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ARE COASTAL UPWELLINGS AFFECTING THE SPATIAL ECOLOGY OF
JUVENILE HAWKSBILL SEA TURTLES? INSIGHTS FROM A SMALL BAY IN
THE EASTERN TROPICAL PACIFIC

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DEDICATORIA

A mis padres, quienes han dado gran parte de sí por sus hijos y por vernos alcanzar nuestras metas.

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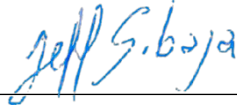
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RESUMEN

Comprender cómo se mueven los animales dentro y entre distintos hábitats y los factores que afectan estos movimientos es crucial para la gestión espacial de las especies en peligro de extinción. Este estudio analizó la abundancia y ecología espacial de las tortugas carey (*Eretmochelys imbricata*) en el Área Marina de Manejo Bahía Santa Elena (AMMBSE), en el Pacífico norte de Costa Rica. El AMMBSE está compuesta por las bahías Matapalito y Santa Elena, en las cuales existe una gran diversidad de hábitats que han sido identificados como importantes para la alimentación de varias especies de tortugas marinas. Además, el AMMBSE es influenciada por un afloramiento costero estacional, con condiciones ambientales marcadas entre las temporadas de afloramiento (diciembre a mayo) y no afloramiento (junio a noviembre). Este estudio investigó cambios estacionales en la abundancia de tortugas carey en la bahía Matapalito, y además determinó la residencia y conectividad espacial dentro del AMMBSE. Para esto, se realizaron censos de tortugas marinas en la Bahía Matapalito entre el 2012 y el 2023. Además, se monitoreó el movimiento y la residencia de tortugas carey en el AMMBSE utilizando telemetría acústica pasiva. Se calculó el índice de residencia en cada área de monitoreo (Bahía Matapalito, Bahía Santa Elena, y toda el AMMBSE) y se determinaron los movimientos entre los hábitats disponibles en Matapalito y las zonas internas y externas de bahía Santa Elena a partir de las detecciones diarias. Se capturaron en promedio 11.2 ± 11.6 tortugas carey por año, en su mayoría identificadas como juveniles. Hubo diferencias significativas en las capturas entre años, pero no se detectaron diferencias significativas en la abundancia de tortugas Carey entre estaciones (afloramiento y no afloramiento). La residencia fue variable entre individuos, pero similar entre las bahías de Matapalito y Santa Elena. En promedio, las tortugas fueron altamente residentes en el AMMBSE (IR promedio \pm DS = 0.6 ± 0.3). La conectividad del hábitat mostró que 85% de los individuos se movieron entre diferentes hábitats. Estos hallazgos resaltan la importancia de esta región para las especies y señalan que la conectividad del hábitat es crucial para el correcto manejo espacial para la conservación de las tortugas marinas.

ABSTRACT

Understanding how animals move within and between different habitats, and what drivers affect these movements, is crucial for spatial management of endangered species. This study looked at the abundance and spatial ecology of Hawksbill sea turtles (*Eretmochelys imbricata*) in Santa Elena Bay Marine Management Area (SEBMMA), in the north Pacific coast of Costa Rica. SEBMMA is composed of Matapalito and Santa Elena bays, where a great diversity of habitats identified as important for feeding of different sea turtle species are available. The SEBMMA is also influenced by seasonal coastal upwelling, with marked environmental conditions between upwelling (December to May) and non-upwelling (June to November) seasons. We studied the seasonal changes in the abundance of hawksbill sea turtles in Matapalito Bay, and determined their residency, habitat use and spatial connectivity withing SEBMMA. We conducted sea turtle surveys in Matapalito Bay between 2012 and 2023 to assess total and seasonal abundance of hawksbill sea turtles in the Bay. Secondly, we used passive acoustic telemetry to monitor the movement and residency of hawksbill sea turtles in the SEBMMA. We calculated the residency index in each area monitored (Matapalito Bay, Santa Elena Bay, and the entire SEBMMA), and to determine movements between the available habitats in Matapalito Bay, and the inner and outer zones of Santa Elena Bay using daily detections. We captured an average of 11.2 ± 11.6 hawksbill turtles per year, most of them juveniles. There was a significant difference in the number of captures between years, but there was no significant difference between the seasons (upwelling and the non-upwelling). Residency was variable between individuals, but similar between Matapalito and Santa Elena Bays. On average, the turtles were highly resident to the SEBMMA (RI mean \pm SD = 0.6 ± 0.3). Habitat connectivity showed that 85% of the individuals moved between different habitats. These findings highlight the importance of this region for species and point to habitat connectivity being crucial for the correct spatial management for the conservation of sea turtles.

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LISTA DE ABREVIATURAS

AMMBSE	Área Marina de Manejo Bahía Santa Elena
IR	Índice de Residencia
PTO	Pacífico Oriental Tropical
ENOS	El Niño Oscilación Sur
BSEMMA	Santa Elena Bay Marina Management Area
RI	Residency Index
ETP	Eastern Tropical Pacific
CCL	Curved Carapace Length
CCW	Curved Carapace Width
ENSO	El Niño Southern Oscillation

INTRODUCCIÓN

Entender los factores que influyen los patrones de movimiento y uso de hábitat de los animales es crucial para implementar estrategias de manejo efectivamente, en especial para las especies altamente amenazadas (Allen & Singh, 2016). Los animales utilizan hábitats que son críticos para la sobrevivencia sus poblaciones (Hall et al., 1997; Rosenfeld & Hatfield, 2006), por lo que requieren de un manejo especial o protección (Camaclang et al., 2014). Su movimiento entre y dentro de estos hábitats y ecosistemas se dan en respuesta a factores biológicos, ecológicos y ambientales (Joo et al., 2022). Estas respuestas se han registrado para diferentes grupos animales, por ejemplo, cambios en distribución espacial y de profundidad en el océano en respuesta al cambio climático (Poloczanska et al., 2016). También Giffin et al. (2019) reportaron que peces arrecifales están cambiando el uso de hábitat entre estadíos, y las tortugas cabezonas (*Caretta caretta*) han mostrado que la competencia intraespecífica puede afectar las áreas que usan como refugio o para alimentarse (Dujon et al., 2018). Estos ejemplos enfatizan la importancia de entender cómo se mueven los animales entre hábitats en respuesta a diferentes factores, y cómo conectan estos hábitats a pequeñas y grandes escalas espaciales y temporales (Ogburn et al., 2017). Sin embargo, estudiar el movimiento animal es retardador, especialmente para especies marinas con grandes áreas de distribución y ciclos de vida complejos como las tortugas marinas.

La tortuga carey (*Eretmochelys imbricata*) es una especie críticamente amenazada con distribución global en aguas tropicales y subtropicales (Mortimer & Donnelly, 2008). La subpoblación del Océano Pacífico Oriental tropical (PTO) es una de las más amenazadas y menos estudiadas (Gaos et al., 2010). Esta subpoblación es mayormente afectada por la pesca incidental con técnicas como el trasmallo (Liles et al., 2017) y la pesca con explosivos (Liles et al., 2011). Sin embargo, otras amenazas como el saqueo, la pérdida y la degradación de su hábitat natural también han sido identificadas como factores importantes en el declive poblacional (Gaos et al., 2010).

En el PTO, las tortugas carey utilizan una amplia variedad de hábitats disponibles que difieren de los de otras subpoblaciones. Por ejemplo, los manglares y estuarios sobresalen como áreas de alimentación y reproducción importantes (Gaos, Lewison, Yañez, et al., 2012); sin embargo, una porción de las carey de esta subpoblación también utiliza arrecifes rocosos y de coral para alimentarse y playas arenosas para anidar (Martínez-Estévez et al., 2023). Esta plasticidad en el uso de distintos hábitats se refleja en las adaptaciones de las tortugas carey en el PTO a condiciones de la región al (i) usar diferentes hábitats disponibles para alimentarse y reproducirse, (ii) explotar una amplia variedad de presas (e.g. algas e invertebrados como esponjas, tunicados, caracoles y gusanos (Carrión-Cortez et al., 2013; Méndez-Salgado et al., 2020; Reynolds et al., 2023), y (iii) al restringir sus movimientos a ambientes más protegidos, como manglares y arrecifes coralinos (Gaos, Lewison, Yañez, et al., 2012). Sin embargo, información de cuándo y dónde se mueven las tortugas carey en escalas temporales y espaciales relativamente pequeñas, y cómo estas conectan diferentes hábitats costeros sigue siendo limitado, particularmente para individuos pequeños que aún no han alcanzado la madurez sexual. Por lo tanto, estudiar el movimiento y uso de diferentes hábitats costeros de las tortugas carey es crucial para realizar una gestión espacial efectiva, fortalecer las estrategias de conservación regionales, y para promover la recuperación de su población en el PTO (Gaos, Lewison, Wallace, et al., 2012; Llamas et al., 2017)

Los estudios de ecología de movimiento se han convertido de gran importancia para la planificación de manejo y la conservación (Allen & Singh, 2016). El uso de tecnologías de telemetría y las métricas de movimiento desarrolladas, como la residencia (el tiempo que un animal pasa en un área determinada) o el rango de hogar (el área donde los animales viven y desarrollan sus actividades), entre otras, ha dado forma al conocimiento de la ecología del movimiento de animales terrestres y marinos durante la última década (Allen & Singh, 2016; Joo et al., 2022). Para las tortugas carey, estudios previos han mostrado pueden pasar de meses a años en áreas de menos de 1 km² (Berube et al., 2012; Blumenthal et al., 2009; Hart et al., 2013), caracterizándolas de una residencia alta a sus áreas de alimentación y refugio. Sin embargo, algunos estudios han mostrado casos de tortugas que presentan largas

distancias de desplazamiento (por ejemplo, 6.8-39.8 km en Belice Chevis et al., 2017) y grandes rangos de hogar (31.2 ha \pm 32.6 en Belice, Scales et al., 2011). En estos casos, se han sugerido diferentes comportamientos de movimiento para las carey, según el tiempo que pasan en diferentes áreas y cómo se mueven entre ellas, tales como alta residencia (los individuos que pasan más de 60% del tiempo en la misma área), residencia secuencial (los individuos que pasan semanas a meses en un área antes de moverse a otra) y comportamiento transitivo (los individuos que pasan solo unos días en un área antes de moverse a otra y repetir el comportamiento) (Chevis et al., 2017). Para la subpoblación de PTO, las tortugas carey también han mostrado alta fidelidad a áreas pequeñas (Llamas et al., 2017; Martínez-Estevez et al., 2021), además de una divergencia ontogenética en su preferencia de hábitat, ya que las carey que utilizan los ambientes de manglar para alimentarse y reproducirse tienen poco intercambio genético con aquellas que lo hacen en ambientes arrecifales (Gaos et al., 2016). Investigaciones recientes en diferentes áreas de alimentación a lo largo del PTO respaldan esto, al encontrar un alto nivel de fidelidad de los individuos a un hábitat específico, ya sea estuarino, arrecifal o arenoso (i.e. Baja California, Martínez-Estevez et al., 2021, Costa Rica, Carrión-Cortez et al., 2013).

El PTO es influenciado por eventos como El Niño Oscilación Sur (ENOS) y varios afloramientos costeros que afectan las condiciones ambientales de áreas costeras (Fiedler & Lavín, 2017; Lavín et al., 2006). Específicamente los afloramientos costeros se dan cuando los vientos alisios del este causan el desplazamiento de las aguas superficiales, con lo cual surgen aguas profundas frías y ricas en nutrientes, que reducen drásticamente la temperatura y la concentración de oxígeno del agua (Kämpf & Chapman, 2016). En el PTO se pueden encontrar tres áreas principales donde se dan afloramientos costeros estacionales, ubicados en México (afloramiento de Tehuantepec), Costa Rica (afloramiento de Papagayo) y Panamá (afloramiento del golfo de Panamá) (Pennington et al., 2006). A pesar de que estas tres áreas son utilizadas por tortugas marinas, aún no está claro si estos eventos afectan sus patrones de movimiento y distribución, o si benefician a estas especies durante alguna de sus etapas de vida.

El efecto de los afloramientos costeros en las tortugas marinas ha sido estudiado en otras regiones. Por ejemplo, en la costa Pacífica de Sur América, donde el afloramiento de Humboldt afecta la costa de Chile y Perú a lo largo del año, se han estudiado las agregaciones de tortuga verde (*Chelonia mydas*) y se han comparado a otras en zonas de ecotono. Estos estudios han encontrado que, en general, los individuos de tallas pequeñas son más abundantes que los adultos en las áreas de afloramiento (Quiñones et al., 2022; Velez-Zuazo et al., 2014). Además, en áreas de afloramiento, las tortugas verde tuvieron una mayor tasa de crecimiento (Velez-Zuazo et al., 2014) y los componentes de su dieta también fueron distintos (Quiñones et al., 2022). Sin embargo, no está claro si las diferencias entre las tasas de crecimiento y la dieta de las tortugas marinas se pueden atribuir a la etapa de vida en la que se encuentran (adultos versus juveniles) o a las condiciones del afloramiento. Aunque estos estudios establecen una base importante para la ecología de las tortugas marinas en áreas de afloramiento, difícilmente pueden ser extrapolados a las condiciones que generan los afloramientos costeros en el PTO, ya que son eventos estacionales e influyen ecosistemas tropicales, donde los cambios provocados por la surgencia son más drásticos.

Costa Rica cuenta con seis áreas principales donde se ha registrado un significativo número de tortugas carey (Carrión-Cortez et al., 2013; Chacón-Chaverri et al., 2016; Heidemeyer et al., 2015). Estos sitios son dominados por hábitats de arrecifes rocosas y de coral, pero además tienen otros hábitats disponibles (e.g., manglares, bahías y estuarios) que las tortugas marinas pueden acceder (Carrión-Cortez et al., 2013; Chacón-Chaverri et al., 2016). La bahía Matapalito (Matapalito de ahora en adelante) es uno de estos sitios de alimentación importantes para las tortugas carey en el Pacífico norte de Costa Rica. Se ha sugerido que Matapalito cumple un rol importante como área de alimentación para tortugas juveniles, resaltando su importancia para la conservación de esta especie en el PTO (Heidemeyer et al., 2015). Matapalito se ubica en el Golfo de Santa Elena, un área con alta biodiversidad y una amplia variedad de hábitats costeros que pueden facilitar el desplazamiento de las tortugas entre estos. Además, esta área es influenciada por un afloramiento costero temporal que puede afectar la distribución de las especies y

el uso de hábitat (Eisele et al., 2021), por lo tanto, provee una oportunidad para cuantificar la residencia, el movimiento y la conectividad de hábitat de las tortugas carey. En este estudio, se utilizaron muestreos de abundancia y telemetría acústica para investigar los patrones de abundancia estacional y la ecología espacial de tortugas carey juveniles en Matapalito y los hábitats del Golfo Santa Elena. Específicamente, (i) se determinaron los cambios estacionales en la abundancia de las tortugas carey en Matapalito a lo largo de un período de 10 años, y (ii) se cuantificaron los patrones de residencia y de conectividad de hábitat en Matapalito y los hábitats costeros adyacentes. Ya que Matapalito ha sido identificada como una importante área de alimentación para las tortugas carey en el Pacífico norte de Costa Rica, y que la especie es conocida por tener rangos de hogar relativamente pequeños a lo largo de su distribución, se espera que las carey presenten una abundancia estable a lo largo de los años en la bahía. Además, ya que las tortugas carey han presentado una alta fidelidad de sitio a hábitats específicos en otras áreas del PTO, se espera que presenten una alta residencia a Matapalito por largos períodos de tiempo (hasta 2 años), usando los hábitats disponibles en Matapalito, con desplazamientos limitados a otras áreas costeras. Sin embargo, debido a los drásticos cambios en las condiciones ambientales causados por el afloramiento estacional en el área, se espera que cambie la abundancia y la residencia de las tortugas carey durante estos eventos, aumentando ambos factores ya que los animales podrían aprovechar la alta productividad causada por el afloramiento.

CAPÍTULO 1

Residency and habitat connectivity of juvenile hawksbill sea turtles across coastal environments

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1. INTRODUCTION

Understanding what drives animal movement and habitat use is crucial for implementing effective spatial management approaches, especially for highly threatened species (Allen & Singh, 2016). Animals often use specific habitats that are critical to the survival of their populations (Hall et al., 1997; Rosenfeld & Hatfield, 2006) and may therefore require special management considerations or protection (Camaclang et al., 2014). Animals move within and across habitats and ecosystems in response to biological, ecological and environmental drivers (Joo et al., 2022). These responses have been reported for different animal taxa; for example, shifts in the spatial and depth distribution in the ocean in response to climate change (Poloczanska et al., 2016). Giffin et al. (2019) reported reef fishes shifting their habitat use amongst different life stages, and the Loggerhead sea turtles (*Caretta caretta*) have shown intra-specific competition affecting the habitat that they use for foraging or refuge (Dujon et al., 2018). These examples highlight the importance of understanding how animals move within and between habitats in relation to different drivers, and how these habitats are connected at small and large spatial and temporal scales (Ogburn et al., 2017). However, studying animal movement is challenging, especially for large, wide-ranging marine species with complex life cycles such as sea turtles.

The Hawksbill sea turtle (*Eretmochelys imbricata*) is a Critically Endangered species with a global distribution in tropical and subtropical marine and estuarine waters (Mortimer & Donnelly, 2008). The Eastern Tropical Pacific (ETP) subpopulation of hawksbills is one of the most threatened and poorly studied (Gaos et al., 2010). This subpopulation is mainly affected by incidental fishing mortality attributed to gillnets (Liles et al., 2017) and blast fishing (Liles et al., 2011). However, other threats such as poaching, and the loss and degradation of their natural habitats have also been identified as important contributors of population decline (Gaos et al., 2010).

In the ETP, hawksbills use a wide range of habitats available compared to other subpopulations. For example, mangrove and estuarine habitats stand out as important habitats for feeding and reproduction (Gaos, Lewison, Yañez, et al., 2012); however, a portion of the hawksbills population in this region still uses coral and rocky reef

habitats for feeding and sandy beaches for nesting (Martínez-Estévez et al., 2023). Changes in habitat use show how hawksbills in the ETP have adapted to the conditions of this region by (i) using different habitats available during their life cycle, (ii) exploiting a wide range of prey (e.g. algae and invertebrates such as sponges, tunicates, snails and worms (Carrión-Cortez et al., 2013; Méndez-Salgado et al., 2020; Reynolds et al., 2023)), and (iii) restricting their movements to more sheltered environments such as mangroves and coral reefs (Gaos, Lewison, Yañez, et al., 2012). However, knowledge of when and where hawksbills move at relatively small spatial scales, and the extent to which they connect different habitats is still limited, particularly in smaller individuals that have not reached sexual maturity. Therefore, understanding how they use specific coastal areas can help inform spatial planning, strengthen regional conservation approaches, and ultimately facilitate species population recovery efforts (Gaos, Lewison, Wallace, et al., 2012; Llamas et al., 2017).

Movement ecology studies have shown to be highly important in management planning and conservation (Allen & Singh, 2016). The use of tracking technology and movement metrics such as residency (the time an animal spends in a given area), home range (the areas where animals live and develop their activities), among others, have shaped the movement ecology knowledge of terrestrial and marine animals during the last decade (Allen & Singh, 2016; Joo et al., 2022). For hawksbill turtles, previous studies have shown that sea turtles can spend months to years in areas of less than 1 km² (Berube et al., 2012; Blumenthal et al., 2009; Hart et al., 2013), characterizing them as having high residency to their foraging and resting sites. However, few studies have shown cases of hawksbill turtles presenting larger displacement (for example 6.8-39.8 km in Belize Chevis et al., 2017) and large home ranges (a mean of 31.2 ha ± 32.6 in Belize, Scales et al., 2011). In these cases, different movement behaviors have been suggested for hawksbill turtles, according to the amount of time they spent in different areas and how they move between them, as high residency (spending over 60% of their time in the same area), sequential residency (spend weeks to months in one area before moving to another one) and transient behavior (spend just a few days in an area before moving to another one) (Chevis et al., 2017). For the ETP subpopulation, hawksbill turtles also show high site

fidelity to small areas (Llamas et al., 2017; Martinez-Estevez et al., 2021), but they also show an ontogenetic divergence in their habitat preference, as the individuals that use mangrove habitats for feeding and reproduction have little genetic mixing with those in reef habitats (Gaos et al., 2016). This is supported by recent findings from foraging grounds along the ETP, which show a high degree of site fidelity of individuals to a particular habitat, whether estuarine, rocky reef or in sandy areas (i.e. Baja California, Martinez-Estevez et al., 2021, Costa Rica, Carrión-Cortez et al., 2013).

The ETP region is also influenced by the El Niño Southern Oscillation (ENSO) and some areas by regional upwelling that are known to influence the environmental conditions of coastal areas (Fiedler & Lavín, 2017; Lavín et al., 2006). Specifically, coastal upwellings in the ETP region occur when strong trade winds push surface water away from the coast, bringing in cool, nutrient-rich water from the seafloor, drastically reducing temperature and oxygen levels (Kämpf & Chapman, 2016). There are three main areas along the ETP coast where these events happen seasonally, one in southern Mexico (Tehuantepec upwelling), one in Costa Rica (Papagayo upwelling) and one in Panama (Panama Gulf upwelling) (Pennington et al., 2006). Although these three areas are highly used by different species of sea turtles, it is not clear how these events affect their movement and distribution patterns, or whether they benefit these species at any life stages.

The effect of upwellings on sea turtles has been studied in other regions. For example, on the Pacific coast of South America, where the Humboldt upwelling affects the coast of Chile and Peru all year round, green sea turtle (*Chelonia mydas*, “green turtles” from here on) aggregations have been studied and compared with others in ecotone areas. These studies have found that smaller individuals are generally more abundant than adults in the cooler upwelling areas (Quiñones et al., 2022; Velez-Zuazo et al., 2014). Green turtles in the upwelling areas also show a faster growth rates (Velez-Zuazo et al., 2014), and dietary differences (Quiñones et al., 2022), although it is unclear whether these differences are due to ontogenetic changes (juveniles vs. adult) or upwelling conditions. While these findings provide an important basis for understanding sea turtle ecology in upwelling areas, they are difficult to extrapolate to tropical seasonal upwelling conditions typical in the ETP.

There are six main sites in Costa Rica where significant numbers of hawksbills have been identified (Carrión-Cortez et al., 2013; Chacón-Chaverri et al., 2016; Heidemeyer et al., 2015). Most of these sites are predominantly coral and rocky reef habitats, but there are also other habitats available (e.g., mangroves, bays and estuaries) that hawksbills can access (Carrión-Cortez et al., 2013; Chacón-Chaverri et al., 2016). Matapalito Bay, hereafter referred to as Matapalito, is one of these important hawksbill feeding sites on the north Pacific coast of Costa Rica. Previous work suggests that Matapalito plays an important role as a feeding area for juvenile hawksbills, highlighting its importance for the conservation of the species in the ETP (Heidemeyer et al., 2015). Matapalito is located in the Gulf of Santa Elena, an area of high biodiversity, with a wide variety of coastal habitats that may facilitate sea turtle connectivity. This area is also subject to a strong seasonal upwelling, which can affect the distribution and habitat use of marine species (Eisele et al., 2021), and therefore provides an ideal opportunity to quantify the residency (i.e. the proportion of time individuals spend in an area), movement, and habitat connectivity of hawksbill turtles.

In this study, we used abundance surveys and acoustic telemetry to investigate seasonal abundance patterns and the spatial ecology of juvenile hawksbill turtles in Matapalito and nearby habitats from the Gulf of Santa Elena. Specifically, we (i) determined seasonal changes in the abundance of hawksbill turtles in Matapalito over a 10-year period, and (ii) we quantified the residency patterns and habitat connectivity in Matapalito and other adjacent coastal habitats. Given that Matapalito has been identified as an important foraging ground for hawksbills in the northern Pacific region of Costa Rica, and that the species is known to have relatively small home ranges throughout their distribution, we expect hawksbills to exhibit stable abundance in the Bay between years. Since hawksbill turtles have shown high site fidelity to specific habitats in other areas of the ETP, we also expect them to exhibit high residency to Matapalito over long periods (up to 2 years or more), using the habitats available within Matapalito, with limited movement to other coastal areas. However, because of the drastic change in conditions caused by the seasonal upwelling in the area, we also expected hawksbills sea turtles change their abundance and the residency, increasing both as animals would take advantage of the high productivity caused by the upwelling.

2. MATERIALS AND METHODS

2.1 Study site

Matapalito is a small bay (less than 1 km²) located in the north Pacific coast of Costa Rica (Fig. 1). This bay has a wide range of habitats, including sandy bottoms with coral patches, macroalgal pads, small seagrass beds, and rocky reefs (Heidemeyer et al., 2015; Samper-Villarreal et al., 2020). Matapalito is directly connected through a channel during high tides or around a small islet during low tides to Santa Elena Bay, a much larger (approx. 7 km²) embayment with rocky reefs in the outer parts transitioning to mangrove estuarine habitats in the innermost parts. This complex of two bays forms the Santa Elena Bay Marine Management Area (MMA), hereafter referred to as Santa Elena Bay MMA, an area that was created in 2017 to protect approximately 50% of the habitats and where fishing activities are restricted to low-impact gears (e.g. hand lines, sportfishing) (SINAC, 2017). The Santa Elena Bay MMA also has multiple zoning categories that manage commercial, recreational and scientific activities, ranging from minimum to high intervention zones (SINAC, 2017). The Santa Elena Bay MMA is also located in a region subject to a seasonal coastal upwelling between December and April, where strong east trade winds push surface waters west, bringing in cool, nutrient-rich water from the seafloor to the surface (Stuhldreier et al., 2015). During the upwelling months, water temperature can decrease from an average of 29 °C to close to 15 °C, while there is an increase in nutrients (e.g. phosphate, ammonia and nitrate) and chlorophyll- α concentrations (Cortés et al., 2014; Stuhldreier et al., 2015).

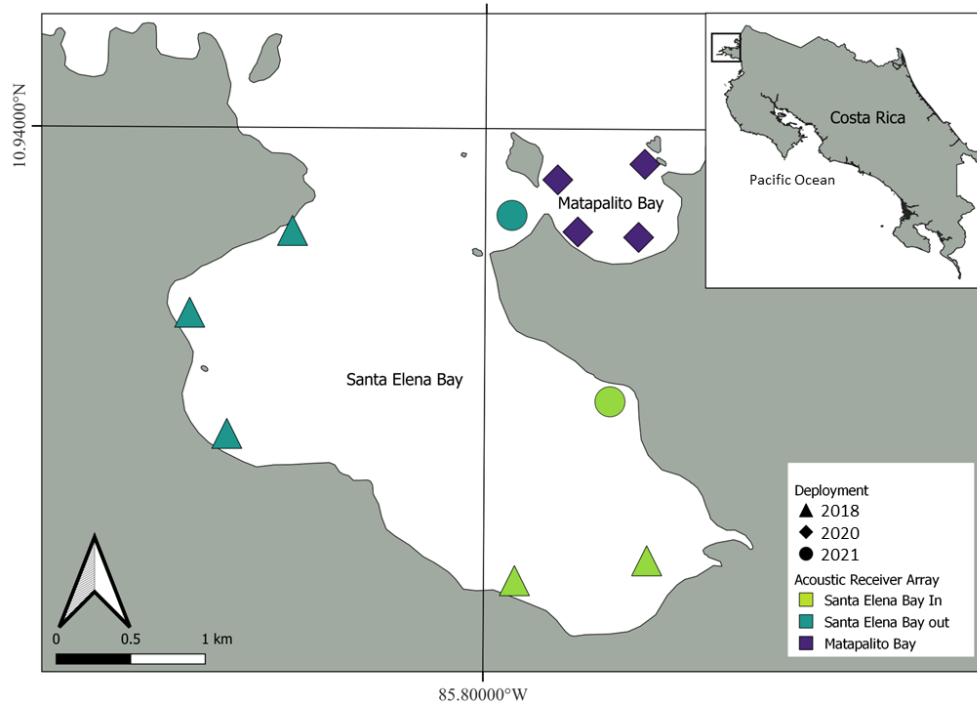


Fig. 1. Study area located in the north Pacific coast of Costa Rica. Symbols represent the location of acoustic receivers deployed through time and divided in different arrays (by color).

2.2 Seasonal patterns of abundance

Between March 2012 and July 2023, sea turtle surveys were conducted in Matapalito to examine seasonal patterns of abundance. The surveys were conducted at least twice a year, once in the upwelling season (December to May) and once in the non-upwelling season (June to November) (Alfaro & Cortés, 2012), with most years being monitored between 4 and 7 times. Sea turtles were captured using three multifilament nets (80 × 6 m, 45 cm stretch mesh size) tied continuously with buoys every 2 m at the top edge to keep the net afloat and weights at the bottom to keep it vertical in the water column without making it too heavy for the turtles to be able to surface to breathe, (Heidemeyer et al., 2015). Depending on the tide, nets were set parallel to the coastline and set 10-15 m away from the reef, with one end of the net set at the shallowest part of the reef (about 2 m deep) and the other end at the deepest part of the reef (up to 9 m deep). The nets were left in the water for 3 to 4 hrs and were checked every 15-30

min. The nets were set only during daylight hours. While the nets were in the water, between two and five people were searching for sea turtles on the reef. If an animal was seen resting on the bottom or between rocks or coral, an attempt was made to capture it by hand. Two trips were conducted at nighttime with only snorkelers hand-capturing the sea turtles, with two hrs of monitoring each night.

All captured turtles were brought to the boat, measured with a flexible measuring tape (curved carapace length- CCL- and curved carapace width-CCW) and weighed (kg). In addition, individuals were tagged for identification with an external metal INCONEL (style 681, National Band and Tag Company, Newport, Kentucky) tag in the skin adjacent to the first inner scale of each hind flipper. In addition, a passive integrative transponder (PIT) tag (AVID Identification systems) was placed on the front shoulder for identification.

2.3 Acoustic tagging

Acoustic transmitters with an external case (Vemco V16-6H-69 kHz, 115 mm length x 16 mm wide, 15 g in water weight, high power output 158dB, 3035 days of nominal battery life) were be fitted to 12 turtles over 4 kg (approximately 35-40 cm CCL). The tags were set to pulse every 60 to 90 s with a random delay to reduce signal collision from multiple individuals being detected simultaneously within the study site. The tags were attached to the marginal posterior scute following the methodology described by (Smith et al., 2019), using two or three wires to secure it through holes drilled on the edge of the carapace (Fig. 2). Marine epoxy (JB marine weld) was used to cover and reinforce the attachment of the transmitter when possible. Individuals were kept out of the water for a maximum of two hours, with their head covered with moist towels to reduce stress and dehydration.

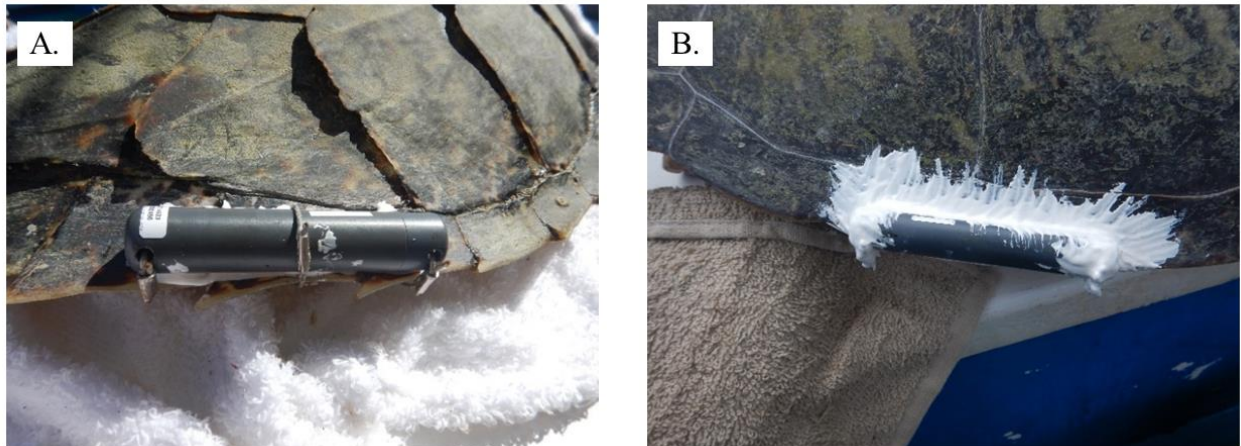


Fig. 2. Deployment of the acoustic transmitter on sea turtles tagged in Matapalito Bay, north Pacific coast of Costa Rica. A. with three anchor points and marine Weld epoxy on the base, B. with two anchor points and marine Weld epoxy securing all the transmitter.

2.4 Acoustic monitoring array

We deployed four acoustic receivers (Vemco VR2Tx-69 kHz) in Matapalito at depths between 3 and 11 m during September 2020 (Fig. 1). Each receiver was attached to a line (approx. 1 m from the seabed) with an underwater buoy that anchored to a cement base. Receivers were placed at distances of 400-600 m to maximize acoustic coverage of the entire bay, but also to cover different habitats (e.g. coral reef, rocky reef or sandy bottom with macroalgae). Five receivers (Vemco VR2W-69 kHz) were deployed throughout Santa Elena Bay in 2018, as part of an ongoing monitoring project for Pacific nurse sharks (*Ginglymostoma unami*) (Madrigal-Mora et al., in press). Two additional receivers (Vemco VR2Tx-69 kHz) were deployed in Santa Elena Bay in June 2021; one was placed in the channel that connects Matapalito and Santa Elena during high tide, and the other was placed in a transitional mangrove habitat in the east side of Santa Elena Bay (Fig. 1). Range tests of the receivers in Matapalito varied from 200-600 m, with an average detection range of 400 m (Valverde-Cantillo et al., unpublished data). In Santa Elena Bay, range tests were conducted in two zones of the bay: the

inner and outer bay. The inner bay is characterized for having mangrove forests along the shore and soft-mud and fine-course gravel bottom. The outer bay transitions into scattered rocky reefs along the shore and sandy-gravel bottoms. Range tests in the inner bay varied from 300-700 m; in the outer bay range tests varied from 200-400 m (Espinoza et al. unpublished data). Using a nominal detection radius of 400 m per receiver for both bays (Matapalito and Santa Elena Bay), estimate detection coverage of 100% of Matapalito Bay and 24% of Santa Elena Bay at the start of the study (2020) and a coverage of 100% of Matapalito Bay, 32.7% of Santa Elena Bay after two additional acoustic receivers were deployed in Santa Elena Bay in 2021. For the entire area, we had a coverage of 38.4% at the start of the study and 46.6% after the last two receivers were added in 2021. The receivers deployed in Santa Elena Bay between 2018 and 2021 used the same mooring system as the receivers of Matapalito. These receivers were placed to monitor nurse sharks in estuarine and rocky reef habitats available in Santa Elena Bay, but they were further apart (800 to 2100 m) and covered a smaller percentage of the Bay.

2.5 Environmental Conditions

Sea floor water temperature was monitored throughout the entire study period using either temperature sensors integrated into the VR2Tx acoustic receivers (± 0.1 resolution, ± 0.5 accuracy) or with a HOBO Pro v2 temperature datalogger (U22-01, ± 0.1 resolution, ± 0.2 accuracy, Onset Computer Corporation) that was attached to the VR2W receiver. Water temperature was averaged daily from the area where the receivers were placed (e.g. Matapalito, Santa Elena inner bay and Santa Elena outer bay) to examine daily variation over the study period. Temperature data were plotted using “*ggplot2*” (Wickham, 2016) with and without a smoother method *glm* in R (v. 4.3.1, R Core Team, 2021). Wind speed and rain fall data for the region were obtained from the National Meteorological Institute (No. 72153 and No. 72191, Instituto Meteorológico Nacional – IMN) for the La Cruz Station (lat, lon). The data was averaged daily and plotted using “*ggplot2*” (Wickham, 2016).

2.6 Data analysis

Data from sea turtle surveys conducted in Matapalito between 2012 and 2023 was used to determine (i) the number of hawksbill turtles captured per year, (ii) changes in abundance between seasons (upwelling and non-upwelling), and (iii) the size frequency distribution of individuals using the Bay. Due to the large variation in sample size over the study period and between seasons, capture data were standardized as the relative abundance of sea turtles captured per trip. Relative abundance data was log-transformed to meet the assumptions of normality and homoscedasticity. The effect of the season and year on number of captured turtles was analyzed using a two-way ANOVA. Results were graphed using “*ggplot2*”.

Daily detection data were used to determine the presence/absence of hawksbills in three areas: (i) Matapalito (tagging site), (ii) Santa Elena Bay, and (iii) the entire Santa Elena Bay MMA. To avoid false detections, we only used the days when individuals had two or more detections in each area (Kraft et al., 2023). Daily detection plots for each individual throughout the study period were used to examine visitation patterns in Matapalito and Santa Elena Bay. Santa Elena Bay was divided into inner and outer bay based on the different environments available to determine if hawksbills had different visitation patterns between within Santa Elena Bay. Turtles were divided into three groups according to the length of time they spent in the study area: (i) individuals that stayed for less than 2 weeks; (ii) individuals that stayed between 3 and 6 months; and (iii) individuals that stayed for more than 9 months.

For the individuals detected over 30 days ($n = 7$), daily detections were used to calculate two residency indexes (RI) for each area (Appert et al., 2023). In RI_A , we calculated the number of days individuals were detected in each of the study area (e.g. Matapalito, Santa Elena Bay, and Santa Elena Bay MMA) relative to the number of days at liberty (i.e. number of days from the date of tagging to the last date an individual was detected) (see Eq. 1). In RI_B , we calculated the number of days individuals were

detected in each of the study area (e.g. Matapalito, Santa Elena Bay, and Santa Elena Bay MMA) relative to the number of days that they were monitored (i.e. number of days from the date of tagging to the last date of the study or the end of battery life of the transmitter) (see Eq. 2).

$$RI_A = \frac{\text{days detected in the area}}{\text{days at liberty}} \quad \text{Eq. 1}$$

$$RI_B = \frac{\text{days detected in the area}}{\text{days monitored}} \quad \text{Eq. 12}$$

To understand how hawksbill turtles move within Matapalito and/or connect Matapalito with other areas, Santa Elena Bay receivers were grouped in two zones: the inner Santa Elena Bay characterized by mangrove and muddy areas, and outer Santa Elena Bay with gravel and rocky reef habitats (Fig. 1) We analyzed the degree of connectivity by quantifying the daily movements of individuals between the three areas (Matapalito, inner Santa Elena Bay and outer Santa Elena Bay). We only used daily detections from individuals that were detected over 30 days ($n = 7$) to determine which areas they used each day. If an individual was detected in more than one area per day, we used the area with the most detections, and if the individual was not detected in any of the study areas, the location was defined as “unknown”. A matrix with the sum of movements within and between arrays (including movements to unknown locations) was constructed following the methods by Espinoza et al., 2021. A modified circular plot (“connectivity plot”) was used to visualize the movements of each individual between areas. Secondly, a similar movement analysis was used to determine how many individuals moved between areas throughout the study period. Using the same movement matrix created before, if the number was >1 , meaning this individual moved in that direction, then this was added to a final matrix as one individual moving on each direction. The resulting matrix represented the total number of individuals moving between areas. A modified circular plot (“connectivity plot”) was used to visualize the number of individuals moving between zones. Connectivity plots

were created using the “`circos.trackPlotRegion`” function from the “`circlize`” package (Gu et al., 2014).

3. RESULTS

3.1 Environmental conditions

Water temperature data during the monitoring period showed marked differences between the upwelling and non-upwelling seasons (Fig. 3), as well as a lower temperature in Matapalito compared to the other areas (Fig. 3A). Wind speed data for the region showed high peaks during the upwelling season that were consistent with low water temperatures in Santa Elena and Matapalito (Fig. 3B). Rain fall data showed peaks opposite to wind speed, with higher values reported during the non-upwelling seasons (Fig. 3C).

3.2 Inter-annual and seasonal abundance patterns

Between March 2012 and July 2023, 127 monitoring trips were conducted in Matapalito (Table 1), during which a total of 136 individuals were captured (mean \pm SD: 11.2 \pm 11.6 individuals per year), with a mean relative abundance of 0.99 \pm 0.55 turtles per trip (Fig. 4).

Hawksbill turtles were captured each year during both seasons, with a total of 83 individuals captured during the non-upwelling and 52 individuals captured during the upwelling seasons (Fig. 4). Although there was an inter-annual effect in the number of hawksbill turtles captured across years ($F_{(11,11)} = 7.26$, $P < 0.05$), there was no seasonal effect ($F_{(1,11)} = 0.73$, $P > 0.05$).

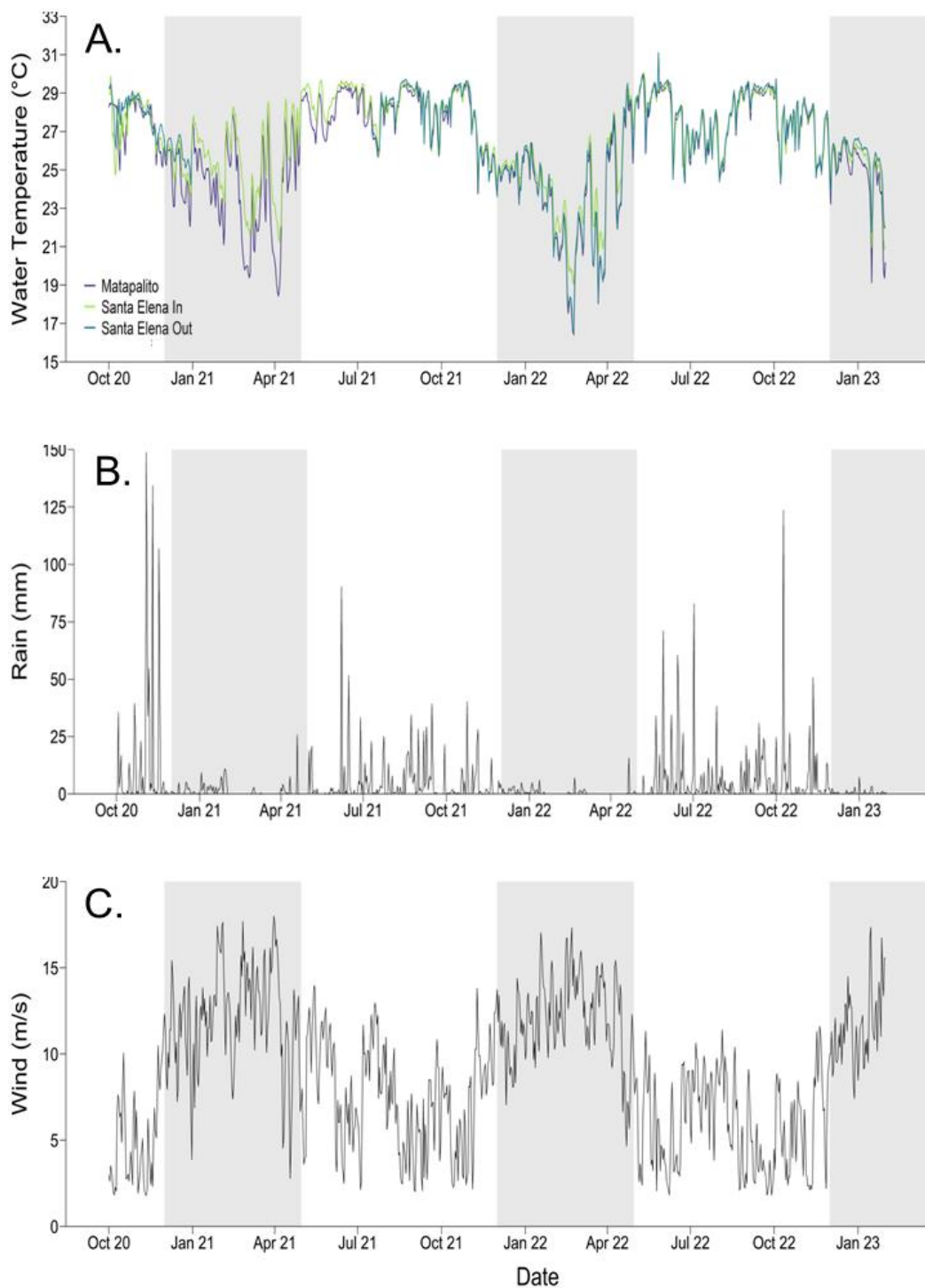


Fig. 3. Environmental conditions data for the region for the study period. A. water temperature for the AMMBSE. B., C. Wind and rain data for the region. Grey panels mark the upwelling season.

Table 1. Sea turtle monitoring trips conducted between 2012 and 2023 in Matapalito Bay, north Pacific coast, Costa Rica.

Year	Total No. Trips	Upwelling season		Non-upwelling season	
		Trips	Captures	Trips	Captures
2012	4	3	7	1	2
2013	7	2	2	5	5
2014	2	1	1	1	1
2015	7	2	2	5	5
2016	13	5	3	8	8
2017	22	10	8	12	10
2018	19	6	12	13	33
2019	16	8	5	8	6
2020	5	3	3	2	2
2021	20	6	3	14	10
2022	7	4	2	3	0
2023	5	3	4	2	1
Total	127	53	52	74	83

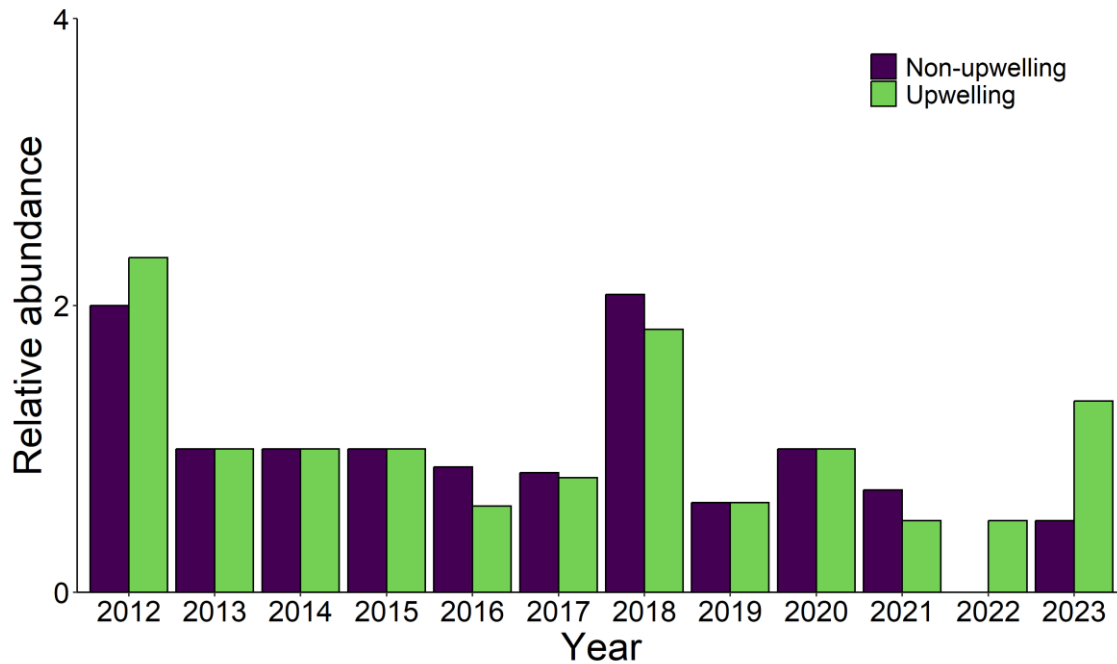


Fig. 4. Relative abundance by season of hawksbill turtles (*Eretmochelys imbricata*) captured in Matapalito Bay, north Pacific coast of Costa Rica, between 2012 and 2023.

The size of captured turtles ranged from 30 to 85 cm CCL (mean \pm SD: 44.6 ± 8.7 CCL), with the majority of turtles in the 35 to 40 cm and 40 and 45 cm CCL size classes and weighing between 2 and 50 kg (9.0 ± 6.4 kg). Captured individuals below 60 cm CCL were assumed to be juveniles (Fig. 5).

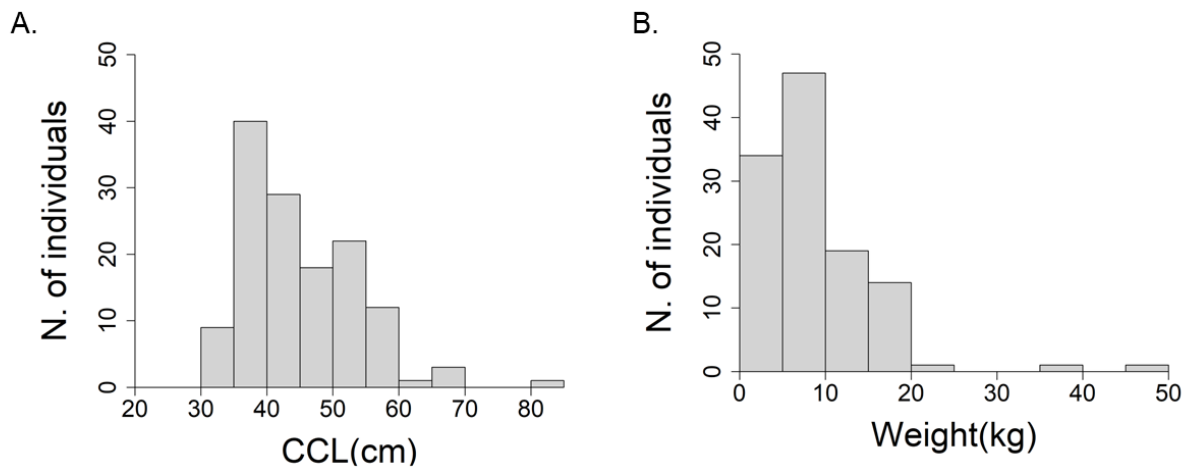


Fig. 5. Size histograms of hawksbill sea turtles captured in Matapalito Bay, north Pacific coast of Costa Rica, between 2012 and 2019.

3.4 Spatial Ecology of hawksbill turtles

Thirteen individuals fitted with acoustic transmitters were monitored between 96 and 924 days (Table 2). Seven of these individuals were included in further analysis, as they were detected for more than 30 days. The RI_A to Matapalito was highly variable between individuals, ranging from 0.07 to 0.75 (mean \pm SD: 0.3 ± 0.3). Eighty-five percent of the individuals were recorded in Santa Elena Bay and had a similar RI_A compared to their tagging site (mean \pm SD: 0.3 ± 0.2). For the entire Santa Elena Bay MMA, the RI_A ranged from 0.2 to 1.0 (mean \pm SD: 0.6 ± 0.3 , Table 2). The RI_A of hawksbills was higher than the RI_B in all three areas (e.g. Matapalito, Santa Elena Bay and Santa Elena Bay MMA) (Table 2, Fig. 6).

Table 2. Detection data for Hawksbill turtles (*Eretmochelis imbricata*) tagged with acoustic receivers at Matapalito Bay for each area (Matapalito Bay, Santa Elena Bay and the Santa Elena Bay MMA) for the study period.

ID	Date Tagged (MM/DD /YY)	CCL (cm)	CCW (cm)	Weight (kg)	Days Monitor	Days at Liberty	Matapalito				Santa Elena Bay				Santa Elena MMA			
							Days Det.	# Dets.	RI _A	RI _B	Days Det.	# Dets.	RI _A	RI _B	Days Det.	# Dets.	RI _A	RI _B
2170	10/16/20	51	40.9	8.8	924	716	108	7345	0.15	0.12	12	1796	0.02	0.01	107	9141	0.17	0.13
2164	10/16/20	41	34.5	7	924	261	192	4787	0.74	0.21	0	0	0	0	180	4787	0.74	0.21
2167	12/6/20	37.5	32.5	4.3	873	19	13	493	0.68	0.01	0	0	0	0	13	493	0.68	0.01
2171	1/27/21	36.5	30.5	4	821	22	3	109	0.14	0.00	5	544	0.23	0.01	8	653	0.36	0.01
2165	1/27/21	35.5	30	4.2	821	197	39	4049	0.20	0.05	104	13256	0.53	0.13	139	17305	0.73	0.17
63764	3/16/21	45	41	9	773	104	62	2950	0.60	0.08	43	10873	0.41	0.06	104	13823	1.00	0.13
63762	5/1/21	38.7	33.5	5	727	1	1	7	1.00	0.00	0	0	0	0	1	7	1.00	0.00
63759	7/4/21	35	31.5	4.1	663	622	161	52328	0.26	0.24	304	23011	0.49	0.46	416	75339	0.63	0.59
63756	7/18/21	52	14	14	649	622	79	23590	0.13	0.12	44	2283	0.07	0.07	110	25873	0.18	0.18
2912	11/18/21	35.9	31	4.3	526	1	1	14	1.00	0.00	1	728	1.00	0	1	742	1.00	0.00
14633	2/9/22	45	32.5	8	443	147	10	759	0.07	0.02	78	20909	0.53	0.18	84	21668	0.59	0.19
14632	4/28/22	43	37.5	7	365	3	3	116	0.07	0.01	0	0	0	0	3	116	0.07	0.01
57808	1/22/23	39.3	35.5	14	96	4	3	319	0.75	0.03	0	0	0	0	4	319	0.75	0.03

CCL: Curved Carapace Length; CCW: Curved Carapace Width; Days monitor: days between tagging date and last day of the study; Days at liberty: days between date tagged and last detection; RI_A: residency index based on days at liberty; RI_B: residency index based on days monitored.

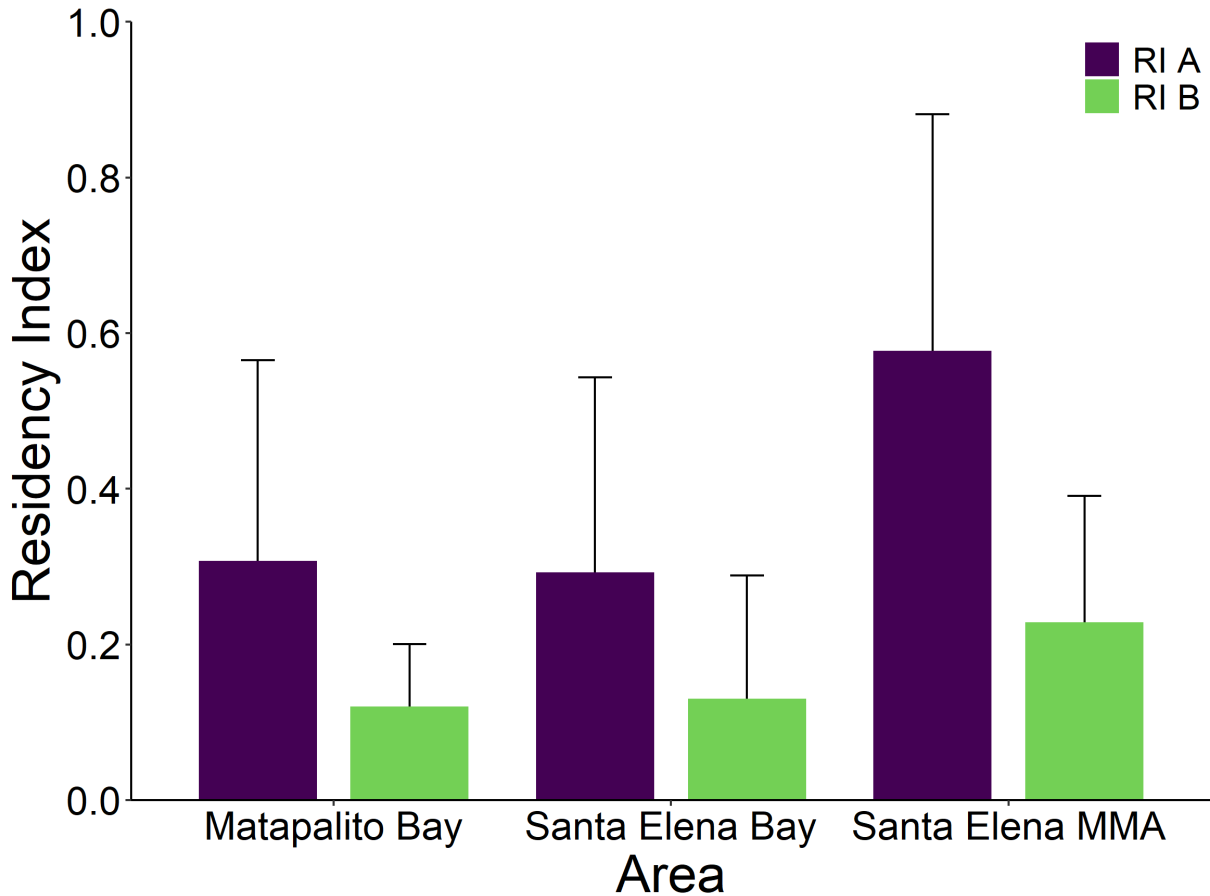


Fig. 6. Average residency of hawksbill turtles (*Eretmochelis imbricata*) for each area calculated based on days at liberty (RI_A) and total days tracked (RI_B), north Pacific coast of Costa Rica.

According to the time spent in the monitored area, group one (less than two weeks) had most tagged individuals ($n = 6$), followed by the third group (more than 9 months, $n = 4$), and then the second group (three to six months, $n = 3$). Of all the turtles tagged, two individuals returned to the study site after being undetected for up to 15 months (Fig. 7, turtles 63756 and 2170).

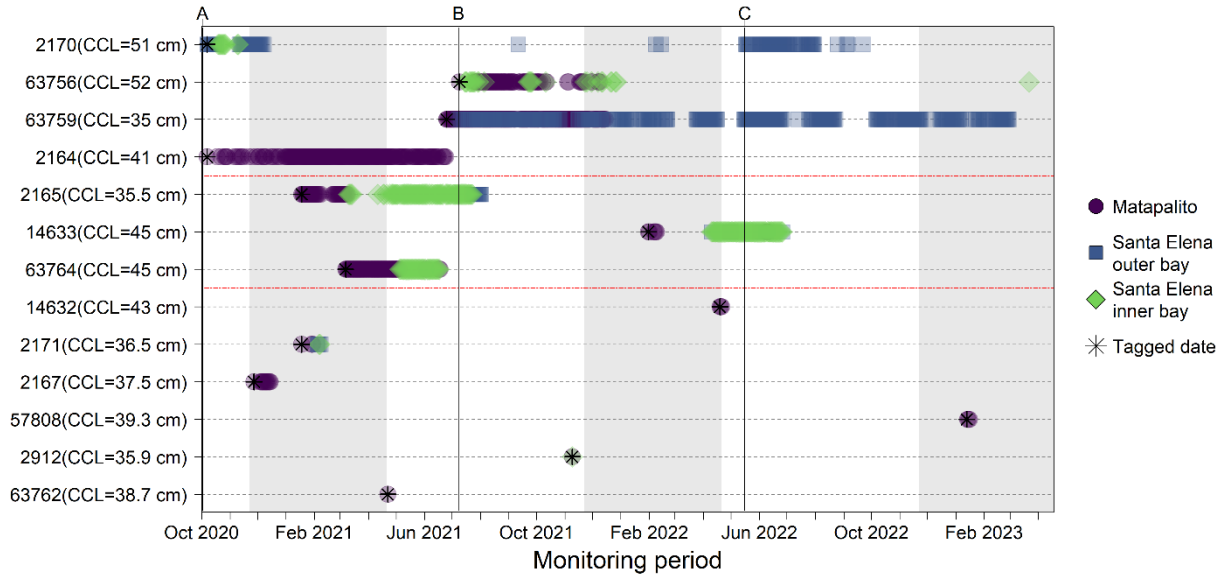


Fig. 7. Daily detections for sea turtles tagged in Matapalito Bay, north Pacific coast of Costa Rica. Marks represent presence in each zone and gray areas mark upwelling season. Letters on the upper axis represent the number of receivers monitoring the study area: A. 4 receivers in Matapalito, 2 receivers in Santa Elena in, 3 in Santa Elena out; B. 1 receiver added to Santa Elena in and 1 to Santa Elena out, C. 4 receivers added to Santa Elena out, 1 receiver added to Matapalito. Red lines represent the groups by category of time spent in the study area from least (less than 1 month) to most (over 9 months).

3.5 Habitat connectivity

Of all individuals detected for more than 30 days ($n = 7$), 85% moved between habitats of the different study areas several times before leaving the study area (Fig. 8). Five individuals moved between the coral reef and sandy habitats in Matapalito and mangrove habitats of Santa Elena inner bay, before moving to the scattered rocky reefs in Santa Elena outer bay (Fig. 9). A small number of animals moved back from both Santa Elena inner and outer bays to Matapalito bay (Fig. 9). Overall, 70% of the hawksbills showed high use of Matapalito, and only 30% were detected in all three areas (Fig. 9).

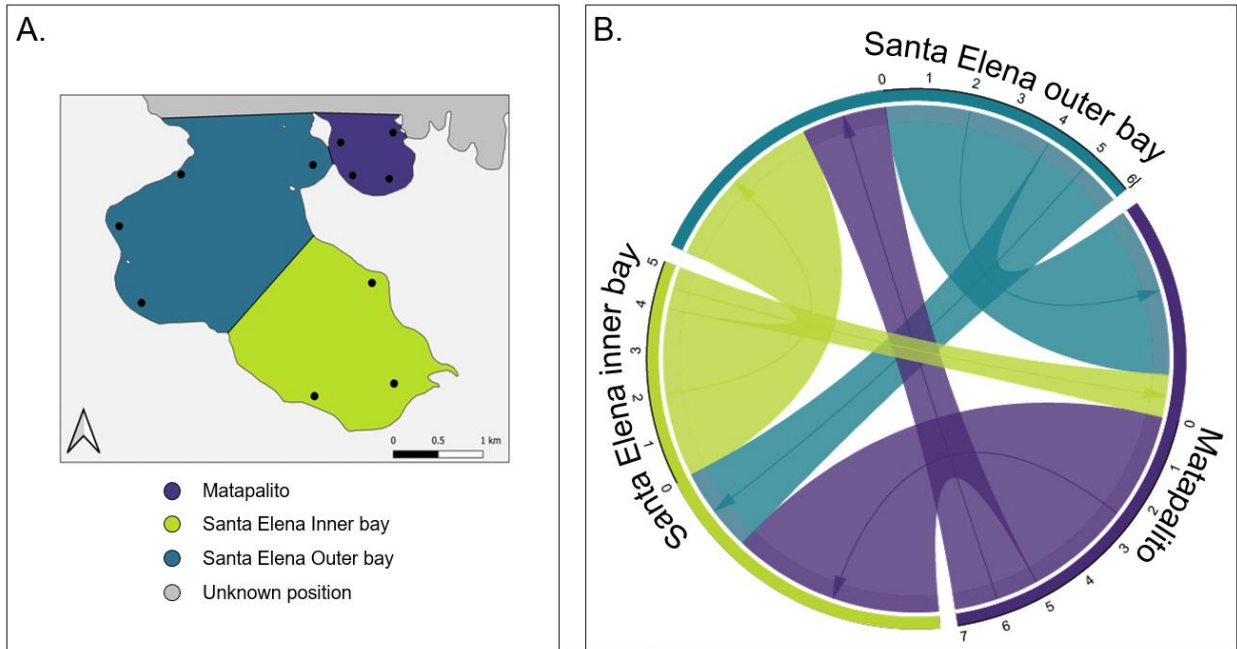


Fig. 8. A. Map of the study area divided by zone. B. Number of individuals (outer numbers) of hawksbill turtles (*Eretmochelis imbricata*) tagged with acoustic transmitters in Matapalito moving between zones.

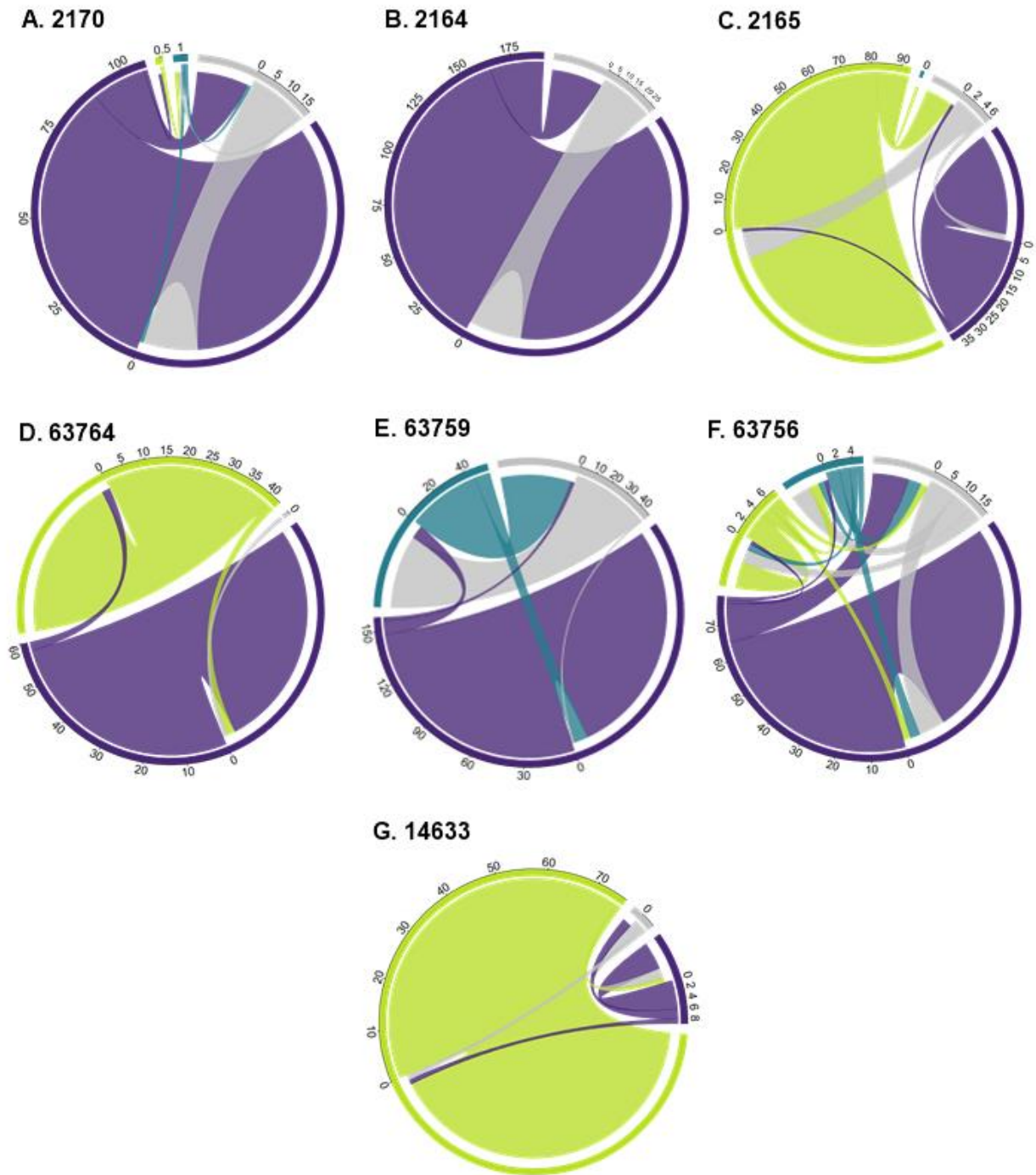


Fig. 9. Connectivity plot for individual Hawksbill turtles tagged in Matapalito Bay, north Pacific coast of Costa Rica. Links show the number of days (outer numbers) each individual moved between each zone.

4. DISCUSSION

This study sheds light on the spatial ecology of juvenile hawksbill turtles in the Eastern Tropical Pacific, a region that has been poorly studied, but faces many challenges in protecting this critically endangered species. Our data revealed that the abundance of juvenile hawksbills in the northern Pacific coast of Costa Rica have remained stable over the last decade. We also showed that this species uses a wide range of coastal habitats available, connecting coral and rocky reefs with estuarine and mangroves at multiple spatial and temporal scales. However, the relatively low residency values reported in this study suggest that the species requires a larger area to meet its energetic needs.

Matapalito was previously identified as one of the most important foraging sites for juvenile hawksbill turtles in the north Pacific coast of Costa Rica (Heidemeyer et al., 2015). Based on regular abundance surveys conducted between 2012 and 2023, the degree of use of Matapalito by juvenile hawksbills appears to vary over the years but was seasonally stable. Considering that this area is subject to strong seasonal upwelling and El Niño-Southern Oscillation (ENSO) events, the use of Matapalito by the juvenile hawksbills throughout the 10-year monitoring period may indicate that this bay offers stability during the upwellings but might still be affected by other major oceanographic events. ENSO events represent an important factor in the region's environmental conditions (Alfaro & Cortés, 2012) that can affect coastal upwellings intensity as well (Graco et al., 2017). Positive stages of ENSO (El Niño years) have shown to affect the feeding ecology (Carrión-Cortez et al., 2010), migration and nesting patterns of different species of sea turtles in the ETP (Quiñones et al., 2010; Ramírez et al., 2021; Saba et al., 2008). However, it is still unclear how they may affect juvenile sea turtles at their tropical feeding grounds. In Matapalito bay, ENSO events are possibly affecting the sea turtles feeding in the area, as warm water conditions can change the seasonal availability of food resources and decrease the productivity, causing a relaxation of the upwelling at the same time. Considering that ENSO events will possibly intensify with future climate change conditions (Guilyardi, 2006), and its

relationship with the upwelling, it is important to further study how the dynamic between the two conditions can affect populations of endangered species.

The prevalence of smaller size classes suggests that Matapalito is an important development site for this critically endangered species. Recruitment of hawksbill turtles is thought to occur when individuals are between 20 and 35 cm CCL (Liles et al., 2017; Llamas et al., 2017) and reach maturity at 72.2 cm CCL according to mean nesting size in nearby nesting beaches (Carrión-Cortez et al., 2013). During the juvenile stage, sea turtles are highly vulnerable to predators such as sharks (Heithaus et al., 2008), making recruitment sites critical for their survival (Mazaris et al., 2006). Other sites have shown feeding areas to be used by a mix of size classes, were smaller juveniles mix sometimes with subadults (Blumenthal et al., 2009). The rare capture of adult hawksbills (>72.2 cm CCL) may indicate that this site has a very low rate of size class mixing. This can be caused by the food type and availability (Ferreira et al., 2018), shelter availability (Matley et al., 2021) or even competition for resources with other species such as green turtles, which are known to occur in the same areas (*Chelonia mydas*, Clyde-Brockway et al., 2022).

Hawksbill turtles are known to use small to medium-sized areas for foraging, ranging from a few m² to 10 km² (Berube et al., 2012; Wood et al., 2017), and they remain in these areas for several years (Matley et al., 2021). However, hawksbill turtles tagged in Matapalito had relatively low residency values to the tagging site, and even when considering a larger area (e.g. Santa Elena Bay MMA), most individuals remain less than 60% of the time. In other areas of the ETP, similar size classes of hawksbills are known to have residency values of over 87% for periods of over 4 years (Martinez-Estevez et al., 2021). This may indicate that hawksbills in the Gulf of Santa Elena regularly move around and use broader areas where similar habitats are available (e.g., coral/rocky reefs and mangroves), and that Matapalito, although an important site for the species, is one of several sites used by juveniles for feeding. However, it is important to note that the relatively low acoustic coverage of the receivers in Santa Elena Bay may underestimate our ability to detect sea turtles in this area, and consequently our estimates of residency times.

In the western Atlantic, hawksbills have home ranges of less than 1.1 km (Berube et al., 2012; Wood et al., 2017). In the ETP, although studies quantifying the home range of hawksbills are scarce, they suggest that individuals have a higher variability in the areas used. For example, Martinez-Estevez et al. (2021) reported home ranges up to 17 km² in Baja California, while Carrión-Cortez et al., 2013 reported home ranges up to 1.26 km² in Punta Coyote. This variability in spatial use of the ETP subpopulation may depend on the type of habitat and environmental conditions in each of the study areas and may be more pronounced in foraging areas where a variety of suitable habitats are available for the turtles (Chevis et al., 2017; Martinez-Estevez et al., 2021). Matapalito is the only site in the Gulf of Santa Elena where an ongoing survey provide key information to identify an important foraging ground for hawksbills. However, constant sightings of juvenile hawksbill turtles in other sites in the Gulf (Equipo Tora Carey, personal observation, Diving Center Cuajiniquil, personal observation) further point to these turtles using a much larger area. Monitoring a wider area that includes Matapalito and other sites from the Gulf of Santa Elena could confirm whether Matapalito is more of a core area for hawksbills while they are in the region, and if so, how large an area is being used by the species.

Hawksbill turtles have been identified as coral reef inhabitants where they feed mostly on sponges and have shown very little habitat variability in other regions (Carr & Stancyk, 1975; León & Bjorndal, 2002; Meylan, 1988). For the ETP population, habitat variability has been identified as an important adaptation of this population to the conditions of the region (Gaos, Lewison, Yañez, et al., 2012), and most studies have shown individuals restrict their movements to one habitat type (Gaos et al., 2016; Martinez-Estevez et al., 2021), with even little genetic exchange between mangrove and reef residents, pointing to an important genetic segregation by habitat preference (Gaos et al., 2016). These findings differ from our results, which show that a large percentage of the hawksbill turtles tagged in Matapalito move to other adjacent coastal areas, including mangroves and rocky reefs. This may be particularly true for the turtles in Matapalito due to the abundance of prey, intra and interspecific competition for resources, or the high accessibility of different habitats on a small spatial scale, providing opportunities for hawksbills to move between them.

Although there was no indication of seasonal patterns in the residency or habitat use of the area, we decided not to test this as the small sample size could cause artifacts in the suggestions. However, it would make sense that sea turtles as ectothermic secondary consumers would be affected by the drastic change in environmental conditions during the upwelling season. These responses could be seen as a decrease in activity or residency during the cold-water months or a variability of energy intake with the increase in ocean productivity. Further studies on these important ecological aspects are needed to properly understand the spatial needs of sea turtles and to make appropriate conservation decisions.

5. CONCLUSIONS

Our study is one of the first long-term studies of an important foraging ground for juvenile hawksbill turtles in the north Pacific coast of Costa Rica. Monitoring efforts of these areas is crucial to understand specific aspects of their life history and the level at which certain habitats are connecting the population. A detailed understanding of the movement patterns and the degree of habitat connectivity of juvenile hawksbill turtles at different spatial and temporal scales can also help to identify key habitats that are critical for the persistence of the species. Given that most of the coastline cannot be fully protected, it is important to ensure the connectivity of a species between critical habitats that have some form of protection or management. Future studies should focus on determining the extent of the area used by hawksbill turtles in this region. This can be achieved by expanding monitoring efforts in other areas, and by expanding passive acoustic telemetry networks and inclusion of other methods such as satellite tagging, animal borne cameras, genetic approaches, and sharing information with other monitored areas in the region.

CONCLUSIONES

Este estudio representa uno de los primeros análisis de largo plazo de una importante área de alimentación para las tortugas carey juveniles en el Pacífico norte de Costa Rica. Nuestros resultados dan generan información sobre la ecología espacial de esta especie amenazada en una región donde ha sido poco estudiada, pero que enfrenta muchos desafíos para su recuperación. Encontramos que las tortugas carey juveniles en esta región utilizan una amplia variedad de hábitats costeros, conectando arrecifes rocosos y de coral con estuarios y manglares a diferentes escalas temporales y espaciales. Sin embargo, la residencia de las tortugas en áreas menores como Bahía Matapalito es baja, lo que sugiere que ocupan un área mayor para su desarrollo.

Los esfuerzos de muestreo de las áreas de alimentación de las tortugas marinas son cruciales para entender aspectos específicos de sus ciclos de vida. En este estudio se encontró que la abundancia de tortugas carey en Bahía Matapalito es constante a lo largo de los años y entre las temporadas de afloramiento y no afloramiento, lo que sugiere una estabilidad en esta área para las tortugas juveniles. Sin embargo, se encontró que las tortugas presentan baja residencia a esta bahía, pero una estancia por mayor tiempo en el área mayor del Área Marina de Manejo Bahía Santa Elena. Esto sugiere que las tortugas carey en esta región utilizan áreas mayores para su alimentación en comparación a las áreas reportadas para otros sitios. Finalmente, las tortugas carey monitoreadas con telemetría acústica mostraron un alto nivel de conectividad entre áreas, con varios individuos moviéndose entra ambientes rocosos, arrecifales y estuarinos.

Los estudios de movimiento en la región del Golfo Santa Elena subrayan la importancia de proteger hábitats claves, aún a pequeña escala, y las rutas que conectan estas áreas, tanto a escalas locales como regionales. En el futuro, es importante determinar la extensión real del área que utilizan las tortugas carey en esta región. Esto se puede lograr con monitoreo constante de diferentes sitios en la región, combinado con otras técnicas como telemetría satelital, cámaras animales o estudios genéticos, e incentivando la colaboración entre los diferentes sitios de la región.

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