VARIACIÓN INTRAESPECÍFICA Y ECOLOGÍA TRÓFICA DE *Chelonia mydas* EN EL PARQUE NACIONAL NATURAL GORGONA

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RESUMEN

Las tortugas verdes *Chelonia mydas* presentan dos morfotipos que se distinguen entre sí por su color y forma, así como por su distribución. Las tortugas negras se encuentran predominantemente en el Pacífico oriental, mientras que las amarillas tienen distribución circumglobal. El Parque Nacional Natural Gorgona (PNN Gorgona) es el único sitio conocido de forrajeo de juveniles de esta especie en el Pacífico colombiano, y es de los pocos lugares en el mundo donde coexisten los dos morfotipos. Las tortugas de morfotipo amarillo tienen mayor tamaño de madurez sexual y crecimiento somático que las de morfotipo negro, y una alimentación basada principalmente en algas en el Pacífico, mientras que las de morfotipo negro ingieren mayor cantidad de invertebrados. Se esperaría que estas diferencias se encuentren también entre los individuos de los dos morfotipos presentes en el PNN Gorgona. Para llevar a cabo esta comparación se contó con datos morfométricos de tortugas muestreadas entre octubre 2003 y diciembre 2012 por parte del personal de la Estación Científica Henry von Prahl del PNN Gorgona; con datos de arrastres de zooplancton obtenidos por el Grupo de Investigación en Ecología Animal de la Universidad del Valle entre agosto 2005 y septiembre 2006; y con datos colectados entre noviembre 2011 y diciembre 2012. En este último año se tomaron datos biométricos de tortugas, se hicieron lavados esofágicos de las tortugas, se determinó la abundancia de alimentos potenciales en los principales arrecifes, se llevó a cabo un análisis proximal de algunas de las algas presentes en los arrecifes, y se tomaron datos para análisis isotópicos de las tortugas y de sus principales alimentos potenciales.El número de tortugas amarillas capturadas en el PNN Gorgona aumentó entre 2007 y 2012. Las tortugas negras fueron más grandes y pesadas que las amarillas, pero estas últimas tuvieron mejor condición corporal. La tasa de crecimiento somático de los dos morfotipos no fue significativamente diferente, y fue

comparable a la reportada en otras localidades del Pacífico oriental. El análisis de la disponibilidad de alimentos en la columna de agua mostró que los tunicados son un alimento ocasional, ya que la abundancia de individuos no fue constante a lo largo del año, con picos de abundancia muy alta en septiembre 2005 y marzo 2006. Este alimento constituiría un recurso esporádico del cual las tortugas se pueden aprovechar oportunistamente. La abundancia de alimentos potenciales en el arrecife no fue significativamente diferente a lo largo del año. Se encontró mayor abundancia de algas rojas incrustantes, así como de tapete algal. El número total de especies de algas en el PNN Gorgona es menor que el que se ha reportado para otras zonas de forrajeo de tortugas marinas, y para zonas cercanas en el Pacífico oriental. Es probable que la baja abundancia de algas lleve a las tortugas verdes a aprovechar otros recursos alimenticios, tales como las plantas terrestres y los invertebrados. La dieta estimada por medio de lavados esofágicos (n=77) indicó un consumo alto de plantas terrestres, y en menor medida de algas e invertebrados. No hubo diferencia significativa (ANOSIM, $p = 0.41$) entre los dos morfotipos. El índice de selectividad de Ivlev indicó que el morfotipo negro seleccionó el alga verde *Cladophora* sp., mientras que el morfotipo amarillo evitó esta alga. Ambos morfotipos seleccionaron las algas *Dictyota* sp. e *Hypnea pannosa*. El análisis proximal indicó que *Dictyota* sp. tuvo mayor cantidad de lípidos y proteínas que las demás algas analizadas, y es probable que por ello ambos morfotipos la seleccionen. El análisis isotópico mostró mayor variabilidad en los valores isotópicos de las tortugas amarillas que de las negras, lo cual sugiere que las tortugas de morfotipo negro tienen una dieta más especializada. El nivel trófico obtenido para los dos morfotipos indica que hubo consumo de materia animal, probablemente de invertebrados grandes o incluso de peces, que ubicaron a las tortugas al nivel de carnívoros primarios. Sería por lo tanto necesario continuar los estudios tróficos para determinar cuál es el principal alimento que está siendo asimilado por las tortugas en el PNN Gorgona.

PALABRAS CLAVE

Análisis isotópico, *Chelonia mydas,* dieta, disponibilidad de alimentos, distribución de tallas, morfotipo amarillo, morfotipo negro, nutrientes, posición trófica, tasa de crecimiento

ABSTRACT

Green turtles *Chelonia mydas* have two morphotypes that differ in their shape and color, as well as their distribution. Black turtles can be found mainly in the eastern Pacific, whereas yellow turtles have a circumglobal distribution. Gorgona National Natural Park (GNNP) is the only known foraging site of juveniles of this species in the Colombian Pacific, and is one of the few places in the world where both morphotypes coexist. Yellow morphotype turtles have a larger size at sexual maturity and faster somatic growth than black turtles. They also have a diet based mainly on algae in the Pacific, whereas black morphotype turtles ingest a higher amount of invertebrates. These differences should also be evident in the individuals of both morphotypes present at GNNP. In order to compare the two morphotypes, green turtle biometric data were obtained between October 2003 and December 2012 by personnel from the Henry von Prahl Scientific Station of GNNP; zooplankton abundance data were obtained by the Animal Ecology Group of the Universidad del Valle between August 2005 and September 2006; data on green turtle trophic ecology were obtained during the field phase of this research between November 2011 and December 2012. During this last year biometric turtle data were taken, esophageal lavages were carried out, the abundance of potential food items on the reef was estimated, a proximate analysis of the most abundant algae on the reef was undertaken, and isotopic analyses of green turtles and their main potential food items were obtained. The number of yellow turtles captured at GNNP increased between 2007 and 2012. Black turtles were larger and heavier than yellow turtles, although yellow turtles had a better body condition. The somatic growth rate of both morphotypes was not significantly different, and was comparable to that reported at other eastern Pacific locations. The analysis of food availability in the water column showed that tunicates are an occasional food item for green turtles at GNNP, since tunicate abundance was

not constant during the year, with very high abundance peaks in September 2005 and March 2006. Tunicates are a sporadic resource that green turtles can take advantage of opportunistically. The abundance of potential food items on the reef was not significantly different during the year. There was higher abundance of red encrusting algae and algal turf. The total number of algae at GNNP is lower than what has been reported for other green turtle foraging areas, and for nearby areas in the eastern Pacific. It is probable that the low algal abundance has led green turtles to take advantage of other food resources, such as terrestrial plants and invertebrates. The diet estimated through esophageal lavages (n = 77) indicated high consumption of terrestrial plants, and a lower proportion of algae and invertebrates. There was no significant difference in diet between the two morphotypes (ANOSIM, p = 0.41). Ivlev´s electivity index indicated that the black morphotype selected the green alga *Cladophora* sp. whereas the yellow morphotype avoided this alga. Both morphotypes selected the algae *Dictyota* sp. and *Hypnea pannosa*. The proximate analysis indicated that *Dictyota* sp. had a higher amount of lipids and proteins that the other analyzed algae, which is probably why both morphotypes selected this alga. The isotopic analysis showed higher variability in isotopic values of yellow turtles than black turtles, which suggests that black turtles had a more specialized diet. The trophic level obtained for both morphotypes indicated consumption of animal matter, possibly large invertebrates or even fish, which placed turtles at the level of primary carnivores. It is therefore necessary to continue trophic analyses to determine the main food component that is being assimilated by green turtles at GNNP.

KEY WORDS

black morphotype, *Chelonia mydas*, diet, food availability, growth rate, isotopic analysis, nutrients, trophic position, size distribution, yellow morphotype

INTRODUCCIÓN GENERAL

Taxonomía

Las tortugas marinas tienen una larga historia evolutiva. Las primeras tortugas marinas de la familia Cheloniidae aparecieron a finales del Mesozoico, hace 100 mil años, mientras que el primer fósil del género *Chelonia* data de hace 20 mil años (Baker 1978, Márquez 2000). Esta familia incluye en la actualidad a las especies *Eretmochelys imbricata, Lepidochelys olivacea, Lepidochelys kempii, Caretta caretta, Natator depressus* y *Chelonia mydas.* La otra familia de tortugas marinas es Dermochelidae, la cual sólo incluye en el presente a la especie *Dermochelys coriacea*.

El estatus taxonómico de las tortugas verdes *Chelonia mydas* se ha debatido por años. Las tortugas verdes del Pacífico occidental y oriental han sido consideradas como especies diferentes por algunos autores, quienes consideraban que en el Pacífico occidental estaba distribuida la especie *Chelonia mydas*, mientras que en el Pacífico oriental se encontraba la especie *Chelonia agassizii* (Pritchard 1971; Carr 1980; Hirth 1997). Otros autores han considerado a las tortugas verdes del Pacífico oriental como una subespecie, *Chelonia mydas agassizii* (Amorocho & Reina 2007; Rodríguez-Barón *et al.* 2011). La distinción entre las tortugas del Pacífico oriental y occidental se ha basado principalmente en parámetros morfológicos. Sin embargo, la falta de evidencia genética sustancial ha llevado a varios autores a concluir que las poblaciones del Pacífico occidental y oriental de tortuga verde son simplemente diferentes morfotipos de una única especie, *Chelonia mydas* (Bowen *et al.* 1992; Parham & Zug 1996; Parker *et al.* 2011; Wallace *et al.* 2010). Esta es la clasificación taxonómica utilizada por la Unión Internacional por la Conservación de la Naturaleza (IUCN por sus siglas en inglés, Seminoff 2004a), y será la clasificación que se utilizará en esta tesis.

A pesar de ser consideradas una misma especie, se han reportado diferentes haplotipos para los dos morfotipos de *C. mydas* (Amorocho *et al.* 2012; Correa-Cárdenas 2013), y existen marcadas diferencias morfológicas, de historia de vida y entre las poblaciones de los dos grupos.

Historia de vida de las tortugas verdes

El ciclo de vida de las tortugas verdes *C. mydas* incluye una fase oceánica luego de la eclosión, durante la cual las tortuguitas se desplazan pasivamente en los grandes giros oceánicos. Luego de varios años los juveniles migran a zonas neríticas donde forrajean hasta alcanzar el tamaño de madurez sexual (Bolten 2003). Los adultos migran entre zonas de forrajeo y de reproducción, pudiendo usar zonas costeras de forrajeo así como oceánicas, dependiendo de la población (Seminoff 2004a; Hatase *et al.* 2006).

En general todas las especies de tortuga marina tienen supervivencia baja y variable de huevos y neonatos, y supervivencia más bien alta y constante en juveniles grandes y adultos (sin tomar en cuenta amenazas antropogénicas), larga vida (55-60 años en Australia; Hamman *et al*. 2003) con una fase juvenil larga, crecimiento lento, y determinación sexual dependiente de la temperatura, con producción de sólo machos a temperaturas por debajo de los 28 ºC, y sólo hembras por encima de los 30.5 ºC (Wibbels 2003). La anidación es infrecuente y variable, y la fecundidad se ve limitada por el tamaño de los huevos (Heppell *et al.* 2003). La variabilidad en anidación es influenciada por factores ambientales como la distancia migratoria al sitio de anidación y la calidad del sitio de forrajeo, y factores intrínsecos como la historia reproductiva y la edad (Hamman *et al.* 2003). Estos factores afectan a los individuos y a las poblaciones de manera desigual y por lo tanto no se ha podido cuantificar exactamente la variabilidad en la fecundidad de las tortugas verdes (Hamman *et al.* 2003).

La edad de madurez sexual de *C. mydas* es variable y depende de la distribución geográfica de sus poblaciones, puede variar entre individuos de una misma población o de poblaciones diferentes (Hirth 1997). Se piensa que la vida reproductiva dura en promedio 19 años y que una generación dura entre 35.5 y 49.5 años (Seminoff 2004a).

Morfotipo negro

Este morfotipo tiene un caparazón gris oscuro o negro de forma acorazonada, a veces con puntos más claros, y generalmente el caparazón se estrecha a la altura de las aletas traseras (Hirth 1997; Amorocho & Reina 2007; Parker *et al.* 2011). El morfotipo negro se encuentra distribuido en la margen oriental del Océano Pacífico, desde Perú hasta California, USA (Márquez 1990; Wallace *et al.* 2010). Ha sido reportado en California, Golfo de California, Michoacán, Istmo de Tehuantepec, Islas Revillagigedo, El Salvador-Nicaragua en el Golfo de Fonseca, Costa Rica, Islas Coco, Ecuador, Isla de Cañas en Panamá, Galápagos, Colombia, y norte de Perú (península de Paracas). En años muy cálidos han llegado a ser reportadas en British Columbia y en el sur hasta Coquimbo, Chile (Márquez 2000). La presencia de tortugas negras también ha sido reportada ocasionalmente en el Pacífico central (archipiélago de Hawaii; Balazs & Chaloupka 2004).

El tamaño promedio de madurez sexual de la tortuga negra en Michoacán se estima en 77.3 cm de largo recto de caparazón (LRC), y en las islas Galápagos en 79.4 cm LRC (Koch *et al.* 2007; Zárate 2004). Para las tortugas negras el tamaño de reclutamiento a zonas neríticas en Baja California es de 35-40 cm LRC, y pasan de 10 a 20 años en sus hábitats de desarrollo (Koch *et al.* 2007).

Las principales áreas de anidación del morfotipo negro de *C. mydas* en el Pacífico oriental son Michoacán y las islas Revillagigedo en México, y las islas Galápagos en Ecuador (Green 1983;

Blanco *et al.* 2013). En Colombia se ha reportado anidación de *C. mydas* en el departamento de Chocó (playa La Cuevita) y esporádicamente en Playa Palmeras, en el PNN Gorgona (Barrientos & Ramírez 2010, citado en Barreto-Sánchez 2011). Entre las principales áreas conocidas de forrajeo en el Pacífico oriental de las tortugas negras están Baja California, Perú, las islas Galápagos, y el PNN Gorgona en Colombia (Seminoff *et al.* 2002a; Amorocho & Reina 2007; Velez-Zuazo *et al.* 2014). Se sabe de la existencia de otras áreas de forrajeo sobre cuyas características aun no existen publicaciones, pero que son probablemente importantes para la especie (Seminoff 2004a).

Las hembras del morfotipo negro de *C. mydas* producen entre 65 y 90 huevos por desove (Hirth 1997) y desovan aproximadamente 3 veces por año (se ha reportado hasta 3.7 desoves por año; Blanco *et al.* 2011), con 12 a 15 días entre puestas. Sin embargo, las hembras no desovan todos los años, y dependiendo de la especie los desoves ocurren entre cada 1 y 3 años. Los huevos tardan 48-72 días en eclosionar (Hirth 1971). Las crías miden en promedio 4.7 cm de largo de caparazón (Márquez 2000).

La dieta de este morfotipo en el Pacífico oriental se basa principalmente en algas (Seminoff *et al.* 2002a; López-Mendilaharsu *et al.* 2008). Sin embargo, se ha reportado en algunos sitios una ingestión a veces importante de invertebrados, tales como tunicados en el PNN Gorgona (73.8 frecuencia de ocurrencia, FO%; Amorocho & Reina 2007), cnidarios y sifonóforos entre otros en las Islas Galápagos (26.15 FO%; Carrión-Cortés *et al.* 2010), esponjas, moluscos, equinodermos y cnidarios en la costa occidental de Baja California Sur, México (20.18 FO%; Rodríguez-Barón 2010), anélidos, esponjas, cnidarios y moluscos entre otros en la costa oriental de Baja California, México (38.5 - 42.8 FO%; Seminoff *et al*. 2002a), y moluscos en la Bahía de San Diego (Lemons *et al.* 2011).

El crecimiento es lento comparado con las poblaciones de *C. mydas* de morfotipo amarillo del Caribe. Las tasas de crecimiento más bajas reportadas fueron observadas en las Islas Galápagos (0.11 – 0.45 cm/año; Green 1993), en Baja California se reportó un crecimiento de 1.0 – 1.9 cm/año (Seminoff *et al.* 2002b), mientras que las más altas se reportaron en la costa de Chile (2.83 a 6.77 cm/año; Vélez-Zuazo et al. 2014).

Morfotipo amarillo

El morfotipo amarillo de *C. mydas* se distingue por tener un caparazón redondeado y una coloración amarilla a café claro con rayas negras o café (Parker *et al.* 2011). Este morfotipo tiene distribución pantropical. La presencia de tortugas amarillas en el Pacífico oriental ha sido reportada en las Islas Galápagos, aunque estas tortugas no anidan en esa zona (Pritchard 1971; Green 1981). A modo de ilustración, de 6743 adultos de *C. mydas* marcados por Green (1981) en las Islas Galápagos entre 1976 y 1980, sólo 23 pertenecieron al morfotipo amarillo. Para el PNN Gorgona, Amorocho *et al.* (2012) reportaron presencia de 85% de tortugas con haplotipos característicos del morfotipo negro, y 15% de tortugas con haplotipos característicos del morfotipo amarillo.

El tamaño reportado para adultos de tortugas amarillas en Australia es de 85-120 cm de largo curvo de caparazón (LCC), cuya edad fue estimada en >32 años. Se consideran juveniles las tortugas amarillas que miden entre 40 y 65 cm LCC, y subadultas las tortugas entre 65 y 90 cm LCC (Chaloupka & Limpus 2005). El tamaño de reclutamiento a los hábitats neríticos de las tortugas de morfotipo amarillo es de 40 cm LCC en Australia (Chaloupka *et al.* 2004), y se estima que los juveniles pequeños pasan 5-6 años en la zona pelágica (Limpus & Chaloupka 1997). En Hawaii el tamaño promedio de madurez sexual de la tortuga amarilla es de 80 cm LRC, y el tamaño de reclutamiento a zonas neríticas es de 35 cm LRC (Balazs & Chaloupka

2004). Se ha estimado la edad de madurez sexual en 18-30 años para *C. mydas* de morfotipo amarillo en Florida (Mendonca 1981), en 35-50 años en Hawaii (Balazs & Chaloupka 2004), y en 25-50 años en Australia (Limpus & Chaloupka 1997). Las hembras de morfotipo amarillo en el Pacífico ponen entre 97 y 118 huevos por desove, y ponen entre 3 y 5.5 veces por temporada, con 10.5 a 14.9 días en promedio entre puestas (Hirth 1997).

La alimentación de las tortugas de morfotipo amarillo en el Caribe se basa principalmente en pasto marino (*Thalassia testudinum*) (Bjorndal 1997). En otros lugares donde hay disponibilidad de pasto marino se ha visto consumo de este recurso complementado a veces con algas e invertebrados (Mendonca 1981; Gilbert 2005; Cardona *et al.* 2009). En Australia la dieta de *C. mydas* de morfotipo amarillo se compone principalmente de algas, con aportes de mangle e invertebrados (Forbes 1996; Arthur *et al.* 2009). En Hawaii la dieta de este morfotipo incluye mayoritariamente algas, con consumo adicional de cianobacterias (Arthur & Balazs 2008).

El crecimiento reportado para el morfotipo amarillo en el Caribe es alto (1.9 – 8.4 cm/año, Bjornal & Bolten 1988). En Hawaii también se han reportado tasas de crecimiento somático altas (0.6 – 4.4 cm /año; Zug *et al.* 2002), mientras que en Australia las tasas de crecimiento son menores (0.75 – 1.46 cm/año; Zug & Glor 1998).

Estudio de *C. mydas* en el PNN Gorgona

La dificultad de evaluar a las especies que tienen distribución global como *Chelonia mydas* para inclusión en la lista roja de la IUCN, es que no siempre se toman en cuenta las tendencias poblacionales locales, y el riesgo de extinción que aplica para la especie globalmente no necesariamente aplica a nivel local o regional (Seminoff 2004b; Seminoff & Shanker 2008). Por lo tanto estudiar la estructura poblacional, crecimiento y ecología trófica de los diferentes stocks genéticos a nivel local puede ayudar a llenar vacíos de información que permitan tener una idea

más clara del estado en que se encuentran las poblaciones de *C. mydas* en ciertas zonas del mundo. Asimismo, las evaluaciones regionales son más útiles para los administradores y conservacionistas locales (Seminoff 2004b).

Se han reportado diferentes tasas de crecimiento en diferentes stocks genéticos de tortugas, ligadas a diferentes condiciones climáticas y disponibilidad de alimento (Bjorndal *et al.* 2000; Braun-McNeill *et al.* 2008). Casale *et al.* (2009) también recomendaron determinar las tasas de crecimiento específicas de las diferentes poblaciones, ya que las tasas de crecimiento generales de un área dada no pueden tomarse como representativas de todas las poblaciones que allí se encuentran.

La habilidad de los individuos para utilizar los recursos disponibles y el riesgo que presentan los depredadores dependen en gran medida del tamaño individual (Werner & Gillam 1984). En consecuencia las tortugas presentan cambios ontogenéticos en sus hábitats y en los recursos que utilizan. Cada etapa de vida enfrenta diferentes amenazas y utiliza diferentes recursos, y por lo tanto es importante estudiar las características biológicas de cada una de las fases de la historia de vida de las tortugas marinas. Braun-McNeill *et al.* (2008) enfatizaron la importancia de determinar cuáles son los parámetros demográficos para cada población, así como para cada etapa de vida de las tortugas, incluyendo el determinar cuándo (a qué edad) empieza cada etapa, y cuál es su duración. Por lo tanto es importante determinar y comparar el crecimiento de tortugas negras y amarillas en el PNN Gorgona, que provienen de diferentes orígenes geográficos (las negras provienen de las Islas Galápagos y de Michoacán, México, y las tortugas amarillas provienen de Polinesia Francesa y de Hawaii; Amorocho *et al*. 2012) y tienen diferente información genética (las tortugas amarillas de Australasia presentan los haplotipos CMP21, CMP22 y CMP97, mientras que las tortugas del Pacífico central y oriental presentan los haplotipos CMP4, CMP8, CMP5 y CMP17; Amorocho *et al*. 2012).

Ambos morfotipos emprenden procesos migratorios de gran escala durante su historia de vida (Bolten 2003), los cuales conllevan gastos energéticos importantes. Estos gastos necesitan una utilización eficiente de los recursos, y las migraciones pueden tener consecuencias sobre la reserva energética del individuo, y a largo plazo sobre su *fitness* (la habilidad de reproducirse y pasar sus genes a la siguiente generación) (Crossin *et al.* 2014). Las tortugas marinas son "capital breeders", es decir que pueden almacenar energía en aras de una reproducción futura (Hamman *et al.* 2003). Este almacenamiento de energía se ve afectado por la disponibilidad de recursos alimenticios, de tal manera que cada proceso migratorio implica un balance entre quedarse en un lugar con recursos conocidos, o pasar a otro lugar que tenga potencialmente mejores recursos o más abundantes (Godley *et al* 2003; Crossin *et al.* 2014).

La adquisición de nutrientes tiene efectos sobre las tasas de crecimiento somáticas, los tiempos de residencia, la demografía de las poblaciones, la bioenergética y presupuestos energéticos, y está limitada por factores tanto fisiológicos como ambientales (Karasov & Martínez del Río 2007). Por lo tanto, el lugar donde se encuentren las tortugas tendrá consecuencias sobre su crecimiento, condición corporal, y determinará cuándo ocurran las migraciones y a qué distancia puedan llegar.

El PNN Gorgona es de los pocos lugares en el mundo donde coexisten los dos morfotipos conocidos de *Chelonia mydas* durante su fase juvenil. Dado que estos morfotipos tienen diferentes características como tamaño de madurez sexual (las tortugas amarillas tienen mayor tamaño de madurez sexual), rutas migratorias (las tortugas negras migran entre las Islas Galápagos y el PNN Gorgona o Michoacán y el PNN Gorgona, y las amarillas migran entre el Pacífico central/occidental y el PNN Gorgona), crecimiento (las amarillas crecen más rápido que las negras) y alimentación (las tortugas negras incluyen más invertebrados en la dieta que las

amarillas), se esperaría que los individuos que se encuentran en el PNN Gorgona presenten características acordes con su morfotipo.

Amorocho *et al*. (2012) hicieron un análisis genético de individuos presentes en el PNN Gorgona y reportaron 85.45% con haplotipos característicos de sitios de anidación del Pacífico oriental y de morfotipo negro, y 14.55% con haplotipos característicos de sitios de anidación del Pacífico central/occidental y de morfotipo amarillo. La hipótesis del primer capítulo de esta investigación es que la población de *C. mydas* en el área de forrajeo del PNN Gorgona está constituida en un 85.45% por el morfotipo negro que es lo reportado para la región, y la hipótesis alterna es que el porcentaje de morfotipo amarillo en el PNN Gorgona es mayor que lo reportado. Adicionalmente, se esperaría que los valores encontrados para el PNN Gorgona fueran de por lo menos 1.27, ya que en el Pacífico oriental se han reportado índices de condición corporal que varían entre 1.27 y 1.55 (Velez-Zuazo *et al*. 2014).

En la segunda fase de esta investigación se determinó la tasa de crecimiento somático de los dos morfotipos, comparando la tasa de crecimiento anual calculado a partir de medidas lineales y las tasas de crecimiento de cada clase de tamaño (Capítulo 2). El crecimiento se ve afectado por parámetros ambientales como la temperatura. Al estar sometidos ambos morfotipos al mismo rango de temperaturas, se esperaría igual crecimiento si los individuos de los dos morfotipos permanecen durante el mismo tiempo en la zona de forrajeo del PNN Gorgona. Adicionalmente, los dos morfotipos encontrados en el parque incluyen únicamente individuos juveniles, que deberían tener el mismo metabolismo, y por lo tanto no deberían presentar diferencias en su crecimiento. Sin embargo, se ha encontrado que hay crecimiento más rápido en reptiles que tienen una talla de madurez sexual mayor (Stamps *et al*. 1998). Las tortugas amarillas tienen un tamaño promedio de madurez sexual mayor que el de las negras, y por lo tanto se esperaría que

primen las características de historia de vida del morfotipo, y se dé un crecimiento más rápido en las tortugas amarillas que en las negras presentes en el PNN Gorgona.

Amorocho & Reina (2007) reportaron que el alimento más consumido por las tortugas muestreadas en el PNN Gorgona fueron los tunicados (salpas y doliolos). Si este es el alimento más consumido por las tortugas verdes en la zona de estudio se esperaría que hubiera abundancia del mismo durante todo el año, y que estuviera presente en gran abundancia alrededor de la isla. La hipótesis del tercer capítulo de esta investigación es que los tunicados serían abundantes en todos los meses del año y en todas las estaciones alrededor de la Isla Gorgona.

En el cuarto capítulo de esta investigación se evaluó la ecología trófica de los juveniles de *C. mydas* en el PNN Gorgona. Dado que no se ha encontrado diferencia en la alimentación de juveniles pelágicos de los dos morfotipos (Parker *et al*. 2011), tampoco se esperaría encontrar diferencias en la dieta de juveniles neríticos en el PNN Gorgona. De acuerdo a la Teoría del Forrajeo Optimo (MacArthur & Pianka 1966), se esperaría que los individuos de ambos morfotipos maximicen el consumo de nutrientes, seleccionando el alimento más nutritivo, y que su alimento se encuentre disponible todo el año. Por esto no se esperaría que los tunicados fueran el alimento principal de la dieta de las tortugas verdes en el PNN Gorgona, y se esperaría obtener una posición trófica por encima del nivel de los herbívoros si las tortugas verdes incluyen invertebrados en su dieta como ha sido reportado anteriormente en el parque y en otros sitios del Pacífico (Heithaus *et al*. 2002; Amorocho & Reina 2007; Carrión-Cortez *et al*. 2010).

Esta investigación suministra información sobre la estructura poblacional, crecimiento somático y ecología trófica de los dos morfotipos de *C. mydas* presentes en el PNN Gorgona, describiendo qué tantos recursos comparten los dos morfotipos en esta localidad y cuantificando la diferencia en su comportamiento alimentario, información que es de gran interés por el debate que todavía existe sobre si se trata de dos especies o de diferentes morfotipos de la misma especie. También

proporciona información relevante para fortalecer las estrategias de manejo establecidas para esta especie por los funcionarios del PNN Gorgona, lugar conocido de alimentación de los juveniles de *C. mydas* en el Pacífico Oriental tropical, y además proporciona información de utilidad a nivel regional, ya que podrían identificarse otras posibles zonas de alimentación basándose en la descripción realizada del tipo de alimento que consumen y los lugares donde estos se encuentran.

CAPÍTULO 1

Green turtle *Chelonia mydas* (Cheloniidae) intraspecific variation at the Gorgona National Park Foraging Area (Colombian Pacific)

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Green turtle *Chelonia mydas* (Cheloniidae) intraspecific variation at the Gorgona National Park Foraging Area (Colombian Pacific)

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Abstract

The size distribution and body condition of the two known morphotypes of green turtle (*Chelonia mydas*) foraging at Gorgona National Park (GNP) in the Colombian Pacific was assessed from 2003 to 2012. Measurements of straight carapace length (SCL), curved carapace length (CCL), weight, and body condition of 1,023 turtles captured at the GNP reefs were taken. More black turtles (n = 747) than yellow turtles (n = 276) were captured, all were juveniles. Black turtles were significantly larger and heavier than yellow turtles. The size of recruitment to the neritic zone was 40.0-49.9 cm SCL for both morphotypes, but there were more yellow than black turtles in this size class, indicating variations in the recruitment pattern. The body condition index of yellow turtles was significantly higher than that of black turtles, which could indicate differences in resource use. Based on our results, we suggest that GNP might function as a recruitment area for yellow turtles, which arrive at smaller sizes, and as part of a coastal migratory route for black

turtles, which arrive at larger sizes and maintain residence at this location for an unknown period of time.

Key words: black morphotype, condition index, foraging ground, size-frequency distribution, yellow morphotype

Resumen

Se comparó la distribución de tallas y condición corporal de los dos morfotipos conocidos de tortuga verde (*Chelonia mydas*) en el área de forrajeo del Parque Nacional Natural Gorgona (PNNG) en el Pacífico colombiano, entre 2003 y 2012. Se tomaron medidas de largo recto de caparazón (LRC), largo curvo de caparazón (LCC), peso y condición corporal de 1,023 tortugas capturadas en los arrecifes del PNG. Se capturaron más tortugas negras (n = 747) que amarillas (n = 276), siendo todas juveniles. Las tortugas negras fueron significativamente más grandes y pesadas que las amarillas. El tamaño de reclutamiento a la zona nerítica fue de 40.0-49.9 cm para ambos morfotipos, pero hubo más tortugas amarillas que negras en este intervalo de tamaños, lo cual sugiere una variación en el patrón de reclutamiento. El índice de condición corporal de las tortugas amarillas fue significativamente más alto que el de las tortugas negras, lo cual podría indicar diferencias en la utilización de recursos. Con base en los resultados obtenidos se sugiere que el PNNG podría funcionar como un área de reclutamiento para las tortugas amarillas, las cuales llegan más pequeñas a esta zona; y como parte de la ruta migratoria costera de las tortugas negras, las cuales llegan más grandes, e incluso residen en esta localidad durante un lapso de tiempo desconocido.

Palabras clave: área de forrajeo, distribución de frecuencia de tamaño, índice de condición corporal, morfotipo amarillo, morfotipo negro

INTRODUCTION

As they go through their different life stages, *Chelonia mydas* individuals, like those of other sea turtle species, inhabit widely different environments. After hatching, the young sea turtles move to epipelagic areas, where they spend several years, migrating then to neritic foraging areas where they remain until reaching sexual maturity. Adults migrate between breeding and foraging areas (Meylan *et al*., 2011). Since each life stage is subject to different pressures and threats, management and conservation strategies need to be geared toward the specific challenges that each life stage confronts, helping generate effective conservation plans (Heppell *et al*., 2003). Determining the size of recruitment to neritic areas (size at arrival), the time of residency and the size at maturity (size at departure) is important for implementation of conservation measures (Heppell *et al*., 2003; Meylan *et al*., 2011).

The protection of sea turtles during their different life stages is critical, particularly for areas that include animals from different stocks, such as foraging areas where animals share the same resources and face the same threats (Bass *et al*., 2004). The environmental conditions at a given foraging ground affect the health of individuals from different stocks that will migrate to different breeding areas, so that conditions at the foraging ground will ultimately have an effect on the conservation status of geographically distant breeding populations (Lahanas *et al*., 1998; Engstrom *et al*., 2002; Heppell *et al*., 2003).

Chelonia mydas has a worldwide distribution. In the Eastern Pacific, however, *C. mydas* individuals have a distinct coloration and shape that sets them apart from the all other populations (Parker *et al*., 2011). The black morphotype (known locally as the black turtle or East Pacific green turtle) can be found along the eastern margin of the Pacific Ocean, from Chile to California, USA (Wallace *et al*., 2010). It has a dark grey to black heart-shaped carapace, sometimes with lighter dots (Fig.1A; Pritchard, 1998; Amorocho and Reina, 2007). The yellow

morphotype, which can be found over the remaining distribution of *C. mydas*, has a distinctive yellow to light brown coloration with black streaks (Fig. 1B; Hirth, 1997). The distribution of this morphotype in the Eastern Pacific is limited, with published reports only from the Galápagos Islands, Ecuador (Pritchard, 1971; Green, 1981) and Gorgona National Park (Amorocho *et al*., 2012).

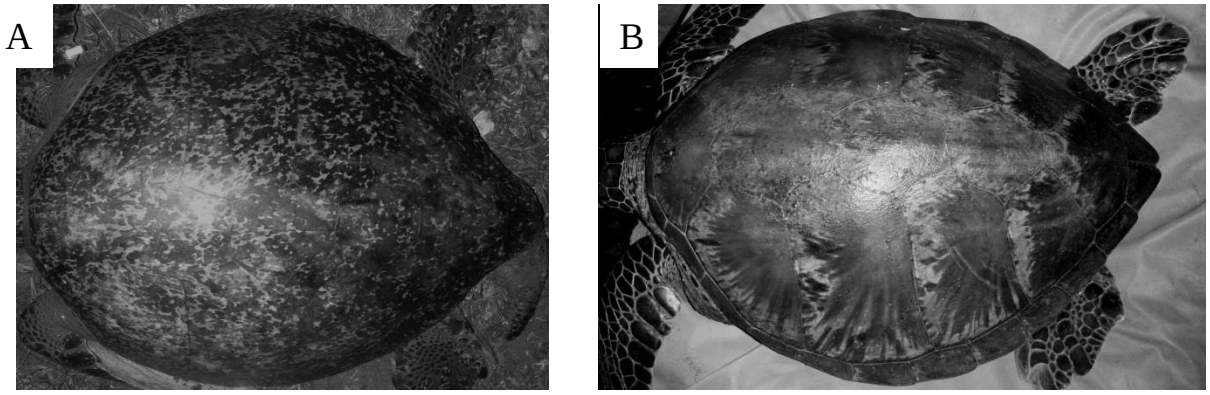

Figure 1. Phenotypic carapace differences between the black (A) and yellow (B) morphotypes of *Chelonia mydas* at the Gorgona Island foraging ground.

The black morphotype is known to forage in neritic and offshore waters of many areas from Chile to the United States (Seminoff *et al*., 2012). Gorgona National Park (GNP) is the only known foraging ground for *C. mydas* in the Colombian Pacific. This area is important regionally because it protects one of the most developed coral reef formations in the Eastern Tropical Pacific (Cortés *et al.* 1997; Zapata 2001), and is also one of the few places in the world where both morphotypes of *C. mydas* co-exist (Pritchard, 1971; Márquez, 1990; Amorocho *et al*., 2012). Black turtles have only been reported to nest in the Eastern Pacific, where yellow turtles have not been seen nesting (Pritchard, 1971; Márquez, 1990).

The fact that these two morphotypes co-exist year-round in this foraging area provides a unique opportunity to compare intraspecific phenotypic variations and body condition of organisms that share the same habitat and are probably consuming the same resources.

The present study was undertaken to describe and compare the size structure and the body condition of the two *C. mydas* morphotypes present at GNP, a mixed stock foraging ground. This information is vital to develop efficient conservation strategies, geared towards a specific life stage whose conservation could have repercussions on the survival of other life stages.

MATERIALS AND METHODS

STUDY AREA

Gorgona National Park (GNP) is located off the southwestern coast of Colombia (between 2º49´ and 3º06´N, and between 78º06´ and 78º18´W), approximately 30 km from the mainland. GNP measures 616.8 km^2, comprising the islands of Gorgona and Gorgonilla, and a marine area that makes up 97.5% of the park (Fig. 2). Fringing reefs occur on the eastern side of Gorgona Island. The two main reefs, La Azufrada (11.2 ha) and Playa Blanca (10.86 ha), are composed mainly of corals of the genus *Pocillopora* (Glynn *et al*., 1982; Zapata *et al*. 2001). These reefs provide shelter for several species of fish, invertebrates, and algae, and offer resources for large vertebrates such as manta rays and whale sharks (Acevedo-Bueno *et al*., 2004; Sampson & Giraldo, 2014).

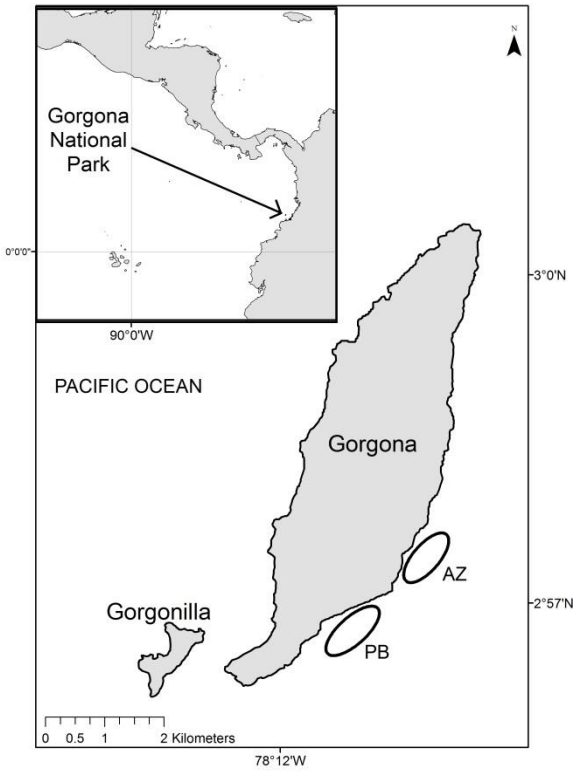

Figure 2. Study area – Gorgona National Park in the Colombian Pacific. Black ellipses show location of reefs where *C. mydas* individuals were captured (AZ = Azufrada, PB = Playa Blanca).

TURTLE CAPTURE AND MEASUREMENTS

Since 2003 a monitoring study of *C. mydas* has been carried out at GNP. Between 2003 and 2006 surveys were carried out by the National Park service in conjunction with CIMAD (Centro de Investigación para el Manejo Ambiental y el Desarrollo); between 2006 and 2008 the Colombian National Park service and WWF Colombia were in charge; and between 2008 and 2012 surveys were carried out solely by the Colombian National Park service. Turtles were captured by hand at night while two to five people searched the reef area using snorkelling gear. When a turtle was sighted it was grabbed by the carapace and transferred to an outboard motor boat. The searching continued for one hour (8 p.m. to 9 p.m.) or until five turtles had been captured. The same monitoring protocol has been followed during all years of this study; however, due to the

variations in personnel involved over the years and the lack of data on time effort, no catch per unit effort data were calculated.

The turtles were brought to shore where straight carapace length (SCL) and curved carapace length (CCL) were measured from the nuchal notch to the posterior notch, and mass was recorded. Straight measurements were taken using forestry callipers with 0.05 cm accuracy; curved measurements were taken with a flexible tape with 0.05 cm accuracy; mass was measured using a spring scale with 0.5 kg accuracy. The carapace color was noted at the time of capture. Turtles were tagged on the trailing edge of the right or left front flipper, using numbered Inconel tags (No. 681, National Band and Tag Co., Newport, Kentucky, USA). Data obtained from tagged turtles (recaptures and growth) will be published separately (Sampson *et al*., in prep).

BODY CONDITION INDEX

A condition index (CI), which can be used as a proxy for individual health and can be used to infer quality of available resources (Bolger *et al*. 1989), was calculated for each morphotype, year and size class as:

$$CI = \frac{Mass}{SCL^3} x1000$$

Where mass is given in kg and SCL in cm (Bjorndal *et al*., 2000). The condition index (CI) was calculated for each morphotype separately; data from 745 black turtles and 270 yellow turtles was used to calculate CI.

STATISTICAL ANALYSES

Measurement data (SCL, CCL and mass) and CI data were checked for normality using Lilliefor´s test, and for homogeneity of variances using Levene´s test. To compare CI between color morphs Welch´s t tests were used when data failed the normality assumption. To compare size measurements between morphs and years, and CI values between morphs and years,

Kruskal-Wallis tests were used when data failed the normality assumption. Post-hoc multiple comparisons with Bonferroni corrections were carried out to detect differences between samples. All analyses were carried out using Statsoft v. 8.0.

RESULTS

TURTLE CAPTURES

Measurements of 1,023 *C. mydas* turtles were taken from 2003 to 2012; 747 were black and 276 were yellow. There were only five yellow morphotype turtles caught at GNP before 2007; four were caught in 2003 and one in 2004. After 2007 the number of yellow morphotype turtles caught has increased from 30 turtles in 2007 to 79 in 2012 (Fig. 3).

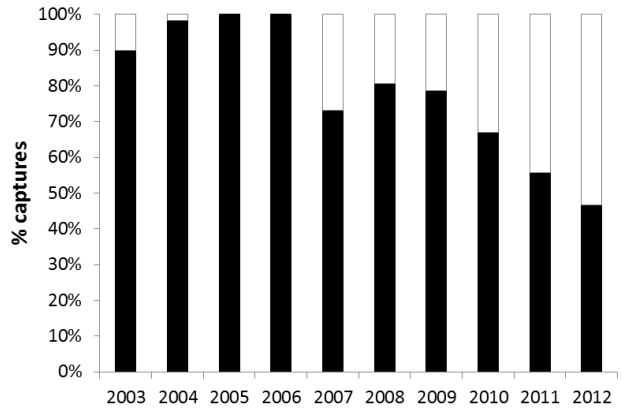

Figure 3. Percent captures of black and yellow *Chelonia mydas* captured at the Gorgona National Park foraging area between October 2003 and December 2012. Black morphotype turtles are shown in black and yellow morphotype turtles in white.

TURTLE MEASUREMENTS

Black morphotype turtles were significantly larger (SCL and CCL) and heavier than yellow turtles (Kruskal-Wallis, $H=191.9$, $p<0.01$; Fig.4). Mean SCL of black turtles was 60.2 cm (min= 36.0, max= 78.0 cm), mean CCL was 64.0 cm (min = 37.9, max = 82.7), and mean weight was 31.1 kg (min = 5, max = 63). Mean SCL of yellow turtles was 53.6 cm (min= 40.2, max= 72.5

cm), mean CCL was 57.5 cm (min = 43.7, max = 77.3), and mean weight was 23.7 kg (min = 9, max = 50).

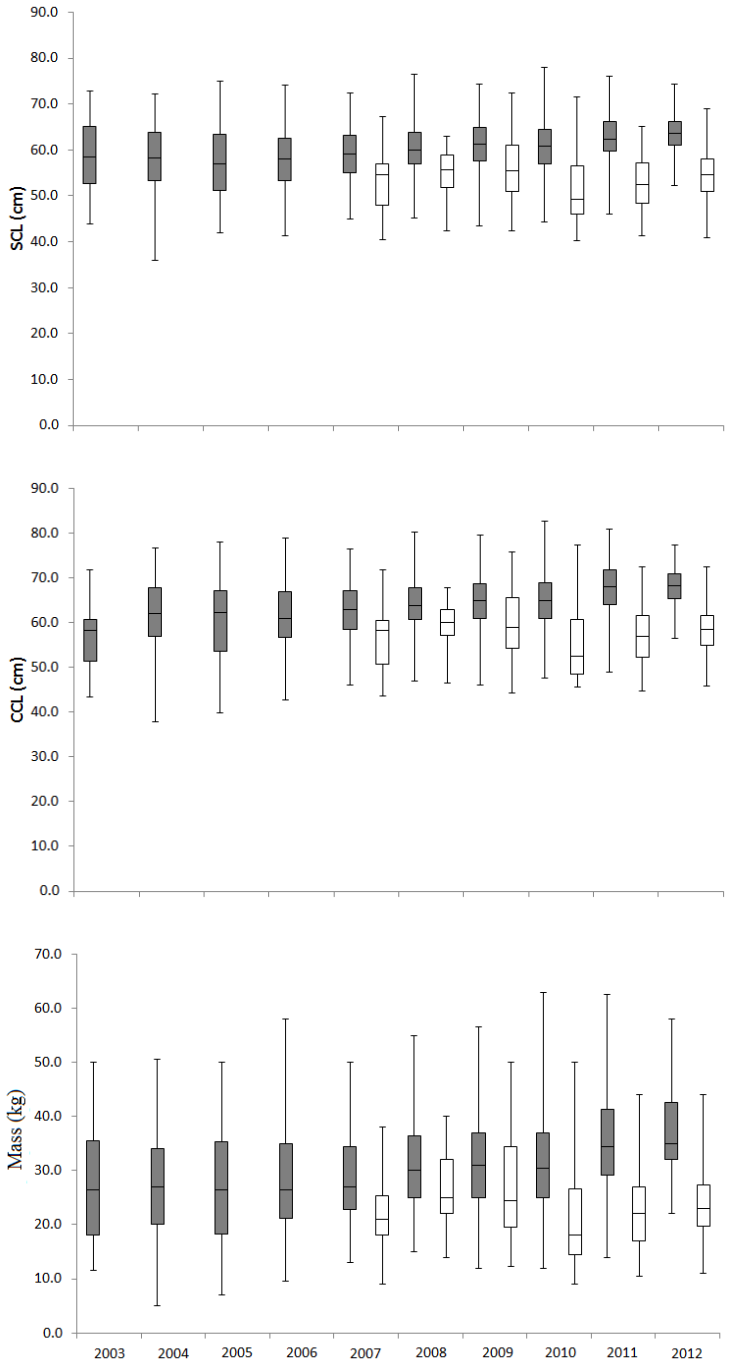

Figure 4. Straight (SCL) and curved (CCL) carapace length and weight of black (grey boxes) and yellow (white boxes) morphotype *C. mydas* captured at the GNP foraging ground between 2003 and 2012. Median, 25%, 75%, minimum and maximum are shown.

There were significant differences in the size and mass of black turtles among years (SCL: Kruskal-Wallis, H=9, p<0.01; CCL: Kruskal-Wallis H=9, p<0.01; mass: H=9, p<0.01). The size of black turtles in the last two years of sampling was statistically different from size during 2004-2008, indicating an increase in the size of sampled turtles (Multiple comparisons of mean ranks, p<0.01). Yellow turtle size and weight also varied significantly among years (SCL: Kruskal-Wallis, H=5, p=0.0190; CCL: Kruskwal Wallis H=5, p=0.0076; mass: H=5, p=0.0033). For yellow turtles 2010 was statistically different, indicating a smaller size of turtles in that year (Multiple comparisons of mean ranks, p<0.01).

The size at maturity (SM) of *C. mydas* individuals was calculated as a weighted mean of the SM at the rookeries from which turtles at GNP originate. Approximately 88.5% of black turtles come from the Galápagos Islands (SM = 79.7 cm SCL) and 11.5% come from Michoacán (SM = 77.3 cm SCL), while approximately 1.7% of yellow turtles come from French Frigate Shoals (SM = 80.0 cm SCL) and 96.3% come from French Polynesia (SM = 96.3 cm SCL) (Hirth, 1997; Márquez 1990; Balazs and Chaloupka 2004; Zárate 2004; Amorocho *et al.* 2012; Correa-Cárdenas, 2013). The estimated SM of black turtles at GNP was 79.4 cm SCL and that of yellow turtles was 96.0 cm SCL. All captured turtles in this study measured less than SM, indicating that they were all at the juvenile or sub-adult stage and were likely not sexually mature.

SIZE-FREQUENCY DISTRIBUTION

Only 2 turtles measuring between 30 and 39.99 cm SCL were caught, indicating that the size of recruitment to the neritic zone of GNP was 40 to 49.9 cm SCL for both morphotypes (Fig. 5). There were no significant differences in size distribution between the two morphotypes (Welch´s t test, t=15.04, p>0.05). However, most black turtles (86.1%) measured between 50 and 69.9 cm SCL, whereas most yellow turtles (83.1%) were smaller, measuring between 40 and 59.9 cm SCL (Table 1).

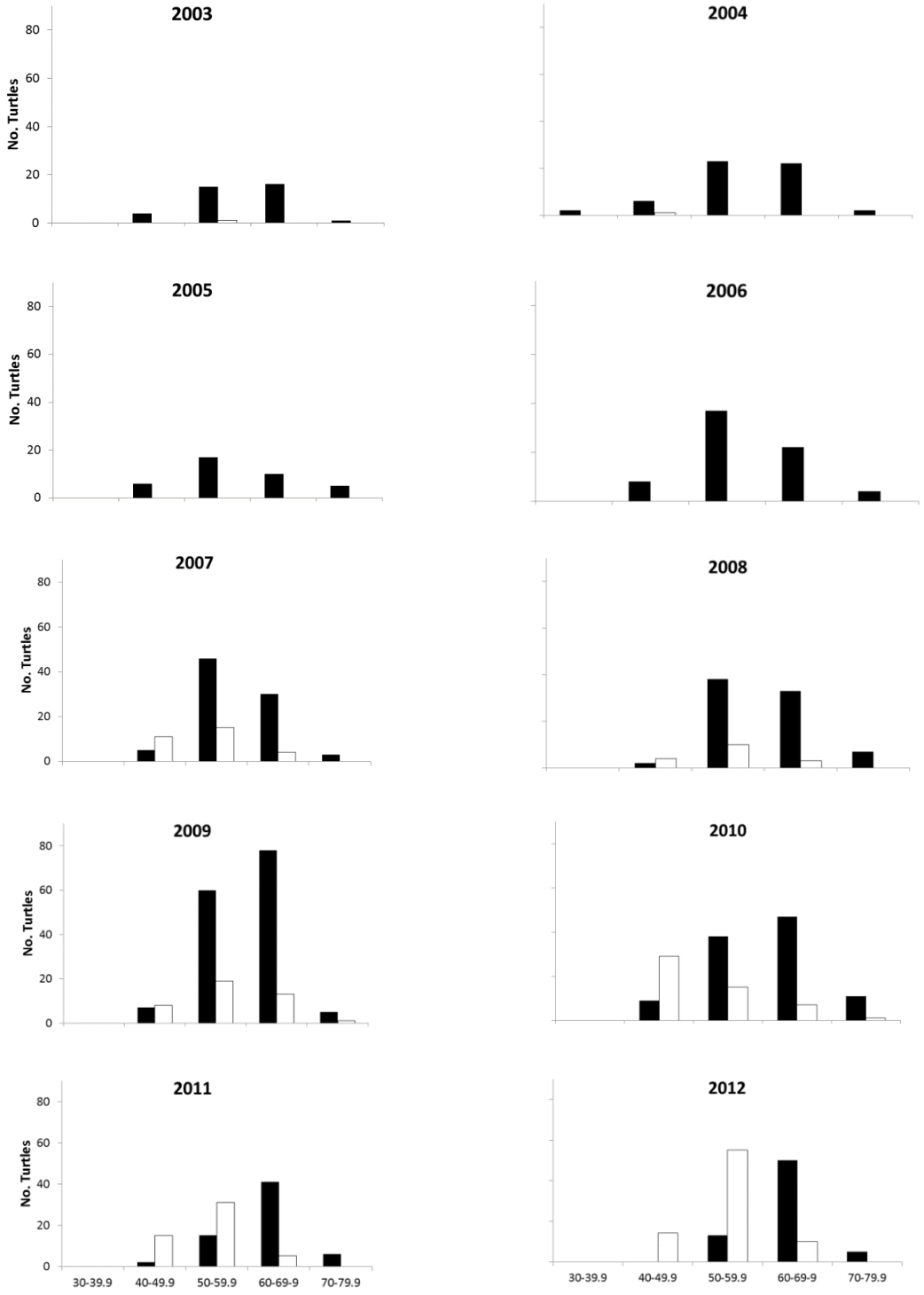

Figure 5. Number of black (black bars) and yellow (white bars) *C. mydas* individuals captured at the GNP foraging area between 2003 and 2012 by size class.

Table 1. Number and proportion of *C. mydas* in each size class for 2003-2012 (black turtles) and 2007-2012 (yellow turtles).

	Black			Yellow		
Size class (cm)	**N**	**%**	**Cumulative %**	**N**	**%**	**Cumulative %**
30-39.9	2	0.3	0.3	0	0	0.0
40-49.9	47	6.3	6.6	81	29.8	29.8
50-59.9	281	37.7	44.2	145	53.3	83.1
60-69-9	361	48.4	92.6	44	16.2	99.3
70-79.9	55	7.4	100.0	2	0.7	100.0

There were more yellow turtles recruiting at the 40-49.9 cm SCL size class (29.8% of all individuals captured), while only 6.3% of all black turtles captured belonged to this size class (Table 1). The number of black turtle recruits ranged from 0 in 2012 to 9 in 2010, while yellow turtles recruits ranged from 1 in 2004 to 28 in 2010.

BODY CONDITION INDEX

The overall CI (all years and size classes combined) of black morph turtles had a mean value of 1.38 (SD = 0.15), and ranged from 0.80 to 2.46, while that of yellow morph turtles had a mean value of 1.49 (SD=0.22), and ranged from 0.80 to 3.16 (Table 2). The mean CI of the two morphotypes were statistically different (Welch´s t test, $t=-9.12$, $p<0.01$).

Table 2. Condition index values of black *C. mydas* at other locations in the Eastern Pacific and values found for black and yellow turtles in this study.

Source	Location	Mean	Range
Koch *et al.* (2007)	Bahía Magdalena, BC, Mexico	1.67	1.03 - 1.70
López-Castro *et al.* (2010)	Baja California Peninsula, Mexico	1.2 - 1.4	0.67 - 2.30
Rodríguez-Barón *et al.* (2011)	Bahía Vizcaíno, BCS, Mexico	1.48	1.25 - 2.06
Seminoff *et al.* (2003)	Bahía de Los Angeles, BC, Mexico	1.42	1.03 - 2.19
Black turtles, this study	Gorgona National Park, Colombia	1.38	0.80 - 2.46
Yellow turtles, this study	Gorgona National Park, Colombia	1.49	0.80 - 3.16

A comparison of CI values among size classes for each morphotype was carried out, taking all sampled years for each morphotype separately (2003-2012 for black turtles, 2007-2012 for yellow turtles). This analysis showed that for both morphotypes the different size classes were

statistically different (Kruskal-Wallis, H=17.46, p=0.001 for black turtles and H=23.86, p<0.01 for yellow turtles). For black turtles, the 50-59.9 cm size class had a higher CI than the 60-69.9 cm class, while for yellow turtles, the smaller turtles 40-49.9 cm had a higher CI than larger turtles (Fig. 6A; Multiple comparisons of mean ranks, p<0.01).

There were significant differences in the CI of black turtles among years (2003 to 2012) (Kruskal-Wallis, H=37.34, p<0.01), with 2003 being significantly lower than 2006, 2008, 2011 and 2012, and 2011 being significantly higher than 2007 (Fig. 6B; Multiple comparisons of mean ranks, p<0.05). Mean CI of yellow turtles was not statistically different among years (2007 to 2012) (Fig. 6B; Kruskal-Wallis, p>0.01; Multiple comparisons of mean ranks, p>0.05).

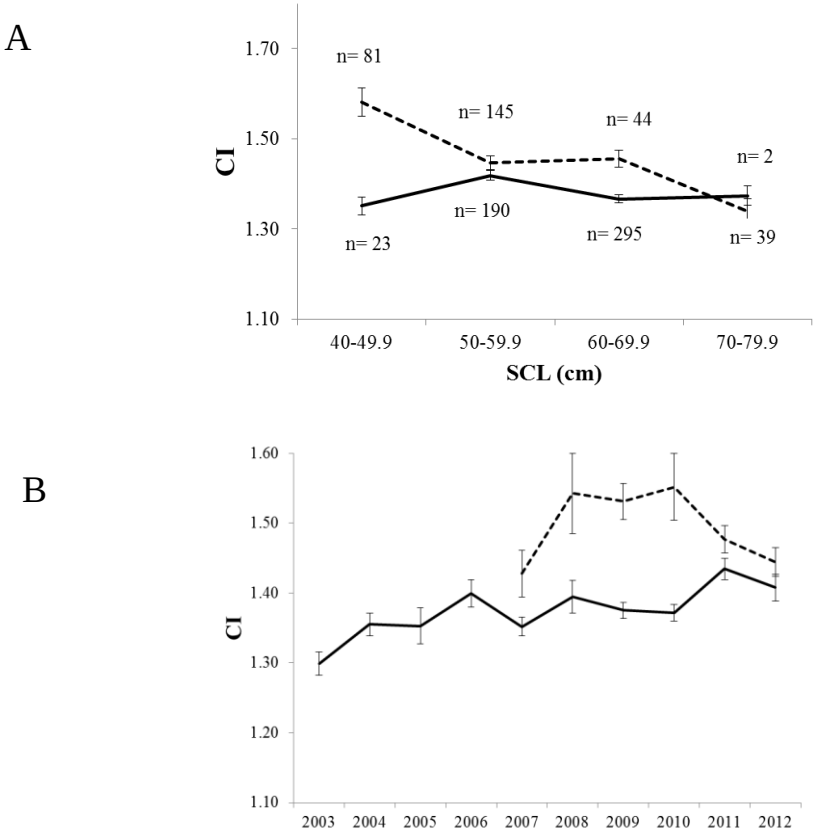

Figure 6 . Condition Index by size class (A) and year (B) of black (solid line) and yellow (dashed line) morph *C. mydas* captured at the Gorgona National Park foraging area between October 2003 and December 2012. The error bars show standard error.

DISCUSSION

All *C. mydas* individuals captured at the GNP foraging area were below the mean size at maturity (SM). It is therefore safe to say that GNP is a juvenile developmental habitat used by black and yellow *C. mydas*. There were reports in the 90s of eight black morphotype *C. mydas* nesting at a beach on the western side of Gorgona Island (McCormick-Anzola, 1996), but there were no reports of nesting activity during the years of the present study.

There were more black than yellow turtles captured from 2003 to 2012, which is in accordance with what has been reported for the Galápagos Islands (Pritchard, 1971; Green, 1993). Of 6,743 *C. mydas* adults tagged between 1976 and 1980 at the Galápagos Islands, only 23 were of the yellow morphotype (Green, 1981). However, there was an increase in the number of yellow turtles captured at GNP since 2007, which could be indicative of changes in the migratory routes taken by this morphotype. It should be noted that since capture effort was not quantified, the change in numbers of captured turtles could be an artifact of sample effort. However, we do not think there was bias in the captures, and we believe that our sample is representative of the proportion of black and yellow turtles present at GNP during the years of this study.

Most black and yellow turtles arrived at GNP at >40 cm SCL, (except two black morphotype turtles 36-38 cm SCL). Green turtles arrive to Hawaiian foraging grounds at 35cm SCL (Arthur and Balazs 2008), at 35-40 SCL to foraging grounds in Baja California (Seminoff *et al*., 2003), and at 40 cm CCL in the southwestern Pacific Ocean (Chaloupka *et al*., 2004). Parker *et al*. (2011) proposed that the black eastern Pacific turtles remain longer in the oceanic region than the yellow morphotype, which would explain a larger recruitment size at GNP than at Hawaii.

There were more yellow turtles at the smaller size class. This difference in the proportion of small turtles (40-49.9 cm SCL) could be due to black turtles recruiting to the neritic foraging

ground of GNP at a larger size (>50 cm SCL) than yellow turtles (Table 1). It might also be indicative of a difference in the migratory behavior of black and yellow turtles, because the fact that two black turtles <40 cm SCL were captured indicates that this morphotype can arrive at this size to coastal areas. Black turtle juveniles could be recruiting to coastal areas other than GNP and moving along the coast to this foraging area, while yellow turtles could be arriving directly to GNP from the open ocean.

Yellow turtles captured at GNP are travelling mainly from rookeries in the western Pacific (French Polynesia and Hawaii), probably being transported along west-east currents, while black turtles arrive from the Galápagos and Michoacán rookeries (Amorocho *et al*., 2012; Correa-Cárdenas, 2013). Satellite telemetry studies would be necessary to confirm the movements of both morphotypes in the region, and future stable isotope analyses comparing the carbon values of these two morphotypes could also help elucidate their migratory behavior.

Black turtles reached larger sizes than yellow turtles at this study site, which indicates that black turtles stay in the neritic zone of GNP until almost reaching their SM (~79.4cm SCL), while yellow turtles would only be using the area for part of their migratory developmental phase, since their SM is much larger (~96.0cm SCL). Tagging data indicate that *C. mydas* individuals stay at GNP for several years (Sampson *et al*. in prep). GNP is probably a stopover point in the migratory route of both *C. mydas* morphotypes.

The data showed that black turtles were significantly larger during the last years of this study (2011 and 2012), and that yellow turtles were smaller in 2010. This could be indicative of a change in the contribution of the different rookeries (SM of Galápagos turtles is larger than that of Michoacán turtles, and that of Hawaii turtles is smaller than that of French Polynesia turtles), or to more time being spent by these turtles at different locations before arriving to GNP. According to genetic analyses, there were more turtles from Hawaii in 2010 than from French

Frigate shoals, which would explain the smaller size of these turtles in that year (Correa-Cárdenas, 2013).

The CI values reported by several authors for eastern Pacific *C. mydas* are similar to those found in this study (Table 2). This indicates that the resources available for turtles at the GNP foraging area are equivalent to those of turtles further north (Baja California), since their CI is similar, and that resources at GNP are sufficient to maintain a healthy CI for *C. mydas* juveniles in the area. The lower availability and abundance of algae in GNP compared to Baja California might be compensated by the availability of other resources such as tunicates that provide a high-protein food source (Amorocho and Reina, 2007; Fernández-García *et al*., 2011; Sampson and Giraldo, 2014).

Condition indices have been proposed as indicators of individual health; these indices can be used to compare the well-being of individuals from different populations and can be indicators of changes in the food supply (Bolger *et al*., 1989). The mean CI of yellow morphotype turtles was significantly higher than that of black turtles. This could be due to yellow turtles consuming more or better quality food, and coincides with the report by Pritchard (1971) of yellow turtles being larger and fattier than black turtles at the Galápagos Islands. It could also be due to smaller-sized turtles arriving to the foraging area with a higher CI: The mean CI of 40-49.9 cm SCL yellow turtles was 1.58, while the mean CI of 50-69.9 cm SCL turtles was 1.45, which would give support to the hypothesis that yellow turtles arrive at GNP in better condition (Fig. 6A). This suggests that when yellow turtles recruit to the neritic area and switch from their protein-based oceanic diet their condition decreases slightly, assuming that turtles stay in the neritic area and don´t go back and forth from the oceanic to the neritic area.

The CI of black morphotype turtles varied significantly among the years of this study, while that of yellow morphotype turtles did not. This could be explained by the larger sample size of black

turtles (2003-2012, n=745) compared to that of yellow turtles (2007-2012, n=270) that would better reflect possible changes in CI among years. It could also be a consequence of yellow turtles recruiting to the GNP foraging area as their initial neritic foraging ground, and therefore reflecting conditions in the ocean, while black turtles had probably been feeding in other coastal areas and were dependent on coastal conditions that are more variable in terms of food availability.

Meylan *et al*. (2011) reported that at most Pacific sites the developmental habitats of juveniles overlap with the foraging range of adults. This is not the case at GNP where no adults were observed. This site would function in a similar manner to those observed by Meylan *et al*. (2011) in the Caribbean and Florida, where only juveniles are present.

The variation in sizes at this foraging ground that point to variations in the migratory routes of the two morphotypes studied makes evident the importance of protecting oceanic migratory areas as well as coastal areas that provide resources for turtles that come from geographically separate rookeries.

CONCLUSIONS

GNP is a foraging ground used by both yellow and black morphotypes of *C. mydas*. These two morphotypes share the reef habitat of GNP while they grow to the size at sexual maturity. Most black turtles arrive at a larger size than yellow turtles, and remain until they reach larger sizes. Yellow turtles seem to arrive to GNP and to move out of the foraging area at smaller sizes. These turtles are possibly using GNP as a stopover point during their migration in the eastern Pacific before reaching their rookeries of origin. The black turtles seem to be using GNP until they reach their maturity size and then move either to the Galápagos or the Michoacán rookeries. The fact that the number of yellow turtles using the GNP habitat has increased in recent years, and the

variation in the size of both morphotypes, imply changes in the migratory behavior of this species.

GNP is a foraging area where the stocks from different breeding areas converge to feed, making it an important area for conservation, since several populations are relying on this stopover point in their migratory route for growth.

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REFERENCES

Acevedo-Bueno CI, Beltrán-León BS, Caicedo-Tulante RA. Plan básico de manejo 2005-2009 Parque Nacional Natural Gorgona. Cali: Parques Nacionales Naturales de Colombia. Dirección Territorial Suroccidente;2004.

Amorocho DF, Reina RD. Feeding ecology of the East Pacific green sea turtle *Chelonia mydas agassizii* at Gorgona National Park, Colombia. Endanger. Species Res. 2007;3: 43-51.

Amorocho DF, Abreu-Grobois FA, Dutton PH, Reina RD. Multiple distant origins for green sea turtles aggregating off Gorgona Island in the Colombian Eastern Pacific. PLoS ONE. 2012; 7(2): e31486.

Arthur KE, Balazs GH. A comparison of immature green turtle (*Chelonia mydas*) diets among seven sites in the main Hawaiian Islands. Pac Sci. 2008;62(2): 205-217.

Bass AL, Epperly SP, Braun-McNeill J. Multi-year analysis of stock composition of a loggerhead turtle (*Caretta caretta*) foraging habitat using maximum likelihood and Bayesian methods. Conserv Genet. 2004;5: 783-796.

Bjorndal KA, Bolten AB, Chaloupka MY. Green turtle somatic growth model: evidence for density dependence. Ecol Appl. 2000; 10(1): 269-282.

Bolger T, Connolly PL. The selection of suitable indices for the measurement and analysis of fish condition. J Fish Biol. 1989; 34: 171-182.

Chaloupka M, Limpus C, Miller J. Green turtle somatic growth dynamics in a spatially disjunct Great Barrier Reef metapopulation. Coral Reefs. 2004; 23: 325-335.

Correa-Cárdenas CC. Spatial-temporal analyses of Eastern Pacific green turtles (*Chelonia mydas/Chelonia agassizii*) foraging as mixed stock in Gorgona NNP, Colombian Pacific Ocean. [Master´s thesis] Departamento de Ciencias Biológicas, Universidad de los Andes; 2013, 67p.

Cortés, J. Biology and geology of eastern Pacific coral reefs. Coral Reefs. 1997;15: S39-S46.

Engstrom TN, Meylan PA, Meylan AB. Origin of juvenile loggerhead turtles (*Caretta caretta)* in a tropical developmental habitat in Caribbean Panamá. Anim Conserv. 2002;5: 125-133.

Fernández-García C, Riosmena-Rodríguez R, Wysor B, Tejada OL, Cortés J. Checklist of the Pacific marine macroalgae of Central America. Bot Mar. 2001;54: 53-73.

Glynn PW, von Prahl H, Guhl F. Coral reefs of Gorgona Island, Colombia with special references to corallivores and their influence on community structure and reef development. An Inst Inv Mar Punta Betín. 1982;12: 185-214.

Green D. The green sea turtle project in Galápagos: past, present and future. Noticias de Galápagos 33. 1981;17-20.

Green D. Growth rates of wild immature green turtles in the Galápagos Islands, Ecuador. J Herpetol. 1993; 27(3): 338-341.

Heppell SS, Snover ML, Crowder LB. Sea turtle population ecology. In: Lutz PL, Musick J, Wyneken J, editors. The biology of sea turtles, Vol. II. Boca Raton: CRC Press;2003. p. 275-306.

Hirth H. Synopsis of the biological data of the green turtle, *Chelonia mydas* (Linnaeus, 1758). U.S. Fish and Wildlife Service Biological Report;1997. 120 pp.

Koch V, Brooks LB, Nichols WJ. Population ecology of the green/black turtle (*Chelonia mydas*) in Bahía Magdalena, Mexico. Mar Biol. 2007;153: 35-46.

Lahanas PN, Bjorndal KA, Bolten AB, Encalada SE, Miyamoto MM, Valverde RA, Bowen BW. Genetic composition of a green turtle (*Chelonia mydas*) feeding ground population: evidence for multiple origins. Mar Biol. 1998;130: 345-352.

López-Castro MC, Koch V, Mariscal-Loza A, Nichols WJ. Long-term monitoring of black turtles *Chelonia mydas* at coastal foraging areas off the Baja California Peninsula. Endanger. Species Res. 2010;11: 35-45.

McCormick-Anzola CC. Contribución al conocimiento de la ecología y biología reproductiva de las tortugas marinas en la Isla Gorgona. [Tesis de pregrado]. Cali: Departamento de Biología, Facultad de Ciencias, Universidad del Valle; 1996. 91p.

Márquez MR. An annotated and illustrated catalogue of sea turtle species known to date. FAO Fish. 1990;125(11): 1-81.

Meylan PA, Meylan AB, Gray, JA. The ecology and migrations of sea turtles 8. Tests of the developmental habitat hypothesis. Bull. Am. Mus. Nat. Hist. 2011;357: 3-62.

Parker DM, Dutton PH, Balazs GH. Oceanic diet and distribution of genotypes for the green turtle, *Chelonia mydas*, in the central North Pacific. Pac. Sci. 2011;65(4): 419-431.

Pritchard PCH. Galápagos sea turtles: preliminary findings. J Herpetol. 1971;5(1/2):1-9.

Pritchard PCH. Evolution, Phylogeny, and Current Status. In: Lutz PL and Musick JA (editors). The Biology of Sea Turtles. Boca Raton: CRC Press;1998. pp. 1- 28.

Rodríguez-Barón JM, Riosmena-Rodríguez R, Seminoff JA, Hernández-Carmona G. *Chelonia mydas agassizii* diet. Herpetol Rev. 2011;42(2): 264.

Sampson L, Giraldo A. Annual abundance of salps and doliolids (Tunicata) around Gorgona Island (Colombian Pacific), and their importance as potential food for green sea turtles. Rev Biol Trop. 2014;62(1):149-159.

Sampson L, Giraldo A, Payán LF, Amorocho DF, Eguchi T, Seminoff JA. Somatic growth of juvenile black and yellow morphotype *Chelonia mydas* at the Gorgona National Park foraging ground (Colombian Pacific). Manuscript in preparation.

Seminoff JA, Alfaro Shigueto J, Amorocho D, Arauz R, Baquero A, Chacón D, *et al*. Biology and conservation of sea turtles in the eastern Pacific Ocean: A general overview. In: Seminoff JA and Wallace BP (editors). Sea Turtles of the Eastern Pacific Ocean: research advances, conservation challenges and signs of success. Tucson: University of Arizona Press;2012. p. 11-38.

Seminoff JA, Jones TT, Resendiz A, Nichols WJ, Chaloupka MY. Monitoring green turtles (*Chelonia mydas*) at a coastal foraging area in Baja California, Mexico: multiple indices to describe population status. J Mar Biol Assoc UK. 2003;83: 1355-1362.

Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM, Bolten AB, Chaloupka MY, *et al*. Regional Management Units for marine turtles: A novel framework for prioritizing conservation and research across multiple scales. PLoS ONE 2010;5(12): e15465.

Zapata FA, Vargas-Ángel B, Garzón-Ferreira J. Salud y conservación de las comunidades coralinas. In: Barrios LM, López-Victoria M, editors. Gorgona marina: contribución al conocimiento de una isla única. Santa Marta: INVEMAR, Ser. Pub. Esp. 7;2001. p. 41-50.

Zárate P. Informe final proyecto anidación de la tortuga verde, *Chelonia mydas*, durante la temporada de anidación 2002-2003. Fundación Charles Darwin. Presentado al National Marine Fisheries Service y Parque Nacional Galápagos;2004. 105 p.

CAPÍTULO 2

Somatic growth of juvenile green turtle (*Chelonia mydas*) morphotypes in the Colombian Pacific

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Somatic growth of juvenile green turtle (*Chelonia mydas*) morphotypes in the Colombian Pacific

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ABSTRACT

Somatic growth rates of green turtles (*Chelonia mydas*) are affected by foraging success and influence their survival and reproduction. Gorgona National Park (GNP) in the Colombian Pacific (2°58´03´´N, 78°10´49´´W) is an insular foraging site that offers a unique opportunity to study the black (occurring only in the eastern Pacific) and yellow (with western Pacific nesting beach origins) morphotypes of green turtles during their juvenile phase. A total of 995 turtles were captured and marked between October 2003 and December 2012. Recapture rates were low (20 black morphotype and 13 yellow morphotype turtles) but suggested that at least some turtles remain in the area for extended periods (>5 years). Mean growth rate was slightly higher for black morphotype (mean = 0.92 ± 0.24 cm y^{-1}) than yellow morphotype turtles (mean = 0.74 ± 0.26 cm y^{-1}), and both morphotypes displayed a non-monotonic growth pattern. Black morphotype turtles grew faster at intermediate sizes, similar to black turtles at other locations in

the eastern Pacific, whereas yellow morphotype turtles had slowest growth at intermediate sizes. Our data underscore the importance of GNP as a foraging habitat for *C. mydas* individuals from distinct nesting populations, and indicate that these morphotypes have different growth patterns while residing at the same foraging site.

INTRODUCTION

The green turtle (*Chelonia mydas*), like most marine turtle species, utilizes different habitats during its life cycle. These ontogenetic habitat shifts involve moving from pelagic areas during the first years of life to neritic areas as juveniles, and moving between reproductive and feeding areas as adults (Bolten 2003). Green turtles also migrate between feeding grounds during their juvenile years; these developmental migrations can occur as a response to several factors, such as when water temperatures change (Limpus & Chaloupka 1997; Kubis *et al*. 2009) or as a response to prevailing currents (Bass *et al.* 2006) and changing habitat quality (Godley *et al*. 2003). Ontogenetic habitat shifts are usually correlated with maximization of growth rates, with turtles moving to habitats that allow the greatest nutrient intake (Bjorndal and Bolten 1988; Koch *et al*. 2007). Large-scale migrations of juveniles to foraging grounds have been reported for green turtles in Brazil (up to 670 km; Godley *et al*., 2003) and in Malaysia (up to 1670 km; Pilcher 2010). The resources available to sea turtles at different developmental habitats are important because they affect their ability to grow and eventually reproduce (Bjorndal *et al.* 2000; Kubis *et al*. 2009).

Distinct populations of the same sea turtle species may have different growth rates as a result of varying habitat quality and resource availability at the respective foraging habitats within which they reside (Bjorndal and Bolten 1988; Heppell *et al.* 2003). Comparing growth rates among geographic regions and foraging groups can elucidate the drivers of ontogenetic habitat shifts, because available resources in a given area will have differential effects on growth, age and size

at sexual maturity, and reproductive output (Balazs and Chaloupka 2004; Kubis *et al*. 2009; Bjorndal *et al*. 2013).

The life history of green turtles, including developmental migrations and wide-ranging juvenile movements among foraging areas, hinders studies on juvenile growth, and requires long-term monitoring of populations to garner sufficient information about somatic growth within a population (Bjorndal *et al.* 2000). Gorgona National Park (GNP), in the Colombian Pacific, is a protected foraging area that provides shelter and resources for juvenile green turtles. This park protects one of the most developed coral reefs in the eastern tropical Pacific and provides resources for a large diversity of marine species, including sea turtles (Zapata 2001; Zapata and Vargas-Ángel 2003). The green turtle black morphotype occurs only in the eastern Pacific (Márquez 1990), whereas the yellow morphotype occurring in this region is known to originate from nesting beaches in the central and/or western Pacific (Amorocho *et al.* 2012). Both morphotypes occur at GNP (Sampson *et al.* 2014), which offers a unique opportunity to study this life stage.

The juvenile life stage is demographically important, as it has been shown that reductions in mortality of neritic juveniles and subadults significantly impact population growth rate (Crouse *et al.* 1987). Juvenile green turtles are vulnerable because they preferentially occupy neritic areas, which often have substantial anthropogenic impacts from fisheries bycatch and habitat degradation that result in high mortality (Bolten 2003; Rees *et al.* 2013). Thus, studying juvenile sea turtles in this neritic foraging area will provide much needed information to managers and an estimate of growth of this ectothermic species in a tropical habitat with limited food resources. Here we undertake the first study to determine somatic growth rates of green turtles in the Colombian Pacific. To our knowledge, this is the first-ever study to compare growth of two genetically distinct groups within the same foraging area. This study will help clarify whether

somatic growth rates are more affected by intrinsic characteristics of the individual or by the environment it inhabits. In the first case black and yellow morphotypes should have significantly different growth rates, and in the latter both morphotypes should have similar growth rates since they inhabit the same foraging area and presumably use the same resources.

Other locations in the eastern Pacific where somatic growth rates of black turtles have been estimated reported values ranging widely from 0.15 cm y^{-1} for black morphotype turtles at the Galapagos Islands (Green 1993) to 6.43 cm y^{-1} at Chilean neritic areas (Velez-Zuazo *et al*. 2014).Our data will provide greater context about the variability in green turtle growth among foraging areas throughout the eastern Pacific Ocean.

MATERIALS AND METHODS

Study site

Gorgona Island is in the Colombian Pacific, approximately 30 km from the mainland; together with Gorgonilla it makes up 2.4% of Gorgona National Park (GNP; 2°58´03´´N, 78°10´49´´W), which encompasses a 616.8 km^2 area (Fig. 1). Giraldo (2008) reported an average sea surface temperature of 26.8-28.6ºC for the study area. Local oceanographic processes are influenced by the Panama wind jet and by the intertropical convergence zone moving over the study area (Giraldo 2008). The main reefs are located on the eastern side of the island (La Azufrada, 11.2 ha and Playa Blanca, 10.86 ha) and are dominated by the scleractinean corals *Pocillopora damicornis* and *P. elegans*.

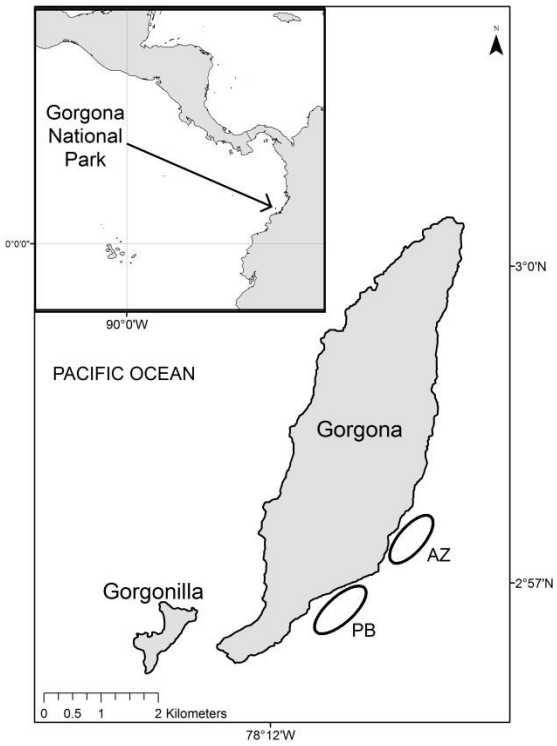

Fig. 1 Study area, Gorgona National Park. Black ellipses show location of reefs where *C. mydas* individuals were captured (AZ = Azufrada, PB = Playa Blanca). Source data of inset map: www.naturalearthdata.com

Seagrass, which is an important component in the diet of green turtles in several regions of the world (Bjorndal and Bolten 1988; Heithaus *et al.* 2013; Williams *et al.* 2014), is not distributed in the eastern tropical Pacific (Short *et al*. 2007). A diet based mainly on algae has been reported for green turtles in the central and eastern Pacific, including Hawaii (Arthur and Balazs 2008), Baja California, Mexico (Seminoff *et al*. 2002), the Galapagos Islands (Carrión-Cortez *et al*. 2010), and Peru (Santillán-Corrales 2008). Reefs in the eastern tropical Pacific are few and far between (Glynn 2001), making GNP an important stopover point for green turtles of both morphotypes. Although it sustains less algae species than other eastern tropical Pacific locations (84 species were reported by Bula-Meyer 1995 at GNP, while Fernández-García *et al*. 2011 reported 146 species at El Salvador, 216 species at Costa Rica and 174 at Panama), this park provides

resources for a green turtle juvenile aggregation that has been monitored since 2003 (Sampson *et al*. 2014).

Turtle Measurements

Growth rates were assessed for green turtles captured at GNP between October 2003 and December 2012. Survey effort (measured as number of turtles captured per sampling trip) was higher in 2003 and 2004 than in subsequent years (One-way ANOVA, $F = 3.07$, $df = 9$, $p = 0.003$), but there were no seasonal differences in survey effort (measured as number of turtles caught per trip per month; One-way ANOVA, $F = 1.74$, $df = 11$, $p = 0.80$). Turtles were captured by hand at night by two to five people, while snorkelling at the two reefs on the eastern side of Gorgona Island (Fig. 1). Measurements of all captured individuals were taken once on shore. Straight carapace length (SCL) from the nuchal notch to the posterior notch and straight carapace width (SCW) at the widest point of the carapace were obtained with forestry calipers, whereas curved carapace length (CCL) was measured with a flexible measuring tape to the nearest 0.5 cm. Turtles were weighed with a spring scale to the nearest 0.5 kg. Turtles were tagged on the trailing edge of the front flippers using numbered Inconel tags (No. 681, National Band and Tag Co., Newport, Kentucky, USA). Due to budget constraints approximately 50% of all captured turtles were tagged on both flippers, while the other 50% were tagged on either the right or left front flipper. Individuals belonging to each morphotype were identified based on external characteristics such as carapace color (black morphotype turtles are dark gray with lighter blotches; yellow morphotype turtles are dark brown with lighter streaks) and carapace shape (black morphotype turtles are more highly arched and with a tapered end; yellow morphotype turtles are rounder) (Márquez 1990; Hirth 1997). External morphological differences have been corroborated by the distinct haplotypes characteristic of each morphotype (Amorocho *et al.* 2012).

Growth analysis

Individual annual linear somatic growth rates were calculated as:

$$Growth = \frac{(Measurement_2 - Measurement_1)}{time\ at\ large}$$

where time at large is the time in years between the initial capture and recapture of a given individual and measurements are SCL in cm.

Only times at large > 6 months were included in the calculation of linear growth rates, to account for measurement error. The reason given in other studies for including only recaptures of > 11 months is that seasonal environmental parameters could affect sea turtle growth rates (Limpus and Chaloupka 1997); however, GNP is a tropical foraging ground, therefore no marked seasonal effects are expected. Negative growth rates were included to avoid bias linked to measurement error, and because there is no statistical reason to exclude them (Bjorndal and Bolten 1988; Limpus and Chaloupka 1997). To avoid pseudoreplication when individuals were recaptured more than once only the first recapture greater than 6 months was used to measure linear somatic growth rates.

Analyses of covariance (ANCOVA) were used to compare the relationship between SCL and CCL, SCW, and the natural logarithm of mass [ln(mass)]. All analyses were conducted using Statistica v.8 (Statsoft). If the regression slopes of the two morphotypes were not significantly different, the extent of the difference in the elevation of the slopes was calculated by subtracting the adjusted means of the two lines.

RESULTS

A total of 995 turtles were captured and tagged from October 2003 to December 2012. Of these, 20 black morphotype and 13 yellow morphotype turtles were recaptured at least once (Fig. 2). The size at initial capture of black morphotype turtles ranged from 43.0 to 71.0 cm SCL, whereas

the size at initial capture of yellow morphotype turtles ranged from 44.1 to 65.9 cm SCL (Fig. 3). The time at large (interval between the first and last capture) of black morphotype turtles ranged from 0.57 to 5.89 years (207 to 2,150 days), with a median of 1.99 years (727 days), and time at large of yellow morphotype turtles ranged from 0.59 to 5.34 years (215 to 1,948 days), with a median of 1.30 years (475 days) (Table 1).

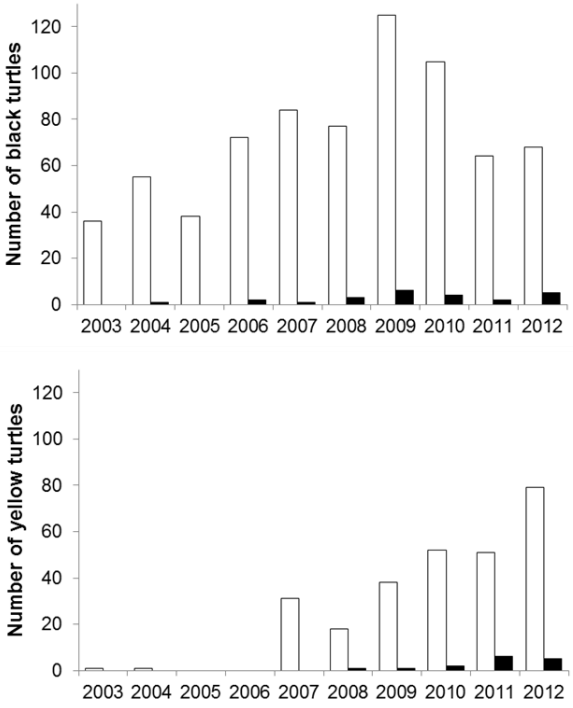

Figure 2. Number of captured and recaptured turtles at Gorgona National Park between 2003 and 2012. White bars: captures, black bars: recaptures.

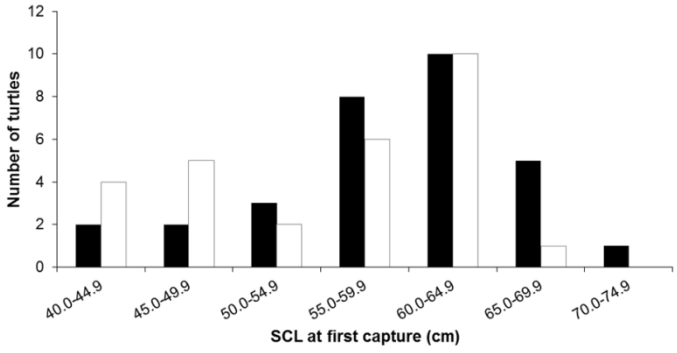

Figure 3. Initial size of black (grey bars) and yellow (white bars) morphotype *C. mydas* captured at Gorgona National Park (2003 - 2012). This graph shows only turtles that were marked then subsequently recaptured.

Table 1. Sample size (N), days at large, size at first capture as cm SCL, and growth in cm y^{-1} of black and yellow turtles captured at Gorgona National Park between 2003 and 2012. Mean ± SD (range)

	Black	**Yellow**
N	20	13
Days at large	894.0 ± 655.3 (207 – 2150)	599.8 ± 452.6 (215 – 1948)
SCL (cm)	57.9 ± 8.3 (43.0 – 71.0)	55.4 ± 7.5 (44.1 – 65.9)
Growth (cm y^{-1})	0.92 ± 1.05 (-0.09 – 3.50)	0.74 ± 0.93 (-0.85 – 2.74)

Somatic growth rates of black morphotype turtles ranged from -0.09 to 3.50 cm y^{-1} (mean=0.92 cm y^{-1}; SE=0.20; n=20), whereas those of yellow morphotype turtles ranged from -0.85 to 2.74 cm y^{-1} (mean=0.74 cm y^{-1}; SE=0.26; n=13) (Fig. 4, Table 1). There were no significant differences in growth rates between the two morphotypes (t test, t=0.49, N_1=20, N_2=13, p=0.62). There were no statistical differences in growth rates among size classes for either black morphotype turtles (ANOVA, F (3, 16) = 6.10, p=0.26), or yellow morphotype turtles (ANOVA, F (2, 10) =3.57, p= 0.07). However, black morphotype turtle somatic growth rates seemed to have a non-monotonic pattern, with fastest growth in the 50.0-59.9 cm SCL size class, while yellow morphotype turtles displayed the opposite pattern, with faster growth rates in the smallest size class (40.0-49.9 cm SCL; Fig. 4).

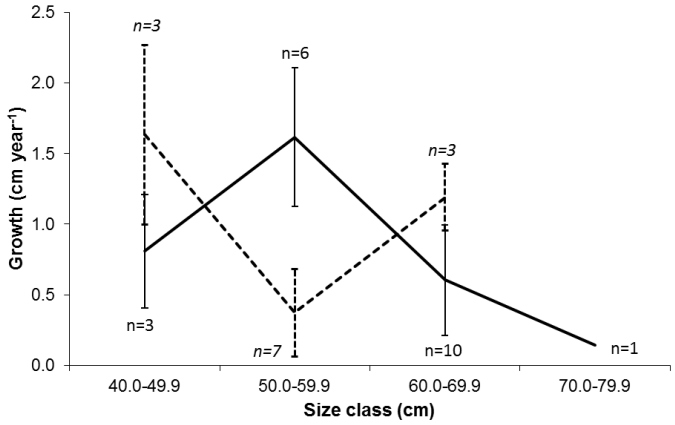

Figure 4. Growth in cm y^{-1} of black (black line) and yellow (dashed line) morphotype *C. mydas* captured at Gorgona National Park (2003 – 2012). Error bars show the standard error, n denotes the number of turtles caught (number of yellow turtles is shown in italics)

The relationships between SCL and CCL, and between SCL and SCW of black and yellow morphotype turtles were linear. The relationship between SCL and ln(mass) was linear for both morphotypes. The analyses of covariance comparing the regression lines obtained for the two morphotypes showed that the slopes of the lines were not significantly different between black and yellow morphotype turtles for SCL vs. CCL, SCL vs. SCW, or SCL vs. ln(mass) (ANCOVA, $p>0.3$; Table 2).

Table 2. ANCOVA results for comparisons of slopes and elevations of relationships between SCL, CCL, SCW (in cm) and ln(mass) of yellow and black turtles captured at Gorgona Island National Park between 2003 and 2012.

	Mean	Adjusted mean	Slope	Slope comparison	Elevation comparison
SCL vs CCL					
Black	64.03	62.20	1.05	F = 0.373	F = 9.117
Yellow	57.41	62.48	1.04	p = 0.541	p = 0.002
SCL vs SCW					
Black	44.42	47.73	0.68	F = 0.0003	F = 11.35
Yellow	49.49	48.28	0.68	p = 0.985	p = 0.0008
SCL vs mass					
Black	3.38	3.29	0.049	F = 0.3535	F = 29.31
Yellow	3.10	3.34	0.050	p = 0.552	p = $7.68e^{-08}$

For all three relationships the elevation of the slopes were significantly different between the two morphotypes (ANCOVA, $p<0.05$). The difference in elevation (black minus yellow) between the lines of SCL vs. CCL was 0.27; for SCL vs. SCW it was 0.56, and for SCL vs. ln(mass) it was -0.27. These results indicated that black morphotype turtles were significantly longer and wider than yellow morphotype turtles, whereas yellow morphotype turtles were heavier. The relationships between SCL and the other measured parameters were not significantly different between the two morphotypes (Table 2). A comparison of growth rates found in this study and those reported for other Pacific Ocean locations is presented in Table 3.

Table 3. Size-specific growth rates of *Chelonia mydas* at different locations in the Pacific.

		Growth rate per size class (cm y^{-1})							
Source	**Study area**	**20-30**	**30-40**	**40-50**	**50-60**	**60-70**	**70-80**	**80-90**	**90-100**
Limpus and Walter (1980)[a]	Heron Island, Australia			0.75	0.95	1.43	1.46	1.1	
Balazs (1982)[a]	Hawaiian Archipelago		1.08	1.33	2.13				
Green (1993)	Galápagos Islands, black turtles			0.4	0.45	0.15	0.12	0.11	
Green (1993)	Galápagos Islands, yellow turtles				1.57				
Zug and Glor (1998)	Hawai´i Island		1.3	1.8	1.8	1.3	0.4		
	French Frigate Shoals		0.98	0.94	1.0				
Zug *et al.* (2002)	Hawaiian Archipelago	4.4	3.5	2.1	2.3	2.2	2.1	1.3	0.6
Seminoff *et al.* (2002)	Baja California				1.0	1.4	1.2	1.9	1.0
Black turtles, this study	Gorgona National Park			0.81	1.62	0.60	0.14		
Yellow turtles, this study	Gorgona National Park			1.63	0.37	1.19			

[a] Limpus and Walter 1980, Balazs 1982 cited in Zug and Glor (1998)

DISCUSSION

There have been few published studies of green turtle growth rates at eastern Pacific locations (Table 3). The present study provides somatic growth rates for a green turtle aggregation composed of individuals from different genetic stocks (Amorocho *et al*. 2012) at a tropical foraging ground. The average growth rates of the two green turtle morphotypes compared in this study were not significantly different, hinting at a greater effect of the environment on growth rates rather than of the genetic stocks the individuals belong to, as has been seen at other foraging areas where individuals from different rookeries co-occur (Patricio *et al*. 2014).

The different growth rate patterns that were evident when taking into account size classes, however, suggest that the individual´s life history could also affect growth rates. As a genetic study indicated, green turtles at this coastal foraging ground arrive from distant nesting beaches (Amorocho *et al*. 2012). Differences in oceanic conditions over the migratory paths taken by individual turtles may be affecting the observed growth patterns. This possibility underscores the importance of protecting migratory corridors such as the Eastern Pacific Tropical Marine Corridor that would help ensure that juvenile green turtles can move between protected areas that they use as developmental habitat.

Recapture rate

The number of recaptures in this study was relatively low, with only 8% recaptures of black morphotype turtles and 10% recaptures of yellow morphotype turtles, compared with other locations where reported recapture rates have been much higher, such as Australia (32%; Chaloupka *et al.* 2004), the Bahamas (41%; Bjorndal *et al.* 2000), Florida (61%; Kubis *et al*. 2009), and Baja California (up to 32%; Koch *et al.* 2007). However, the cumulative number of captured turtles increased with the years of study, with time at large of up to 5.9 years. Recaptured turtles could be staying at the GNP feeding ground during all this time or could be

moving to nearby feeding areas that are within the reported range of coastal movements of juvenile turtles (up to ~670 km, Godley *et al*. 2003). It should be noted that tag loss can occur, and residence times at GNP could be longer than observed. Given that only half of all captured turtles were double-tagged, losses could potentially be high. However, absence of scar tissue on captured turtles indicated that this was probably not an issue. Future surveys should establish double-tagging to comply with recommended standards, and PIT tags could be introduced to further decrease tag loss (Balazs 1999). If turtles were moving out of the area constantly, the cumulative number of captures would not have increased with time. The low recapture rates in this study could be indicative of low resource availability that would result in turtles moving in and out of the study area to feed elsewhere, or that the number of turtles in the area was so high that with the limited sampling effort, tagged turtles were not recaptured during the study period. There might be a mixture of resident and transient green turtles at GNP, as some individuals were recaptured several times over the years. Given all possible causes of observed low recapture rates, it is important to continue marking green turtles at this foraging site in order to obtain better capture-recapture data, and to examine movements in and out of this foraging area through the use of telemetry.

Linear growth rates

Mean somatic growth rates of the two morphotypes were not significantly different. The regressions of SCL vs. CCL, SCW and ln(mass) indicated no significant difference in the slopes of the regression lines between the two morphotypes, which indicates that turtles of both morphotypes were similarly shaped.

The size-specific mean growth rate of black morphotype turtles showed a non-monotonic pattern, with highest growth rates in the 50.0-59.9 cm size class, and a subsequent decline in the largest size classes, similar to what has been reported for black morphotype turtles in the Galápagos

Islands and in San Diego Bay (Green 1993; Eguchi *et al.* 2012), and for yellow morphotype turtles in the Hawaiian Archipelago (Balazs and Chaloupka 2004). Yellow morphotype turtles at GNP displayed the opposite pattern, with slowest growth at intermediate sizes and highest growth rates in the smallest size class (40.0-49.9 cm SCL). This type of growth pattern has not been reported elsewhere and might be an artifact of small sample size and large variability. The increase in growth rates of black morphotype turtles after recruitment to the neritic area of GNP could be an effect of the ontogenetic change in habitat, with its associated change in resource consumption.

Growth rates and resource availability

It is apparent that black morphotype turtles at GNP have similar growth patterns to other black morphotype populations in the eastern Pacific, whereas there is a declining trend in yellow morphotype growth rates at intermediate sizes, although this was not statistically significant (Fig. 4). The higher growth rates found for smaller yellow morphotype turtles coincide with higher condition index values found for this size class in yellow morphotype turtles at GNP (Sampson *et al*. 2014). This suggests that when small yellow morphotype turtles arrive at GNP they are in better condition and grow faster, but that after changing to a neritic habitat both the condition index and growth rates decline. This could be indicative of the metabolic changes that occur when turtles recruit to the neritic zone or could be reflecting resource availability in the study area. However, ANCOVA results showed that yellow morphotype turtles were heavier than black morphotype turtles at a given length. This could be a morphological characteristic and would therefore make comparisons of condition index values between the two morphotypes more complicated.

Resource availability has been linked to growth rates in green turtles, for example, Kubis *et al*. (2009) found slower growth rates in green turtles that consumed a lower number of algae species

in Florida. Turtles at the location with slower growth rates ate available algae, jellyfish, fish carcasses and floating vegetation – similar to what occurs at GNP, where turtles eat available algae and supplement their diet with invertebrates and floating vegetation (Amorocho & Reina 2007). High growth rates (2.83 - 6.77 cm y^{-1}) reported for green turtles near high-productivity locations in Chile also support the link between environmental quality and growth rates (Velez-Zuazo et al. 2014).

The observed growth pattern of yellow morphotype turtles could be due to the small size range of captured turtles, or it could be due to this morphotype having a different life history than that of the black morphotype, with different migrations and a larger size at maturity that results in different somatic growth rates. This result should be investigated further with continued monitoring of this population. Identifying the precise origin of yellow morphotype turtles at GNP would also help elucidate the differences between the life histories of these two morphotypes at this location.

In summary, this marine protected area is an important neritic foraging ground for individuals of the two known morphotypes of green turtle that originate from different nesting beaches. This is an important location for the two morphotypes, functioning as a foraging area for juveniles and subadults of both sexes, and its conservation is therefore essential. GNP could also act as an index site for the source populations of individuals captured there. Further long-term capture-recapture data could provide estimates of important parameters such as abundance, survival rates, and life stage duration.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

REFERENCES

Amorocho DF, Reina R (2007) Feeding ecology of the East Pacific green sea turtle *Chelonia mydas agassizii* at Gorgona National Park, Colombia.

Amorocho DF, Abreu-Grobois FA, Dutton PH, Reina RD (2012) Multiple distant origins for green sea turtles aggregating off Gorgona Island in the Colombian Eastern Pacific. PLoS ONE 7(2): e31486. doi:10.1371/journal.pone.0031486

Balazs GH, Chaloupka M (2004) Spatial and temporal variability in somatic growth of green sea turtles (*Chelonia mydas*) resident in the Hawaiian Archipelago. Mar Biol 145: 1043-1059. doi: 10.1007/s00227-004-1387-6

Bass AL, Epperly SP, Braun-McNeill J (2006) Green turtle (*Chelonia mydas*) foraging and nesting aggregations in the Caribbean and Atlantic: Impact of currents and behavior on dispersal. J Heredity 97(4): 346-354. doi: 10.1093/jhered/esl004

Bjorndal, KA, Bolten, AB (1988) Growth rates of immature green turtles, *Chelonia mydas*, on feeding grounds in the southern Bahamas Copeia 3: 555-564

Bjorndal KA, Bolten AB, Chaloupka MY (2000) Green turtle somatic growth model: evidence for density dependence. Ecol Appl 10(1): 269-282.

Bjorndal, KA, Parsons, J, Mustin, W, Bolten, AB (2013) Threshold to maturity in a long-lived reptile: interactions of age, size, and growth. Mar Biol 160(3): 607-616. doi: 10.1007/s00227-012-2116

Bolten AB (2003) Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. In: Lutz PL, Musick J, Wyneken J (eds) The biology of sea turtles, Vol. II. CRC Press, Boca Raton, pp. 243-257.

Bula-Meyer G (1995). Macroalgas de la Isla de Gorgona (Pacífico Colombiano) con nuevos registros y una explicación de la baja diversidad y biomasa. La isla de Gorgona, nuevos estudios biológicos. Instituto de Ciencias Naturales-Museo de Historia Natural, Santafé de Bogotá, Colombia.

Carrión-Cortez JA, Zárate P, Seminoff JA (2010) Feeding ecology of the green sea turtle (*Chelonia mydas*) in the Galapagos Islands. J Mar Biol Assoc UK 90(5): 1005-1013. doi: 10.1017/S0025315410000226

Chaloupka M, Limpus C, Miller J (2004) Green turtle somatic growth dynamics in a spatially disjunct Great Barrier Reef metapopulation. Coral Reefs 23: 325-335. doi: 10.1007/s00338-004-0387-9

Crouse DT, Crowder LB, Caswell H (1987) A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68(5): 1412-1423. doi: http://dx.doi.org/10.2307/1939225

Eguchi T, Seminoff JA, LeRoux RA, Prosperi D, Dutton DL, Dutton PH (2012) Morphology and growth rates of the green sea turtle (*Chelonia mydas*) in a Northern-most temperate foraging ground. Herpetologica 68(1): 76-87 doi: 10.1655/HERPETOLOGICA-D-11-00050.1

Fernández-García C, Riosmena-Rodríguez R, Wysor B, Tejada OL, Cortés J (2011) Checklist of the Pacific marine macroalgae of Central America. Bot Mar 54: 53-73 doi: 10.1515/bot.2011.001

Giraldo A (2008) Variabilidad espacial de temperatura, salinidad y transparencia en el ambiente pelágico del PNN Gorgona durante septiembre 2007 y marzo 2008. Boletín Científico CIOH 26: 157-163

Glynn PW (2001) Eastern Pacific coral reefs: new revelations in the twentieth century. Atoll Res Bull 494(8): 119-158. doi: 10.5479/si.00775630.494-8.119

Godley BJ, Lima EHSM, Akesson S, Broderick AC, Glen F, Godfrey MH, Luschi P, Hays GC (2003) Movement patterns of green turtles in Brazilian coastal waters described by satellite tracking and flipper tagging. Mar Ecol Prog Ser 253: 279-288. doi: 10.3354/meps253279

Goshe LR, Avens L, Scharf FS, Southwood AL (2010) Estimation of age at maturation and growth of Atlantic green turtles (*Chelonia mydas*) using skeletochronology. Mar Biol 157: 1725-1740. doi: 0.1007/s00227-010-1446-0

Green D (1993) Growth rates of wild immature green turtles in the Galápagos Islands, Ecuador. J Herpetol 27(3): 338-341.

Heppell SS, Snover ML, Crowder LB (2003) Sea turtle population ecology. In: Lutz PL, Musick J, Wyneken J (eds) The biology of sea turtles, Vol. II. CRC Press, Boca Raton, pp 275-306.

Heithaus MR, Vaudo JJ, Kreicker S, Layman CA, Krützen M, Burkholder DA, Gastrich K, Bessey C, Sarabia R, Cameron K, Wirsing A, Thomson JA, Dunphy-Daly M (2013) Apparent resource partitioning and trophic structure of large-bodied marine predators in a relatively pristine seagrass ecosystem. Mar Ecol Prog Ser 481: 225-237. doi:10.3354/meps10235

Hirth H (1997) Synopsis of the biological data of the green turtle, *Chelonia mydas* (Linnaeus, 1758). U.S. Fish and Wildlife Service Biological Report.

Koch V, Brooks LB, Nichols WJ (2007) Population ecology of the green/black turtle (*Chelonia mydas*) in Bahía Magdalena, Mexico. Mar Biol 153: 35-46. doi: 10.1007/s00227-007-0782-1

Kubis S, Chaloupka M, Ehrhart L, Bresette M (2009) Growth rates of juvenile green turtles *Chelonia mydas* from three ecologically distinct foraging habitats along the east central coast of Florida, USA. Mar Ecol Prog Ser 389: 257-269. doi: 10.3354/meps08206

Limpus C, Chaloupka M (1997) Nonparametric regression modelling of green sea turtle growth rates (southern Great Barrier Reef). Mar Ecol Prog Ser 149: 23-34. doi: 10.3354/meps149023

Márquez MR (1990) An annotated and illustrated catalogue of sea turtle species known to date. FAO Fish 125(11): 1-81.

Patricio R, Diez CE, van Dam RP (2014) Spatial and temporal variability of immature green turtle abundance and somatic growth in Puerto Rico. Endang Species Res 23: 51-62. doi: 10.3354/esr00554

Pilcher N (2010) Population structure and growth of immature green turtles at Mantanani, Sabah, Malaysia. J Herpetol 44(1): 168-171. doi: http://dx.doi.org/10.1670/08-115.1

Rees AF, Margaritoulis D, Newman R, Riggall TE, Tsaros P, Zbinden JA, Godley BJ (2013) Ecology of loggerhead marine turtles *Caretta caretta* in a neritic foraging habitat: movements, sex ratios and growth rates. Mar Biol 160: 519-529. doi: 10.1007/s00227-012-2107-2

Sampson L, Payán LF, Amorocho DF, Seminoff JA, Giraldo A (2014) Intraspecific variation of the green turtle, *Chelonia mydas* (Cheloniidae), in the foraging area of Gorgona Natural National Park (Colombian Pacific). Acta Biol Colomb 19(3): 461-470. doi: http://dx.doi.org/10.15446/abc.v19n3.42615

Santillán-Corrales LA (2008) Composición del contenido estomacal de Chelonia mydas agassizzi en Bahía de Sechura. In: Kelez S, van Oordt F, de Paz N, Forsberg K (eds) Libro de resúmenes II Simposio de tortugas marinas en el Pacífic sur oriental, Lima, Peru, p. 16.

Seminoff JA, Resendiz A, Nichols WJ, Jones TT (2002) Growth rates of wild green turtles (*Chelonia mydas*) at a temperate foraging area in the Gulf of California, México. Copeia 3: 610-617.

Short F, Carruthers T, Dennison W, Waycott M (2007) Global seagrass distribution and diversity: A bioregional model. J Exp Mar Biol Ecol 350: 3-20. doi: 10.1016/j.jembe.2007.06.012

Velez-Zuazo X, Quiñones J, Pacheco AS, Klinge L, Paredes E, Quispe S, Kelez S (2014) Fast growing, healthy and resident green turtles (*Chelonia mydas*) at two neritic sites in the central and northern coast of Peru: implications for conservation. PLoS ONE 9(11): e113068. doi: 10.1371/journal.pone.0113068

Williams NC, Bjorndal KA, Lamont MM, Carthy RR (2014) Winter diets of immature green turtles (*Chelonia mydas*) on a Northern feeding ground: Integrating stomach contents and stable isotope analyses. Estuar Coast 37: 986-994. doi:10.1007/s12237-013-9741-x

Zapata FA (2001) Formaciones coralinas de isla Gorgona. In: Barrios LM, López-Victoria M (eds) Gorgona marina: contribución al conocimiento de una isla única. INVEMAR, Ser. Pub. Esp. 7, Santa Marta, pp 27-40.

Zapata FA, Vargas-Ángel B (2003) Corals and coral reefs of the Pacific coast of Colombia. In: Cortes J (ed) Coral reefs of Latin America. Elsevier Science, Amsterdam, pp 419-447.

Zug GR, Glor RE (1998) Estimates of age and growth in a population of green sea turtles *Chelonia mydas* from the Indian River lagoon system, Florida: a skeletochronological analysis. Can J Zool 76: 1497–1506. doi: 10.1139/z98-090

Zug GR, Balazs GH, Wetherall JA, Parker DM, Murakawa SKK (2002) Age and growth of Hawaiian green seaturtles (*Chelonia mydas*): an analysis based on skeletochronology. Fish B-NOAA 100: 117-127.

CAPÍTULO 3

Annual abundance of salps and doliolids around Gorgona Island (Colombian Pacific), and their importance as potential food for green sea turtles

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Annual abundance of salps and doliolids around Gorgona Island (Colombian Pacific), and their importance as potential food for green sea turtles

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ABSTRACT: Gorgona National Park protects fertile waters that support large filter-feeding vertebrates, including green sea turtles *Chelonia mydas*. Gelatinous zooplankton constitute a resource that can be found year-round in Gorgona Island´s coastal waters. This study was carried out to determine the abundance of salps and doliolids around Gorgona Island over a year, and to determine whether this is a resource that could be used reliably year-round by green turtles and other large plankton-feeding predators. The monthly abundance of salps and doliolids at eight coastal stations around Gorgona Island (Colombian Pacific) was determined between September 2005 and August 2006. Oblique tows were carried out from 50m to the surface, total zooplankton biomass was measured and the number of salps and doliolids per tow, and frequency of occurrence per station and month were determined. Superficial and bottom sea temperature, superficial and bottom salinity, and chlorophyll-*a* concentration were recorded at each station. There were tunicate abundance peaks in September 2005 and March 2006. The high abundances

in March were probably due to a cold water intrusion into the study area, which resulted in colder saltier water and a shallower thermocline. Tunicates were probably advected to the area by currents from the southwest and aggregated due to the underwater topography. In September, the influence of continental river discharge as well as inputs from rainfall over the island could have provided increased nutrients and resulted in higher abundances. The large filter-feeding vertebrates that feed on tunicates include green sea turtle juveniles, which use coastal waters of Gorgona Island as feeding grounds, as part of their migration route in the Eastern Tropical Pacific. These turtles could be using tunicates opportunistically, as a sporadic resource that is available at certain times of the year.

Key words: *Chelonia mydas*, tunicates, Salpidae, Doliolidae, Gorgona Island, opportunistic trophic behaviour, advection

RESUMEN

Se determinó la abundancia de salpas y doliólidos en ocho estaciones costeras alrededor de Isla Gorgona (Pacífico colombiano), entre septiembre 2005 y agosto 2006. Se hicieron arrastres oblicuos desde 50m hasta la superficie; se midió la biomasa zooplanctónica total, el número de salpas y doliólidos por arrastres, y la frecuencia de ocurrencia por estación y por mes. Se registró la temperatura superficial y de fondo, la salinidad superficial y de fondo, así como la concentración de clorofila *a* en cada estación. Se observaron picos de abundancia de tunicados en septiembre 2005 y marzo 2006. Las altas abundancias en marzo fueron probablemente debidas a una intrusión de agua fría a la zona de estudio, la cual resultó en aguas más frías y saladas, y en una termoclina más somera. Los tunicados fueron probablemente advectados hacia el área por corrientes provenientes del suroeste, y la topografía subacuática causó una agregación de estos organismos. En septiembre, la influencia de las descargas de los ríos continentales, así como aportes por la precipitación sobre la isla pudieron haber provisto mayor cantidad de nutrientes y

resultado en mayores abundancias. Los grandes vertebrados marinos filtradores que se alimentan de tunicados incluyen tortugas verdes juveniles, las cuales usan las aguas de Isla Gorgona como zona de forrajeo, como parte de su ruta de migración en el Pacífico Oriental Tropical. Estas tortugas podrían estar utilizando los tunicados oportunistamente, como un recurso esporádico que está disponible en ciertas épocas del año.

INTRODUCTION

Gorgona National Park protects the most developed reef on the Eastern Tropical Pacific, and coastal waters around the island provide resources for a variety of plant and animal life (Zapata et al., 2001; Giraldo & Valencia, 2012). Several large plankton-feeding vertebrates such as manta rays, devil rays and whale sharks feed in Gorgona Island´s coastal waters (Acero & Franke, 2001). The oceanographic conditions of the island provide a setting that fosters the presence of a diverse zooplankton community that includes mostly copepods, decapods and polychaetes. Gelatinous zooplankton, including pelagic tunicates (salps and doliolids) can be found in coastal waters year-round (Soto et al., 2001).

Pelagic tunicates are large transparent animals that can measure up to 25 cm (Lavaniegos & Ohman, 2003). They are mainly herbivorous filter feeders that feed on diatoms, dinoflagellates, radiolarians and foraminiferans, among others (Alldredge & Madin, 1982; Kremer, 2002). Their life cycle alternates between sexual solitary structures and asexual colonies that reproduce by gemmation, and can produce hundreds of thousands of individuals. This allows rapid increases in population numbers (Graham et al., 2001). Sudden increases in tunicate populations possibly linked to increases in food abundance have been observed in previous studies, with densities of up to 7 000 ind/m^3 being recorded (Alldredge & Madin, 1982).

Several large predators consume pelagic tunicates, such as sea turtles, tuna, cod, ocean sunfish, flying fish, jellyfish, siphonophores, ctenophores, and heteropod molluscs (Alldredge & Madin,

1982; Dewar et al., 2010; Hays et al., 2009; Madin et al., 1996; Montenegro et al., 1984; Potter et al., 2011). Leatherback turtles *Dermochelys coriacea* are known to feed mainly on gelatinous organisms such as jellyfish, salps and pyrosomes, and the olive ridley turtle *Lepidochelys olivacea* occasionally feeds on salps (Hays et al., 2009, Montenegro et al., 1984). The green turtle *Chelonia mydas* has a mainly herbivorous diet, but in the eastern Pacific, where seagrass pastures are not available, green sea turtles also include animal protein in their diet (Bjorndal, 1985; Amorocho & Reina, 2007). Gorgona Island is the only known feeding ground for juvenile green turtles in the Colombian Pacific, and in this area pelagic tunicates can make up a large component of their diet (66% dry weight, Amorocho & Reina, 2007).

Of the known predators of pelagic tunicates present around Gorgona Island, the green sea turtle is the only species that is the focus of a Management Plan for Gorgona National Park (Acevedo-Bueno et al., 2004), and determining the availability of this resource for the turtles would be beneficial for future management actions. The objective of this study was therefore to determine the abundance of salps and doliolids in coastal waters of Gorgona Island over the course of a year, and to determine whether this is a resource that could be used reliably year-round by green turtles and other large plankton-feeding predators.

MATERIALS AND METHODS

Study area: Gorgona National Park is located off the Pacific coast of Colombia; it encompasses a 6033 km^2 marine area that includes Gorgona Island (13.3 km^2). It is located within the Inter-Tropical Convergence Zone, which has a marked influence on local winds, temperature and precipitation (Rodríguez-Rubio et al., 2003). The coastal oceanography of Gorgona Island is influenced by cyclonic gyres generated by the trade winds. Two contrasting oceanographic periods have been detected for the area: a warm, low-salinity period with a deep thermocline (47 m) from May to December (rainy season), and a cold, high-salinity period with a shallow

thermocline (7.5 m) from January to April (dry season; Giraldo et al., 2008; Giraldo et al., 2011). Circulation patterns also show two contrasting periods: one during the northern hemisphere summer, with currents moving towards the south-west, and another one during the northern hemisphere winter, with currents moving towards the north-east (Rodríguez-Rubio et al., 2003; Giraldo et al., 2008).

The fringing coral reefs on the eastern side of the island provide habitat and resources for a variety of organisms, including fish, echinoderms, polychaetes, mollusks, crustaceans, bryozoans, hydroids, sponges and algae, among others (Barrios-Suárez & López Victoria, 2001; Acevedo-Bueno et al., 2004; Zapata et al., 2010). The pelagic zone also offers food resources, with 136 species of phytoplankton (75% diatoms and 23% dinoflagellates in October; 69% diatoms and 30% dinoflagellates in March), and 96 zooplankton families having been reported (Soto et al. 2001; Giraldo et al., 2011; Giraldo et al., 2013).

Gorgona Island´s coastal zone does not include seagrasses or mangroves, which are food resources used by *C. mydas* in other parts of the world (Bjorndal, 1985; Acevedo-Bueno et al., 2004). There are eighty-five algae species (17 Chlorophyta, 15 Phaeophyta, and 54 Rhodophyta) with a predominance of encrusting red algae (Bula-Meyer, 1995), which is noticeably lower than the number of species reported for Baja California (998 sp.), the Galápagos Islands (316 sp.), and Hawaii (400 sp.), places where *C. mydas* has been reported to feed mainly on algae (López-Mendilaharsu et al., 2008, Arthur & Balazs, 2008, Carrión-Cortez et al., 2010; Fernández-García et al., 2011).

Field sampling, laboratory work and data analysis: Oblique diurnal tows were carried out once a month from 50m to the surface, at eight coastal stations (see Fig. 3 for station numbers and locations), from September 2005 to August 2006, using a 30cm mouth diameter bongo net with 250µm mesh size. A flowmeter (General Oceanics) was placed in the center of the net to

determine filtered volume (11.09m^3 on average were filtered during each tow). All samples were preserved in 10% formalin. Temperature and salinity were recorded at the surface and at the bottom (or at 50m, depending on depth at each station), in September, November and December 2005, and March and June 2006, using a CTD (Seabird-19). Superficial chlorophyll-*a* concentrations were recorded from February to August 2006, using an AquaFluor® handheld fluorometer (Turner Designs). The thermocline was determined as the depth where the temperature was 20ºC.

Separation and quantification of samples was done at the Animal Ecology Laboratory of the Universidad del Valle. Total zooplankton biomass in wet weight was recorded and the total number of organisms counted (Giraldo et al. 2011). A subsample (½ or ¼) was taken, and all tunicates (salps and doliolids) were separated and counted using a stereoscope. Unfortunately, organisms could not be identified to species due to sample deterioration caused by prolonged storage. Tunicate abundances were classified according to the following categories: 1) 1-3 ind/m^3, 2) 4-17 ind/m^3, 3) 18-80 ind/m^3, 4) 80-350 ind/m^3, and 5) 350-1500 ind/m^3 (Frontier et al., 1969; Ménard et al., 1994).

The salp and doliolid frequency of occurrence was calculated for each station as $FO\%_{station}$=(months with salps or doliolids present at each station/total number of stations) x 100, and for each month as $FO\%_{month}$=(months with salps or doliolids present each month/total number of stations) x 100. The number of tunicates (number of salps or doliolids/m^3) obtained during each tow was calculated as number of salps or doliolids per tow/total filtered volume in m^3. The percentage of tunicates compared to all other zooplankton was calculated as tunicate%= (number of salps or doliolids/m^3 /total zooplankton in m^3) x 100.

Kruskal-Wallis tests, post-hoc non-parametric multiple comparisons and Spearman´s correlations were used to compare abundances, salinity, temperature and chlorophyll-*a* concentrations

between stations and months, using Statistica v. 8.0 (StatSoft). ArcMap 10.0 was used to create maps depicting the proportion of tunicates vs. zooplankton at each station.

RESULTS

Environmental variables: There were annual variations in sea surface temperature (SST), sea bottom temperature (SBT), sea surface salinity (SSS) and sea bottom salinity (SBS) (Kruskal-Wallis, $p<0.05$). SST was more variable in March (range of 23.8–27.5ºC) than during the rest of the year (average±st. dev, 27.2ºC±0.37ºC). SSS was variable in September, ranging from 26.2UPS to 30.7UPS, while the rest of the year the average was 30.7±0.96. SBT and SBS had no defined pattern, ranging from 15.1 ºC to 27.5ºC and 28.9UPS to 34.9UPS, respectively.

Thermocline depths varied during the year (Table 1). In March the thermocline was shallower (10.6m) than the rest of the year (average 46.5m). This shallower thermocline was also detected by Giraldo *et al*. (2013) during March 2011. Chlorophyll *a* values were also significantly different during the year (Kruskal-Wallis, $p<0.05$), with higher values in April (Table 2).

Table 1. Sea surface temperature (SST), Sea bottom temperature (SBT), Sea surface salinity (SSS), Sea bottom salinity (SBS), and Thermocline depth from September 2005 to June 2006

	SST (ºC)*	SBT (ºC)	SSS	SBS	Thermocline depth (m)
Sep-05	27.26 ± 0.08	24.25 ± 3.94	29.46 ± 1.50	32.19 ± 1.44	47.68
Nov-05	26.93 ± 0.10	22.45 ± 5.85	29.92 ± 0.20	32.13 ± 2.32	39.75
Dec-05	26.99 ± 0.12	23.00 ± 4.76	30.22 ± 0.48	32.73 ± 1.49	47.56
Mar-06	26.17 ± 1.19	18.95 ± 3.79	31.41 ± 0.81	34.27 ± 0.95	10.57
Jun-06	27.80 ± 0.17	25.70 ± 2.78	31.33 ± 0.96	32.89 ± 0.86	50.91

* = average ± standard deviation

Table 2. Monthly chlorophyll-*a* concentrations, salp and doliolid abundances from September 2005 to August 2006

	Salps (ind/m^3) *	Doliolids (ind/m^3)	Chlorophyll-*a* (μg/L)
Sep-05	9.60 (±12.54)	83.32 (±174.84)	N.D.
Oct-05	0.16 (±0.24)	1.24 (±1.18)	N.D.
Nov-05	1.07 (±1.34)	2.10 (±2.46)	N.D.
Dec-05	0.02 (±0.06)	10.57 (±6.50)	N.D.
Jan-06	0.44 (±0.73)	1.12 (±1.03)	N.D.
Feb-06	19.81 (±32.07)	0.00	0.310 (±0.24)
Mar-06	9.43 (±11.90)	164.06 (±373.11)	0.442 (±0.20)
Apr-06	0.17 (±0.25)	1.10 (±0.95)	0.653 (±0.25)
May-06	0.00	0.11 (±0.21)	0.301 (±0.24)
Jun-06	1.24 (±0.92)	2.08 (±1.93)	0.320 (±0.13)
Jul-06	1.74 (±1.49)	1.41 (±2.16)	0.132 (±0.02)
Aug-06	0.00	2.22 (±3.25)	0.134 (±0.02)

* = average ± standard deviation

Tunicate annual abundances: There was a significant difference in doliolid abundance during the year (Kruskal-Wallis, $p<0.05$), with maximal abundances (categories 3 to 5) in September 2005 (515.4 ind/m^3, Station 1) and March 2006 (1 085.1 ind/m^3, Station 1). The rest of the year there were very few doliolids (<18 ind/m^3; Fig. 1). In September doliolids comprised 17.2% of total zooplankton and in March 2006 they made up 23.1% of total zooplankton (Fig. 3).

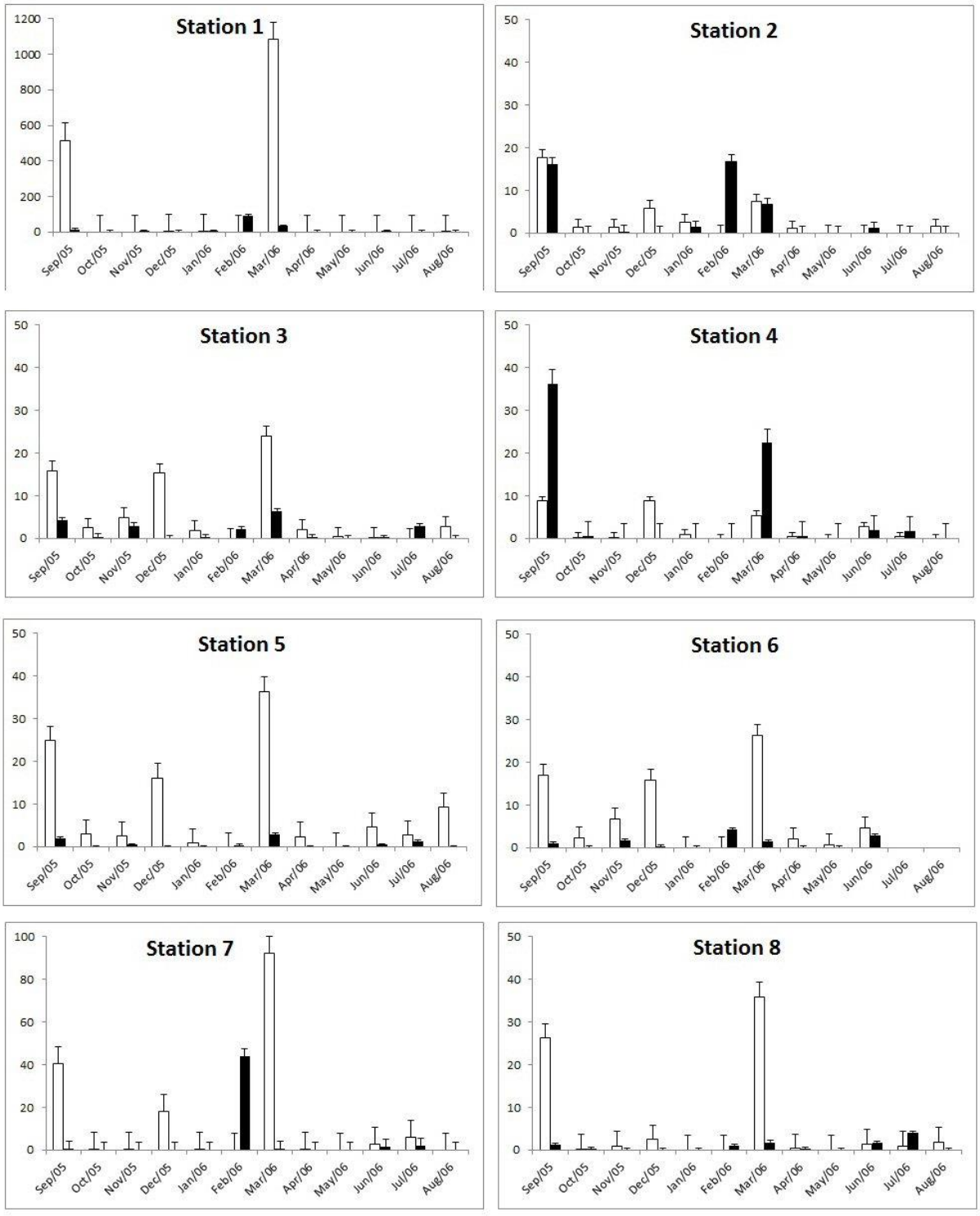

Fig. 1. Salp (black bars) and doliolid (white bars) abundance in ind/m^3 between September 2005 and August 2006, at coastal stations around Gorgona Island. Note: Station 1 is on a different scale due to the high abundance at this station.

Salp abundances were also statistically different during the year (Kruskal-Wallis, $p<0.05$). Maximal abundances (categories 3 to 4) were observed in September 2005 (36.14 ind/m^3, Station 4), February 2006 (90.1 ind/m^3, Station 1), and March 2006 (43.9 ind/m^3, Station 7), while the rest of the year abundances were <18 ind/m^3 (Fig. 1). Salps made up 1.98% of total zooplankton in September 2005, 4.27% in February 2006 and 12.05% in March 2006 (Fig 3).

Figure 2 shows that tunicates were collected at all stations around the island, although they occurred in higher abundances at some locations (salps: stations 1, 10 and 19; doliolids: stations 1, 7, 13, 16, 19 and 22). Although no salps were recorded in May or August 2006 and no doliolids were recorded in February 2006, the frequency of occurrence by month showed that tunicates were available around Gorgona Island year-round.

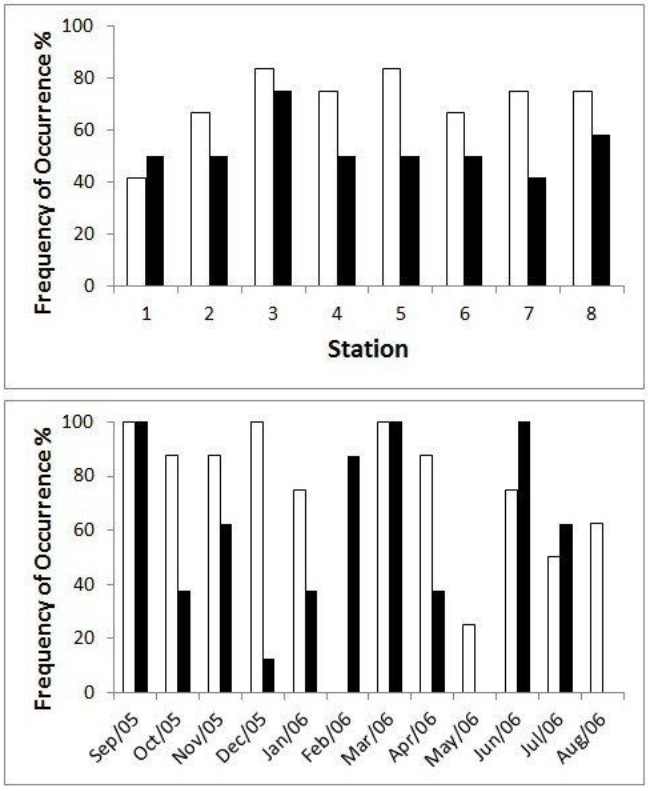

Fig. 2. Salp (black bars) and doliolid (white bars) frequency of occurrence between September 2005 and August 2006 around Gorgona Island.

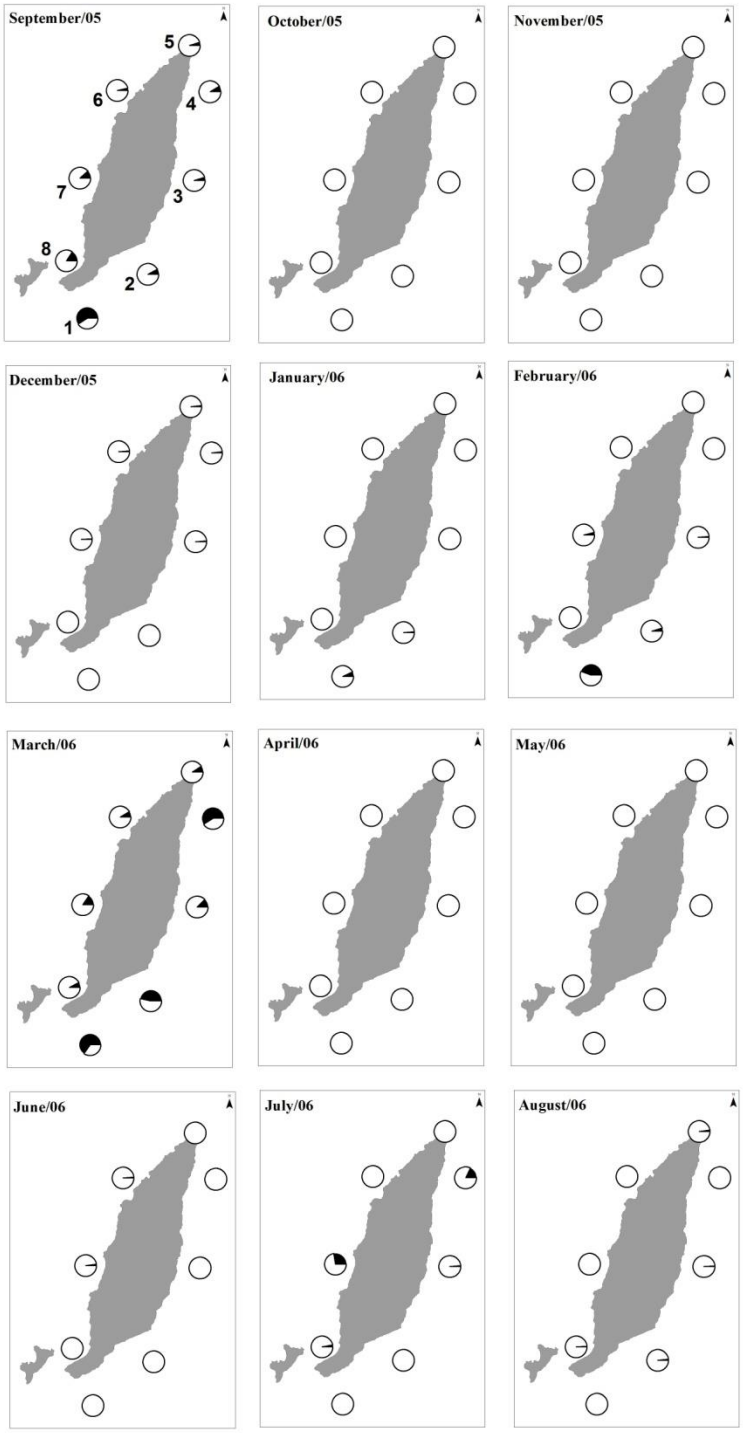

Fig. 3. Proportion of tunicates vs. total zooplankton from September 2005 to August 2006.

No differences in tunicate abundances were detected among stations (Kruskal-Wallis, $p>0.05$); however, the highest abundances of salps and doliolids were detected at Station 1. Spearman

correlations indicated that in December 2005 doliolid abundances were significantly correlated with SBT (r_s= 0.85, p<0.05), while salps were significantly correlated with SBT in March 2006 (r_s= -0.71, p<0.05). In December, SBT was 23ºC on average, while in March it was 19ºC on average (Table 2).

Salps were significantly correlated with chlorophyll *a* concentrations in February (r_s=0.83, p<0.05) and April 2006 (r_s=-0.76, p<0.05). April had the highest chlorophyll *a* concentrations (0.653 mg/L), while February had an intermediate concentration of 0.310 mg/L (Table 2). It seems therefore that salps do not occur in high abundances when chlorophyll *a* concentrations are high, and that their abundances are higher when chlorophyll *a* concentration is intermediate.

DISCUSSION

There was a clear seasonal pattern of tunicate abundance around Gorgona Island in 2005-2006. March 2006 was characterized by a shallower thermocline and very high abundances of salps and doliolids. This is the driest month of the year, part of the dry season that goes from January to April, with higher salinity and lower temperatures (Giraldo et al., 2008; Blanco, 2009). The shallow thermocline is indicative of intrusions of colder water masses that are probably coming from the southwest during the northern hemisphere winter (Rodríguez-Rubio et al., 2003). This is supported by the fact that Station 1, located at the southern tip of the island, had the highest tunicate abundances.

Giraldo et al. (2008) described a change in current patterns in February compared to June; they reported that during February and March there was a stronger influence of the Colombia current, which could be advecting tunicates towards the area. It is possible that this change resulted in the advection of tunicates towards coastal stations. These currents could be responsible for the changes in temperature and salinity observed during the present study. Station 1 is characterized by being shallower (the bottom was encountered 5-16m from the surface). If water masses move

towards the island from the southwest and collide against underwater topography at the southern tip of the island, tunicates would get aggregated in this area, explaining the high abundances observed.

In September 2005 high abundances of salps and doliolids were also observed. This month was characterized by warmer temperatures, a deeper thermocline and less saline water, with the highest range in SSS (4.46UPS). High variability in salinity during September was also reported by Giraldo et al. (2008), and could be explained in part by the increased rainfall over Gorgona Island from April to December, and in part by the influence of the continental rivers of the Patía-Sanquianga complex over the study area (Giraldo, 2008; Blanco, 2009). River discharge could bring nutrients to the study area and tunicates could benefit by feeding on small particles and microbes, thereby increasing their numbers (Pagès & Gili, 1991; Deibel & Paffenhöfer, 2009).

Graham et al. (2001) stated that there are two kinds of blooms: those due to productivity changes, in which the local abundance of tunicates increases, and those due to currents, in which increases in tunicate numbers are due to passive transport to a given place, such as tunicate aggregations that occur near coasts due to transport, and retention by winds and by local hydrology that interact with topography. The high abundances observed were probably not due to upwelling, since for high abundances of zooplankton to be observed, an increase in chlorophyll *a* in the area would have to be observed first, which was not the case during this study. The population increase that was observed was probably due to an accumulation of individuals, resulting from the interaction of topography and mesoscale currents (Genin et al., 2004). The mesoscale advective processes observed in coastal waters of Gorgona Island in 2005-2006 could be an example of increases in zooplankton biomass due to currents and not upwelling (Pagès & Gili, 1991).

The lack of an increase in tunicate population size with an increase in chlorophyll *a* indicates that the maximum abundance recorded for tunicates was not due to an increase in prey abundance. Additionally, Alldredge & Madin (1982) suggested that no tunicates are usually found during phytoplankton blooms, because tunicates cannot change their filtering velocity according to food availability. If the food concentration is too high, the filters become saturated and the tunicates stop feeding.

Tunicates are important links in the trophic chain, as they are effective filter-feeding predators that can ingest a wide range of particle sizes (Kremer, 2002). They can increase their population numbers in a very short time and consume large amounts of phytoplankton, transferring large amounts of carbon as fecal pellets to the aphotic zone (Deibel & Paffenhöfer, 2009). They are also consumed by a large number of predators that range in size from siphonophores to tuna and sunfish (Alldredge & Madin, 1982; Madin et al., 1996; Potter et al., 2011).

Gelatinous organisms are the main prey items in the diet of leatherback sea turtles *Dermochelys coriacea*, and have also been recorded in the diet of the olive ridley sea turtle *Lepidochelys olivacea* and the green sea turtle *Chelonia mydas* (Montenegro-Silva et al., 1984, Amorocho & Reina, 2007; Hays et al., 2009). Green sea turtles are mainly herbivorous in the Atlantic, consuming seagrasses and algae, whereas in other areas such as the eastern Pacific and Africa they also include animal protein in their diets (Bjorndal, 1985).

Green sea turtle juveniles arrive at Gorgona Island as part of their migratory route in the Eastern Pacific Ocean, and use the island´s coastal waters as feeding grounds for an unknown period of time (Alvarado & Figueroa, 1992; Amorocho & Reina, 2008). Green sea turtles reach the juvenile phase at around 35cm curved carapace length in the Pacific, and this development phase is when the fastest growth occurs in wild sea turtles (Zug et al., 2002); it has been hypothesized that a diet rich in protein would allow green turtles to reach their maturation size at a faster rate

(Amorocho & Reina, 2007). The availability of an easily captured prey such as tunicates would therefore be an important resource for green turtles around Gorgona Island. Although tunicates are gelatinous organisms that are 95% water, sea turtles could take advantage of high-density patches that provide more energy (Alldredge & Madin, 1982; Genin et al., 2004). It is probable that the diversity and abundance of algae around Gorgona Island is not sufficient to support a completely herbivorous diet for *C. mydas*, and other food sources, such as tunicates, could potentially be an important source of nutrients.

Tunicates as a food resource seem to occur in high abundances seasonally around Gorgona Island. In other locations high punctual abundances have also been reported, with population numbers being affected by local productivity, currents, topography, and temperature (Graham et al., 2001, Hereu et al., 2006). Furthermore, in some tropical areas the salp community composition can change over time, with species appearing and disappearing, without changes in water masses (Madin et al., 1996).

Although this study was carried out over only one year, it is probable that the fluctuations observed in tunicate numbers occur in roughly the same pattern every year, since the oceanographic and climatic influences that favor tunicate increases occur in the same fashion every year. Seasonal patterns in the occurrence of abundance peaks of salps have also been observed in other areas (Ménard et al., 1994; Licandro et al., 2006; Deibel & Paffenhöfer, 2009). Tunicates could be a seasonal food resource for sea turtles and other filter-feeding vertebrates if their abundance is directly linked to recurring oceanographic patterns.

According to Worms et al. (2003), biodiversity hotspots are places of high food concentration resulting from oceanographic processes that increase productivity. Morales (2008) also noted that there is higher plankton productivity around oceanic islands than in the open ocean. Around Gorgona Island large predators such as sharks, whales and manta rays can be observed as well as

sea turtles (Barrios-Suárez & López-Victoria, 2001; Acevedo-Bueno et al., 2004); therefore, Gorgona Island might be a place of high food concentration that sea turtles benefit from, explaining the fact that green sea turtle juveniles use the area as a feeding ground.

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REFERENCES

Acero, A. & R. Franke. 2001. Peces del parque nacional natural Gorgona, p. 123-131. *In*: Barrios, L.M. & M. Lopéz-Victoria (eds.). Gorgona marina: Contribución al conocimiento de una isla única, Serie Publicaciones Especiales No 7, Instituto Investigaciones Marinas y Costeras – INVEMAR. Santa Marta, Colombia.

Acevedo-Bueno, C.I., B.S. Beltrán-León & R.A. Caicedo-Tulante. 2004. Plan básico de manejo 2005-2009 Parque Nacional Natural Gorgona. Parques Nacionales Naturales de Colombia. Dirección Territorial Suroccidente, Cali, Colombia.

Alldredge, A.L. & L.P. Madin. 1982. Pelagic tunicates: unique herbivores in the marine plankton. BioScience. 32: 655-663.

Alvarado, J. & A. Figueroa. 1992. Recapturas post-anidatorias de hembras de tortuga marina negra (*Chelonia agassizii*) marcadas en Michoacán, México. Biotropica. 24: 560-566.

Amorocho, D.F. & R.D. Reina. 2007. Feeding ecology of the East Pacific green sea turtle *Chelonia mydas agassizii* at Gorgona National Park, Colombia. Endang. Species Res. 3: 43-51.

Amorocho, D.F. & R.D. Reina. 2008. Intake passage time, digesta composition and digestibility in East Pacific green turtles (*Chelonia mydas agassizii*) at Gorgona National Park, Colombian Pacific. J. Exp. Mar. Biol. Ecol. 360: 117-124.

Arthur, K.E. & G.H. Balazs. 2008. A comparison of immature green turtle (*Chelonia mydas*) diets among seven sites in the main Hawaiian Islands. Pac. Sci. 62: 205-217.

Barrios, L.M. & López-Victoria, M. (eds). Gorgona marina: Contribución al conocimiento de una isla única, Serie Publicaciones Especiales No 7, Instituto Investigaciones Marinas y Costeras – INVEMAR. Santa Marta, Colombia.

Bjorndal, K.A. 1985. Nutritional ecology of sea turtles. Copeia 3: 736-751.

Blanco, J.F. 2009. The hydroclimatology of Gorgona Island: Seasonal and ENSO-related patterns. Actual. Biol. 31: 111-121.

Bula-Meyer, G. 1995. Macroalgas de la Isla Gorgona (Pacífico Colombiano) con nuevos registros y una explicación de la baja diversidad y biomasa, p. 23-45. *In*: P. Pinto (ed.). La Isla Gorgona, nuevos estudios biológicos. Editorial Guadalupe Ltda, Bogotá, Colombia.

Carrión-Cortez, J.A., P. Zárate & J.A. Seminoff. 2010. Feeding ecology of the green sea turtle (*Chelonia mydas*) in the Galapagos Islands. J. Mar. Biol. Assoc. UK. 90:1005-1013.

Deibel, D. & G.A. Paffenhöfer. 2009. Predictability of patches of neritic salps and doliolids (Tunicata, Thaliacea). J. Plankton Res. 31: 1571-1579.

Dewar, H., T. Thys, S.L.H. Teo, C. Farwell, J. O´Sullivan, T. Tobayama, M. Soichi, T. Naktasubo, Y. Kondo, Y. Okada, D.J. Lindsay, G.C. Hays, A. Walli, K. Weng, J.T. Streelman & S.A. Karl. 2010. Satellite tracking the world´s largest jelly predator, the ocean sunfish, *Mola mola*, in the Western Pacific. J. Exp. Mar. Biol. Ecol. 393: 32-42.

Fernández-García, C., R. Riosmena-Rodríguez, B. Wysor, O.L. Tejada & J. Cortés. 2011. Checklist of the Pacific marine macroalgae of Central America. Bot. Mar. 54: 53-73.

Frontier, S. 1969. Sur une méthode d´analyse faunistique rapide du zooplancton. J. Exp. Mar. Biol. Ecol. 3: 18-26.

Genin, A., J.S. Jaffe, R. Reef, C. Richter & P.J.S. Franks. 2004. Swimming against the flow: A mechanism of zooplankton aggregation. Science. 308: 860-862.

Giraldo, A. 2008. Variabilidad espacial de temperatura, salinidad y transparencia en el ambiente pelágico del PNN Gorgona durante septiembre 2007 y marzo 2008. Bol. Cient. CIOH. 26: 157-163.

Giraldo, A. & Valencia, B. (eds). 2012. Isla Gorgona. Paraíso de biodiversidad y ciencia, 223p. Programa Editorial Universidad del Valle. Cali, Colombia.

Giraldo, A., E. Rodríguez-Rubio & F. Zapata. 2008. Condiciones oceanográficas en isla Gorgona, Pacífica oriental tropical de Colombia. Lat. Am. J. Aquat.Res. 36: 121-128.

Giraldo, A., B. Valencia & D.G. Ramírez. 2011. Productividad planctónica y condiciones oceanográficas locales en isla Gorgona durante julio 2006. Bol. Invest. Mar. Cost. 40: 185-201.

Giraldo, A., B. Valencia, J.D. Acevedo & M. Rivera. 2013. Variación estacional del fitoplancton y zooplancton en Isla Gorgona, Pacífico Colombiano, y su relación con algunas variables hidrográficas. Rev. Biol. Trop.

Graham, W.M., F. Pagès & W.M. Hamner. 2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia. 451: 199-212.

Hays, G.C., M.R. Farquhar, P. Luschi, S.L.H. Teo & T.M. Thys. 2009. Vertical niche overlap by two ocean giants with similar diets: Ocean sunfish and leatherback turtles. J. Exp. Mar. Biol. Ecol. 370: 134-143.

Hereu, C.M., B.E. Lavaniegos, G. Gaxiola-Castro & M.D. Ohman. 2006. Composition and potential grazing impact of salp assemblages off Baja California during the 1997-1999 El Niño and La Niña. Mar. Ecol. Prog. Ser. 318: 123-140.

Kremer, P. 2002. Towards an understanding of salp swarm dynamics. ICES publication CM2002. N: 12. Copenhagen, Denmark.

Lavaniegos, B.E. & M.D. Ohman. 2003. Long-term changes in pelagic tunicates of the California Current. Deep-Sea Res. II. 50: 2473-2498.

Licandro, P., F. Ibañez & M. Etienne. 2006. Long-term fluctuations (1974-1999) of the salps *Thalia democratica* and *Salpa fusiformis* in the northwestern Mediterranean Sea: Relationships with hydroclimatic variability. Limnol. Oceanog. 51: 1832-1848.

López-Mendilaharsu, M., S.C. Gardner, R. Riosmena-Rodríguez & J.A. Seminoff. 2008. Diet selection by immature green turtles (*Chelonia mydas*) at Bahía Magdalena foraging ground in the Pacific Coast of the Baja California Peninsula, México. J. Mar. Biol. Assoc. UK. 88: 641-647.

Madin, L.P, P. Kremer & S. Hacker. 1996. Distribution and vertical migration of salps (Tunicata, Thaliacea) near Bermuda. J.Plankton Res. 18: 747-755.

Ménard, F., S. Dallot, G. Thomas & J.C. Braconnot. 1994. Temporal fluctuations of two Mediterranean salp populations from 1967 to 1990. Analysis of the influence of environmental variables using a Markov chain model. Mar. Ecol. Prog. Series.104:139-152.

Montenegro-Silva, B.C., Bernal-González, N.G. & A. Martínez-Guerrero. 1984. Estudio del contenido estomacal de la tortuga marina *Lepidochelys olivacea*, en la costa de Oaxaca, México. Méx. An. Inst. Cienc. del Mar y Limnol. 13:121-32.

Morales-Ramírez, A. 2008. Caracterización cualitativa del zooplancton del Área de Conservación Marina Isla del Coco (ACMIC), Océano Pacífico de Costa Rica. Rev. Biol. Trop. 56: 159-169.

Pagès, F. & J.M. Gili. 1991. Effects of large-scale advective processes on gelatinous zooplankton populations in the northern Benguela ecosystem. Mar. Ecol. Prog. Ser. 75: 205-215.

Potter, I.F., B. Galuardi & W.H. Howell. 2011. Horizontal movement of the ocean sunfish, *Mola mola*, in the northwest Atlantic. Mar. Biol. 158: 531-540.

Rodríguez-Rubio, E., W. Schneider, & R. Abarca del Río. 2003. On the seasonal circulation within the Panama Bight derived from satellite observations of wind, altimetry and sea surface temperature. Geophys. Res. Lett. 30: 1410-1413.

Soto, P.A., S.L. Sánchez. & C. Fernández. E. 2001. Comunidades planctónicas marinas, p. 93-105. *In*: L.M. Barrios. & M.L. Victoria (eds.). Gorgona Marina: Contribución al conocimiento de una isla única, Serie Publicaciones Especiales No 7, Instituto Investigaciones Marinas y Costeras – INVEMAR. Santa Marta, Colombia.

Worm, B., H.K. Lotze & R.A. Myers. 2003. Predator diversity hotspots in the blue ocean. PNAS 100: 9884-9888.

Zapata, F.A. 2001. Ecología de peces arrecifales en Gorgona: composición, abundancia, diversidad e historia de vida temprana, p. 111-122. *In*: Barrios, L.M. & López-Victoria, M. (eds). Gorgona marina: Contribución al conocimiento de una isla única, Serie Publicaciones Especiales No 7, Instituto Investigaciones Marinas y Costeras – INVEMAR, Santa Marta, Colombia.

Zapata, F.A., A. Rodríguez-Ramírez, C. Caro-Zambrano & J. Garzón-Ferreira. 2010. Mid-term coral-algal dynamics and conservation status of a Gorgona Island (Tropical Eastern Pacific) coral reef. Rev. Biol. Trop. 58: 81-94.

Zug, G.R., G.H. Balazs, J.A. Wetherall, D.M. Parker & S.K.K. Murakawa. 2002. Age and growth of Hawaiian green seaturtles (*Chelonia mydas*): an analysis based on skeletochronology. Fish. Bull. 100: 117-127.

CAPÍTULO 4

Trophic ecology of green turtle (*Chelonia mydas*) juveniles in the Colombian Pacific

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Trophic ecology of green turtle *Chelonia mydas* juveniles in the Colombian Pacific

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Abstract

Gorgona National Park (GNP) protects the only known feeding aggregation of juvenile green turtles *Chelonia mydas* on the Pacific coast of Colombia. The two morphotypes of *C. mydas* (black and yellow) can be found on two fringing reefs in the park, where food resources such as algae and invertebrates can be found. This study was undertaken to determine green sea turtle diet as well as availability and quality of food resources at GNP. Diet was determined through esophageal lavages and isotopic analysis of epidermal tissue of black and yellow morphotype turtles captured between February and December 2012. Food quantity (availability on the reef) was estimated by determining percent cover in 0.5 x 0.5 m quadrats randomly placed on the reefs. Food quality of algae species consumed by black and yellow morphotype turtles, and of abundant algae on the reef, was estimated by proximate analysis. Food selection was estimated using Ivlev´s electivity index, comparing available and ingested food. Potential food items

(algae, aquatic and terrestrial plants, phytoplankton and zooplankton) were collected and compared to sea turtle isotopic values, and the trophic level of sea turtles at GNP was calculated. A of 30 black (mean = 63.9 cm SCL) and 47 yellow (mean = 54.3 cm SCL) morphotype *C. mydas* were lavaged, with 8 invertebrate and 9 algae food items identified. The most frequently found and abundant items in lavages were terrestrial plants, followed by plastic fibers, invertebrates, and algae. No significant difference in diet between the two morphotypes could be determined through lavage or isotopic analysis (black morphotype turtles mean $\delta^{13}C$ = -16.82, $\delta^{15}N$ mean = 13.85; yellow morphotype turtles mean $\delta^{13}C$ = -16.57, $\delta^{15}N$ mean = 13.65). A total of 27 items, including 15 algae species, were identified on the reefs, of which *Cladophora* sp. was selected by black turtles, and *Hypnea pannosa* and *Dictyota* sp. were selected by both morphotypes. This last species had the highest protein and lipid content, and lower lignin content. A trophic level of 3.6 for black and 3.5 for yellow morphotype turtles was calculated.

Key words

Esophageal lavage, stable isotope analysis, availability, selectivity, proximate analysis, *Chelonia mydas* morphotypes, trophic level, Gorgona National Park

Introduction

Understanding the trophic ecology of populations allows making inferences about other parameters of the population, such as growth and size at sexual maturity. The quality and abundance of resources available to a population at a given location affect the ability of individuals to grow to reach their size at maturity, as diet quality determines growth rates and eventually how soon size at maturity is reached (Bjorndal et al., 2000). Gorgona National Park (GNP) is part of the migratory developmental route of black and yellow morphotype *Chelonia mydas* (Linnaeus, 1758) that belong to geographically

separate rookeries (Amorocho et al., 2012). Black morphotype turtles occur only in the eastern Pacific, from California to Chile (Márquez 1990), while yellow morphotype turtles found at GNP belong to rookeries from the central and/or western Pacific (Amorocho et al., 2012). The individuals of both morphotypes that arrive to GNP waters are juveniles (black turtles <79.4 cm SCL, yellow turtles <96.0 cm SCL), and use the park´s coastal waters to feed and rest (Sampson et al., 2014).

This is one of few locations in the eastern Pacific used exclusively by juveniles (Heppell et al., 2003; Velez-Zuazo et al., 2014), and the only known feeding aggregation of juvenile green turtles in Colombia (Amorocho and Reina, 2007).

The diet of green turtles in the eastern Pacific comprises mostly algae, with a sometimes important invertebrate component (Seminoff et al., 2002; Carrión-Cortez et al., 2010; Lemons et al., 2012). Black morphotype green turtles have been reported to feed mainly on tunicates (74 % frequency of occurrence, %FO) and terrestrial plants (30 %FO) at GNP (Amorocho and Reina, 2007). Yellow morphotype turtles from the central Pacific have been reported to eat algae almost exclusively (Arthur and Balazs 2008), while yellow morphotype turtles from Australia eat mostly algae but can also include gelatinous invertebrates in their diet when available (Heithaus et al., 2002; Arthur et al., 2008).

Amorocho and Reina (2007) speculated that green turtles might be using the GNP reefs as resting areas, and feeding on tunicates and leaves in current convergences around the island, instead of consuming food items available on the reefs. Tunicates, however, are a sporadic resource at GNP, since high abundances only occur at certain times of year (Sampson and Giraldo 2014). An assessment of the diet of green turtles and of food availability during the year would help clarify the use of resources at GNP. Although Parker et al. (2011) found no difference in the diet of black and yellow morphotype

pelagic juveniles, neritic juveniles might have differing diets, as the amount of invertebrates reported in the diet of black morphotype turtles tends to be greater than that reported for yellow morphotype turtles (Heithaus et al. 2002; Arthur et al. 2008; Amorocho & Reina 2007; Carrión-Cortez et al. 2010). We compared the diet of individuals from the two morphotypes at GNP, using esophageal lavages and stable isotope analysis, to determine whether diet of neritic juveniles can be linked to their morphotype.

According to the Optimal Foraging Theory, animals should adopt a strategy of either time minimization or nutrient maximization when foraging (MacArthur and Pianka, 1966). There are no large predators of sea turtles at GNP, such as tiger sharks, that would put pressure on time spent foraging (Acevedo-Bueno et al., 2004), so the strategy of nutrient maximization is probably at play at this location. Animals select forage items according to food quality (Manly et al., 2002), which can be determined by analyzing nutrient composition. This type of analysis provides information on protein and fat content, as well as on the amount of fiber, which impacts digestibility (Karasov and Martínez del Río, 2007). To confirm whether green turtles at GNP are selecting food items based on nutritional quality we performed proximate analyses of some algae species present on the reef.

Trophic levels are indicative of the functional roles of organisms within a given ecosystem and can also help quantify energy flow through communities. We calculated the trophic level of black and yellow morphotype *C. mydas* at GNP using isotopic values of turtle epidermis and taking algae as the base of the trophic web. The use of stable isotope values to estimate trophic levels allows a calculation of trophic level that is continuous and reflects better the role of the organism in the system (Post, 2002).

In summary, the present study was carried out in order to determine resource use by the black and yellow morphotypes of *C. mydas* present at GNP over one year. In order to examine the diet of green turtles at GNP, we 1) determined the diet of turtles captured on the reefs through esophageal lavages and stable isotope analysis of epidermis and of potential food items, 2) determined food availability on the reefs and selectivity by the turtles, 3) analyzed the nutrient content of some reef algae available to the turtles, and 4) calculated the trophic position of green turtles at this foraging site.

Methods

Study Area

Gorgona National Park (GNP) is located in the Colombian Pacific and comprises a 6 033 km^2 marine area and a 13.3 km^2 island; the closest location to the mainland is 30 km away (Fig. 1). Two fringing reefs are located off the south-eastern end of Gorgona Island (La Azufrada and Playa Blanca). Monthly precipitation on the island ranges from 180 to 400 mm during the dry season (January-March), and from 550 to 750 mm during the rainy season (April-December) (Giraldo et al., 2014). A total of 715 terrestrial plant species have been recorded on the island, and 85 algae have been identified in the coastal zone (Bula-Meyer, 1995; Giraldo et al., 2014). Unlike many other green sea turtle foraging grounds, there are no seagrass pastures or mangroves in the study area (Acevedo-Bueno et al., 2004). Of algae identified by Murillo-Muñoz and Peña-Salamanca (2014), 55.8% belonged to the Rhodophyta, 27.9% belonged to Chlorophyta, and 14% belonged to Heterokontophyta.

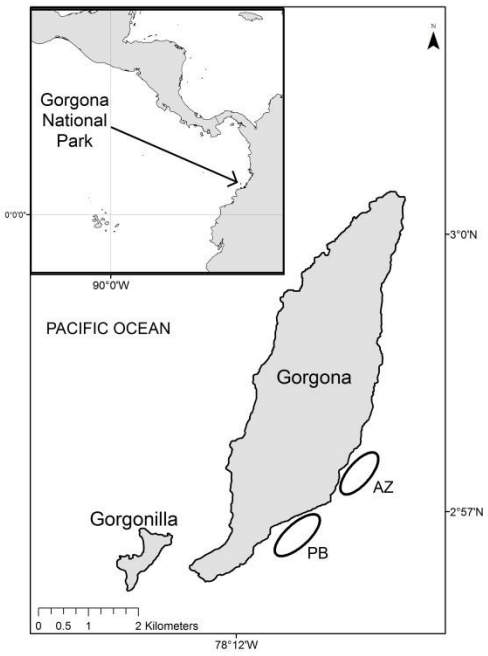

Figure 1. Study site. Black ellipses show two main reefs where *Chelonia mydas* individuals were captured.

Turtle capture and ID

C. mydas individuals were captured by hand at night in February, April, August, October and December 2012. Two to five persons entered the water and searched for turtles over the reefs of La Azufrada and Playa Blanca. Turtles were taken to shore where morphotype was recorded and measures of straight carapace length (SCL in cm), and weight (in kg) were taken for each individual. Each turtle was tagged with a uniquely-numbered INCONEL tag (No. 681, National Band and Tag Co., Newport, Kentucky, USA) in either the left or right front flipper. Sampling was conducted with help from personnel from the Henry von Prahl research station of Gorgona National Park.

Esophageal lavage

Turtles were restrained using a vest with Velcro straps and placed on a tire on their carapace, with the head at a lower height. The mouth was pried open using a flat screw driver, and a short PVC pipe covered with rubber was used as a gag. Two flexible

lubricated plastic tubes with rounded ends were inserted into the esophagus; the retrieval tube measured 12 or 16 mm diameter by 1 m, depending on turtle size, and the injection tube measured 5.0 mm diameter by 3 m. A maximum of 4L of fresh water were pumped through the injection tube. A bucket was placed under the turtle´s head to collect the flushed water; this was later strained through a 20μm mesh and stored in 4% formaldehyde solution (Forbes, 1999).

Identification and quantification of lavage samples

Samples were filtered using a 20 μm mesh net, then placed in a Petri dish, adding distilled water to homogenize the sample. A 0.5 x 0.5 cm grid was placed under the Petri dish, and each item that fell under the grid points was counted. There were 266 grid points under each Petri dish. A Nikon SMZ-1500 stereoscopic microscope and a Nikon Eclipse Ni upright microscope were used to identify food items to the lowest possible taxonomic level. Each food type was separated into broad categories (plants, algae, invertebrates, sand, and plastic). Algae were identified to the lowest possible taxonomic level using the guides by Bula-Meyer (1995), Guiry and Guiry (2014), Murillo-Muñoz and Peña-Salmanca (2014), Schnetter and Bula-Meyer (1982), and Taylor (1945).

The following indices were used to characterize the diet (Hyslop, 1980):

Frequency of Occurrence (FO%)

$$FO\% = \frac{Number\ of\ turtles\ with\ food\ item\ i}{Total\ number\ of\ turtles\ sampled} x100$$

Number %

$$N\% = \frac{Number\ of\ grid\ points\ covered\ by\ item\ i}{Total\ number\ of\ grid\ points\ for\ all\ samples} x100$$

The frequency of occurrence of diet items that contributed > 5 % and > 50 % of total sample volume was also calculated (Arthur and Balazs, 2008). Weight % was not calculated, as the amounts of sample recovered were very small.

Available food items

The available food items present on the two largest reefs at GNP (La Azufrada and Playa Blanca) were quantified using fifteen 0.5 x 0.5 m quadrats randomly placed on each reef. Sampling trips to evaluate food availability were carried out in November 2011, February, April, August, October and December 2012. The percent cover of each substratum type was estimated using a 10 x 10 grid.

Food selection

The availability of resources and the items consumed by each morphotype were compared using Ivlev´s electivity index, calculated with the following equation:

$$E_i = \frac{(r_i - p_i)}{(r_i + p_i)}$$

where r_i is the available proportion of item *i* in the habitat, and p_i is the proportion of item *i* consumed by the predator (Manly et al., 2002). This index takes on values from -1 (item is avoided) to +1 (item is selected).

Nutrient content

A proximate analysis of algae consumed by black and yellow morphotype turtles as well as abundant algae on the reef was carried out. The humidity, ash, protein, ether extract, crude fiber, lignin, NDF and ADF content of samples were evaluated at the Analytical processes laboratory of the International Center for Tropical Agriculture (CIAT) in Cali, Colombia. This type of analysis identifies broad chemical compounds as follows: ashes represent minerals; ethereal extract represents fats; fiber represents the least digestible structural materials (cellulose, hemicellulose, cutin-suberin, pectin and

lignin), NDF represents cellulose, hemicellulose and lignin, and ADF represents cellulose and lignin (Karasov and Martínez del Río, 2007).

Stable isotope analysis

Before the lavage was performed a 6-mm sample of turtle epidermis from the neck area was obtained using a scalpel. Samples of resources available on the reef including algae, aquatic and terrestrial plants, phytoplankton, and zooplankton were also collected from November 2011 to December 2012. The following potential food resources were collected for isotopic analysis: four Chlorophyta species (*Bryopsis* sp., *Cladophora* sp., *Polysiphonia* sp., *Caulerpa racemosa*), three Phaeophyta species (*Dictyota humifusa*, *Dictyota adnata* , *Lobophora* sp.), three Rhodophyta species (*Gelidium* sp., *Hypnea pannosa*, *Jania* sp.), turf algae, a cyanobacteria (*Phormidium* sp.), aquatic plants (mangrove fruit and water hyacinth leaves), terrestrial plants (leaves of *Ficus* sp., *Hibiscus* sp., a palm and climbing plant), phytoplankton, zooplankton, and gelatinous invertebrates (siphonophores, tunicates, jellyfish and invertebrate eggs). Samples were kept in NaCl for less than a week then dried at 60ºC for 24 h. It has been shown that NaCl has no effect on isotopic values (Barrow et al., 2008). Prior to drying, turtle epidermis samples were cut finely with a scalpel and any connective tissue was removed (Reich and Seminoff, 2010).

Samples were ground and approximately 1 mg of sample was packed in 5 x 9mm tin capsules. Turtle samples were analyzed at the Stable Isotope Facility of the University of California at Davis. A PDZ Europa ANCA-GSL elemental analyzer was interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Habitat samples were analyzed using a continuous-flow isotope-ratio mass spectrometer at the Stable Isotope Laboratory of the University of Florida, Gainesville USA. A Costech ECS 4010 elemental combustion system was interfaced via a ConFlo III device

(Finnigan MAT, Bremen, Germany) to a Deltaplus gas isotope-ratio mass spectrometer (Finnigan MAT, Bremen, Germany).

Isotopic values are expressed as δ values relative to international standards (Vienna PeeDee Belemnite for carbon and air for nitrogen) in the following manner:

$$\delta = \left[\left(R_{sample}/R_{standard}\right) - 1\right] * 1000$$

where R_{sample} and $R_{standard}$ are the ratios of heavy to light isotopes in the sample and the standard ($^{13}C/^{12}C$ and $^{15}N/^{14}N$). The C%, N% and C:N ratio of potential food items were also determined.

Data analysis

The similarity of the diet between the two morphotypes was tested with non-metric multidimensional scaling analysis (NMDS) using a Bray-Curtis similarity matrix, followed by a similarity analysis (ANOSIM) to test the effect of the morphotype over the diet components. These analyses were carried out using the software PAST v 2.17. Data were tested for normality using Kolgomorov-Smirnov tests and for homogeneity of variances using Levene´s test. Isotopic values of the two morphotypes were compared with a Student t test.

Individual $\delta^{15}N$ and $\delta^{13}C$ values and SCL were compared with a linear regression to examine whether ontogenetic changes in diet could be detected. Monthly $\delta^{15}N$ and $\delta^{13}C$ values of each morphotype were compared with a one-way ANOVA, followed by a HSD Tukey test if results were significant. If data failed the normality of residuals and homogeneity of variance assumptions Kruskal-Wallis non-parametric tests were used. Analyses were carried out using Statistica v. 8 (Statsoft).

Trophic level was calculated with the following equation proposed by Post (2002):

$$TL = \frac{\left(\delta^{15}N_{top\ predator} - \delta^{15}N_{baseline}\right)}{discrimination\ factor} + \lambda$$

where $\delta^{15}N_{baseline}$ is the value of the organism chosen to represent the base of the trophic food web, λ is the trophic level of that organism, and the discrimination factor is the change in $\delta^{15}N$ values in ‰ between one trophic level and the next. The mean value of algae was used as $\delta^{15}N_{baseline}$, using a λ of one. A discrimination factor of 3.3 was used, calculated as the mean of the discrimination factors estimated for green sea turtles by Seminoff et al. (2006) and by Vander Zanden et al. (2012).

The MixSIAR model (Stock and Semmens, 2013) was used to determine the most probable food source consumed by the black and yellow *C. mydas* morphotypes at GNP. Prey items were first grouped into large groups (algae, aquatic plants, cyanobacteria, terrestrial plants and plankton), and isotopic differences among groups were tested with a Kruskal-Wallis test. Isotopic discrimination factors specific to green turtles were incorporated into the model (-0.17±0.03 for $\delta^{13}C$ and +2.80±0.20 for $\delta^{15}N$; Seminoff et al., 2006).

Results

Turtle capture and ID

A total of 30 black morphotype and 47 yellow morphotype *C. mydas* were sampled (for lavage, stable isotope analysis and measurements) from February to December 2012. The size of black turtles ranged from 52.3 cm to 73.2 cm SCL (mean = 63.9 cm) and yellow turtles measured from 40.9 cm to 68.9 cm SCL (mean = 54.3 cm). The body mass of black turtles ranged from 23.0 kg to 52.0 kg (mean = 36.7 kg), whereas the body mass of yellow turtles ranged from 11.0 kg to 41.5 kg (mean = 23.2 kg). The body condition index of black turtles ranged from 1.12 to 1.70 (mean = 1.38) and that of yellow turtles ranged from 1.14 to 1.83 (mean = 1.43).

Esophageal lavage

A total of 19 items were identified, including 8 invertebrates and 9 algae (Table 1). A study of the digestive apparatus of green turtles by Magalhaes et al. (2012), found that there are no glands associated to the oesophagus, which indicates that there is no digestion in this part of the digestive apparatus. Therefore, cells found in the lavages correspond to the turtle´s own epithelial cells and not to half-digested food. Most samples contained these epithelial cells, accidentally scraped from the turtles´ esophagus during the lavages, and sand particles, probably incidentally ingested during the turtles´ foraging. These two items were excluded from later analyses.

Plastic fibers were found in 73% samples from black turtles and 85% from yellow turtles. The non-metric multidimensional scaling analysis showed high overlap in diet components between the two morphotypes (Fig. 2), and the ANOSIM showed that there were no significant differences in the diet of yellow and black morphotypes during the study period ($R = 0.010$, $p = 0.41$). However, yellow turtles consumed fewer invertebrates than black turtles, whereas black turtles consumed fewer algae than yellow turtles. No yellow turtles consumed *Cladophora* sp. Both morphotypes ingested large amounts of terrestrial plants (leaves and seeds) (Table 1).

Table 1. Frequency of occurrence (FO%) and percent volume (N%) of items recovered from lavage samples of black and yellow morphotype *Chelonia mydas* sampled at Gorgona National Park from February to December 2012. >5% and >50% represent the percentage of turtles in which the diet item contributed over 5% and 50% of relative volume (N%).

	Black				**Yellow**			
Item	**FO %**	**N %**	**> 5 %**	**> 50 %**	**FO %**	**N %**	**> 5 %**	**> 50 %**
Invertebrates	**53.33**	**6.28**	**26.67**	**3.33**	**44.68**	**3.86**	**14.89**	**4.26**
Salps	10.0	3.00	10.0	3.33	2.13	0.04	0	0
Amphipods	13.33	0.36	0	0	10.64	0.28	2.13	0
Copepods	16.67	0.93	6.67	0	2.13	0.09	0	0
Ostracods	3.33	0.02	0	0	4.26	0.17	2.13	0
Isopods	6.67	0.33	3.33	0	4.26	0.17	2.13	0
Eggs	0	0	0	0	23.40	0.52	0	0
Insects	20.0	0.96	10.0	0	6.38	1.31	0.02	2.13
Unidentified	16.67	0.68	3.33	0	6.38	1.31	0.02	2.13
Algae	**36.67**	**8.58**	**26.67**	**3.33**	**36.17**	**16.67**	**27.66**	**17.02**
Chlorophyta								
Cladophora sp.	10.0	4.44	10.0	3.33	0	0	0	0
Phaeophyta								
Dictyota sp.	10.0	1.07	3.33	0	21.28	7.42	19.15	10.64
Chnoospora pannosa	10.0	0.44	3.33	0	10.64	1.27	6.38	0
Rhodophyta								
Jania sp.	6.67	1.47	6.67	0	12.77	1.01	8.51	0
Hypnea pannosa	16.67	1.09	6.67	0	21.28	6.60	17.0	4.26
Ceramium sp.	3.33	0.03	0	0	12.77	0.18	0	0
Gelidium sp.	0	0	0	0	8.51	0.14	0	0
Bostrychia sp.	0	0	0	0	2.13	0.01	0	0
Unidentified	3.33	0.04	0	0	2.13	0.03	0	0
Terrestrial Plants	**96.67**	**39.15**	**83.33**	**30.0**	**100**	**36.54**	**82.98**	**27.66**
Plastic	**73.33**	**12.47**	**50.0**	**3.33**	**85.11**	**13.70**	**65.96**	**6.38**

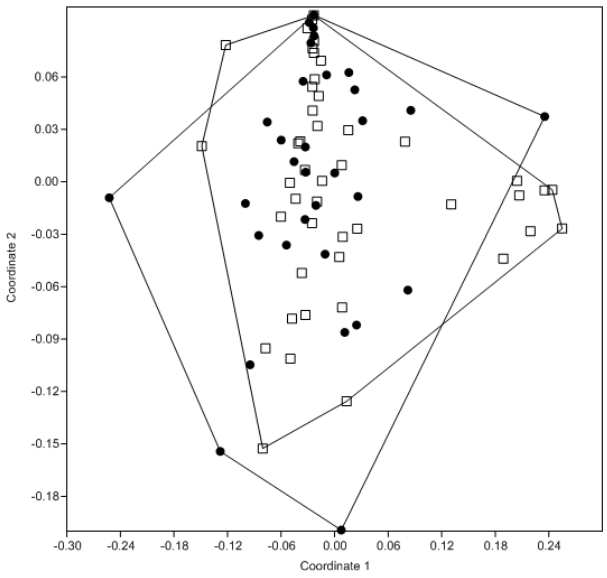

Figure 2. Non-metric multidimensional analysis of diet components of black (black circles) and yellow (white squares) *Chelonia mydas* sampled from February to December 2012 at Gorgona National Park.

Available food items

A total of 27 items were identified in the quadrats on the reefs, including 15 algae species (4 Chlorophyta, 5 Phaeophyta, 6 Rhodophyta), and turf algae mats which include several small green and red algae species (Murillo-Muñoz and Peña-Salmanca, 2014). The most abundant items in the quadrans were the coral *Pocillopora* sp. and rodoliths (*Sporolithon* sp.; Table 2). Availability was not significantly different during the year for any of the algae recorded on the reef ($H=5$, $N=11$, $p>0.05$).

Table 2. Percent cover of potential food items identified at the two main reefs of Gorgona National Park between November 2011 and December 2012.

Item	Relative abundance %
Chlorophyta	
Cladophora albida	3.21
Bryopsis galapagensis	0.04
Caulerpa racemosa	0.05
Parvocaulis parvulus	0.58
Phaeophyta	
Dictyota adnata	0.35
Dictyota humifusa	0.20
Lobophora variegata	0.04
Chnoospora pannosa	0.03
Liagora fragilis	0.02
Rhodophyta	
Amphiroa crosslandii	0.16
Jania capillacea	0.78
Jania ungulata	0.20
Hypnea pannosa	0.83
Gelidiopsis intricata	0.09
Sporolithon sp.	28.08
Heterosiphonia crispella	0.07
Turf algae	6.25
Total algae	**40.98**
Cyanobacteria	
Phormidium sp.	1.13
Total cyanobacteria	**1.13**
Corals	
Pocillopora sp.	44.88
Dead *Pocillopora* sp.	11.29
Psammocora sp.	0.37
Total coral	**56.53**
Other items	
Sand	0.76
Mangrove fruit	0.01
Leaf	0.06
Crab	0.01
Sea urchin	0.48
Sponge	0.02
Nudibranch	0.01
Total other items	**1.35**
Total	**100.00**

Food selection

The electivity index was calculated only for those items that were found in the lavages and in the quadrants (Table 3). *Hypnea pannosa* (Agardh, 1847) and *Dictyota* sp. were selected by both morphotypes, but selection was stronger for yellow turtles. Both turtles selected *Jania* sp., probably because this alga comes attached to *Dictyota* clumps (Schnetter and Bula-Meyer, 1982). *Cladophora* sp. was avoided by yellow turtles but was selected for by black turtles. The high electivity values obtained for *Chnoospora* sp. are probably due to the low availability of this alga on the reef.

Table 3. Ivlev´s electivity values (E_i) obtained for the main items consumed by black and yellow morphotype *Chelonia mydas* captured at Gorgona National Park between February and December 2012.

Item	E_i	
	Black	**Yellow**
Cladophora sp.	0.42	-1.00
Hypnea pannosa	0.40	0.87
Jania sp.	0.46	0.30
Dictyota sp.	0.55	0.92
Chnoospora sp.	0.93	0.98

Nutrient content

A proximate analysis of *Dictyota* sp., *Cladophora* sp., *Colpomenia* sp. and turf algae was carried out. The algae with highest protein content were *Dictyota* sp. and *Cladophora* sp. The brown alga *Dictyota* sp. had the highest humidity content and the lowest ash content. It also had a low lignin amount compared with *Cladophora* sp. and *Colpomenia* sp. Neutral detergent fiber did not differ much between species. Crude fiber was higher in *Cladophora* than in *Dictyota*. Acid fiber was equivalent for the three algae. Ether extract was much higher for *Dictyota* than for the other analyzed algae (Table 4).

Table 4. Results of proximate analysis of algae collected at the two main reefs of Gorgona National Park. Values are given in g/kg, except ash, given as a percentage.

Item	Protein	Humidity	Ash	Ether extract	Crude fiber	NDF	Lignin	ADF
Cladophora sp.	88.01	27.55	63.75	15.60	231.2	293.0	205.8	271.4
Dictyota sp.	89.53	68.84	48.63	58.40	203.2	326.0	118.0	267.2
Colpomenia sp.	39.43	NA	NA	20.80	248.2	260.0	448.8	270.8
Turf algae	66.10	31.92	63.40	23.20	170.8	289.6	43.8	154.4

Stable isotope analysis

A total of 29 black morphotype and 47 yellow morphotype *C. mydas* juveniles were sampled from February to December 2012. Although isotopic values were not significantly different between the two morphotypes ($\delta^{13}C$: t test, t = -1.39, N_1 = 29, N_2 = 47, p = 0.17; $\delta^{15}N$: t test, t = 1.09, N_1 = 29, N_2 = 47, p = 0.28), yellow turtle values were more variable than those of black turtles, as can be seen by the higher SD and wider range (Fig. 3). Mean $\delta^{13}C$ of black turtles was -16.82 (SD = 0.60; range = -18.06 to -15.76), whereas that of yellow turtles was -16.57 (SD = 0.87; range = -19.85 to -14.69). Mean $\delta^{15}N$ of black turtles was 13.85 (SD = 0.40; range = 12.95 to 14.85), whereas that of yellow turtles was 13.65 (SD = 0.95; range = 10.75 to 15.79) (Fig. 4).

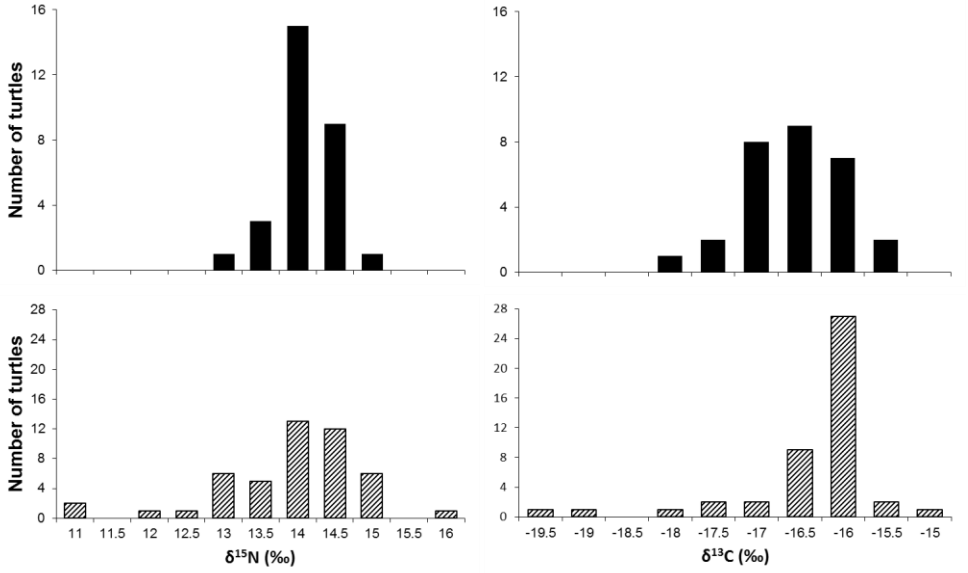

Figure 4. Frequency of $\delta^{15}N$ and $\delta^{13}C$ values of black (black bars) and yellow (stippled bars) *Chelonia mydas* sampled at GNP from February to December 2012.

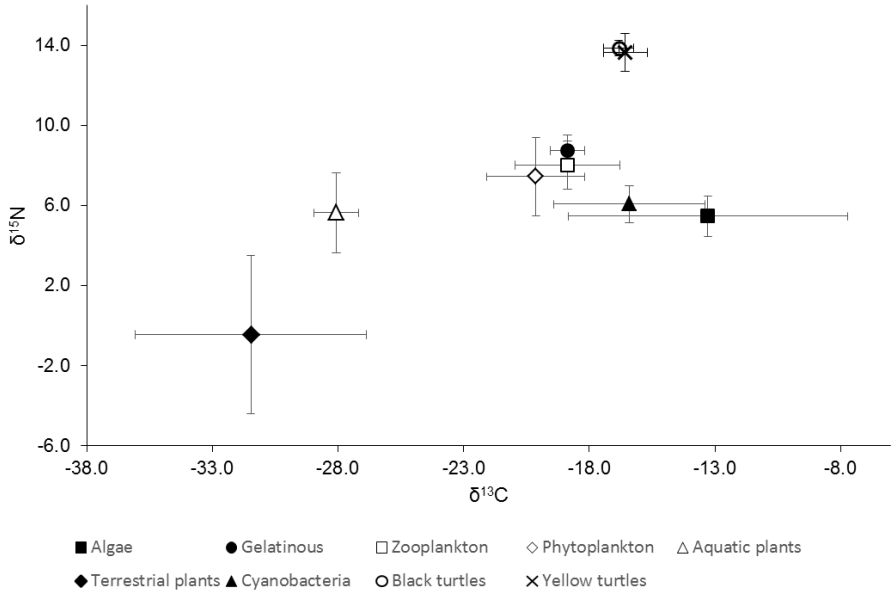

Figure 4. Biplot of $\delta^{15}N$ and $\delta^{13}C$ values of black and yellow *Chelonia mydas* and potential food items sampled at GNP from February to December 2012. *Gelatinous* includes gelatinous invertebrates such as siphonophores, jellyfish and salps; *Aquatic plants* include water hyacinth and mangrove fruit. Error bars denote standard deviation.

There was no significant relationship between $\delta^{13}C$ or $\delta^{15}N$ and carapace size (black: F= 0.19, p = 0.66; yellow: F = 2.91, p = 0.09) (Fig. 5), indicating that the diet of green turtle juveniles at GNP does not change with size (Fig. 5).

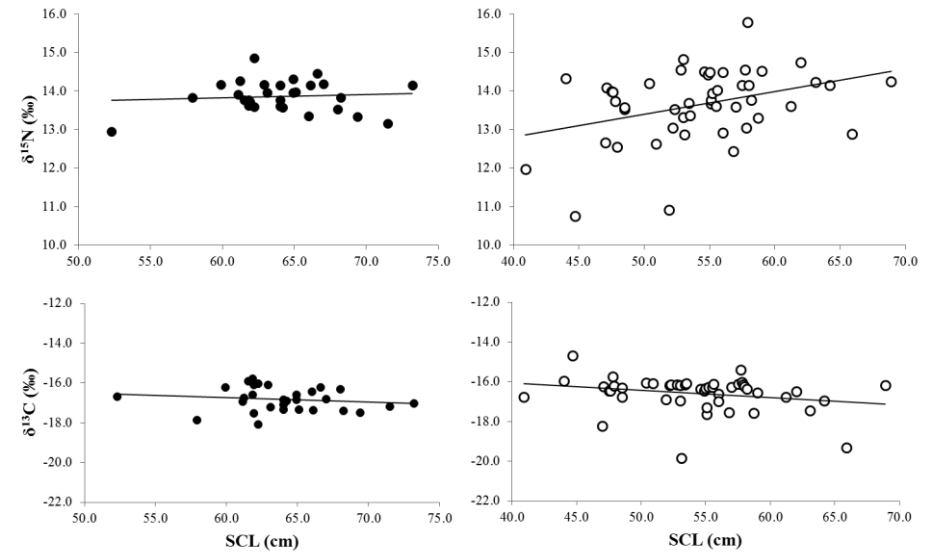

Figure 5. Regression of $\delta^{13}C$ and $\delta^{15}N$ vs. SCL of black (black diamonds) and yellow (white diamonds) *C. mydas* sampled at GNP between February and December 2012. Black $\delta^{13}C$: y = -0.0214x -15.449, R^2= 0.0212; $\delta^{15}N$: y = 0.0085x + 13.317, R^2 = 0.0073; Yellow $\delta^{13}C$: y= -0.0374x – 14.556, R^2 = 0.0612; $\delta^{15}N$: y = 0.0589x + 10.45, R^2 =0.1298.

Isotopic values of black turtles did not change over time ($\delta^{13}C$: F=0.37, p=0.83; $\delta^{15}N$: F=0.78, p=0.55), whereas there was a significant change in isotopic values of yellow turtles over time ($\delta^{13}C$: F=4.60, p=0.004, df= 4; $\delta^{15}N$: F=3.57, p=0.01, df= 4). The $\delta^{13}C$ values of yellow turtles were significantly lower in December, while $\delta^{15}N$ values were significantly higher in August (Unequal N Tukey HSD test, p<0.01; Fig. 6).

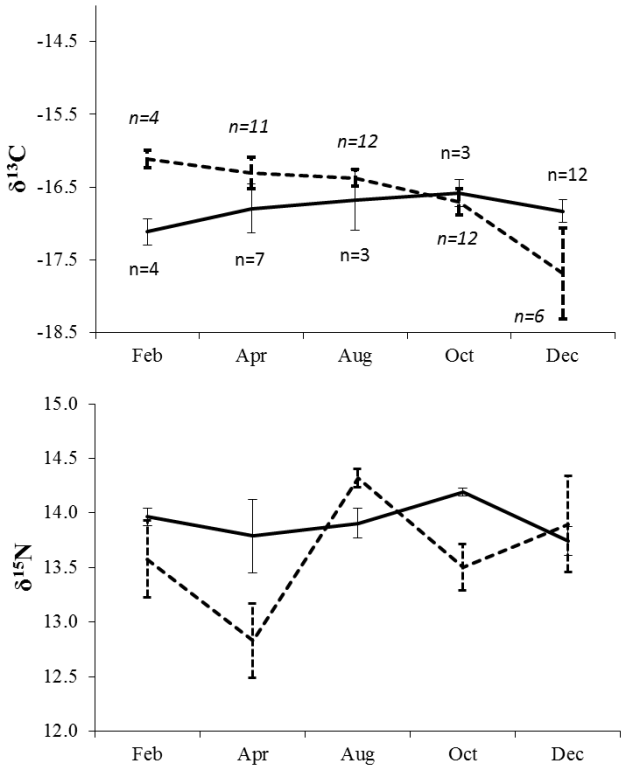

Figure 6. $\delta^{13}C$ and $\delta^{15}N$ values per sampled month for black (solid line) and yellow (dotted line) *C. mydas* caught at GNP between February and December 2012. Number of samples is shown in the upper panel, number of yellow turtles in italics. Error bars denote standard error.

The values of algae, aquatic plants, cyanobacteria, terrestrial plants and plankton were significantly different from each other ($\delta^{15}N$: H(4, n=63) = 31.929, p<0.001; $\delta^{13}C$: H(4, N=63) = 42.9309, p<0.001; Table 5). These different food sources could therefore be used as separate sources in the MixSIAR model, since their isotopic values were significantly different and would occupy different spaces in the isoplot. Running this model, however, did not result in a feasible solution. Additional potential food sources would need to be sampled to obtain results in a mixing model.

Table 5. $\delta^{13}C$ and $\delta^{15}N$ values of black and yellow morphotype *Chelonia mydas* and potential food items sampled at GNP between November 2011 and December 2012.

	$\delta^{13}C$ (± SD)	**$\delta^{15}N$ (± SD)**	**n**
Sea turtles			
Black morphotype	-16.82 (± 0.60)	13.85 (± 0.40)	29
Yellow morphotype	-16.57 (± 0.87)	13.65 (± 0.95)	47
Plankton			
Gelatinous	-18.86 (± 0.67)	8.74 (±0.77)	6
Zooplankton	-18.87 (± 2.08)	8.01 (±1.20)	4
Phytoplankton	-20.12 (± 1.95)	7.44 (± 1.96)	2
Algae			
Chlorophyta	-15.23 (± 1.18)	5.55 (± 0.84)	9
Phaeophyta	-11.22 (± 3.97)	5.63 (± 0.92)	12
Rhodophyta	-15.72 (± 5.59)	5.59 (± 0.74)	11
Cyanobacteria	-16.41 (± 3.00)	6.06 (± 0.92)	6
Aquatic plants	-28.07 (± 0.88)	5.62 (± 2.00)	8
Terrestrial plants	-31.47 (± 4.59)	-0.45 (± 3.96)	5

The calculation of TL using the equation proposed by Post (2002) requires a homogeneous isotopic signal of the baseline. In this study algae were sampled over one year (November 2011 to December 2012), so that variations in isotopic values were taken into account. A Kruskal-Wallis test showed that algal isotopic values (Chlorophyta, Rhodophyta and Phaeophyta) were not significantly different from each other ($H (2, N=32) =0.1429$) so the overall mean of algae isotopic values (5.59‰) was used as $\delta^{15}N$ baseline, and $\lambda = 1$. The calculated trophic level using stable isotope values was 3.6 for black turtles and 3.5 for yellow turtles.

Discussion

There was no significant difference in the diet of black and yellow morphotype juveniles at GNP, which indicates that individuals are sharing the same resources at this foraging site. Terrestrial plants were the most frequently consumed item, whereas

invertebrates comprised a low percentage by frequency and by volume of the diet, and tunicates occurred infrequently. Mangrove fruits and leaves have been reported in the diet of green turtles from the Galapagos Islands (Carrión-Cortez et al., 2010), Bahía Magdalena, Mexico (López-Mendilaharsu et al., 2005), and Australia (Read and Limpus, 2002), but the only other study to report terrestrial plant matter as an important part of the diet of neritic green turtles was that of Amorocho and Reina (2007) at the same foraging site. The consumption of terrestrial plants represents the use of a terrestrial resource by a marine species, which indicates nutrient cycling from terrestrial to marine areas through marine turtles. These plants could have entered the ocean from the coastal area of the park or could have been carried over from the continent.

In their study, Amorocho and Reina (2007) reported that green sea turtles at GNP consumed large amounts of salps. The turtles in that study belonged to the black morphotype, as yellow morphotype turtles were very rarely observed in GNP at the time (Sampson et al., 2014) and were not included in that analysis. However, tunicates are not available at GNP in high abundance year-round (Sampson and Giraldo, 2014), and it is possible that black morphotype turtles have evolved a behavior where they use pulses of invertebrate resources whereas yellow turtles maintain a diet mainly based on algae. This would explain the higher incidence of invertebrates in black turtle lavages compared to yellow turtles. Sea turtles at GNP seemed to rely on opportunistic ingestion of terrestrial plants and invertebrate pulses, while selecting a few algae species from what was available on the reefs. Non-selectivity and opportunism in the diet of green turtles have been reported at other locations, such as Nicaragua (Mortimer 1981), Queensland, Australia (Read and Limpus, 2002), Western Australia (Heithaus et al., 2002), Bahía Magdalena, Mexico (López-Mendilaharsu et al., 2005), the south-west Pacific (Boyle and Limpus, 2008), and Hawaii (Arthur and Balazs, 2008).

The number of algae species present at GNP (85 species; Bula-Meyer, 1995) is relatively low compared with nearby eastern Pacific locations: 216 algae species at Costa Rica, 174 algae species at Panama, 146 algae species at El Salvador (Fernández-García et al., 2011), and compared with other sea turtle foraging areas: 115 algae species on Heron Reef, Australia (Forbes 1996), ~400 algae species in the Hawaiian Islands (Arthur and Balazs, 2008). The rodolith *Sporolithon* sp. was found to be the most abundant alga on both reefs during this study, while turf algae (an assemblage of several small filamentous green and red algae), and the green alga *Cladophora* sp. were the most important in terms of relative abundance. Murillo-Muñoz and Peña-Salamanca (2014) also reported *Sporolithon* sp. as the most abundant alga at La Azufrada reef, but the most abundant algae found by these authors at Playa Blanca reef were *Lithophyllum* sp., *Gelidium pusillum*, *Sporolithon* sp., *Amphiroa crosslandii*, *Hypnea valentiae* and *Polyphysa clavata.* The difference in results could be due to sampling protocol or timing of the samples, as not all algae species were found in every sampled month during this study.

The main algae consumed by green turtle juveniles at GNP were *Cladophora* sp., *Dictyota* sp., and *Hypnea pannosa*. Both black and yellow morphotype turtles selected the brown alga *Dictyota* sp., which had the highest protein and fat content of the analyzed algae, as well as the lowest ash content, and less fiber than *Cladophora* sp. This latter species had high protein content but higher lignin and fiber content than *Dictyota* sp., making it less nutritionally advantageous to turtles, as high lignin content is indicative of low nutritional value (Karasov and Martínez del Río, 2007). *Thalassium testudinum* blades analyzed by Bjorndal (1979) in the Bahamas had lower lignin content than the algae in this study and the terrestrial plants analyzed by Amorocho and Reina (2007). It would appear that green turtle diet in GNP is of lower nutritional value than

that of turtles in the Bahamas and would explain the low growth rates found at GNP (Sampson et al., *in press*). Higher growth rates than those found at GNP were also reported for black morphotype turtles at high-productivity locations off the coast of Peru (Velez-Zuazo et al., 2014). The difference in growth rates between these geographic locations could be due to higher quality or more abundant resources being consumed at the Bahamas and Peru locations, which resulted in faster growth rates. The fact that condition indices are similar (1.49 and 1.55 at the Peru locations; 1.38 for black and 1.43 for yellow turtles at GNP), however, points to resources at GNP being sufficient for green turtles at this location to result in good body condition (Sampson et al., 2014; Velez-Zuazo et al. 2014).

Compared with the range of isotopic values reported by Burkholder et al. (2011) for yellow turtles in Australia, the $\delta^{13}C$ variability of turtles at GNP was relatively low, which could be indicative of residency in the coastal area. In this study sea turtles had low isotopic variance, which indicates that they stayed within the GNP foraging area during the turnover time of epidermis (3-4 months for loggerhead turtle *Caretta caretta* Linnaeus, 1758 epidermis; Reich et al. 2008). Turtles sampled had probably already spent some time in the neritic zone, integrating the isotopic values of neritic food consumed within GNP over the last few months. The wider range in yellow turtle isotopic values indicated greater diversification in the diet of yellow turtle individuals, with black turtles possibly being more specialized.

The low variability in $\delta^{15}N$ values indicates a similarity in the diet and physiology of individuals of both morphotypes present at GNP. Since all individuals sampled were juveniles within a narrow range of sizes, we did not expect large physiological differences. The low variance of isotopic values of both morphotypes (black turtle $\delta^{15}N$ SD = 0.40; yellow turtles $\delta^{15}N$ SD = 0.95) could indicate specialization in feeding, or it

could be due to synchronous changes in diet in the population, for example when taking advantage of resource pulses (Bearhop et al., 2004).

The lack of relationship found in this study between SCL and isotopic values is similar to other studies, such as that of Godley et al. (1998), who found no significant relationship between $\delta^{15}N$ and green turtle size (SCL) for bone and scute tissue of turtles from Cyprus and Turkey. The lack of a significant regression could be due to the choice of tissue analyzed. The use of scute tissue, which reflects long-term changes in diet, could have given a significant result, because it can reflect ontogenetic changes in diet from oceanic to neritic areas (Reich et al., 2007). If small juveniles consume prey in oceanic areas their isotopic values should be much lower than those of large juveniles consuming prey in neritic areas. The epidermis tissue analyzed in this study gives values over the previous months and only reflected isotopic values of the food chain within GNP. Variations at the bottom of the food chain (algae) were not reflected as variations in the isotopic values of the consumers, indicating that the analyzed tissue (epidermis) has a turnover time that is sufficient to integrate isotopic variations at the base of the food web, and reflects diet assimilated at the study site.

The tissue of black turtles did not change significantly during the study period, whereas $\delta^{15}N$ values of yellow turtles were higher in August 2012, and $\delta^{13}C$ were lower in December 2012. These differences could be reflecting an actual change in the isotopic baseline of the environment, but given the lack of difference in diet between the two morphotypes, it is probably due to individual isotopic differences of the turtles sampled during those months. It is possible that the yellow turtles captured in August and December had recently arrived to GNP and were reflecting isotopic signals of a different geographic location, or that they had moved out of the study area to forage.

We used the isotopic values of several algae species collected over one year in order to obtain an isotopic baseline value that integrated temporal variability. There was large variability in $\delta^{13}C$ values of algae both among and within species, but $\delta^{15}N$ variability was much lower, allowing us to use this food source as $\delta^{15}N_{baseline}$. The high $\delta^{13}C$ variability detected among algae species as well as within species over time is typical of what has been reported for algae (Cornelisen et al., 2007). The calculated trophic level for black and yellow morphotype sea turtles at GNP (3.5 and 3.6 respectively) is higher than expected. If green sea turtles were entirely herbivorous, they should have a trophic level around 2, and if they included only small invertebrates in their diet, their trophic level should be similar to that reported for *Cetorhinus maximus*, a zooplanktivorous shark, by Estrada et al. (TL = 3.1; 2003). The trophic level calculated in this study is indicative of a diet that includes diet items higher up the food chain (large invertebrates or possibly even fish). The higher $\delta^{15}N$ and higher calculated trophic position found in this study point to green turtles at GNP not being completely herbivorous, because the inclusion of animal matter would increase their trophic level.

Potential food items had significantly different isotopic values, which allowed their use in the MixSIAR model as independent food sources (Stock and Semmens, 2013). No feasible solution could be found with this model, however. The lack of solution of the MixSIAR model was caused by the position of sea turtle isotopic values on the isotopic biplot above that of sampled habitat samples, because in order to find a solution the consumer´s isotopic values should be located midway between those of their potential prey (Stock and Semmens, 2013). Cardona et al. (2009) studied green turtles in Mauritania, and found that fish had to be included in the model, as the inclusion of jellyfish only, in addition to seagrasses and macroalgae, did not result in feasible solutions. Habitat samples collected for isotopic analysis were selected based on what

was identified in lavage samples. No large invertebrates were identified in lavages, so these items were not collected, resulting in turtles being placed at a high position on the biplot. This is a result of the bias inherent to lavages, which only allow the collection of samples below a certain diameter of the collection tube.

The high position of sea turtles in the isotopic biplot could be explained by the effect of decomposition on isotopic values of free-floating vegetation. If turtles fed on leaves that had been floating in the ocean for several days/weeks the decomposition of that material probably resulted in changes to the isotopic values, as has been reported for example for water hyacinth in Brazil, where $\delta^{15}N$ values of decomposing plants increased over time (Fellerhoff et al., 2003).

Another possible explanation is that individuals at GNP are not in good nutritional condition and therefore their values are more elevated, as it has been reported that individuals that are in poor nutritional condition have elevated $\delta^{15}N$ values (Hobson et al., 1993). However, the fact that condition indices at GNP were similar to those obtained off Peru where growth rates are quite high would tend to discard this explanation (Velez-Zuazo et al., 2014).

In conclusion, black and yellow morphotype juvenile *C. mydas* captured at GNP did not have a significantly different diet; both consumed mostly terrestrial plants and a lower proportion of invertebrates and algae. There was a difference, however, in selectivity and in variability of isotopic values, which indicated higher specialization in black turtles than yellow turtles. The trophic level of green turtles at GNP as well as the lack of a feasible mixing model solution indicated that these juveniles are consuming prey higher on the food chain than would be expected from esophageal lavages alone.

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References

Acevedo-Bueno, C.I., Beltrán-León, B.S., Caicedo-Tulante, R.A., 2004. Plan básico de manejo 2005-2009 Parque Nacional Natural Gorgona. Parques Nacionales Naturales de Colombia. Dirección Territorial Suroccidente, Cali, Colombia, 253pp.

Amorocho, D.F., Reina, R., 2007. Feeding ecology of the East Pacific green sea turtle Chelonia mydas agassizii at Gorgona National Park, Colombia. Endanger. Spec. Res. 3, 43-51.

Amorocho, D.F., Abreu-Grobois, F.A., Dutton, P.H., Reina, R.D., 2012. Multiple distant origins for green sea turtles aggregating off Gorgona Island in the Colombian Eastern Pacific. PLoS ONE 7(2), e31486.

Arthur, K.E., Balazs, G.H., 2008. A comparison of immature green turtle (Chelonia mydas) diets among seven sites in the main Hawaiian Islands. Pac. Sci. 62(2), 205-217.

Arthur, E., Boyle, M.C., Limpus, C.J., 2008. Ontogenetic changes in diet and habitat use in green sea turtle (*Chelonida mydas*) life history. Mar. Ecol. Prog. Ser. 362, 303-311.

Barrow, L.M., Bjorndal, K.A., Reich, K.J., 2008. Effects of preservation method on stable carbon and nitrogen isotope values. Phys. Biochem. Zool. 81(5), 688-693.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., Macleod, H., 2004. Determining trophic niche width: a novel approach using stable isotope analysis. J. Animal. Ecol. 73, 1007-1012.

Bjorndal, K.A., 1979. Cellulose digestion and volatile fatty acid production in the green turtle, *Chelonia mydas*. Comp. Biochem. Physiol. 63, 127-133.

Bjorndal, K.A., Bolten, A.B., Chaloupka, M.Y., 2000. Green turtle somatic growth model: evidence for density dependence. Ecol. Appl. 10(1), 269-282.

Boyle, M.C., Limpus, C.J., 2008. The stomach contents of post-hatchling green and loggerhead sea turtles in the southwest Pacific: an insight into habitat association. Mar. Biol. 155, 233-241.

Bula-Meyer, G., 1995. Macroalgas de la Isla de Gorgona (Pacífico Colombiano) con nuevos registros y una explicación de la baja diversidad y biomasa. In: Pinto, P. (ed) La isla de Gorgona, nuevos estudios biológicos. Instituto de Ciencias Naturales-Museo de Historia Natural, Santafé de Bogotá, Colombia. 78pp.

Burkholder, D.A., Heithaus, M.R., Thomson, J.A., Fourqurean, J.W., 2011. Diversity in trophic interactions of green sea turtles *Chelonia mydas* on a relatively pristine coastal foraging ground. Mar. Ecol. Prog. Ser. 439, 277-293.

Cardona, L., Aguilar, A., Pazos, L., 2009. Delayed ontogenic dietary shift and high levels of omnivory in green turtles (Chelonia mydas) from the NW coast of Africa. Mar. Biol. 156, 1487-1495

Carrión-Cortés, J.A., Zárate, P., Seminoff, J.A., 2010. Feeding ecology of the green sea turtle (Chelonia *mydas*) in the Galapagos Islands. J. Mar. Biol. Assn. U.K. 90(5),1005-1013

Cornelisen, C.D., Wing, S.R., Clark, K.L., Bowman, M.H., Frew, R.D., Hurd, C.L., 2007. Patterns in the δ13C and δ 15N signature of Ulva pertusa: Interaction between physical gradients and nutrient source pools. Limnol. Oceanog. 52(2), 820-832.

Estrada, J.A., Rice, A.N., Lutcavage, M.E., Skomal, G.B., 2003. Predicting trophic position in sharks of the north-west Atlantic Ocean using stable isotope analysis. J. Mar. Biol. Assn. U.K. 83,1347-1350.

Fellerhoff, C., Voss, M., Wantzen, K.M., 2003. Stable carbon and nitrogen isotope signatures of decomposing tropical macrophytes. Aquatic Ecol. 37, 361-375.

Fernández-García, C., Riosmena-Rodríguez, R., Wysor, B., Tejada, O.L., Cortés, J., 2011. Checklist of the Pacific marine macroalgae of Central America. Bot. Mar. 54, 53-73.

Forbes, G.A., 1996. The diet and feeding ecology of the green sea turtle (*Chelonia mydas*) in an algal-based coral reef community. PhD thesis, James Cook University, Queensland, Australia. 340pp.

Forbes, G.A., 1999. Diet sampling and diet component analysis. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., Donnelly, M. (Eds.), Research and management techniques for the conservation of sea turtles. IUCN/SSC Marine Turtle Specialist Group Publication No.4. pp.144-148.

Giraldo, A., Valencia, B., Ramírez, D.G., 2014. Isla Gorgona, enclave estratégico para los esfuerzos de conservación en el Pacífico Oriental Tropical. Rev. Biol. Trop. 62(1), 1-12.

Godley, B.J., Thompson, D.R., Waldron, S., Furness, R.W., 1998. The trophic status of marine turtles as determined by stable isotope analysis. Mar. Ecol. Prog. Ser. 166, 277-284.

Guiry, M.D., Guiry, G.M., 2014. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org; searched on 13-11-2014.

Heithaus, M.R., McLash, J.J., Frid, A., Dill, L.M., Marshall, G.J., 2002. Novel insights into green sea turtle behavior using animal-borne video cameras. J. Mar. Biol. Ass. U.K. 82, 1049-1050.

Heppell, S.S., Snover, M.L., Crowder, L.B. 2003. Sea turtle population ecology. In: Lutz PL, Musick J, Wyneken J, editors. The biology of sea turtles, Vol. II. Boca Raton: CRC Press p. 275-306.

Hobson, K.A., Alisauskas, R.T., Clark, R.G., 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. Condor 95(2), 388-394.

Hyslop, E.J., 1980. Stomach contents analysis - a review of methods and their application. J. Fish. Biol. 17, 411-429.

Karasov, W.H., Martínez del Río, C., 2007. Physiological Ecology: How animals process energy, nutrients, and toxins. Princeton University Press, Princeton. 744pp.

Lemons, G., Lewison, R., Komoroske, L., Gaos, A., Lai, C.T., Dutton, P., Eguchi, T., LeRoux, R., Seminoff, J.A., 2011. Trophic ecology of green sea turtles in a highly urbanized bay: Insights from stable isotopes and mixing models. J. Exp. Mar. Biol. Ecol. 405, 25-32.

López-Mendilaharsu, M., Gardner, S.C., Seminoff, J.A., Riosmena-Rodríguez, R., 2005. Identifying critical foraging habitats of the green turtles (Chelonia mydas) along the Pacific coast of the Baja California peninsula, Mexico. Aquatic Conserv.: Mar. Freshw. Ecosyst. 15, 259-269.

MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. Amer. Nat. 100 (916), 603-609.

Magalhaes, M. dos S., Barsante Santos, A.J., da Silva, N.B., de Moura, C.E.B., 2012. Anatomy of the digestive tube of sea turtles (Reptilia: Testudines). Zoologia 29(1), 70-76.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P., 2002, Resource selection by animals. Statistical Design and Analysis for Field Studies. Kluwer Academic Publishers, Dordrecht, The Netherlands. 221 pp.

Márquez, M.R., 1990. An annotated and illustrated catalogue of sea turtle species known to date. FAO Fish 125(11), 1-81.

Mortimer, J.A., 1981. The feeding ecology of the West Caribbean green turtle (Chelonia mydas) in Nicaragua. Biotropica 13(1), 49-58.

Murillo-Muñoz, M., Peña-Salamanca, E.J., 2014. Algas marinas bentónicas de la Isla Gorgona, costa pacífica colombiana. Rev. Biol. Trop. 62(1), 27-41.

Parker, D.M., Dutton, P.H., Balazs, G.H., 2011. Oceanic diet and distribution of genotypes for the green turtle, Chelonia mydas, in the central North Pacific. Pac. Sci. 65(4), 419-431.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83(3), 703-718.

Read, M.A., Limpus, C.J., 2002. The green turtle, Chelonia mydas, in Queensland: feeding ecology of immature turtles in Moreton Bay, Southeastern Queensland. Mem. Queensl. Mus. 48(1), 207-214.

Reich, K.J., Bjorndal, K.A., Bolton, A.B., 2007. The 'lost years' of green turtles: using stable isotopes to study cryptic lifestages. Biol. Letters 3, 712-714.

Reich, K.J., Bjorndal, K.A., Martínez del Río, C., 2008. Effects of growth and tissue type on the kinetics of 13C and 15N incorporation in a rapidly growing ectotherm. Oecologia 155, 651-663.

Reich, K.J., Seminoff, J.A., 2010. Standardizing sample collection, preparation, and analysis of stable isotopes of carbon and nitrogen in sea turtle research. Second Workshop in Stable Isotope Techniques in Sea Turtle Research, 30th Annual Symposium on Sea Turtle Biology and Conservation in Goa, India, 27-29 April.

Sampson, L., Payán, L.F., Amorocho, D.F., Seminoff, J.A., Giraldo, A., 2014. Intraspecific variation of the green turtle, *Chelonia mydas* (Cheloniidae), in the foraging area of Gorgona Natural National Park (Colombian Pacific). Acta Biol. Colomb. 19(3), 461-470.

Sampson, L., Giraldo, A., 2014. Annual abundance of salps and doliolids (Tunicata) around Gorgona Island (Colombian Pacific), and their importance as potential food for green sea turtles. Rev. Biol. Trop. 62(1), 149-159.

Sampson, L., Giraldo, A., Payán, L.F., Amorocho, D.F., Eguchi, T., Seminoff, J.A., in press. Somatic growth of green turtle (*Chelonia mydas)* morphotypes in the Colombian Pacific. Mar. Biol.

Schnetter, R., Bula-Meyer, G., 1982. Algas marinas del litoral pacífico de Colombia. Gartner Verlag, Germany, 282 pp.

Seminoff, J.A., Resendiz, A., Nichols, W.J., 2002. Diet of East Pacific Green Turtles (Chelonia *mydas*) in the Central Gulf of California, Mexico. J. Herpetol. 36(3), 447-453.

Seminoff, J.A., Jones, T.T., Eguchi, T., Jones, D.R., Dutton, P.H., 2006. Stable isotope discrimination ($\delta^{13}C$ and $\delta^{15}N$) between soft tissues of the green sea turtle Chelonia mydas and its diet. Mar. Ecol. Prog. Ser. 308, 271-278.

Stock, B.C., Semmens, B.X., 2013. MixSIAR GUI User Manual, version 1.0. Available from http://conserver.iugo-cafe.org/user/brice.semmens/MixSIAR.

Taylor, W.R., 1945. Pacific marine algae of the Allan Hancock expeditions to the Galapagos Islands. The University of Southern California, Vol. 12, Los Angeles, USA. 556 pp.

Vander Zanden, H.B., Bjorndal, K.A., Mustin, W., Ponciano, J.M., Bolten, A.B., 2012. Inherent variation in stable isotope values and discrimination factors in two life stages of green turtles. Physiol. Biochem. Zool. 85(5), 431-441.

Velez-Zuazo, X., Quiñones, J., Pacheco, A.S., Klinge, L., Paredes, E., Quispe, S., Kelez, S., 2014. Fast growing, healthy and resident green turtles (*Chelonia mydas*) at two neritic sites in the central and northern coast of Peru: implications for conservation. PLoS ONE 9(11), e113068.

DISCUSIÓN GENERAL

En esta tesis se evaluaron las diferencias en la estructura de la población, crecimiento somático y ecología trófica de los dos morfotipos de *Chelonia mydas* presentes en el PNN Gorgona. Para esto se comparó la distribución de tallas, condición corporal, tasa de crecimiento somático, dieta, posición trófica, selección de alimentos, y cantidad y calidad de alimentos disponibles para los dos morfotipos de *C. mydas* en esta localidad.

Los hallazgos de esta investigación son de importancia local, regional y global. A nivel local estos resultados se pueden utilizar para fortalecer y actualizar el Plan de Manejo del Parque Nacional Natural Gorgona, ya que se identificaron los alimentos más frecuentemente consumidos por esta especie en el área marina protegida; se midió el tamaño de los individuos que habitan esta área; se calculó la tasa de crecimiento y se estimó la proporción de cada morfotipo. A nivel regional, se obtuvo información sobre el morfotipo negro en un área tropical con menor disponibilidad de alimento que en otras zonas de forrajeo cercanas, obteniéndose información relevante sobre el comportamiento alimenticio de esta especie. A nivel global se aportó información sobre las diferencias y similitudes entre los dos morfotipos de esta especie, los cuales comparten una misma área de forrajeo en el Pacífico oriental tropical.

Estructura de la población

Los tamaños de las tortugas capturadas entre 2003 y 2012 indican que el PNN Gorgona es un área de forrajeo para juveniles de *C. mydas* de los dos morfotipos estudiados. Se destaca así la importancia de esta zona de estudio como hábitat de alimentación durante una etapa de vida importante para la especie, ya que la cantidad y calidad de alimentos consumidos por los juveniles determinará la rapidez con que puedan llegar al tamaño de madurez sexual, y qué tan pronto puedan seguir hacia otras áreas de desarrollo, siguiendo con sus rutas migratorias (Bjorndal *et al.* 2000; Bolten 2003). En el Pacífico

oriental se han reportado pocos lugares de forrajeo en los que se encuentren exclusivamente juveniles, lo cual resalta la importancia que tiene el PNN Gorgona para las tortugas verdes *C. mydas*.

Como era de esperarse, dada la distribución global así como la proporción de los dos morfotipos reportada para el PNN Gorgona (Amorocho *et al*. 2012), se capturaron más tortugas de morfotipo negro que amarillo durante este estudio, aunque el número de tortugas amarillas capturadas aumentó en los años más recientes. Se pasó de 73% negras y 27% amarillas en 2007 a 46.6% negras y 53.4% amarillas en 2012. Este aumento podría deberse a un cambio en la ruta migratoria de las tortugas amarillas, las cuales probablemente provienen en su mayoría de Polinesia Francesa y de Hawaii (Amorocho *et al*. 2012). Aunque este factor no hace parte de los objetivos de la tesis, han sido reportadas recientemente variaciones significativas en los campos de corriente superficial en el Pacífico suroriental, los cuales podrían afectar los desplazamientos de los neonatos de las tortugas de morfotipo amarillo, llevándolas hacia las costas del Pacífico oriental (Cai *et al*. 2005; Poloczanska *et al*. 2009).

Las tortugas de morfotipo amarillo que llegaron a la zona costera del PNN Gorgona durante el estudio fueron de menor tamaño que las de morfotipo negro. Esto podría estar indicando que las tortugas de morfotipo amarillo tienen un tamaño de reclutamiento a la zona costera menor que el de las de morfotipo negro, o que estas últimas llegan a otras zonas costeras antes de llegar a Isla Gorgona. Es posible que las tortugas de morfotipo negrode las Islas Galápagos lleguen a zonas costeras más al sur y luego utilicen las corrientes costeras de Humboldt y la corriente de Colombia para llegar al PNN Gorgona, y que las tortugas de morfotipo negrode Michoacán utilicen la Corriente de México y viajen a lo largo de la costa, mientras que las tortugas de morfotipo amarilloprobablemente llegan directamente del océano abierto.

También se encontró una diferencia entre los dos morfotipos en cuanto al tamaño máximo de las tortugas capturadas en el PNN Gorgona. Las tortugas de morfotipo negroalcanzaron mayor tamaño de caparazón respecto al tamaño máximo reportado para ese morfotipo que las tortugas de morfotipo amarillo. Las tortugas de morfotipo negrotienen un tamaño estimado de madurez sexual de 79.4 cm LRC en el PNN Gorgona (Hirth 1997; Zárate 2004; Sampson *et al.* 2014), y su talla máxima durante el estudio fue de 78.0 cm LRC, lo cual indica que este morfotipo utiliza la zona de estudio casi hasta alcanzar su talla de madurez sexual. Las tortugas de morfotipo amarillo, por otra parte, tienen una talla de madurez sexual estimada en 96.0 cm LRC, y la talla máxima alcanzada por los individuos muestreados durante este estudio fue de 72.5 cm LRC, muy por debajo de la talla de madurez sexual. Dado el rango de tamaños de las tortugas capturadas, se sugiere que las tortugas de morfotipo amarilloutilizan el PNN Gorgona sólo como una etapa relativamente corta durante su migración en el Pacífico oriental, mientras que las tortugas de morfotipo negro utilizan esta área protegida durante un tiempo proporcionalmente mayor de su ciclo de vida.

La condición corporal calculada para los dos morfotipos fue similar a la reportada para Baja California por Seminoff *et al.* (2002a) y para las costas de Perú por Velez-Zuazo *et al.* (2014), es decir que los dos morfotipos están utilizando los recursos alimenticios de la zona en manera similar, obteniendo una buena condición corporal (>1.4; Vander Zanden *et al.* 2012). La condición corporal se calcula como la proporción entre el cubo del LRC y masa de la tortuga; un peso mayor a un mismo tamaño resultará en un índice de condición corporal mayor. Este índice fue significativamente mejor para las tortugas de morfotipo amarillo que para las de morfotipo negro, lo cual indica que las de morfotipo amarillo hicieron una mejor utilización de los recursos disponibles, o tal vez que llegaron con mejor condición corporal a la zona de estudio.

Desafortunadamente, debido a que el protocolo de monitoreo implementado en el PNN Gorgona no lo contempla, no fue posible incluir datos de esfuerzo de muestreo (calculado como el número de tortugas capturadas por tiempo de búsqueda y número de personas en el agua), los cuales hubieran podido utilizarse para estimar el tamaño de la población. Sería recomendable en el futuro modificar este protocolo para poder contar con esta información.

Crecimiento

En esta tesis se presentan los primeros datos de crecimiento de tortuga verde *C. mydas* en el Pacífico colombiano. El número de tortugas recapturadas fue bajo, lo cual indica baja permanencia en el área de estudio. Sin embargo, el número acumulado de recapturas aumentó con el tiempo, lo cual sugiere que las tortugas no salieron del área de estudio luego de ser marcadas. Es posible también que haya habido pérdida de marcas, lo cual resultaría en bajas recapturas. De todas las tortugas marcadas entre 2003 y 2012 sólo el 50% fueron marcadas en ambas aletas. Aunque el tipo de marca utilizado en este estudio (Inconel) no tiende a corroerse con el tiempo, es posible que por deficiente aplicación de la marca o por alteraciones en el tejido del animal (por ejemplo con el crecimiento), ésta se caiga, y por lo tanto se recomienda marcar las dos aletas para minimizar la pérdida de información (Balazs 1999). No obstante el hecho de que la ausencia de cicatrices o rasgaduras del tejido en las aletas de las tortugas recapturadas sea indicadora de que no ocurrió esto, se debe considerar la posibilidad de que si la única marca aplicada a la mitad de las tortugas en este estudio se cayó, se podría haber perdido así la información de recaptura.

El tiempo entre recapturas fue de más de 5 años para los dos morfotipos. Esto indica que la zona de estudio funciona como área de forrajeo para juveniles durante buena parte de su desarrollo, el cual se calcula que puede durar hasta 21.9 años (Seminoff *et*

al. 2002b). Es probable que estos individuos hagan un uso prolongado de la zona marina del PNN Gorgona, lo cual realza la importancia de conservar los recursos necesarios para la alimentación y crecimiento de esta especie en esta área protegida.

El patrón de crecimiento de las tortugas negras fue similar al reportado para las Islas Galápagos, la Bahía de San Diego, y las Islas Hawaii (Green 1993; Balazs & Chaloupka 2004; Eguchi *et al*. 2012). Este patrón es no-monotónico, con un crecimiento más alto en la clase de 50.0-59.9 cm LRC. El patrón de crecimiento observado en las tortugas de morfotipo amarillo del PNN Gorgona fue el opuesto, con crecimiento menor en la clase intermedia de 40.0-49.9 cm LRC. Esto sugiere que las tortugas de morfotipo negro tienen un crecimiento más rápido luego de llegar a la zona nerítica del PNN Gorgona, mientras que las de morfotipo amarillo sufren el proceso contrario. Es posible entonces que las tortugas de morfotipo negro logren aprovechar mejor los recursos de la zona que las de morfotipo amarillo, las cuales presentan además un índice de condición corporal menor con relación a los tamaños más grandes. Sin embargo, es posible que los patrones de crecimiento observados fueran afectados por el tamaño de muestra pequeño (N= 20 y N=13 para tortugas de morfotipo negro y amarillo, respectivamente), así como por la gran variabilidad en los datos, que no permitió establecer una relación clara en el crecimiento para cada morfotipo.

Se había hipotetizado que las tortugas amarillas crecerían más rápido que las de morfotipo negro ya que su tamaño de madurez sexual es mayor. Sin embargo no se encontró diferencia en la tasa de crecimiento somático entre los dos morfotipos. Es probable que las condiciones ambientales a las que están expuestos los individuos de ambos morfotipos (temperatura, recursos alimenticios) tengan mayor impacto sobre la tasa de crecimiento que las características intrínsecas de cada morfotipo. Es necesario no obstante obtener datos más confiables que permitan discernir las posibles diferencias

en el crecimiento somático de estos dos morfotipos, y se requiere llevar a cabo un monitoreo y marcaje mayor en el tiempo.

El tiempo para alcanzar la madurez sexual entre las tortugas provenientes de diferentes stocks genéticos que forrajean en el PNN Gorgona probablemente tenga consecuencias diferentes sobre las poblaciones a las que pertenecen los individuos. Las tortugas de morfotipo amarillo deberán pasar varios años más en otras áreas de desarrollo a lo largo de su ruta migratoria antes de alcanzar las áreas de apareamiento, mientras que las tortugas de morfotipo negro salen del área de estudio casi habiendo alcanzado su tamaño mínimo de madurez sexual.

Ecología trófica

Lavados esofágicos

El aparato bucal y digestivo de *C. mydas* está adaptado a una dieta herbívora, con un pico filoso y aserrado que le permite cortar algas y plantas. Los individuos también desarrollan la flora microbiana necesaria para digerir plantas (Bjorndal 1997, Márquez 1990). Esta especie no tiene adaptaciones para comer moluscos y triturarlos como *Caretta caretta* y *Lepidochelys olivacea*, ni el pico alargado de *Eretmochelys imbricata* que le permite buscar alimento entre los huecos del coral, y por lo tanto está limitada a consumir animales que estén encima del arrecife y sean de cuerpo blando, o que estén en la columna de agua.

En el caso de las tortugas de Gorgona, al haber relativamente pocas algas, pareciera que ingieren una dieta mixta de plantas terrestres, algas y animales. En este caso tendrían una menor eficiencia digestiva porque la flora intestinal tendría que adaptarse al tipo de comida que estén ingiriendo (Bjorndal 1979), pero esto se compensa por el hecho de que pueden ingerir varios tipos de alimento en mayor cantidad que si sólo comieran algas. El diversificar e incluir proteína animal en la dieta permitiría a las tortugas no

depender totalmente de recursos específicos con poca disponibilidad, aprovechando así su condición omnívora. También es probable que exista competencia por algas en los arrecifes del PNN Gorgona por parte de peces herbívoros y erizos de mar.

En varios estudios se ha reportado el comportamiento trófico oportunista de *C. mydas*, que le permite aprovechar los recursos disponibles en su hábitat (Bjorndal 1997, Cardona *et al.* 2009). Por ejemplo, 82% de tortugas verdes observadas por Heithaus *et al*. (2002) consumieron medusas y ctenóforos cuando estuvieron disponibles en el medio, las cuales son presas fácilmente digeribles que pueden no estar bien representadas en lavados esofágicos debido a que pasan rápidamente por el tracto digestivo. Esta flexibilidad en la alimentación sería beneficiosa para la especie, ya que le permite obtener indistintamente recursos necesarios para su crecimiento y maduración. Una especie del tamaño de *C. mydas* que fuera estrictamente herbívora tendría muchas dificultades para encontrar un hábitat adecuado en sus etapas de vida juvenil y adulta en el Pacífico oriental. La herbivoría estricta limitaría la distribución de *C. mydas* a los lugares que pudieran ofrecerle suficiente cantidad de algas o pasto marino para su desarrollo. En el Pacífico oriental el pasto marino está distribuido desde Panamá hasta Canadá (UNEP-WCMC & Short 2005).

La alta frecuencia de restos de plantas terrestres en los lavados esofágicos de los dos morfotipos (FO% = 96.7 para tortugas de morfotipo negroy FO% = 100 para tortugas de morfotipo amarillo), resalta el papel que cumplen las tortugas marinas en la zona costera del PNN Gorgona en el reciclado de nutrientes terrestres en el ambiente acuático. El subsidio de nutrientes marinos hacia ambientes terrestres ha sido documentado en tortugas marinas; ocurre cuando las hembras desovan en las playas, y las cáscaras de huevos, los huevos no eclosionados, así como los huevos y neonatos depredados pasan a hacer parte de la cadena trófica terrestre (Bouchard & Bjorndal 2000). En el caso del

PNN Gorgona se daría un proceso inverso, en que nutrientes terrestres pasan a hacer parte de la cadena trófica marina por medio del consumo de las tortugas marinas.

Se reportó la presencia de hojas y frutos de mangle en la dieta de *C. mydas* en las Islas Galápagos (~17 FO%; Carrión-Cortez *et al*. 2010), en Bahía Magdalena, México (~17 FO%; López-Mendilaharsu *et al*., 2005), y en Australia (~40 FO %; Read & Limpus 2002). Sin embargo, no se han reportado altas frecuencias de espermatofitas terrestres en los lavados esofágicos de tortugas marinas en otras zonas del mundo, lo cual hace del PNN Gorgona un lugar único en cuanto al comportamiento alimenticio de esta especie.

Disponibilidad de alimentos en la columna de agua y en los arrecifes

Columna de agua

La disponibilidad de alimento en la columna de agua, representada por la abundancia de tunicados (salpas y doliolos) alrededor de la Isla Gorgona, no fue constante durante todo el año de estudio. Se encontraron picos de abundancia, con mayor concentración de individuos en marzo y en septiembre. El pico de marzo ocurrió durante la estación seca, y fue probablemente provocado por el incremento en velocidad de la Corriente de Colombia que ocurre durante la primera parte del año, y la subsiguiente advección de individuos hacia la estación de muestreo más somera, ubicada al sureste de la isla. Esta estación está ubicada un poco más al sureste de la zona arrecifal donde se encuentran los dos morfotipos de tortuga verdes, y los tunicados agregados allí podrían representar un recurso de fácil acceso para las tortugas. En septiembre se dio un pico durante la época de lluvias. Los picos en abundancia de tunicados pelágicos pueden ocurrir ya sea por advección y agregación de individuos, como ocurrió en marzo 2006, o por aumento en la productividad local, es decir en la cantidad de nutrientes disponibles en la columna de agua (Graham *et al.* 2001). El aumento en la abundancia de tunicados en septiembre pudo ser debido a aportes de nutrientes de las quebradas de la isla, o de nutrientes

provenientes del complejo Patía-Sanquianga. Como lo mencionaron Amorocho & Reina (2007), existen aportes de plantas terrestres acarreadas desde esa zona hasta el área costera de la Isla Gorgona, y es posible que estas mismas corrientes lleven nutrientes suspendidos que puedan ser utilizados por tunicados pelágicos. Es posible también que las corrientes de mesoescala que operan en la zona en conjunto con la topografía local hubieran contribuido a agregar a los individuos en el mes de septiembre 2005 (Graham *et al*. 2001).

En general, este recurso es esporádico, dependiente de las corrientes y de la productividad local, y por lo tanto no se puede considerar como un recurso del cual las tortugas marinas puedan aprovecharse todo el año. Posiblemente se trate de un consumo oportunista y ocasional, aunque para poder afirmar esto habría que hacer un estudio de la zona aledaña a la Isla Gorgona para identificar la ocurrencia y ubicación de los hileros, así como su composición. Estudios de seguimiento de las tortugas marinas que habitan las aguas del PNN Gorgona, tal vez con cámaras subacuáticas (Critter cams) permitirían establecer en qué áreas de esta zona protegida se alimentan las tortugas, así como si obtienen la mayoría de su alimento en los arrecifes, en la columna de agua o en los hileros.

Arrecife

No se encontró diferencia significativa en la abundancia de las diferentes algas identificadas a lo largo del año. La variedad de algas disponibles para las tortugas verdes en el PNN Gorgona es baja, comparada con zonas cercanas del Pacífico oriental, así como con otras zonas de forrajeo en el mundo (Bula-Meyer 1995; Arthur & Balazs 2008; Fernández-García *et al*. 2011). Esta baja disponibilidad de algas resulta en la utilización de otros recursos alimenticios por parte de las tortugas verdes, como por ejemplo invertebrados y plantas terrestres. La cantidad de hojas de plantas terrestres

encontradas en el arrecife fue muy baja; es probable que las tortugas consuman plantas que llegan flotando en hileros desde la costa, como lo sugirieron Amorocho & Reina (2007).

Así como los individuos de tortuga carey del Pacífico oriental se han adaptado a vivir en ambientes diferentes a los preferidos por tortugas carey en otras partes del mundo (Seminoff *et al*. 2012a), es probable que las tortugas verdes del Pacífico colombiano se hayan adaptado a utilizar recursos alimenticios distintos a los que prefieren las tortugas verdes en otras localidades. Ya que los arrecifes de coral son poco abundantes, y que la oferta en abundancia y diversidad de algas es baja, comparada con otras zonas, estas tortugas consumen otros recursos del medio marino que les permiten crecer y alcanzar su talla reproductiva.

El hecho de que los recursos disponibles para esta especie sean tan escasos hace más importante el proteger las áreas utilizadas por las tortugas marinas durante las diferentes fases del ciclo de vida de la especie, y con mayor razón durante la etapa juvenil, la cual es demográficamente importante (Crouse *et al.* 1987). Se sabe que *C. mydas* utiliza zonas costeras e insulares a lo largo del Pacífico oriental, desde Chile hasta California, siendo por lo tanto importante proteger todas y cada una de las zonas que utiliza durante su desarrollo, ya que los impactos en cada zona van a tener un efecto en otras áreas geográficas utilizadas por la especie durante sus otras etapas de vida camino a la madurez. Todas las fases de vida de las tortugas verdes están expuestas a amenazas antropogénicas, y es por tanto importante protegerlas en todas ellas (Seminoff *et al.* 2012a).

Nutrientes

El análisis nutricional llevado a cabo en este estudio mostró que *Dictyota* sp. fue el alga con mayor cantidad de proteína y lípidos de las muestras analizadas, lo cual hace que

sea más apetecible para las tortugas verdes. McDermid *et al*. (2007) reportaron que en Hawaii las algas más consumidas por tortugas verdes también tenían los más altos contenidos de carbohidratos y proteínas. Sin embargo, varias algas con altas cantidades de nutrientes no fueron consumidas por las tortugas en ese estudio, posiblemente por tener otros compuestos nocivos o por tener menor disponibilidad.

Aunque Sotka *et al*. (2003) reportaron que las algas del género *Dictyota* producen alcoholes diterpenos que son disuasorios para la mayoría de herbívoros, encontraron un anfípodo que estaba adaptado a comer esta alga. Es probable que los individuos de *C. mydas* estén adaptados a ingerir esta alga a pesar de las toxinas que pueda contener.

Tolentino-Pablico *et al*. (2008) reportaron entre las algas más consumidas por peces herbívoros a las especies pertenecientes a las Rodofitas, las cuales también han sido reportadas como las más consumidas por *C. mydas* en Baja California (Seminoff *et al*. 2002; López-Mendilaharsu *et al.* 2008), en Australia (Forbes 1996) y en Florida (Gilbert 2005). Este no fue el caso en este estudio, ya que el alimento más consumido fueron las plantas terrestres, y entre las algas consumidas por los dos morfotipos se encontraban algas pertenencientes a las tres divisiones algales. Entre las Phaeophyta más consumidas por peces herbívoros, Tolentino-Pablico *et al.* (2008) reportaron a *Dictyota*, y entre las Chlorophyta a *Cladophora*; ambas algas fueron seleccionadas por los juveniles de *C. mydas* en el PNN Gorgona.

El contenido de celulosa de las algas marinas es más bajo que el de las plantas terrestres, lo cual hace que sean más digeribles, y probablemente sean un alimento preferible para las tortugas marinas en el PNN Gorgona (Baldan *et al*. 2001). Sin embargo, la baja disponibilidad de algas en los arrecifes lleva a las tortugas a complementar su dieta con otros alimentos. Además, la cantidad de celulosa en las algas es variable, y es menor en las algas rojas y pardas que en las verdes (Baldan *et al*.

2001). Esto indica que *Hypnea* sp. y *Dictyota* sp. son algas más digeribles que *Cladophora* sp., y es posible que el consumo de esta alga por parte de las tortugas de morfotipo negro y no de las de de morfotipo amarillo sea debido a competencia entre los dos morfotipos, o a una adaptación de las tortugas de morfotipo negro que no poseen las de morfotipo amarillo.

La eficiencia de asimilación de las proteínas contenidas en algas e invertebrados es mayor que la de las proteínas en plantas terrestres, por lo que se esperaría que las tortugas consuman más algas e invertebrados para maximizar su asimilación de proteína y energía (Bowen *et al.* 1995). Los lavados esofágicos indicaron un mayor consumo de plantas terrestres por parte de las tortugas verdes del PNN Gorgona; sin embargo, el análisis isotópico indicó un consumo importante de invertebrados o peces, lo cual estaría más de acuerdo con la teoría del forrajeo óptimo (MacArthur & Pianka 1966), ya que se esperaría que estas tortugas consuman un alimento con mayor cantidad de proteína y energía que la contenida en plantas terrestres.

Selección de recursos

Según la teoría del forrajeo óptimo los animales tratan de maximizar la cantidad de energía obtenida por unidad de tiempo, a la vez que minimizan los costos y riesgos (MacArthur & Pianka 1966). Los alimentos consumidos por las tortugas verdes en el PNN Gorgona deberían representar los alimentos con mayor cantidad de energía (presumiblemente los más digeribles, con menor cantidad de toxinas), que pueden consumir en la zona de bajo riesgo que representan los arrecifes.

El índice de Ivlev mostró una diferencia entre las algas seleccionadas por los dos morfotipos estudiados, viéndose una selección positiva hacia el alga *Cladophora* sp. por parte de las tortugas de morfotipo negro, mientras que esta alga era evitada por las de morfotipo amarillo. Los dos morfotipos seleccionaron las algas *Dictyota* sp. e *Hypnea*

sp., aunque esta selección fue más marcada por parte de las tortugas de morfotipo amarillo.

Se han reportado aproximadamente 275 especies de algas en lavados esofágicos y contenidos estomacales de tortugas en varios estudios llevados a cabo en Hawaii (McDermid *et al*. 2007), lo cual muestra la variedad de la dieta de esta especie. La dieta de los individuos tiende a variar con su ubicación geográfica, lo cual indica que *C. mydas* puede ser oportunista pero que tiende a tener cierta selectividad en su dieta (Arthur & Balazs 2008).

De casi 500 especies de algas identificadas en Hawaii, se ha reportado el consumo de aproximadamente la mitad por parte de tortugas marinas; sin embargo, sólo unas nueve especies comprendieron la mayoría de la dieta, y varias de estas especies tuvieron alto contenido de carbohidratos, proteínas y vitaminas (McDermid *et al*. 2007). Esto indica que hay selección de ciertas especies por parte de las tortugas de morfotipo amarillo presentes en Hawaii. Esta misma situación se observó en el PNN Gorgona, donde sólo algunas especies de algas de las disponibles fueron encontradas en los lavados esofágicos, lo cual indicaría que existe un comportamiento selectivo por parte de los juveniles de tortuga verde mientras permanecen en las aguas costeras del PNN Gorgona.

Isótopos estables

Los resultados del análisis isotópico difirieron de lo hallado por medio de lavados esofágicos, ya que se encontró que las tortugas ocuparon un nivel trófico superior al esperado. Esto en el caso de que sólo estuvieran consumiendo plantas terrestres, algas y pequeños invertebrados pelágicos. Lo anterior resultó en una falta de soluciones factibles cuando se utilizó el modelo de mezcla MixSIAR, ya que este modelo requiere que el consumidor se encuentre ubicado dentro de un polígono formado por sus presas potenciales en la gráfica de $\delta^{13}C$ vs. $\delta^{15}N$ (Stock & Semmens 2013). Es posible que los

juveniles de *C. mydas* que forrajean en el PNN Gorgona también incluyan en su dieta presas como grandes invertebrados e incluso peces, que se encuentran en niveles de la cadena trófica más altos. Se ha reportado el consumo de restos de peces descartados por la pesquería artesanal en África noroccidental (Cardona *et al*. 2009), y este fenómeno también ocurre en el Parque Nacional Machalilla, Ecuador (observación personal). Es posible que los pescadores artesanales de la zona descarten restos de peces dentro en aguas costeras de la isla y que las tortugas verdes tengan acceso a este recurso.

En un estudio llevado a cabo en Baja California, México, Rodríguez-Barón (2010) encontró valores de $\delta^{15}N$ de 7.92-8.40 ‰ en promedio para tortugas verdes juveniles, similares a los reportados por ese autor para invertebrados marinos. En ese estudio las tortugas consumieron principalmente algas rojas, lo cual les dio valores isotópicos similares a los de consumidores primarios. Los valores isotópicos encontrados en el presente estudio estuvieron muy por encima de los reportados por Rodríguez-Barón (2010), lo cual confirma que las tortugas del PNN Gorgona tienen una alimentación que incluye presas en niveles tróficos más altos.

La diferencia entre lo que se encontró con los análisis esofágicos y el análisis isotópico también puede ser debida a que no todo lo que es ingerido por el animal es asimilado de la misma forma, dado que ciertos ítems alimenticios son asimilados más eficientemente, dando mayor peso a sus valores isotópicos (Phillips *et al*. 2014). Las presas blandas como los invertebrados son digeridas rápidamente por los consumidores y por lo tanto no siempre son recuperadas en los lavados esofágicos o en contenidos estomacales (Stowasser *et al.* 2012).

La técnica del lavado esofágico podría estar sesgada, ya que el tamaño del esófago y del tubo recolector limitan el tamaño de muestra que se puede recolectar. Las presas duras y de mayor tamaño podrían no estar representadas en la muestra recolectada (Chipps &

Garvey 2006). Otra explicación a los valores altos de $\delta^{15}N$ obtenidos para tortugas verdes en el PNN Gorgona es el hecho de que los valores isotópicos de plantas terrestres podrían incrementarse con el tiempo de descomposición. Esto fue reportado por Fellerhoff *et al.* (2003) para el buchón de agua, cuyos valores isotópicos aumentaron con el tiempo de descomposición en el agua. Si las tortugas muestreadas consumieron hojas y semillas de plantas que llevaban varias semanas descomponiéndose antes de ser consumidas, es posible que tuvieran una señal isotópica mayor a la de las plantas terrestres frescas recolectadas y analizadas en este estudio.

Se encontró mayor variabilidad en la señal isotópica de las tortugas de morfotipo amarillo que de las de de morfotipo negro, lo cual estaría indicando una mayor variabilidad en la dieta de ese morfotipo. Al tener una señal menos variable, las tortugas de morfotipo negroposiblemente tengan una dieta más especializada (Araújo *et al*. 2011). La baja variabilidad en los valores del $\delta^{15}N$ indica similitud en la dieta de los individuos, y posiblemente cambios sincronizados en la dieta, como podría ocurrir al aprovecharse de recursos esporádicos, como los picos de abundancias de tunicados que ocurren alrededor de la Isla Gorgona (Sampson *et al*. 2014).

Los valores de $\delta^{13}C$ tuvieron baja varianza, lo cual indica que las tortugas muestreadas estuvieron en el ambiente costero del PNN Gorgona en los meses anteriores a ser capturadas, ya que la señal del carbono se demora de cuatro a seis meses en ser integrada en el tejido del consumidor (Reich *et al.* 2008; Seminoff *et al*. 2012b). Si las tortugas estuvieran desplazándose entre áreas de forrajeo tendrían una señal isotópica mucho más variable (Bearhop *et al.* 2004).

Sin embargo, al analizar los valores isotópicos a lo largo del año, se encontraron diferencias en los valores obtenidos para tortugas de morfotipo amarillo en los diferentes meses. Este morfotipo tuvo valores isotópicos de $\delta^{15}N$ más altos en agosto

2012, y valores de $\delta^{13}C$ más bajos en diciembre 2012. Estas diferencias podrían estar indicando movimientos de estas tortugas para alimentarse en áreas más alejadas, o tal vez el hecho de que los individuos muestreados en esos meses acababan de llegar al área de estudio y estaban reflejando los valores isotópicos de otra zona previa al reclutamiento en el PNN Gorgona.

CONCLUSIONES GENERALES

La agregación de tortugas que forrajea en el PNN Gorgona está compuesta por juveniles de los dos morfotipos conocidos de esta especie. Estos juveniles están compuestos principalmente por el morofotipo negro (73.1% entre 2003 y 2012), aunque el registro de tortugas de morofotipo amarillo ha aumentado paulatinamente a lo largo del tiempo en el PNN Gorgona, pasando a representar el 53.4%. Las tortugas de morfotipo negrocapturadas entre 2003 y 2012 fueron más grandes y pesadas que las tortugas de morfotipo amarillo.

Se obtuvo un muy bajo porcentaje de recaptura, aunque las recapturas de hasta 5.89 años señalan que hay una cierta permanencia de las tortugas en el área de estudio. La baja recaptura puede ser debida a pérdida de marcas, a salida del área de estudio, o una gran cantidad de tortugas en la zona.

No hubo diferencia significativa en la tasa de crecimiento lineal de los dos morfotipos, pero sí se observó mejor condición corporal en las tortugas de morfotipo amarillo. El aumento en la tasa de crecimiento de las tortugas de morfotipo negro al llegar a la zona nerítica podría estar señalando un mejor aprovechamiento de los recursos disponibles en el PNN Gorgona, comparado con el morfotipo amarillo.

La dieta de los dos morfotipos estimada por medio de lavados esofágicos no fue significativamente diferente. Sin embargo, hubo diferencia en los alimentos seleccionados, y en su calidad.

Los valores isotópicos de los dos morfotipos no fueron significativamente diferentes, lo cual confirma que la dieta de las tortugas de morfotipo negro y amarillo no es diferente. Sin embargo, la variabilidad en los valores isotópicos de las tortugas de morfotipo amarillo fue mayor, lo cual indica un consumo más variado de alimentos.

La posición trófica calculada para los dos morfotipos fue de consumidores secundarios. Esto indica que las tortugas verdes del PNN Gorgona incluyen materia animal en su dieta que no fue recolectada por medio de lavados esofágicos.

La falta de diferencias significativas en cuanto a crecimiento somático y dieta de los dos morfotipos estudiados en el PNN Gorgona indica que existen más similitudes que diferencias entre estos dos morfotipos, y se da así soporte a la teoría de que se trata de dos morfotipos de una sola especie y no de dos especies distintas. La filopatría que existe en esta especie ha resultado en diferencias morfológicas, pero no se trata necesariamente de un proceso de especiación, dado que ambos morfotipos comparten hábitats y características de vida, como se vio durante esta investigación.

RECOMENDACIONES

- Se recomienda estandarizar el esfuerzo de muestreo utilizado para realizar el monitoreo mensual de esta especie en el PNN Gorgona, es decir llevar a cabo las búsquedas de tortugas durante un tiempo determinado y con un número determinado de personas en el agua durante cada muestreo. Por ejemplo se puede establecer un tiempo de búsqueda de una hora con 4 personas en el agua. La variabilidad en los tiempos de búsquedas hace imposible el cálculo del esfuerzo de muestreo, y por lo tanto de las capturas por unidad de esfuerzo.
- Se recomienda poner marcas dobles, poniendo una marca en cada aleta anterior, para minimizar la pérdida de información. Al poner sólo una marca se duplica la posibilidad de que la tortuga pierda la marca y ya no pueda ser identificada como recaptura.
- Se recomienda continuar el monitoreo mensual, para aumentar la base de datos y tener más datos para calcular las tasas de crecimiento somático de *C. mydas* en el área del PNN Gorgona.
- Se recomienda hacer lavados esofágicos en otras horas del día para determinar si se obtiene más cantidad de muestra en horas de la tarde o de la mañana. Se podría hacer lavados a las 10:00 y 16:00, comparando con lo que se obtuvo en este trabajo a las 20:00.
- Se recomienda hacer muestreos de otros alimentos potenciales, incluyendo invertebrados grandes y peces, para comparar con la señal isotópica de las tortugas y poder identificar los alimentos asimilados.
- Dada la alta movilidad de esta especie, y la alta probabilidad de que los individuos residentes en el PNN Gorgona también utilicen zonas costeras fuera del área protegida, se recomienda que las autoridades ambientales hagan un trabajo de

educación y promoción de la conservación de las tortugas verdes entre pescadores y comunidades costeras aledañas al parque. Es posible que como se había propuesto anteriormente (Amorocho & Reina 2007), las tortugas verdes del PNN Gorgona utilicen el área arrecifal más como refugio que como sitio de alimentación, y sería necesario brindarles protección en sus posibles zonas de alimentación.

- Se recomienda hacer estudios utilizando telemetría que permitan identificar los hábitats utilizados por las tortugas verdes dentro del PNN Gorgona y en áreas aledañas. También se recomienda continuar con estudios de genética incluyendo mayor número de tortugas de morfotipo amarillo en la muestra, para poder identificar los sitios de proveniencia de los individuos de este morfotipo, y poder inferir sus rutas migratorias.
- El análisis de isótopos estables indicó que las tortugas verdes consumen un alimento alto en proteína que podría estar ubicado fuera de los límites del PNN Gorgona. Ya que el alimento identificado previamente como más importante para las tortugas verdes en el PNN Gorgona (tunicados) no está disponible todo el año, en caso de que Parques decidiera llevar a cabo una estrategia de monitoreo o conservación de los recursos alimenticios utilizados por las tortugas marinas, se requeriría hacer un estudio para identificar el alimento más importante en la dieta de esta especie.
- Por último, ya que está comprobado que esta especie realiza amplias migraciones durante sus diferentes etapas de vida, utilizando recursos que abarcan las jurisdicciones de varios países, y dado que el PNN Gorgona provee hábitat para individuos de varias poblaciones muy alejadas entre sí, se recomienda continuar con la iniciativa del Corredor Marino del Pacífico Este Tropical (CMAR).

LITERATURA CITADA

Acero, A. & R. Franke. 2001. Peces del parque nacional natural Gorgona, p. 123-131. *In*: Barrios, L.M. & M. Lopéz-Victoria (eds.). Gorgona marina: Contribución al conocimiento de una isla única, Serie Publicaciones Especiales No 7, Instituto Investigaciones Marinas y Costeras – INVEMAR. Santa Marta, Colombia.

Acevedo-Bueno, C.I., B.S. Beltrán-León & R.A. Caicedo-Tulante. 2004. Plan básico de manejo 2005-2009 Parque Nacional Natural Gorgona. Parques Nacionales Naturales de Colombia. Dirección Territorial Suroccidente, Cali, Colombia.

Alldredge, A.L. & L.P. Madin. 1982. Pelagic tunicates: unique herbivores in the marine plankton. BioScience. 32: 655-663.

Alvarado, J. & A. Figueroa. 1992. Recapturas post-anidatorias de hembras de tortuga marina negra (*Chelonia agassizii*) marcadas en Michoacán, México. Biotropica. 24: 560-566.

Amorocho, D.F. & R.D. Reina. 2007. Feeding ecology of the East Pacific green sea turtle *Chelonia mydas agassizii* at Gorgona National Park, Colombia. Endang. Species Res. 3: 43-51.

Amorocho, D.F. & R.D. Reina. 2008. Intake passage time, digesta composition and digestibility in East Pacific green turtles (*Chelonia mydas agassizii*) at Gorgona National Park, Colombian Pacific. J. Exp. Mar. Biol. Ecol. 360: 117-124.

Amorocho, D.F., F.A. Abreu-Grobois, P.H. Dutton, R.D. Reina. 2012. Multiple distant origins for green sea turtles aggregating off Gorgona Island in the Colombian Eastern Pacific. PLoS ONE. 7(2): e31486.

Araújo, M.S., Bolnick, D.I. & Layman, C.A. 2011. The ecological causes of individual specialization. Ecology Letters 14: 948-958.

Arthur, K.E. & G.H. Balazs. 2008. A comparison of immature green turtle (*Chelonia mydas*) diets among seven sites in the main Hawaiian Islands. Pac. Sci. 62: 205-217.

Arthur, E., Boyle, M.C. & Limpus, C.J. 2008. Ontogenetic changes in diet and habitat use in green sea turtle (*Chelonida mydas*) life history. Mar. Ecol. Prog. Ser. 362: 303-311.

Arthur, K.E., McMahon, K.M., Limpus, C.J. & Dennison, W.C. 2009. Feeding ecology of green turtles (*Chelonia mydas*) from Shoalwater Bay, Australia. Marine Turtle Newsletter 123: 6-12.

Baker, R.R. 1978. The evolutionary ecology of animal migration. Holmes & Meier Publishers, New York, USA.

Balazs, G.H. 1999. Factors to consider in the tagging of sea turtles. En: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., Donnelly, M. (eds). Research and management techniques for the conservation of sea turtles. IUCN/SSC Marine Turtle Specialist Group Publication No. 4, pp. 101-109.

Balazs, G.H., M. Chaloupka. 2004. Spatial and temporal variability in somatic growth of green sea turtles (*Chelonia mydas*) resident in the Hawaiian Archipelago. Mar. Biol. 145: 1043-1059.

Baldan, B., Andolfo, P., Navazio, L., Tolomio, C. & Mariani, P. 2002. Cellulose in algal cell wall: an "in situ" localization. European Journal of Histochemistry 45: 51-56.

Barreto-Sánchez, L.J. 2011. Diagnóstico del estado actual de las tortugas marinas en el Pacífico Colombiano. Informe Nacional. Comisión Permanente del Pacífico Sur.

Barrios, L.M. & López-Victoria, M. (eds). 2001. Gorgona marina: Contribución al conocimiento de una isla única, Serie Publicaciones Especiales No 7, Instituto Investigaciones Marinas y Costeras – INVEMAR. Santa Marta, Colombia.

Barrow, L.M., Bjorndal, K.A., Reich, K.J., 2008. Effects of preservation method on stable carbon and nitrogen isotope values. Phys. Biochem. Zool. 81(5), 688-693.

Bass, A.L., Epperly, S.P., Braun-McNeill, J. 2004. Multi-year analysis of stock composition of a loggerhead turtle (*Caretta caretta*) foraging habitat using maximum likelihood and Bayesian methods. Conserv. Genet. 5: 783-796.

Bass, A.L., Epperly, S.P., Braun-McNeill, J. 2006. Green turtle (*Chelonia mydas*) foraging and nesting aggregations in the Caribbean and Atlantic: Impact of currents and behavior on dispersal. J Heredity 97(4): 346-354.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., Macleod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. J. Animal. Ecol. 73: 1007-1012.

Bjorndal, K.A. 1979. Cellulose digestion and volatile fatty acid production in the green turtle, *Chelonia mydas*. Comp. Biochem. Physiol. 63: 127-133.

Bjorndal, K.A. 1985. Nutritional ecology of sea turtles. Copeia 3: 736-751.

Bjorndal, K.A., Bolten, A.B. 1988. Growth rates of immature green turtles, *Chelonia mydas*, on feeding grounds in the southern Bahamas Copeia 3: 555-564.

Bjorndal, K.A. 1997. Foraging ecology and nutrition of sea turtles. En: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p. 199-231.

Bjorndal, K.A., Bolten, A.B., Chaloupka, M.Y. 2000. Green turtle somatic growth model: evidence for density dependence. Ecol. Appl. 10(1): 269-282.

Bjorndal, K.A., Parsons, J., Mustin, W., Bolten, A.B. 2013. Threshold to maturity in a long-lived reptile: interactions of age, size, and growth. Mar. Biol. 160(3): 607-616.

Blanco, J.F. 2009. The hydroclimatology of Gorgona Island: Seasonal and ENSO-related patterns. Actual. Biol. 31: 111-121.

Blanco, G.S., Morreale, S.J., Vélez, E., Piedra, R., Montes, W.M., Paladino, F.V., Spotila, J.R. 2011. Reproductive output and ultrasonography of an endangered population of East Pacific green turtles. The Journal of Wildlife Management 9999: 1-6.

Blanco, G.S., Morreale, S.J., Seminoff, J.A., Paladino, F.V., Piedra, R. & Spotila, J.R. 2013. Movements and diving behavior of internesting green turtles along Pacific Costa Rica. Integrative Zoology 8(3): 293-306.

Bolger, T., Connolly, P.L. 1989. The selection of suitable indices for the measurement and analysis of fish condition. J. Fish. Biol. 34: 171-182.

Bolten, A.B. 2003. Variation in sea turtle life history patterns: neritic vs. oceanic developmental stages. En: Lutz PL, Musick J, Wyneken J (eds) The biology of sea turtles, Vol. II. CRC Press, Boca Raton, pp. 243-257.

Bouchard, S.S., Bjorndal, K.A. 2000. Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. Ecology 81(8): 2305-2313.

Boulon, R.H., Frazer, N.B. 1990. Growth of wild juvenile Caribbean green turtles, *Chelonia mydas.* J. Herpetol 24(4): 441-445.

Bowen, B.W., Meylan, A.B., Ross, J.P., Limpus, C.J., Balazs, G.H. & Avise, J.C. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. Evolution 46(4): 865-881.

Bowen, S.H., Lutz, E.V. & Ahlgren, M.O. 1995. Dietary protein and energy as determinants of food quality: trophic strategies compared. Ecology 76(3): 899-907.

Boyle, M.C., Limpus, C.J. 2008. The stomach contents of post-hatchling green and loggerhead sea turtles in the southwest Pacific: an insight into habitat association. Mar. Biol. 155: 233-241.

Braun-McNeill, J., Epperly, S.P., Avens, L., Snover, M.L., Taylor, J.C. 2008. Growth rates of loggerhead sea turtles (*Caretta caretta*) from the Western North Atlantic. Herpetol Conserv Biol 3(2): 273-281.

Bula-Meyer, G. 1995. Macroalgas de la Isla Gorgona (Pacífico Colombiano) con nuevos registros y una explicación de la baja diversidad y biomasa, p. 23-45. En: P. Pinto (ed.). La Isla Gorgona, nuevos estudios biológicos. Editorial Guadalupe Ltda, Bogotá, Colombia.

Burkholder, D.A., Heithaus, M.R., Thomson, J.A., Fourqurean, J.W. 2011. Diversity in trophic interactions of green sea turtles *Chelonia mydas* on a relatively pristine coastal foraging ground. Mar. Ecol. Prog. Ser. 439: 277-293.

Cai, W., Shi., G., Cowan, T., Bi, D., Ribbe, J. 2005. The response of the southern annular mode, the East Australian Current, and the southern mid-latitude ocean circulation to global warming. Geophysical Research Letters 32: L23706.

Cardona, L., Aguilar, A., Pazos, L. 2009. Delayed ontogenic dietary shift and high levels of omnivory in green turtles (*Chelonia mydas*) from the NW coast of Africa. Mar. Biol. 156, 1487-1495.

Carr, A. 1980. Some problems of sea turtle ecology. American Zoologist 20(3): 489-498.

Carrión-Cortez, J.A., P. Zárate & J.A. Seminoff. 2010. Feeding ecology of the green sea turtle (*Chelonia mydas*) in the Galapagos Islands. J. Mar. Biol. Assoc. UK. 90:1005-1013.

Casale, P., Mazaris, A.D., Freggi, D., Vallini, C., Argano, R. 2009. Growth rates and age at adult size of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea, estimated through capture-mark-recapture records. Sci. Mar. 73(3): 589-595.

Chaloupka, M., Limpus, C., Miller, J. 2004. Green turtle somatic growth dynamics in a spatially disjunct Great Barrier Reef metapopulation. Coral Reefs. 23: 325-335.

Chaloupka, M. & Limpus, C. 2005. Estimates of sex- and age-class-specific survival probabilities for a southern Great Barrier Reef green sea turtle population. Marine Biology 146: 1251-1261.

Chipps, S.R & J.E. Garvey. 2007. Assessment of diets and feeding patterns. En: Brown, M.L. and C.S. Guy (eds.). Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland, USA. Pp. 473-514

Cornelisen, C.D., Wing, S.R., Clark, K.L., Bowman, M.H., Frew, R.D., Hurd, C.L. 2007. Patterns in the $\delta^{13}C$ and $\delta^{15}N$ signature of *Ulva pertusa*: Interaction between physical gradients and nutrient source pools. Limnol. Oceanog. 52(2): 820-832.

Correa-Cárdenas, C.A. 2013. Spatial-temporal analyses of Eastern Pacific green turtles (*Chelonia mydas/Chelonia agassizii*) foraging as mixed stock in Gorgona NNP, Colombian Pacific Ocean. Tesis de Maestría, Departamento de Ciencias Biológicas, Universidad de los Andes, 67p.

Cortés, J. 1997. Biology and geology of eastern Pacific coral reefs. Coral Reefs 15: S39-S46.

Crossin, G.T., Cooke, S.J., Goldbogen, J.A., Phillips, R.A. 2014. Tracking fitness in marine vertebrates: current knowledge and opportunities for future research. Mar. Ecol. Prog. Ser. 496: 1-17.

Crouse, D.T., Crowder, L.B., Caswell, H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68(5): 1412-1423.

Deibel, D. & G.A. Paffenhöfer. 2009. Predictability of patches of neritic salps and doliolids (Tunicata, Thaliacea). J. Plankton Res. 31: 1571-1579.

Dewar, H., T. Thys, S.L.H. Teo, C. Farwell, J. O´Sullivan, T. Tobayama, M. Soichi, T. Naktasubo, Y. Kondo, Y. Okada, D.J. Lindsay, G.C. Hays, A. Walli, K. Weng, J.T. Streelman & S.A. Karl. 2010. Satellite tracking the world´s largest jelly predator, the ocean sunfish, *Mola mola*, in the Western Pacific. J. Exp. Mar. Biol. Ecol. 393: 32-42.

Eguchi, T., Seminoff, J.A., LeRoux, R.A., Prosperi, D., Dutton, D.L., Dutton, P.H. 2012. Morphology and growth rates of the green sea turtle (*Chelonia mydas*) in a Northern-most temperate foraging ground. Herpetologica 68(1): 76-87.

Engstrom, T.N., Meylan, P.A., Meylan, A.B. 2002. Origin of juvenile loggerhead turtles (*Caretta caretta)* in a tropical developmental habitat in Caribbean Panamá. Anim. Conserv. 5: 125-133.

Estrada, J.A., Rice, A.N., Lutcavage, M.E., Skomal, G.B. 2003. Predicting trophic position in sharks of the north-west Atlantic Ocean using stable isotope analysis. J. Mar. Biol. Assn. U.K. 83: 1347-1350.

Fellerhoff, C., Voss, M., Wantzen, K.M. 2003. Stable carbon and nitrogen isotope signatures of decomposing tropical macrophytes. Aquatic. Ecol. 37: 361-375.

Fernández-García, C., R. Riosmena-Rodríguez, B. Wysor, O.L. Tejada & J. Cortés. 2011. Checklist of the Pacific marine macroalgae of Central America. Bot. Mar. 54: 53-73.

Forbes, G.A. 1996. The diet and feeding ecology of the green sea turtle (*Chelonia mydas*) in an algal-based coral reef community. PhD thesis, James Cook University, Queensland, Australia. 340pp.

Forbes, G.A. 1999. Diet sampling and diet component analysis. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., Donnelly, M. (Eds.), Research and management techniques for the conservation of sea turtles. IUCN/SSC Marine Turtle Specialist Group Publication No.4. pp.144-148.

Frontier, S. 1969. Sur une méthode d´analyse faunistique rapide du zooplancton. J. Exp. Mar. Biol. Ecol. 3: 18-26.

Genin, A., J.S. Jaffe, R. Reef, C. Richter & P.J.S. Franks. 2004. Swimming against the flow: A mechanism of zooplankton aggregation. Science. 308: 860-862.

Gilbert, E.I. 2005. Juvenile green turtle (*Chelonia mydas*) foraging ecology: feeding selectivity and forage nutrient analysis. Tesis de Maestría, University of Central Florida, Orlando, FL, USA, 47pp.

Giraldo, A. 2008. Variabilidad espacial de temperatura, salinidad y transparencia en el ambiente pelágico del PNN Gorgona durante septiembre 2007 y marzo 2008. Bol. Cient. CIOH. 26: 157-163.

Giraldo, A., E. Rodríguez-Rubio & F. Zapata. 2008. Condiciones oceanográficas en isla Gorgona, Pacífica oriental tropical de Colombia. Lat. Am. J. Aquat.Res. 36: 121-128.

Giraldo, A., B. Valencia & D.G. Ramírez. 2011. Productividad planctónica y condiciones oceanográficas locales en isla Gorgona durante julio 2006. Bol. Invest. Mar. Cost. 40: 185-201.

Giraldo, A. & Valencia, B. (eds) 2012. Isla Gorgona. Paraíso de biodiversidad y ciencia, 223p. Programa Editorial Universidad del Valle. Cali, Colombia.

Giraldo, A., Valencia, B., Ramírez, D.G. 2014a. Isla Gorgona, enclave estratégico para los esfuerzos de conservación en el Pacífico Oriental Tropical. Rev. Biol. Trop. 62(1): 1-12.

Giraldo, A., B. Valencia, J.D. Acevedo & M. Rivera. 2014b. Fitoplancton y zooplancton en el área marina protegida de Isla Gorgona, Colombia, y su relación

con variables oceanográficas en estaciones lluviosa y seca. Rev. Biol. Trop. 62(1): 117-132.

Glynn, P.W., von Prahl, H., Guhl, F. 1982. Coral reefs of Gorgona Island, Colombia with special references to corallivores and their influence on community structure and reef development. An. Inst. Inv. Mar. Punta Betín.12: 185-214.

Glynn, P.W. 2001. Eastern Pacific coral reefs: new revelations in the twentieth century. Atoll Res Bull 494(8): 119-158.

Godley, B.J., Thompson, D.R., Waldron, S., Furness, R.W., 1998. The trophic status of marine turtles as determined by stable isotope analysis. Mar. Ecol. Prog. Ser. 166: 277-284.

Godley, B.J., Lima, E.H.S.M., Akesson, S., Broderick, A.C., Glen, F., Godfrey, M.H., Luschi, P., Hays, G.C. 2003. Movement patterns of green turtles in Brazilian coastal waters described by satellite tracking and flipper tagging. Mar. Ecol. Prog. Ser. 253: 279-288.

Goshe, L.R., Avens, L., Scharf, F.S., Southwood, A.L. 2010. Estimation of age at maturation and growth of Atlantic green turtles (*Chelonia mydas*) using skeletochronology. Mar. Biol. 157: 1725-1740.

Graham, W.M., F. Pagès & W.M. Hamner. 2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia. 451: 199-212.

Green, D. 1981. The green sea turtle project in Galápagos: past, present and future. Noticias de Galápagos 33:17-20.

Green, D. 1993. Growth rates of wild immature green turtles in the Galápagos Islands, Ecuador. J. Herpetol. 27(3): 338-341.

Guiry, M.D., Guiry, G.M. 2014. AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. http://www.algaebase.org; searched on 13-11-2014.

Hamman, M., Limpus, C.J. & D.W. Owens. 2003. Reproductive cycles of males and females. En: Lutz PL, Musick J, Wyneken J (eds) The biology of sea turtles, Vol. II. CRC Press, Boca Raton, pp.136-161.

Hatase, H., Sato, K., Yamaguchi, M., Takahashi, K. & Tsukamoto, K. 2006. Individual variation in feeding habitat use by adult female green sea turtles (*Chelonia mydas*): are they obligately neritic herbivores? Oecologia 149: 52-64.

Hays, G.C., M.R. Farquhar, P. Luschi, S.L.H. Teo & T.M. Thys. 2009. Vertical niche overlap by two ocean giants with similar diets: Ocean sunfish and leatherback turtles. J. Exp. Mar. Biol. Ecol. 370: 134-143.

Heithaus, M.R., McLash, J.J., Frid, A., Dill, L.M. & Marshall, G.J. 2002. Novel insights into green sea turtle behavior using animal-borne video cameras. J. Mar. Biol. Ass. U.K. 82: 1049-1050.

Heithaus, M.R., Vaudo, J.J., Kreicker, S., Layman, C.A., Krützen, M., Burkholder, D.A., Gastrich, K., Bessey, C., Sarabia, R., Cameron, K., Wirsing, A., Thomson, J.A., Dunphy-Daly, M. 2013. Apparent resource partitioning and trophic structure of large-bodied marine predators in a relatively pristine seagrass ecosystem. Mar. Ecol. Prog. Ser. 481: 225-237.

Heppell, S.S., Snover, M.L., Crowder, L.B. 2003. Sea turtle population ecology. In: Lutz PL, Musick J, Wyneken J, editors. The biology of sea turtles, Vol. II. Boca Raton: CRC Press p. 275-306.

Hereu, C.M., B.E. Lavaniegos, G. Gaxiola-Castro & M.D. Ohman. 2006. Composition and potential grazing impact of salp assemblages off Baja California during the 1997-1999 El Niño and La Niña. Mar. Ecol. Prog. Ser. 318: 123-140.

Hirth, H. 1997. Synopsis of the biological data of the green turtle, *Chelonia mydas* (Linnaeus, 1758). U.S. Fish and Wildlife Service Biological Report, 120 pp.

Hobson, K.A., Alisauskas, R.T., Clark, R.G. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. Condor 95(2) : 388-394.

Hyslop, E.J. 1980. Stomach contents analysis - a review of methods and their application. J. Fish. Biol. 17: 411-429.

Karasov, W.H., Martínez del Río, C. 2007. Physiological Ecology: How animals process energy, nutrients, and toxins. Princeton University Press, Princeton. 744pp.

Koch, V., Brooks, L.B., Nichols, W.J. 2007. Population ecology of the green/black turtle (*Chelonia mydas*) in Bahía Magdalena, Mexico. Mar. Biol. 153: 35-46.

Kremer, P. 2002. Towards an understanding of salp swarm dynamics. ICES publication CM2002. N: 12. Copenhagen, Denmark.

Kubis, S., Chaloupka, M., Ehrhart, L., Bresette, M. 2009. Growth rates of juvenile green turtles *Chelonia mydas* from three ecologically distinct foraging habitats along the east central coast of Florida, USA. Mar. Ecol. Prog. Ser. 389: 257-269.

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

Lavaniegos, B.E. & M.D. Ohman. 2003. Long-term changes in pelagic tunicates of the California Current. Deep-Sea Res. II. 50: 2473-2498.

Lemons, G., Lewison, R., Komoroske, L., Gaos, A., Lai, C.T., Dutton, P., Eguchi, T., LeRoux, R., Seminoff, J.A. 2011. Trophic ecology of green sea turtles in a highly urbanized bay: Insights from stable isotopes and mixing models. J. Exp. Mar. Biol. Ecol. 405: 25-32.

Licandro, P., F. Ibañez & M. Etienne. 2006. Long-term fluctuations (1974-1999) of the salps *Thalia democratica* and *Salpa fusiformis* in the northwestern Mediterranean Sea: Relationships with hydroclimatic variability. Limnol. Oceanog. 51: 1832-1848.

Limpus, C., Chaloupka, M. 1997. Nonparametric regression modelling of green sea turtle growth rates (southern Great Barrier Reef). Mar. Ecol. Prog. Ser. 149: 23-34.

López-Castro, M.C., Koch, V., Mariscal-Loza, A., Nichols, W.J. 2010. Long-term monitoring of black turtles *Chelonia mydas* at coastal foraging areas off the Baja California Peninsula. Endanger. Species Res. 11: 35-45.

López-Mendilaharsu, M., Gardner, S.C., Seminoff, J.A., Riosmena-Rodríguez, R. 2005. Identifying critical foraging habitats of the green turtles (*Chelonia mydas*) along the Pacific coast of the Baja California peninsula, Mexico. Aquatic Conserv.: Mar. Freshw. Ecosyst. 15: 259-269.

López-Mendilaharsu, M., S.C. Gardner, R. Riosmena-Rodríguez & J.A. Seminoff. 2008. Diet selection by immature green turtles (*Chelonia mydas*) at Bahía Magdalena foraging ground in the Pacific Coast of the Baja California Peninsula, México. J. Mar. Biol. Assoc. UK. 88: 641-647.

Madin, L.P, P. Kremer & S. Hacker. 1996. Distribution and vertical migration of salps (Tunicata, Thaliacea) near Bermuda. J.Plankton Res. 18: 747-755.

MacArthur, R.H., Pianka, E.R. 1966. On optimal use of a patchy environment. Amer. Nat. 100 (916): 603-609.

Magalhaes, M. dos S., Barsante Santos, A.J., da Silva, N.B., de Moura, C.E.B. 2012. Anatomy of the digestive tube of sea turtles (Reptilia: Testudines). Zoologia 29(1): 70-76.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., Erickson, W.P. 2002, Resource selection by animals. Statistical Design and Analysis for Field Studies. Kluwer Academic Publishers, Dordrecht, The Netherlands. 221 pp.

Márquez, M.R. 1990. An annotated and illustrated catalogue of sea turtle species known to date. FAO Fish.125(11): 1-81.

Márquez, R. 2000. Las tortugas marinas y nuestro tiempo. Fondo de Cultura Económica, México.

McCormick-Anzola, C.C. 1996. Contribución al conocimiento de la ecología y biología reproductiva de las tortugas marinas en la Isla Gorgona. Tesis de pregrado, Cali: Departamento de Biología, Facultad de Ciencias, Universidad del Valle, 91p.

McDermid, K.J., Stuercke, B. & Balazs, G.H. 2007. Nutritional composition of marine plants in the diet of the green sea turtle (*Chelonia mydas*) in the Hawaiian Islands. Bulletin of Marine Science 81(1): 55-71.

Mendonca, M.T. 1981. Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. Copeia 4: 1013-1023.

Ménard, F., S. Dallot, G. Thomas & J.C. Braconnot. 1994. Temporal fluctuations of two Mediterranean salp populations from 1967 to 1990. Analysis of the influence of environmental variables using a Markov chain model. Mar. Ecol. Prog. Series. 104: 139-152.

Meylan, P.A., Meylan, A.B., Gray, J.A. 2011. The ecology and migrations of sea turtles 8. Tests of the developmental habitat hypothesis. Bull. Am. Mus. Nat. Hist. 357: 3-62.

Montenegro-Silva, B.C., Bernal-González, N.G. & A. Martínez-Guerrero. 1984. Estudio del contenido estomacal de la tortuga marina *Lepidochelys olivacea*, en la costa de Oaxaca, México. Méx. An. Inst. Cienc. del Mar y Limnol. 13:121-32.

Morales-Ramírez, A. 2008. Caracterización cualitativa del zooplancton del Área de Conservación Marina Isla del Coco (ACMIC), Océano Pacífico de Costa Rica. Rev. Biol. Trop. 56: 159-169.

Mortimer, J.A. 1981. The feeding ecology of the West Caribbean green turtle (*Chelonia mydas*) in Nicaragua. Biotropica 13(1): 49-58.

Murillo-Muñoz, M., Peña-Salamanca, E.J. 2014. Algas marinas bentónicas de la Isla Gorgona, costa pacífica colombiana. Rev. Biol. Trop. 62(1): 27-41.

Pagès, F. & J.M. Gili. 1991. Effects of large-scale advective processes on gelatinous zooplankton populations in the northern Benguela ecosystem. Mar. Ecol. Prog. Ser. 75: 205-215.

Parham, J.F. & Zug, G.R. 1996. *Chelonia agassizii* - valid or not? Marine Turtle Newsletter 72: 2-5.

Parker, D.M., Dutton, P.H., Balazs, G.H. 2011. Oceanic diet and distribution of genotypes for the green turtle, *Chelonia mydas*, in the central North Pacific. Pac. Sci. 65(4): 419-431.

Patricio, R., Diez, C.E. & van Dam R.P. 2014. Spatial and temporal variability of immature green turtle abundance and somatic growth in Puerto Rico. Endang Species Res 23: 51-62.

Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X., Ward, E.J. 2014. Best practices for use of stable isotope mixing models in food web studies. Canadian Journal of Zoology 92(10): 823-835.

Pilcher, N. 2010. Population structure and growth of immature green turtles at Mantanani, Sabah, Malaysia. J Herpetol 44(1): 168-171.

Poloczanska, E.S., Limpus, C.J. & Hays, G.C. 2009. Vulnerability of marine turtles to climate change. Advances in Marine Biology 56: 152-211.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83(3): 703-718.

Potter, I.F., B. Galuardi & W.H. Howell. 2011. Horizontal movement of the ocean sunfish, *Mola mola*, in the northwest Atlantic. Mar. Biol. 158: 531-540.

Pritchard, P.C.H. 1971. Galápagos sea turtles: preliminary findings. J. Herpetol. 5(1/2):1-9.

Pritchard, P.C.H. 1998. Evolution, Phylogeny, and Current Status. In: Lutz PL and Musick JA (eds). The Biology of Sea Turtles. Boca Raton: CRC Press, pp. 1- 28.

Read, M.A., Limpus, C.J. 2002. The green turtle, *Chelonia mydas*, in Queensland: feeding ecology of immature turtles in Moreton Bay, Southeastern Queensland. Mem. Queensl. Mus. 48(1): 207-214.

Rees, A.F., Margaritoulis, D., Newman, R., Riggall, T.E., Tsaros, P., Zbinden, J.A., Godley, B.J. 2013. Ecology of loggerhead marine turtles *Caretta caretta* in a neritic foraging habitat: movements, sex ratios and growth rates. Mar. Biol. 160: 519-529.

Reich, K.J., Bjorndal, K.A., Bolton, A.B. 2007. The 'lost years' of green turtles: using stable isotopes to study cryptic lifestages. Biol. Letters 3: 712-714.

Reich, K.J., Bjorndal, K.A., Martínez del Río, C. 2008. Effects of growth and tissue type on the kinetics of ^{13}C and ^{15}N incorporation in a rapidly growing ectotherm. Oecologia 155: 651-663.

Reich, K.J., Seminoff, J.A. 2010. Standardizing sample collection, preparation, and analysis of stable isotopes of carbon and nitrogen in sea turtle research. Second Workshop in Stable Isotope Techniques in Sea Turtle Research, 30th Annual Symposium on Sea Turtle Biology and Conservation in Goa, India, 27-29 April.

Rodríguez Barón, J.M. 2010. Afinidad trófica a zonas de alimentación de la tortuga verde (*Chelonia mydas*) en la costa occidental de Baja California Sur, México. Tesis de Maestría, Centro Interdisciplinario de Ciencias Marinas, México, 92p.

Rodríguez-Barón, J.M., Riosmena-Rodríguez, R., Seminoff, J.A., Hernández-Carmona, G. 2011. *Chelonia mydas agassizii* diet. Herpetol. Rev. 42(2): 264.

Rodríguez-Rubio, E., W. Schneider, & R. Abarca del Río. 2003. On the seasonal circulation within the Panama Bight derived from satellite observations of wind, altimetry and sea surface temperature. Geophys. Res. Lett. 30: 1410-1413.

Sampson, L., Giraldo, A. 2014. Annual abundance of salps and doliolids (Tunicata) around Gorgona Island (Colombian Pacific), and their importance as potential food for green sea turtles. Rev. Biol. Trop. 62(1):149-159.

Sampson, L., Payán, L.F., Amorocho, D.F., Seminoff, J.A., Giraldo, A. 2014. Intraspecific variation of the green turtle, *Chelonia mydas* (Cheloniidae), in the foraging area of Gorgona Natural National Park (Colombian Pacific). Acta. Biol. Colomb. 19(3): 461-470.

Sampson, L., Giraldo, A., Payán, L.F., Amorocho, D.F., Eguchi, T., Seminoff, J.A., in press. Somatic growth of juvenile green turtle (*Chelonia mydas*) morphotypes in the Colombian Pacific. Mar. Biol.

Santillán-Corrales LA (2008) Composición del contenido estomacal de Chelonia mydas agassizzi en Bahía de Sechura. In: Kelez S, van Oordt F, de Paz N, Forsberg K (eds) Libro de resúmenes II Simposio de tortugas marinas en el Pacífic sur oriental, Lima, Peru, p. 16.

Schnetter, R., Bula-Meyer, G. 1982. Algas marinas del litoral pacífico de Colombia. Gartner Verlag, Germany, 282 pp.

Seminoff, J.A., Resendiz, A., Nichols, W.J. 2002a. Diet of East Pacific Green Turtles (*Chelonia mydas*) in the Central Gulf of California, Mexico. J. Herpetol. 36(3): 447-453.

Seminoff, J.A., Resendiz, A., Nichols, W.J., Jones, T.T. 2002b. Growth rates of wild green turtles (*Chelonia mydas*) at a temperate foraging area in the Gulf of California, México. Copeia 3: 610-617.

Seminoff, J.A., Jones, T.T., Resendiz, A., Nichols, W.J., Chaloupka, M.Y. 2003. Monitoring green turtles (*Chelonia mydas*) at a coastal foraging area in Baja California, Mexico: multiple indices to describe population status. J Mar Biol Assoc UK. 83: 1355-1362.

Seminoff, J.A. 2004a. *Chelonia mydas*. The IUCN Red List of Threatened Species. Version 2014.3. <www.iucnredlist.org>. Downloaded on 12 January 2011.

Seminoff, J.A. 2004b. Sea Turtles, Red Listing, and the Need for Regional Assessments. Marine Turtle Newsletter 106:4-6.

Seminoff, J.A., Jones, T.T., Eguchi, T., Jones, D.R., Dutton, P.H. 2006. Stable isotope discrimination ($\delta^{13}C$ and $\delta^{15}N$) between soft tissues of the green sea turtle *Chelonia mydas* and its diet. Mar. Ecol. Prog. Ser. 308: 271-278.

Seminoff, J.A. & Shanker, K. 2008. Marine turtles and IUCN Red Listing: a review of the process, the pitfalls, and novel assessment approaches. Journal of Experimental Marine Biology and Ecology 356(1-2): 52-68.

Seminoff, J.A., Alfaro Shigueto, J., Amorocho, D., Arauz, R., Baquero, A., Chacón, D., *et al*. 2012a. Biology and conservation of sea turtles in the eastern Pacific Ocean: A general overview. En: Seminoff JA and Wallace BP (eds). Sea Turtles of the Eastern Pacific Ocean: research advances, conservation challenges and signs of success. Tucson: University of Arizona Press p. 11-38.

Seminoff, J.A., Benson, S.R., Arthur, K.E., Eguchi, T., Dutton, P.H., Tapilatu, R.F., Popp, B.N. 2012b. Stable isotope tracking of endangered sea turtles: validation with satellite telemetry and δ15N analysis of amino acids. PLoS ONE 7:e37403.

Short, F., Carruthers, T., Dennison, W., Waycott, M. 2007. Global seagrass distribution and diversity: A bioregional model. J. Exp. Mar. Biol. Ecol. 350: 3-20.

Sotka, E.E., Wares, J.P. & Hay, M.E. 2003. Geographic and genetic variation in feeding preference for chemically defended seaweeds. Evolution 57(10): 2262-2276.

Soto, P.A., S.L. Sánchez. & C. Fernández. E. 2001. Comunidades planctónicas marinas, p. 93-105. *In*: L.M. Barrios. & M.L. Victoria (eds.). Gorgona Marina: Contribución al conocimiento de una isla única, Serie Publicaciones Especiales No 7, Instituto Investigaciones Marinas y Costeras – INVEMAR. Santa Marta, Colombia.

Stamps, J.A., Mangel, M. & Phillips, J.A. 1998. A new look at relationships between size at maturity and asymptotic size. American Naturalist 152(3): 470-479.

Stock, B.C., Semmens, B.X. 2013. MixSIAR GUI User Manual, version 1.0. Available from http://conserver.iugo-cafe.org/user/brice.semmens/MixSIAR.

Stowasser, G. Atkinson, A., McGill, R.A.R., Phillips, R.A, Collins, M.A. & Pond, D.W. 2012. Food web dynamics in the Scotia Sea in summer: A stable isotope study. Deep-Sea Research II 59-60: 208-221.

Taylor, W.R. 1945. Pacific marine algae of the Allan Hancock expeditions to the Galapagos Islands. The University of Southern California, Vol. 12, Los Angeles, USA. 556 pp.

Tolentino-Pablico, G., Bailly, N., Froese, R., Elloran, C. 2008. Seaweeds preferred by herbivorous fishes. Journal of Applied Phycology 20: 933-938.

UNEP-WCMC, Short, F.T. 2005. Global distribution of seagrasses (version 2). Cambridge, U.K.: UNEP World Conservation Monitoring Centre. http://data.unep-wcmc.org/datasets/7, consultado 3 feb 2015.

Vander Zanden, H.B., Bjorndal, K.A., Mustin, W., Ponciano, J.M., Bolten, A.B. 2012. Inherent variation in stable isotope values and discrimination factors in two life stages of green turtles. Physiol. Biochem. Zool. 85(5): 431-441.

Velez-Zuazo, X., Quiñones, J., Pacheco, A.S., Klinge, L., Paredes, E., Quispe, S., Kelez, S. 2014. Fast growing, healthy and resident green turtles (*Chelonia mydas*) at two neritic sites in the central and northern coast of Peru: implications for conservation. PLoS ONE 9(11): e113068.

Wallace, B.P., DiMatteo, A.D., Hurley, B.J., Finkbeiner, E.M., Bolten, A.B., Chaloupka, M.Y., *et al*. 2010. Regional Management Units for marine turtles: A novel framework for prioritizing conservation and research across multiple scales. PLoS ONE 5(12): e15465.

Werner, E.E., Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15: 393-425.

Wibbels, T. 2003. Critical approaches to sex determination in sea turtles. En: Lutz PL, Musick J, Wyneken J (eds) The biology of sea turtles, Vol. II. CRC Press, Boca Raton, pp. 103-134.

Williams, N.C., Bjorndal, K.A., Lamont, M.M., Carthy, R.R. 2014. Winter diets of immature green turtles (*Chelonia mydas*) on a Northern feeding ground: Integrating stomach contents and stable isotope analyses. Estuar. Coast. 37: 986-994.

Worm, B., H.K. Lotze & R.A. Myers. 2003. Predator diversity hotspots in the blue ocean. PNAS 100: 9884-9888.

Zapata, F.A. 2001. Ecología de peces arrecifales en Gorgona: composición, abundancia, diversidad e historia de vida temprana, p. 111-122. In: Barrios, L.M. & López-Victoria, M. (eds). Gorgona marina: Contribución al conocimiento de una isla única, Serie Publicaciones Especiales No 7, Instituto Investigaciones Marinas y Costeras – INVEMAR, Santa Marta, Colombia.

Zapata, F.A. 2001. Formaciones coralinas de isla Gorgona. In: Barrios LM, López-Victoria M (eds) Gorgona marina: contribución al conocimiento de una isla única. INVEMAR, Ser. Pub. Esp. 7, Santa Marta, pp 27-40.

Zapata, F.A., Vargas-Ángel, B., Garzón-Ferreira, J. 2001. Salud y conservación de las comunidades coralinas. In: Barrios LM, López-Victoria M, editors. Gorgona marina: contribución al conocimiento de una isla única. Santa Marta: INVEMAR, Ser. Pub. Esp. 7, p. 41-50.

Zapata, F.A., Vargas-Ángel, B. 2003. Corals and coral reefs of the Pacific coast of Colombia. In: Cortes J (ed) Coral reefs of Latin America. Elsevier Science, Amsterdam, pp 419-447.

Zapata, F.A., A. Rodríguez-Ramírez, C. Caro-Zambrano & J. Garzón-Ferreira. 2010. Mid-term coral-algal dynamics and conservation status of a Gorgona Island (Tropical Eastern Pacific) coral reef. Rev. Biol. Trop. 58: 81-94.

Zárate, P. 2004. Informe final proyecto anidación de la tortuga verde, Chelonia mydas, durante la temporada de anidación 2002-2003. Fundación Charles Darwin. Presentado al National Marine Fisheries Service y Parque Nacional Galápagos, 105 p.

Zug, G.R., Glor, R.E. 1998. Estimates of age and growth in a population of green sea turtles *Chelonia mydas* from the Indian River lagoon system, Florida: a skeletochronological analysis. Can. J. Zool. 76: 1497–1506.

Zug, G.R., G.H. Balazs, J.A. Wetherall, D.M. Parker & S.K.K. Murakawa. 2002. Age and *growth* of Hawaiian green seaturtles (*Chelonia mydas*): an analysis based on skeletochronology. Fish. Bull. 100: 117-127.

ANEXOS

Lista de tortugas muestreadas en 2012

Número de marca	LCC	LRC	ACC	ARC	LC	AC	LP	AP	LPC	LCCO	LCOCA	ALTURA	PESO
PR692	52.8	47.8	52	39.9	12	17	41	39	7	4	1	21	18.1
PR693	66.6	61.8	66.5	49.5	15	22	53.9	45	8.8	38	NA	23.5	36
PR694	61.3	55.2	60.7	45.2	14	20.2	48.3	42	7.8	3.4	NA	22	26.5
PR695	53.2	47.9	52.7	41.1	13	17.3	43	38.9	5.8	3.5	NA	17.4	19
PR479	53.2	47.1	50.9	41	12.3	18	42	36.2	6.5	3.1	NA	17.1	16.1
PR678	69.3	63.1	66.7	53.9	15.5	22.8	56.5	47.7	7.5	4.5	NA	23.2	36.1
PR700	71.9	66.1	70.6	54.9	16.5	26.6	56.5	52	11	6	2	25.4	48
SIN MARCA	71.9	65.1	70.2	52.8	16	24.4	58.2	51.6	12	6	4	25.8	47
GD721	59.5	57.7	61	38.3	13.8	19.1	47.3	43	9.5	3.5	NA	22.1	29
GD722	55.8	52.2	55.8	47	12	18.3	45.6	42	6	3.6	0.7	20.5	21.5
GD723	58.7	55.5	57.7	43.5	13	19.7	47	39.5	8.5	3.2	NA	25.5	23.6
GD724	66.6	62.9	61.8	49.4	14.3	20.7	51.5	44.5	9.5	4	NA	24	33
GD725	59	56	59	44.9	13	18.4	47.7	39.7	8.3	4	na	26	23.5
GD726	61.2	56.8	68.5	47.9	13.5	21	51.7	44.6	6	3.4	1	22.9	29
GD727	67.5	62.2	63	47.1	15	22.8	52.7	34.4	9	3.7	NA	24.8	34
GD728	62.2	57.8	59.9	49.1	11.8	20.8	47.3	43	7.5	3.6	NA	25.2	29
GD729	65.7	61.1	62	50.5	13.9	21	50.2	44	11	4.8	1	23.1	32
GD730	48.7	44.7	46.8	38	11	17	39.6	36	6.5	2.8	NA	19.1	16
GD731	54.7	50.9	53.4	44.2	13	18.7	42.9	41.4	7	3.2	NA	22	22
PR336	56.5	52.3	55	44.4	13	18.3	45.6	41.2	7	3.5	0.5	25	23
GD735	56	53	55.2	44.6	12.5	18	45	40.1	7.5	3.2	NA	22	22
GD733	56.6	53.5	56.2	45.5	12	18.9	35.5	39.6	7	3.2	NA	22	22
GD734	54.6	51.9	55.2	34.4	13.2	19.5	44.6	39.8	10	3.7	3.8	20.4	23
GD736	61.8	58	68.6	45.1	13.2	19.2	50.1	40	5.5	2.8	NA	21	25
GD737	54.9	52.3	53.8	43.1	12.6	18.1	44.5	39.9	6.6	3.9	1.8	20.5	21
GD738	69.5	66.6	68	54.9	15.5	21.9	54.8	48.9	9.5	4.5	NA	23	37.5
GD739	63	57.9	65.7	49	15.3	20.7	49.5	43	7.5	4.4	NA	24.8	32
GD740	66.7	61.8	65.2	50.5	14.7	21.3	51.8	45.9	12	5.6	4.1	25.2	34
GD786	65.5	61.5	62.8	54.8	15	12	52.5	49	9.5	4.8	1.3	21.8	32
GD787	69.2	63.1	62.8	49	14.7	22.2	54	44.9	11	5.5	5	23	33
GD788	51.9	47.5	51	38.5	11.5	17	41.1	34.2	7	3	1.8	15.4	14
GD789	62	57.5	59.2	48.4	13.7	19.5	47.5	42.8	7.5	4.5	NA	19.5	23.5
GD790	59.6	54.9	58.8	47.6	13	19.5	45.4	41.8	7.5	4	NA	18.2	20.05
GD791	69	64	62	50.7	15.5	22	54.4	44.5	12	5.9	6	22.5	33
GD792	55	50.4	53.8	48.4	12.6	18.5	42.7	37.8	6.5	3	NA	17	17
GD793	60.5	55	58.5	46.1	13.3	19.2	46.9	42	7.5	3.9	NA	19.1	22
GD794	60.1	54.6	61	46.9	13	19	46.6	40.3	7.5	4	NA	24	23
GD795	71	67	70.1	52	15.6	23	55.8	47.5	26	9	23.5	21.8	41
GD796	63	59	61	48.1	13.7	20	50.9	43.5	6.5	3.7	NA	20.9	25
GD797	56	52.8	54.5	43.4	13.4	19.6	46.5	38	7.6	3.7	0.8	16.8	19
GD798	57.6	53.4	58.7	45.9	13	18.5	46	39.3	7	3.1	NA	18.2	21
GD799	64.6	62	62.5	52	14.5	21.4	52	47.1	8.5	5.6	0.7	23.5	32.5
GD800	49	44	47.6	39.8	11.4	17	40.1	35.3	5.5	3	NA	15	12
26	56.2	53	56	41	12.2	19	43.4	39	7.5	3.5	NA	15.2	18
27	64.8	59.9	63.7	52.2	13.5	21	50.5	43.4	11.5	4	2	22.5	27
28	59	54	56.8	46.8	13	20	45.7	41	9.5	4	2	19.8	22
29	60	56	57.4	45	12.5	18.3	46.4	40.9	8.8	4.2	1.1	19.4	23.5
30	45.8	40.9	44.1	36.5	10.5	14.9	37.7	33.2	5.4	2.9	NA	16	11
31	55.5	48.5	55.2	40.8	12.5	18.4	45.8	38.1	7.2	3.6	NA	21.5	20
32	51.1	47	49.6	44.2	11.9	17.5	42.5	40.2	7.4	3.5	2	21.5	19
32	63.9	61.2	62	52	14	19.9	52.9	44.2	6.6	3.6	NA	24.5	31
33	72.5	68.9	71.3	56.7	15.3	22.8	58.1	48.5	12.7	5.1	2.4	25.2	41.5
34	65.1	58.2	60.7	43.5	14.3	21.5	52.2	42.9	8.8	4.3	NA	22.4	28
36	65.6	64	68.4	52.5	15.7	22.2	54.1	46.8	13.5	5.5	7.5	25	34
37	66.5	61.2	65.2	50.5	15.4	22.1	51.8	45.8	13	5.6	4.2	20.5	35.5
38	59.6	55.6	59	50.7	13.5	19.2	46.2	42.6	8	4.2	NA	20.6	23
39	61.5	58.7	58.1	46.9	13.5	19.5	47.9	40.5	8.4	3.3	NA	20.5	23
40	52.9	48.5	54.2	44.7	12	17	43	39.9	7.1	3.6	NA	22.2	18.2
GD747	70	65.8	65	52.4	15.2	22	56.3	49.2	11	5.2	4.5	22.8	39.5
PNG110	77	73.2	69.4	54	15.5	24	59.6	48.1	28.5	9	20	35.2	44
PNG111	67.8	64.2	61	60.3	14.2	21.3	56.4	48.5	10.2	5	3.5	24.8	35
PNG112	58	55.1	59	44.9	13.4	20.9	49.1	39	7.9	3.7	NA	19.5	21.5
PNG113	69.4	65.5	68.2	52.9	15.3	22.6	52	46.3	10.5	4.2	NA	23.9	36
NL349, NL350	55.6	53.1	50.5	42.9	12.2	18.5	45.3	39	7	4.1	1.5	19.2	19.5
PNG114	68.6	64.9	63.9	51	15	21	51.3	44.4	9.5	4.4	NA	22.1	32
PNG116	72.7	69.4	71.4	56.1	14.5	23.8	55	50.9	25	8.7	21.2	23.2	48.5
PNG117	66.5	61.9	67.6	52.1	15.3	23	51.8	46.1	7.5	3.5	NA	23	35
PNG118	65.1	61.9	62.3	51.2	14.8	22	51.8	46.8	10.2	4.3	NA	22.9	30
PNG119	66.8	62.2	67.6	52.4	15.2	21.5	51.6	45.4	9	4.1	NA	21.6	31.5
PNG120	69.5	66	68.4	54.9	15.8	22	56.2	49.3	9.5	5.6	1	24.2	38
PNG121	75.6	71.5	73.7	57.9	16.4	23.6	60.2	52.4	10.3	6.2	NA	27.3	52
PNG122	67	64	65.7	52.9	14.2	22.1	51.7	47.5	20	9.7	16.2	21.2	34
PNG123	72	68.2	71.5	54.5	15.5	23	56	47.5	10	5.3	NA	26.8	42
PNG124	68.2	64.2	66.6	51	15.4	22	53.5	46.4	9	4.9	NA	24.4	34
PNG125	71.2	68	67.5	64.9	14.8	22.2	55.6	48.5	9.5	4	NA	22.1	39
PNG126	51.3	47.6	51.3	41.4	12	16.8	41	37.5	6	3.7	NA	17.3	14.5
PNG127	61	57.9	62.3	50.9	12.5	19.8	48	44.8	8.9	3.7	NA	20.1	31

Abreviaciones: LCC = largo curvo de caparazón; LRC = largo recto de caparazón; ACC = ancho curvo de caparazón; ARC = ancho recto de caparazón; LC = largo de cabeza; AC = ancho de cabeza, LP = largo de plastrón; AP = ancho de plastrón; LPC = largo plastrón-cloaca; LCCO = largo cloaca-cola; LCOCA = largo cola-caparazón

Lista de alimentos muestreados para análisis isotópico en 2012

Ítem	Nov	Feb	Mar	Abr	Ago	Oct	Dic
Algas							
Chlorophyta							
Bryopsis sp.						X	
Caulerpa racemosa					X		
Cladophora sp.		X		X		X	
Polyphysa parvula	X						
Phaeophyta							
Dictyota humifusa				X	X	X	X
Dictyota adnata	X	X		X	X		
Lobophora variegata				X	X		X
Rhodophyta							
Gelidium sp.	X				X		
Hypnea pannosa		X		X			
Jania sp.	X				X		X
Tapete algal	X			X			
Plantas acuáticas							
Fruto de mangle	X	X		X			
Buchón de agua	X						
Cianobacteria							
Phormidium sp.		X				X	X
Plantas terrestres							
Enredadera					X		
Hoja de palma					X		
Hoja de *Hibiscus*					X		
Ficus sp. 1					X		
Ficus sp. 2					X		
Plancton							
Fitoplancton				X		X	
Zooplancton			X		X	X	
Gelatinososo			X				
Tunicados	X		X				
Huevos de invertebrado				X			
Cnidario		X					