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台灣綠蠵龜於覓食棲地之族群生態學及保育

Population Ecology and Conservation of Green Turtles (*Chelonia mydas*) within foraging grounds in Taiwan

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摘要

綠蠵龜（*Chelonia mydas*）被 IUCN 列為瀕危物種，主要分布於亞熱帶與熱帶海域，也是台灣最常見的海龜種類。過往研究多集中於產卵族群，對近岸覓食族群之瞭解相對有限。然而，海龜生命週期中絕大多數的時間都在覓食棲息地發育、生長並累積能量準備繁殖，若能更瞭解覓食族群和棲息地概況，有助於制定保育及管理策略。

本研究結合公眾參與及系統性調查，探討臺灣地區覓食綠蠵龜之族群生態。首先，透過與公民科學家合作建立「海龜點點名」計畫，收集水下海龜目擊資料，並藉由個體辨識，建構台灣沿岸海龜密度地圖、確認覓食熱區與瞭解定居模式。小琉球、恆春和綠島為重要覓食熱點。定居模式估算出約 43.4%的個體會在同一地區停留超過一年，而且成龜的定居時間和目擊次比青年龜和亞成龜來得更久。此外，約有 10%的目擊紀錄，與受傷個體有關，包括漁線纏繞、背甲受傷或其他外觀異常，顯示出人為活動造成的威脅。

其次，我們在覓食熱區小琉球進行兩年的系統性浮潛調查，驗證調查設計對資料有效性的影響，並進一步評估小琉球覓食族群的棲地忠誠度。潮汐狀態和調查設計會影響海龜個體偵測機率：漲潮和滿潮時海龜數量最多，而漲潮和退潮時則有較多不同個體；重覆調查較傳統單次調查記錄到八倍多的目擊數量和快兩倍多的個體及重複目擊率。我們用標準化棲地忠誠指標（SSFI）將海龜個體的定居時間和目擊頻率進行量化，並用階層式群集分析辨識出兩種忠誠度組別，低與

高忠誠度約各佔一半，並其他資料集和不同地區綠蠵龜進行棲地忠誠度的比較，發現小琉球海龜與菲律賓 Oslob 相似，且比公民科學資料提供更好資料解析度。

最後，透過整合公民科學與系統性調查的長期資料，發現在小琉球約 13.3% 野外族群有外傷或疤痕，但 80%的個體都觀察到已復原。本研究觀察到部分受傷個體從一開始受傷到逐漸恢復的完整過程。受傷成因包括螺旋槳擊傷、魚線纏繞和不同原因，復原時間平均皆需一年半。就野外觀察，嚴重傷口平均需約 600 天癒合，而輕微傷口則約 491 天。部分嚴重個案，如因魚線纏繞進而潰爛斷肢，和螺旋槳擊傷造成背甲變形，康復後仍持續在小琉球被目擊達 106 至 2,264 天，顯示其強大的野外康復能力和適應力。但海龜重複受傷的現象和受傷個體大多出沒於港口附近，都顯示設立限速區和娛樂釣魚規範的迫切和重要性。

本研究透過公民科學加深對台灣地區海龜覓食族群生態的瞭解，並針對調查標準化、棲地忠誠度評估與人為威脅提出建議，對臺灣及東印度洋和東南亞區域的海龜族群之保育與管理具有重要參考價值

關鍵字：公民科學、個體辨識、調查設計、棲地忠誠度、人為威脅、野外復原

Abstract

The green turtle (*Chelonia mydas*), listed as Endangered by the IUCN, is primarily distributed in subtropical and tropical waters and is the most commonly sighted marine turtle species in Taiwan. Research has historically focused on the nesting population and stranded individuals, leaving the ecology of foraging populations understudied. Marine turtles spend the majority of their lifetime in foraging grounds, where they seek shelter, grow, and gain energy for breeding and migration. Understanding their population ecology and residency patterns in foraging grounds is crucial for developing effective conservation and management strategies.

This Ph.D. study integrates a citizen science approach and standardized field surveys to understand the population ecology of green turtles in Taiwan. First, a citizen science initiative, TurtleSpot Taiwan, was co-found with citizen scientists to collect sightings of marine turtles and identify individuals through photo identification according to their unique facial scute patterns. Based on five years of nationwide data, several main foraging grounds (Liuqiu Island, Kenting, and Green Island) with a substantial number of foraging aggregations have been identified. Approximately 43.3% of turtles remained in the same area for over a year, with adult-sized turtles having more repetitive sightings and longer residency durations than juveniles and subadults. Approximately 10% of sightings involved turtles with external injuries or anthropogenic threats, including entanglement in fishing lines or hooks, carapace injuries, or missing flippers.

Second, a two-year, multiple-event snorkel-based survey was conducted at a key foraging ground, Liuqiu Island, to validate the survey design and assess the site fidelity of the local aggregation of green turtles. Turtle detection probability was influenced by tidal phase and survey design. More turtles were observed during high and flood tides, and a higher number of unique individuals were observed during flood and ebb tides. Multiple-event surveys recorded over eight times more sightings and nearly twice as many individual turtles and resighting rate as single-event surveys. We used the Standardized Site Fidelity Index (SSFI) to measure site fidelity for each individual, and clustering analysis revealed two distinct fidelity groups (Low Fidelity: 49%; High Fidelity: 51%) at sites. SSFI also allows for comparisons with other regions using open-access photo-ID datasets and found that the site fidelity of green turtles on Liuqiu Island was similar to those at Oslob, the Philippines, and offers a better resolution than citizen science data on Liuqiu Island.

Finally, long-term sightings from citizen science and survey data revealed rare but valuable records of injury recovery in the wild, offering new insights into the resilience and vulnerability of foraging turtles. The prevalence of external injuries among marine turtles at Liuqiu Island is approximately 13.3%, with most exhibiting signs of healing. Regardless of the injury causes (i.e., propeller strike, fishing line entanglement, and unidentifiable cause), the average healing times were about 1.5 years. Severe injuries typically take about 600 days to heal, while minor injuries generally take around 491 days to recover fully. Certain animals recover from severe injuries, such as flipper amputation caused by fishing line entanglement, and propeller strikes leading to carapace deformity permanently; however, the long-term observations after their recoveries for at least 106 to 2,264 days demonstrate remarkable resilience. Individuals with recurring injuries were observed, with tracked individuals showing frequent use of nearshore areas near ports, emphasizing the need for targeted conservation measures specific to port areas and by extension regions with high boat traffic. These include go-slow zones, recreational fishing regulations, and increases in public outreach.

This study demonstrates the value of combining citizen science with systematic monitoring to assess turtle distribution, habitat use, and responses to human impacts. It contributes practical solutions for the foraging population study and marine turtle conservation in Taiwan and can be applied to the broader East Indian and Southeast Asian Regional Management Unit.

Keywords: citizen science, photo-identification, foraging habitat, site fidelity, SSFI, threats, wild recovery

Table of Content

List of Tables

Chapter 2

Chapter 3

Chapter 4

List of Figures

Chapter 1

Chapter 2

Chapter 3

Chapter 4

CHAPTER 1

General Introduction

1.1. Population Ecology and Conservation Context

Population ecology is the study of the distribution, abundance, and dynamics of species populations and how these populations interact with their environment. Understanding species' population ecology is essential for conservation and biodiversity, especially for endangered species (Mace and Lande, 1991). Assessing the current population status and distribution of a target species is the first step when developing a management plan. Hypotheses to explain why the population is decreasing can then be formed, and management actions can be implemented and adjusted based on population monitoring outcomes (Van Dyke, 2008).

The green turtle (*Chelonia mydas*) is listed as endangered by the IUCN, CITES Appendix I, and CMS Appendices I and II. National legislation in many countries, including Taiwan, provides legal protection. The majority of marine turtle records in Taiwan—spanning nesting populations, stranding events, and in-water observations—are attributed to green turtles, which dominate both coastal sightings and bycatch reports (Cheng et al., 2009; I.-J. Cheng et al., 2019; Hoh et al., 2022). Major threats to green turtles include fishery bycatch (i.e., incidental capture of non-target species), coastal development, pollution and pathogens, direct take (e.g., eggs and meat consumption or other turtle products such as stuffed specimens), and climate change (IUCN-SSC MTSG, 2005).

Green turtle hatchlings are omnivores during their early life in pelagic zones, feeding on crustaceans, jellyfish, and ctenophores. As they grow and recruit to neritic habitats when they reach about 35 to 44 cm in curved carapace length (CCL) variated in different regions (Hayashi & Nishizawa, 2015; Limpus et al., 2005), their diet shifts to a predominantly herbivorous one, consisting mainly of macroalgae and seagrass (Bolten et al., 2003). Juveniles often become residents of their feeding grounds and remain there for several years until they mature and leave as adults (above 90 cm in CCL) for breeding migrations. Due to their migratory behavior and widespread distribution, it is particularly challenging to estimate total population size, especially for immature turtles that are more difficult to monitor. As a result, most population assessments rely on nesting counts of adult females (Seminoff & Shanker, 2008).

To improve conservation planning, Wallace et al. (2010) proposed a framework for identifying Regional Management Units (RMUs) for all marine turtle species based on nesting sites, genetic stocks, satellite telemetry, and tagging data and further defined RMUs as groups of marine turtles of the same species that inhabit areas essential for their life stages, including breeding, foraging, and juvenile growth. These turtles experience similar influences on their population dynamics, such as environmental factors, due to their overlapping geographic ranges, which may lead them to follow similar demographic and possibly evolutionary trajectories (Wallace et al., 2023). Eleven RMUs have been identified for green turtles, including two in the Atlantic Ocean, one in the Mediterranean Sea, two in the Indian Ocean, five in the Pacific Ocean, and one spanning the east Indian Ocean and the west Pacific (East Indian and Southeast Asia). Among these, the East Indian and Southeast Asia RMU—which includes Taiwan—was categorized as a Low Threat – Low Risk unit in the latest assessment (Wallace et al., 2025). Over the past decade, targeted conservation actions, which include beach protection, fishery regulations, establishing marine protected areas, and especially reducing direct take, have led to notable population recoveries in many green turtle RMUs (Mazaris et al., 2017; Rees et al., 2016; Senko et al., 2022).

Beyond their ecological roles in maintaining healthy seagrass beds and coral reef ecosystems (Bjorndal & Jackson, 2003; Goatley et al., 2012), green turtles and marine turtles in general also have significant socio-economic and cultural value. Historically, marine turtles were variously harvested for meat and eggs; however, with increasing awareness of population declines and the resulting need for conservation, people are now more inclined to support non-consumptive uses like ecotourism, rather than traditional harvesting (Troëng & Drews, 2004). In many regions, turtle-watching tourism generates greater and more sustainable income than direct exploitation, offering alternative livelihoods to coastal communities. This shift is also evident in Taiwan, where turtles were once widely captured for consumption, taxidermy, or ornamental trade, until they were listed as protected species under the Wildlife Conservation Act in 1989. Today, many people hope to encounter living marine turtles while snorkeling or SCUBA diving, and local marine tourism industries have developed around this interest in sustainable turtle-watching. Beyond being a tourism draw, in response to the increased need for conservation, individuals and businesses have also shown their support by donating to turtle rescue, rehabilitation, and research initiatives. Moreover, a recent study estimated that the annual non-use value of marine turtles in the Asia-Pacific region is approximately USD 25 billion. This increase in conservation-minded interactions with marine turtles has been hypothesized to be driven by motivations such as altruism (maintaining an ecosystem for others), bequest (for future generations), and existence (preservation unrelated to any use) even among people without direct interaction (Brander et al., 2024). Recognizing these multidimensional values is crucial for designing conservation strategies that are not only ecologically sound but also socially equitable and economically viable.

1.2. Foraging Grounds of Green Turtles and Hawksbill Turtles in East Asia

Five of the world's seven marine turtle species – green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys olivacea*), and leatherback (*Dermochelys coriacea*) – have been recorded in the East Asia region (Ng et al., 2024). Among these species, the green turtles and hawksbill turtles are the two most commonly observed species in the waters of Taiwan. Green turtles are endangered worldwide and have a broad distribution from the tropics and north to the coastal areas of central Japan and South Korea in the East Asia region (GBIF.org, 2023; Kim et al., 2021; Nishizawa et al., 2014). The Taiwan Strait, the South China Sea, and the western Pacific are also recognized as important migratory corridors for post-nesting green turtles in this region (Cheng, 2007; I. J. Cheng, 2000; Ng et al., 2018). The critically endangered hawksbill turtle (Mortimer and Donnelly, 2008) is primarily found in southern East Asia and the southern islands of Japan, with a northern range in the Kanto region in central Japan (Ng and Matsuzawa, 2021).

To assess the spatial extent of foraging grounds of green turtles and hawksbill turtles in East Asia, I conducted a literature review using Google Scholar to identify existing knowledge and gaps that informed the design of this PhD study. Search terms included "foraging habitat" or "foraging ground" in combination with "East Asia" or specific country names (e.g., Japan, Korea, China, and Taiwan), along with the common and scientific names of green turtles and hawksbill turtles. This review identified 82 potential foraging sites for green turtles (Fig. 1-1a) and 28 potential foraging sites for hawksbill turtles (Fig. 1-1b), documented through several methods, including satellite telemetry, stable isotope analysis, mark-recapture studies, stranding and bycatch records, and historical observations. For example, Ng et al. (2018) used satellite telemetry and home-range analysis to identify core post-nesting foraging areas of green turtles migrating through Taiwan and the Philippines. Fukuoka et al. (2015) revealed a summer-restricted foraging area in central Japan using bycatch and long-term mark-recapture data, later supported by stable isotope and biologging studies showing seasonal dietary shift (Fukuoka et al., 2019). Other data sources, such as poaching and stranding records, stomach content analyses, interviews with local fishers, and even media reports, have also been used to infer the presence of turtle aggregations (Chan et al., 2007; I.-J. Cheng et al., 2019; Kim et al., 2021; Nishizawa et al., 2010). More recently, Park et al. (2025) analyzed two decades of bycatch and stranding data in South Korea and found an increase in green turtle observations, particularly in the southern coastlines, suggesting previously undocumented developmental foraging grounds in Korean waters.

While this growing body of research has expanded our knowledge of spatial distribution and occurrence across East Asia, critical ecological and demographic information—such as age-class structure, site fidelity, and population dynamics—remains scarce at many sites. In-water surveys and long-term photo-identification or mark-recapture studies remain the most robust methods to confirm foraging ground function, providing quantitative data on local abundance, residency, and seasonal dynamics (W. H. Cheng et al., 2019; Kameda et al., 2023; Su et al., 2015). To date, only a limited number of locations—such as Kuroshima and Yaeyama Islands (Japan), and Liuqiu Island (Taiwan)—have implemented such monitoring efforts. To address these data gaps, coordinated and standardized monitoring approaches, including long-term capture-mark-recapture (CMR) programs, citizen science platforms, satellite tracking, and open-access databases are needed to better evaluate the ecological roles of foraging sites and to guide effective conservation strategies throughout the East Asia region.

While hawksbill turtle records provide valuable insights, they are relatively sparse and often limited to incidental observations (stranded cases) in Taiwan. In contrast, green turtles are more frequently documented and better studied across the region. In Taiwan, most of the in-water sightings and long-term monitoring efforts have focused on this species; therefore, in this thesis, we primarily focus on green turtles to facilitate more detailed analyses of their residency pattern and site fidelity.

1.3. Study objectives

Despite growing regional knowledge of green turtle foraging grounds in East Asia, significant gaps remain in our understanding of foraging green turtles in Taiwan. Most prior research in Taiwan has focused on nesting populations (Chen et al., 2010; Chen et al., 2007; Cheng et al., 2009; King et al., 2013), post-nesting migrations (I.-J. Cheng, 2000; Cheng et al., 2018), and strandings and/or fishery bycatch (I.-J. Cheng et al., 2019; Cheng & Chen, 1997; Huang, 2015), while foraging grounds and populations remain understudied. Although long-term stranding records indicate that juvenile and subadult green turtles frequently occur along Taiwan’s coastlines (I.-J. Cheng et al., 2019), few studies have directly examined the population status of these aggregations in situ.

Recent efforts using facial photo-identification (photo-ID) have confirmed the presence of a foraging aggregation in Liuqiu Island (W. H. Cheng et al., 2019; Su et al., 2015), demonstrating the feasibility of using individual-based monitoring techniques in Taiwanese waters. However, long-term, spatially replicated monitoring efforts across multiple sites are still lacking. As a result, essential demographic information remains poorly understood. These limitations hinder our ability to assess population trends, evaluate residency patterns, or detect emerging threats, all of which are necessary for informed management and conservation planning.

To address these gaps, this thesis focuses on three core objectives:

1. To identify the distribution and demography of foraging green turtles around Taiwan through citizen science and photo-identification (Chapter 2)
2. To quantify site fidelity of green turtles using standardized, multi-event in-water surveys in the foraging hotspot, Liuqiu, Taiwan (Chapter 3)
3. To evaluate the injury status and healing trajectory of injured turtles in the wild through repeated individual observations (Chapter 4).

Together, these efforts aim to fill key data gaps and provide a scalable framework for monitoring foraging marine turtle populations in Taiwan and East Asia.

1.4. Thesis outline

1. **Chapter 1:** General introduction
2. **Chapter 2:** Crowdsourcing Conservation: Unveiling Taiwan's Marine Turtle Foraging Grounds and Residency with Broad Societal Engagement
3. **Chapter 3:** Generating Representative Mark-Resight Data and Applying a Standardized Site Fidelity Index to Study Green Turtle Foraging Aggregations
4. **Chapter 4:** Injury and resilience: wild recovery of green turtles from various anthropogenic damages
5. **Chapter 5:** General discussion

1.5. Terminology and Definitions

This section provides definitions for terms frequently used throughout this thesis. The terms are grouped conceptually for clarity and listed alphabetically within each group.

1.5.1. Habitat use and site descriptions

Foraging habitat / Foraging ground

A geographically defined area or habitat where marine turtles feed, rest, and meet their nutritional needs. These areas are distinct from their nesting habitats and are essential for the survival, growth, and reproductive success of turtles throughout different life stages. These terms are used interchangeably and often refer to coastal or neritic zones supporting long-term occupancy and feeding activities (e.g., seagrass meadows, coral reefs, and algal meadows).

Foraging aggregation

A group of marine turtles utilizes the same foraging ground. These aggregations may consist of individuals of varying life stages and origins, and are often used as the unit for demographic and residency studies.

Main foraging ground

A principal geographic area where a substantial portion of a marine turtle population regularly feeds and sustains itself. In this study, a main foraging ground is defined as an area with over 100 turtle sightings or 50 confirmed individuals, along with direct in-water observations of feeding behavior over the monitored period. This term is used to distinguish such sites from other locations within the broader foraging region where turtles may occur but without clear or consistent evidence of foraging activity.

Foraging hotspot

A specific area within their broader foraging habitat where there is a particularly high concentration or aggregation of turtles feeding. These zones are characterized by especially favorable conditions, such as abundant food resources, optimal environmental parameters, or unique ecological features, causing numerous individuals to use the spot disproportionately more than surrounding areas.

Foraging site

A localized spot within a broader foraging ground where individuals are repeatedly sighted or recorded feeding.

Dive site

A specific location where in-water observations or diving surveys are conducted. These may overlap with foraging sites but are defined by survey effort rather than turtle behavior.

1.5.2. Individual presence and behavior

Minimum Residency Duration (MRD)

The presence of an individual in a given area over time. The MRD for each turtle was estimated based on total duration (days) between the earliest and latest recorded sighting (Hanna et al., 2021). Sometime, the term *residency* is used interchangeably with MRD.

Resident

In this study, individuals that remained within the same area for more than 365 days (one year) were classified as *residents*. This designation is used to distinguish relatively long-term site users from individuals who were observed only briefly or whose observed presence did not exceed one year.

Site fidelity

The tendency of an individual to consistently return to or stay in a specific area (e.g., foraging ground, nesting beach) for a specific period.

Permanence

Permanence is the proportion of time an individual was present in the study area, measured as the time between the first capture and last recapture, over the sampling period. It is used as an indicator of site fidelity.

Periodicity

Periodicity is the recurrence of an individual, determined by the inverse of the average time between successive recaptures. Distinct from permanence, periodicity implies temporary absence and return. It is also used as an indicator of site fidelity.

Standardized Site Fidelity Index (SSFI)

An index developed to quantify an individual's site fidelity based on the number and spacing of its sightings within a survey period. Values range from 0 (single sighting) to a theoretical maximum depending on the survey duration and sighting frequency.

Figures

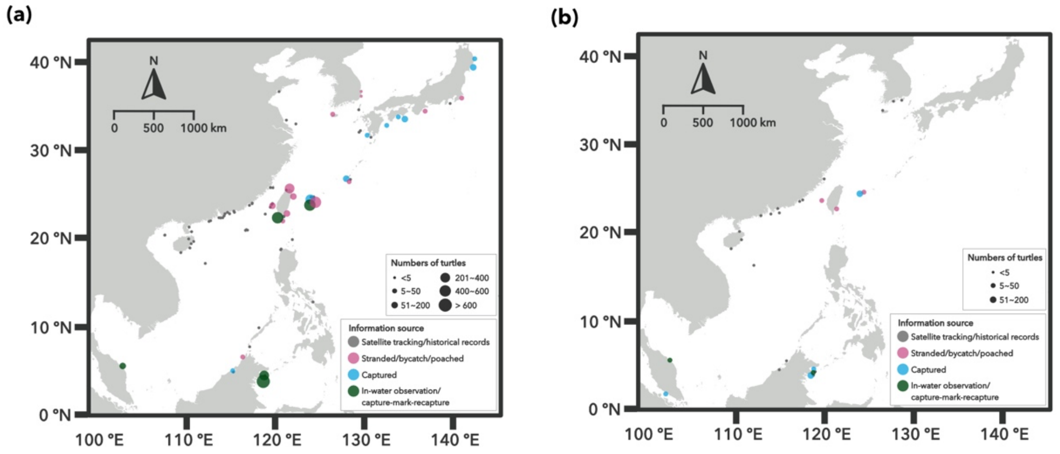

Figure 1-1. Potential foraging grounds of green turtles and hawksbill turtles in East Asia.

(a) Potential foraging grounds of green turtles (n = 82) and (b) potential foraging grounds of hawksbill turtles (n = 27) were identified through a literature review. **Circle colors** indicate the type of data source for each potential foraging ground: Grey represents satellite tracking data, reviews, and historical records with an unknown number of local aggregations; Pink represents the data derived from stranded, bycatch and poached studies, which may include both living and dead turtles; Blue indicates the locations where live turtles were captured for research purposes; Green indicates the sites confirmed through in-water observations or long-term mark-recapture studies, providing evidence of feeding behavior and the numbers of local aggregations.

CHAPTER 2

Crowdsourcing Conservation: Unveiling Taiwan's Marine Turtle Foraging Grounds and Residency with Broad Societal Engagement

2.1. Abstract

Determining marine turtle foraging grounds, emerging threats, and population status are essential for conservation management. Crowdsourced science is a recently recognized approach that enables internet-based data collection, providing important contributions to scientific goals while also benefiting society and public education. This study is based on the published dataset from TurtleSpot Taiwan (2017–2022) to leverage crowdsourced data to determine marine turtle foraging grounds, emerging threats, demography, and residency patterns in Taiwan. We identified three main foraging grounds of green turtle (*Chelonia mydas*) in Taiwan (Liuqiu Island, Kenting, and Green Island), defined as sites with > 100 sightings and direct observations of feeding behavior. Among all sites, Liuqiu Island contributed 77% of the total sightings, suggesting this island is a hotspot. Emerging threats to foraging aggregations of marine turtles in Taiwan were evident from the reported sightings, with ~ 10% of the total sightings involving turtles with fishing line entanglement, ingested debris, missing flippers, or injuries. Most of these sightings occurred in Liuqiu Island, indicating a significant level of human-turtle disturbance. Residency patterns identified from sighting data showed that 43.4% of individuals stayed in the same area for one or more years, with adult-sized turtle residency greater than that of immature turtles. Taiwan supports healthy foraging grounds for green turtles, where adults often stay for more than one year and with dynamic populations of younger individuals. However, despite

a certain number of foraging green turtles observed in Liuqiu Island, many of these turtles displayed injuries. This high population density combined with increased injury frequency suggests that a comprehensive management plan for turtle foraging grounds is urgently needed, including measures to reduce boat speeds in hotspot areas and strict regulations on coastal human activity.

2.2. Introduction

As migratory megafauna, marine turtles have a complex life cycle requiring unique life stage-dependent nesting and foraging habitats (i.e., hatchling, juvenile, sub-adult, and adult) (Spotila, 2011). Historically, marine turtle research and conservation efforts have focused on nesting habitats, while their foraging grounds are less understood (Mazaris et al., 2014; Robinson et al., 2023). Determining the distribution of and the population dynamics within key foraging grounds has been recognized as a global research priority for marine turtle conservation (Hamann et al., 2010), ecology, and conservation management. Despite significant progress in addressing these knowledge gaps, progress remains limited by a bias towards specific questions, species, and regions, highlighting the need for greater engagement with social sciences and a broader range of contributors (Rees et al., 2016).

Five of the world's seven marine turtle species – green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys olivacea*) and leatherback (*Dermochelys coriacea*) – have been recorded in the East Asia region (Ng et al., 2024). Among these species, green and hawksbill turtles are the two most common species historically observed in the waters of Taiwan (I. J. Cheng et al., 2019). Many studies have attempted to identify potential foraging grounds for green and hawksbill turtles in East Asia through various methods, including historical records, bycatch, mark-recapture studies, stable isotope analysis, and satellite tracking (Chan et al., 2007; Ng et al., 2018; Nishizawa et al., 2013; Shimada et al., 2014); however, crucial information such as demography and residency of local aggregations remain lacking. This gap is understandable as both measures require direct in-water surveys and long-term mark-recapture studies, both of which are logistically challenging given the necessary person-hours and financial investments to provide the required resolution of data. Properly moderated citizen science and crowdsourced data collection projects can offer a way to alleviate these logistical hurdles and thereby address the standing knowledge gaps on both local and global scales.

Citizen science (CS) broadly refers to the engagement of the general public in scientific research and has existed for centuries in various forms (Frigerio et al., 2021) but has in recent decades expanded dramatically in both scope and application (Fraisl et al., 2022). The current use of crowdsourced data through CS has proven powerful in generating ecological knowledge (Fraisl et al., 2022), improving conservation science, and enhancing environmental protection (McKinley et al., 2017). The term citizen science is often used interchangeably with related terms such as community science, volunteer monitoring, participatory science, and public science. Notably, the term “citizen” is inclusive and does not imply legal citizenship; rather, it refers to all members of society (e.g., residents, visitors, students, and others) who contribute to scientific inquiry. Crowdsourced science, a subset of CS that utilizing internet connectivity to recruit large groups of volunteers who would otherwise be disconnected for the purpose of problem-solving scientific projects, has the potential to expand societal participation and reduce associated costs of acquiring data (McKinley et al., 2017).

While providing opportunities for increased data collection, including higher temporal and spatial resolution, with minimized logistical limitations to the researcher, CS and crowdsourced conservation projects have their own sets of challenges. These challenges include improving participant engagement and retention, establishing comprehensive project evaluations, and developing better communication strategies (Kelly et al., 2020), while also mitigating potential challenges in data quality, and data coverage (Lukyanenko et al., 2016). For crowdsourced science to provide data in both the quantity and quality needed for scientific purposes, it is necessary for projects to include standardized data collection protocols, means of quality-assurance, engaging community involvement (co-creation), and venues to share data and knowledge with the public (Fraisl et al., 2022; B. L. Jones et al., 2018).

Photographic identification (photo-ID) methods that use unique body patterns for individual identification provide an innovative avenue for researchers and citizen scientists to study animals in their native habitats (Armstrong et al., 2019). The distinctive facial and flipper scale patterns of marine turtles have been validated as reliable natural markers for each individual for studying their in-water biology and ecology (Carpentier et al., 2016; Dunbar et al., 2014; Mills et al., 2023; Schofield et al., 2008). The recent availability of digital platforms, affordable underwater cameras, and photo-ID software (e.g., I3S, HotSpotter, Internet of Turtles) facilitated the emergence of photo-ID CS projects to reveal the population status of foraging turtles (Hancock et al., 2023; Hanna et al., 2021; Hudgins et al., 2023; Long & Azmi, 2017).

TurtleSpot Taiwan is a citizen science project launched in June 2017 on social media platform (https://www.facebook.com/groups/turtlespotintw; Facebook, Meta) with the dual aim of collecting sighting reports of marine turtles for identifying foraging grounds in Taiwan and providing a portal for public education. Engaging over 20,000 group members, TurtleSpot Taiwan’s key innovations were establishing a publicly accessible marine turtle photo-ID database website (https://turtlespottw.org/) that allows users to search and provide optional functions for users to identify their documented/photographed turtles. This database has standardized data collection protocols to enhance data quality, and employs numerous interactive measures to foster community engagement and enhance societal engagement.

Hoh and Fong (2022) and Hoh et al. (2022) previously published occurrence open-access datasets from TurtleSpot Taiwan data between 2017-2022, along with metadata and data collection methodology. Here, we provide the first analysis of these datasets and identify the foraging grounds, emerging threats, demography, and residency of marine turtles in Taiwan. To examine the effectiveness and scope of crowdsourced conservation, we further analyzed citizen scientist participation and retention trends over five years of TurtleSpot Taiwan’s implementation.

2.3. Materials & Methods

2.3.1. Crowdsourced conservation project: TurtleSpot Taiwan

TurtleSpot Taiwan was founded by a group of volunteers from different backgrounds, including scientists, dive instructors, underwater photographers, and ocean advocates. We engaged the public through online interactions, in-person workshops, and educational outreach events throughout the implementation of this project. The online interactions included: (1) Naming turtles: We invited sighting reporters to name the turtles, increasing incentive and building their connections to marine turtles (also see Hoh et al., 2022); (2) Feedback: The group administrator provided feedback, shared photo-ID results, responded to questions, and updated information about individual turtles to sighting posts; and (3) Marine Turtle Nerdy

Award: Each year citizen scientists with the top ten number of reports were announced and acknowledged in the Facebook Group.

A four-step systematic approach to data quality assurance was employed throughout the project (Fig. 2-1). (1) Data submission: The group administrator thoroughly checked the completeness of reported sightings and guided citizen scientists as needed; (2) Photo-ID: The group administrator verified HotSpotter-assigned photo-ID results, checked the correctness of the entered data and downloaded images from the previous step. HotSpotter is a computer-based software that uses pattern recognition algorithms to identify individual animals based on unique natural markings (Crall et al., 2013); (3) Responding to posts with photo-ID results: While replying to the post, the group administrator manually verified the accuracy of the photo-ID result again; (4) Open data preparation: The dataset underwent a comprehensive examination, including verification, cleaning, transformation, and standardization, to ensure compliance with GBIF publication criteria (Hoh & Fong, 2022) under assigned licenses. For a detailed methodology employed in preparing and publishing the dataset, refer to the corresponding data paper (Hoh et al., 2022). The complete dataset described in Hoh et al. (2022) including sighting data and time, dive site location (GPS coordinates and place name), observer information, photographic documentation, turtle species, estimated age-class group, visible injuries or abnormalities, sex (if determinable), observation method (e.g., snorkel, SCUBA, land-based), and, when available, water depth.

Data use and privacy policy terms were described on both the Facebook page and photo-ID database website to protect the copyright of data contributors, authorizing TurtleSpot Taiwan to conduct research and non-profit educational activities while acknowledging that the media copyrights remained with the respective photographers.

Any use of contributed multimedia materials adhered to the Creative Commons Attribution-NonCommercial (CC BY-NC) license.

2.3.2. Marine turtle sighting and distribution in Taiwan

A total of 760 marine turtle individuals were identified and documented on the photo-ID database of TurtleSpot Taiwan, including *C. mydas* (n = 724), *E. imbricata* (n = 35), and *L. olivacea* (n = 1). To study the diversity and abundance of different species of marine turtles around Taiwan, density distribution maps for all marine turtle sightings, individual turtles and participating citizen scientists were generated in R using mapdata (version 2.3.1), sf and ggplot2 (Pebesma & Bivand, 2023; Pebesma, 2018; Wickham, 2016), and modified with Affinity Designer (version 1.10.5).

2.3.3. Foraging grounds, demographic structure and residency of green and hawksbill turtles

Main foraging grounds were identified as areas that have received a high number of sightings (> 100 sightings) along with direct in-water observations of feeding behavior over the monitored period. This study mainly focused on evaluating foraging grounds, demographic structure, and residency for green and hawksbill, as these species are the two most common marine turtles in Taiwan.

To determine the demographic structure of marine turtles, turtle body size was visually estimated from whole-body photographs and categorized into different life history stages (post-hatchling, juvenile, subadult, or adult), combined with the carapace color pattern and marginal scute roundness characteristics and descriptions provided by the reporters. Turtles that lacked a whole-body image and estimated size information were recorded as life stage ‘unknown’. We used previously published straight carapace length (SCL) measurements and carapace characteristics to categorize all sighted turtles into putative age classes as follows: For green turtles, post-hatchling SCL of 10 to 20 cm, juvenile SCL < 65 cm with sunburst patterns on each scute, subadult SCL of 65 to 90 cm with camouflage patterns on each scute, and adult SCL > 95 cm with variously light and dark spotting on the carapace (Caldwell, 1969; Witherington et al., 2006; Witherington & Witherington, 2015; Fig. S2-1). For hawksbill turtles, post-hatchling SCL of 8 to 22 cm, juvenile SCL of 23 to 50 cm, subadult SCL of 50 to 80 cm, and adult SCL > 80 cm (Avens et al., 2021; Meylan & Redlow, 2006; Wood et al., 2017Fig. S2-1). For olive ridley turtles, adult SCL from 53 to 79 cm, with a median size of 60 cm at sexual maturity (Zug et al., 2006). The identification of sex in adult-sized turtles was limited to males, defined as individuals having tail lengths exceeding 25 cm (visually longer than the rear flippers) (Wibbles, 1999). Since it is not possible to definitively determine the sex and sexual maturity of marine turtles with short tails, turtles with tail lengths of 10 to 15 cm (visually shorter than rear flippers) or with no visible tail were classified as sex unknown.

To examine the residency of the marine turtles, minimum residency duration (MRD) of green and hawksbill turtles was calculated and plotted separately. The MRD for each turtle was estimated based on total duration (days) between the earliest and latest recorded sighting (Hanna et al., 2021). Individuals who stayed in the same area for more than 365 days (1 year) were considered residents. To study variations of MRD and number of sightings among estimated age-class groups (i.e., juvenile, subadult, or adult-sized), only green turtles were included due to low sample sizes for other species. Variations in MRD and the number of sightings per individual across different estimated age-class groups were examined using One-Way Analysis of Variance (One-Way ANOVA; factor: estimated age-class groups) in SigmaPlot 11 (Graffiti LLC). The dataset included 428 green turtle individuals from six areas: Northeastern coast, Penghu, Green Island, Liuqiu Island, Kenting, and Hualien. The MRD values passed the equal variance test ($p = 0.509$) without requiring transformations. The number of sightings per individuals were square root transformed twice and passed the equal variance test ($p = 0.118$).

2.3.4. Participation and retention of citizen scientists

The publicly accessible TurtleSpot photo-ID database website houses information and images of documented turtles, featuring a filter function that enables users to search using keywords (e.g., number of the post-ocular scutes, morphological features, location, species, age-class, turtle ID number, or turtle name). This allows citizen scientists to browse through the image database to manually identify the turtles they photographed. To assess citizen science participation, we counted the number of citizen scientists who attempted to identify the turtles they sighted at the individual level, using the photo-ID database website or other means. Regardless of identification accuracy, these attempts were used as an indicator of the involvement level of citizen scientists.

The number of new and retained citizen scientists from previous years was analyzed for each year from 2017-2022 to assess the recruitment and retention trends of TurtleSpot Taiwan. Retention of citizen scientists was calculated as the total duration (in days), including both the first and the last sightings reported by an individual to the Facebook Group. A Pearson correlation coefficient analysis was conducted to examine the correlation between the number of sightings contributed by each participant and their retention time, visualized with a scatter plot in SigmaPlot 11. To avoid bias, sightings directly provided by citizen scientists to us without posting to the Facebook Group were excluded from the above analysis.

2.4. Results

2.4.1. Distribution of foraging grounds and demographics of marine turtles

The majority of the turtles identified from sightings were from Liuqiu Island (83.9%, 3024 sightings and 584 individuals), followed by Kenting (6.6%, 239 sightings and 66 individuals) and Green Island (5.1%, 182 sightings and 57 individuals), all of which serve as foraging grounds for green turtles (Fig. 2-2a). We observed a steady increase in the number of unique individuals recorded over time, with an average of 127 (range: 60 to 201) new individuals recorded each year (Fig. 2-2b), resulting in a total of 760 individuals as of May 2022. For the estimated age-class groups of *C. mydas,* 61.3% (n = 444) of documented turtles were juveniles, 26.2% (n = 190) were subadults, and 12.4% (n = 90) were adults (Fig. 2-2c). Among the adult-sized green turtles, 33 individuals were identified as males. For *E. imbricata,* 74.3% (n = 26) were juveniles, 17.1% (n = 6) were subadults, and 5.7% (n = 2) were adults (one identified male), with one individual identified as a post-hatchling (Fig. 2-2c).

In addition to identifying turtle foraging grounds, sighting data highlighted emerging threats to foraging aggregations of marine turtles in Taiwan, such as boat strikes, propeller injuries, and marine debris. Nearly 10% (n = 358) of total sightings involved turtles with fishing line entanglement or with ingested debris (i.e., plastic bags, fishing lines and ropes) observed protruding from the anus (1.5%, n = 53), missing flippers or injuries to flippers (3.2%, n = 116), or carapace injuries (5.3%, n = 189). There were 114 injury-related turtles, comprising 106 green turtles (346 sightings), 8 hawksbill turtles (10 sightings) and two sightings for which neither species nor individual was identified. Most of these sightings (93.3%, n=334) were from 98 turtle individuals and occurred at Liuqiu Island (Table 2-1), indicating a significant level of human-turtle interaction in this area.

2.4.2. Minimum resident duration (MRD) of turtle individuals

A total of 723 green turtles (sightings n = 3,201) and 35 hawksbill turtles (sightings n = 70) were included in MRD analysis after excluding records with incomplete date information (n = 5). Of these, 295 green and 22 hawksbill turtles were categorized as "non-resighted" because they were only sighted once (green n = 287; hawksbill n = 22) or only had multiple same-day sightings (green n = 8). The resighting rates of green and hawksbill turtles were 59.2% (n = 428) and 37.1% (n = 13), respectively, with the number of re-sightings per individual ranging from 2 to 47 (mean: 4.56, SD: 6.47). Among resighted green turtles (n = 428), 74.3% (n = 318) stayed in the same area for one or more years (i.e., resident turtle), and 25.7% (n = 110) stayed for less than one year (Fig. 2-3a). Resident green turtles (MRD ≥ one year) were mainly distributed in southern Taiwan (Fig. S2-2) at Liuqiu Island (n = 280), Kenting (n = 18), and Green Island (n = 15). Among resighted hawksbill turtles (n = 13), 15.4% (n = 2) stayed for less than one year (Fig. 2-3a) and 84.6% (n = 11) were resident turtles, mainly in Liuqiu Island (n = 6) (Fig. S2-2). Juvenile green turtles contributed more than half of the proportion of non-resighted, < 90 days, 90 – 364 days and 1 – 2 years groups (Fig. 2-3b). However, the proportion of turtles with larger body sizes (estimated as subadults and adults) generally increased with longer MRDs. In the > 2 years MRD category, juveniles accounted for 46.9%, while subadults and adult-sized turtles made up 28.8% and 24.3%, respectively (Fig. 2-3b). Green turtle mean MRD increased with age-class, from juvenile (775 days), subadult (882 days), to adult-sized turtles (1,182 days). Adult-sized turtles had significantly greater MRD than juveniles and subadults (One Way ANOVA, $F_{2, 425} = 13.36$, $p < 0.001$, SNK: adults > juveniles = subadults; Fig. 2-2c). Adult-sized turtles had a significantly higher resighting rate (average 10.12 times per individual) than both juveniles (5.71 times per individual) and subadults (6.75 times per individual) (One way ANOVA, $F_{2, 425} = 14.67$, $p < 0.001$, SNK: adults > juveniles = subadults; Fig. 2-2d).

Additionally, the longest MRD recorded to date was 3,502 days (ID: TW01G0049; 28 sightings), documented in an adult-sized green turtle with carapace injuries and scars, presumably female, from Liuqiu Island. The longest interval between two consecutive sightings was 1,604 days (ID: TW01G0034) documented in a subadult green turtle from Liuqiu Island. This single individual was recorded at a deep boat diving site, which is likely less frequently visited by divers, potentially explaining the extended gap between sightings.

2.4.3. Participation and retention of citizen scientists

From a total of 2,324 sightings contributed by 442 citizen scientists directly to the Facebook group platform, nearly 30% (n = 683) of the sightings were manually identified by 99 individual citizen scientists, indicating their engagement beyond mere data contribution. From June 2017 to May 2022, the annual number of turtle reporters ranged from 95 to 148, with an average of 122 ± 20 citizen scientists per year. In each year, about 67% of reporters were new participants (ranging from 61% to 75%). In comparison, 33% were retained from the previous years (Fig. 2-4a). The consistent influx of new participants in each year highlights sustained public interest in the initiative and the project's effectiveness in recruiting contributors. The number of sightings per citizen scientist ranged from 1 to 339, with 52.7% (n = 233, including one project co-founder who is non-scientist) contributing a single sighting, 34.8% (n = 154) reporting 2 – 5 sightings, 11.1% (n = 49, including one co-founder) reporting 6 – 50 sightings, and 1.4% (n = 6, including one co-founder and one highly involved volunteer, both of whom are non-scientists) reporting more than 50 sightings (Table S2-1). These contributions accounted for 10%, 18.7%, 31.6%, and 39.7% of the total sightings, respectively. Participant retention duration ranged from one day to 1,789 days. Among the citizen scientists, 61.3% (n = 271, including one author) contributed their sightings on a single day, while 19.9% (n = 88) contributed within a one-year period (2 days – 1 year), 8.8% (n = 39) contributed over 1 to 2 years, 3.8% (n = 17) over 2 to 3 years and 4.5% (n = 20, including one author) over 3 to 4 years. Lastly, 1.6% (n = 7, including two authors) contributed sightings consistently across all five years (Table S2-1). A significant moderate positive correlation (Pearson correlation coefficient = 0.44, $p <$ 0.001) was observed between the number of sightings reported by each participant and their retention time (Fig. 2-4b).

2.5. Discussion

2.5.1. Foraging marine turtles in Taiwan

Direct in-water sighting data showed that Taiwan's coastal waters, especially Liuqiu Island, Green Island, and Kenting, are main foraging grounds for green turtles and host a smaller aggregation of hawksbill turtles, represented by individuals of all size groups but dominated by juveniles (61% and 74%, respectively). The foraging grounds of marine turtles surrounding Taiwan exhibit diverse ecological characteristics. Liuqiu Island and Kenting primarily feature fringing reefs, intertidal zones, and small sporadic seagrass beds along their coastlines. Many reefs in these areas are algae-dominated reefs, especially turf algae (Kuo et al., 2023; Lin et al., 2024) making them preferable foraging sites for herbivorous green turtles. This dominance of juveniles in foraging grounds is comparable to that of green turtles in the Japanese Kuroshima Islands (79.9% juveniles) and Yaeyama Islands (1995 – 2003: 88%; 2004 – 2016: 78%) to the north (Kameda et al., 2017; Kameda et al., 2023), as well as Malaysian Mabul Island (78.9%) and Semporna (49%) to the south of Taiwan (Joseph et al., 2022; Palaniappan et al., 2022). In the Great Barrier Reef, foraging grounds typically host a greater mix of life stages, but with juveniles still comprising the majority (approximately 80.5%) (K. Jones et al., 2018). The ratio of juveniles in Taiwan's coastal foraging aggregations (61%) lies in between the values at these other locations. The variation in juvenile dominance among regions may influenced by differences in habitat characteristics and food availability. For example, the foraging habitats in the Great Barrier Reef are coral reef dominated (K. Jones et al., 2018), while Kuroshima Islands and Yaeyama Islands feature coral reef habitats mixed with seagrass and algae (Kameda et al., 2017; Kameda et al., 2023), and Semporna and Mabul Island combines coral reef with seagrass meadows (Bujang et al., 2006; Joseph et al., 2022; Palaniappan & Hamid, 2017; Palaniappan et al., 2022). The foraging grounds in Taiwan are mainly algae-dominated reefs. Variations in food availability among these different habitats may contribute to the differences in the demography of marine turtles across regions. Temporal shifts in food availability can also contribute to different age-class demographics. In Bermuda, a decline in seagrass availability may have driven the emigration of juveniles before maturation, altering the demographic structure of the aggregation (Meylan et al., 2022). Mortality rates of turtles can also affect the demographic composition of foraging aggregations. For instance, in the Yaeyama Islands, the decline of the marine turtle fishery due to increased conservation awareness led to a 10% rise in the proportion of larger-sized turtles during 2004-2016 compared to earlier periods (Kameda et al., 2017). Establishing long-term monitoring programs in Taiwan could help track demographic shifts and provide insights into site-specific ecological roles.

Steady increases in newly sighted individuals each year and a high ratio of juvenile turtles suggest a healthy recruitment pattern in these foraging grounds (Kameda et al., 2017). Our study also found that adult-sized turtles have significantly longer residency durations and higher resighting frequencies than immature turtles. A contrasting trend, where adults have lower residency indices than juveniles and subadult green turtles has been observed in Australian foraging grounds (Pillans et al., 2022). However, home ranges and core areas can be highly variable among tracked turtles (Pillans et al., 2021; Seminoff et al., 2002; Siegwalt et al., 2020), which may influence the resighting probability of turtles in photo-ID-based surveys. Lower resighting rates and shorter residency of juveniles and subadults might present a methodological bias for opportunistic in-water sighting data, or suggest a more dynamic assemblage within these aggregations. Current understanding of their habitat shifts in this region remains limited. Ng et al. (2018) tracked four rehabilitated and released immature green turtles: one turtle released from Dongsha migrated to the Philippines over 143 days, while three turtles released from Kenting remained within Taiwanese waters (tracking duration ranging from 124 to 188 days). Two of these turtles returned from their release sites to the areas where they were originally found stranded or bycaught. These findings suggest that immature turtles can have high variability in home ranges or dynamic movement patterns, with some traveling large geographical distances, making them less frequently observed by volunteer turtle watchers.

Our study showed an increasing temporal trend in marine turtle residency over the past decade. W. H. Cheng et al. (2019) surveyed 432 individual turtles at Liuqiu

Island from 2011 to 2017 and found that around 10% remained for more than one year. Our study found that from 2017 to 2022, of 584 identified individuals, 49% stayed for over a year. It is possible that the habitat conditions of Liuqiu Island have become more suitable for foraging turtles since 2017. Two adult-sized turtles (short tail, presumed female) with flipper tags from the Secretariat of the Pacific Regional Environmental Programme (SPREP) were sighted in Liuqiu Island multiple times each between 2017-2022 and 2022, respectively, indicating this foraging ground is also utilized by adults following ontogenetic emigration. This suggests that the foraging grounds around Taiwan, particularly Liuqiu Island, support all turtle life stages of turtles and are therefore of heightened conservation importance.

Our study also identified a small number of resident turtles on the northeastern coast of Taiwan which supports previous suggestions (I. J. Cheng et al., 2019) that this area could be a foraging ground for green turtles. The benthic community on the northeastern coast consists mainly of turf algae, macroalgae, and non-reefal coral communities (Kuo et al., 2023), which may contain a high abundance of Rhodophyta and Chlorophyta, the main diet of green turtles in reef ecosystems (Santos et al., 2015).

One factor to consider is that the foraging grounds identified in this study may be biased toward sites more accessible for diving. For instance, Penghu has a notable number of marine turtles documented through fishing industry bycatch (I. J. Cheng et al., 2019) but showed low sightings in our data. This may be due to the high turbidity of Penghu’s waters, which likely increased the difficulty of sighting and recording turtles in the area. Potential biases can occur in opportunistic observation databases, such as over-representation of common species (Isaac & Pocock, 2015) and over-sampling of accessible locations (Reddy & Dávalos, 2003) due to uneven sampling efforts. However, such bias can be mitigated by applying photo-ID at the individual level in this study, thereby reducing the likelihood of overestimation. In contrast, Liuqiu Island, a popular diving destination with frequent turtle encounters, yielded significantly more sightings. This higher resolution data enabled more reliable estimates of residency and population trends, offering a closer reflection of reality-based population distribution.

2.5.2. Habitat Connectivity

Sightings of individuals with flipper tags can provide valuable information about their previous foraging grounds or nesting sites, offering insights into habitat connectivity. This project recovered five turtles with flipper tags, three of which had visible tag numbers: An olive ridley turtle (PH1004M/PH1005M) originally tagged and released from Cabangan, Zambales, the Philippines, in January 2018, was found alive (bycatch) in September 2018 along the east coast of Taiwan (Hualien County); a subadult green turtle (KK3 0125) originally tagged and released from Ishigaki Island, Okinawa, Japan, in 2003 was found alive (bycatch) in 2020 along the east coast of Taiwan (Hualien County); a green turtle (R36192; https://turtlespottw.org/turtle-profile/TW01G0082), was an adult nesting female from Ulithi Atoll, Yap State, Federated States of Micronesia, where it nested in 2006 and 2012. Notably, this third turtle was first observed at Liuqiu Island in 2011 and has been frequently seen foraging at the same site from June 2017 to May 2022, indicating that this individual has migrated between Ulithi Atoll and Liuqiu Island (2,500 km apart) at least twice (Fig. 2-5). In additional, both front flipper tags (R36192/R36191) of this turtle were intact during its first sighting in 2011. By 2017, only one tag (R36192) remained, which was subsequently lost in Feb 2020. The information gleaned from these tagged turtles corroborates previous studies using satellite tracking and molecular techniques, which demonstrated that Yap in the Federated States of Micronesia and Yaeyama of Japan are potential source rookeries for the green turtle foraging aggregations around Taiwan (Kolinski et al., 2014; Ng et al., 2024). These observations underscore the importance of understanding marine turtle migratory patterns and habitat use across international boundaries and highlight the scientific significance of the collective efforts of citizen scientists to enhance the conservation of marine turtles.

2.5.3. Operation and maintenance of an extensive crowdsourced conservation network

After seven years of operation (as of 19 August 2024), TurtleSpot Taiwan Facebook Group has more than 21,723 members from diverse sectors of society, including SCUBA and free divers, scientists, schoolteachers, and students, among other members of the general public. Member profile data described a diverse cohort of participants, with a nearly even male-to-female ratio (45% and 55%, respectively), an age range of 13 to +65 years old (majority within the 35-44 range; 39%). However, only about 2% of these members have actively contributed turtle sightings, indicating that much of the engagement represents passive support, such as expressing interest in the initiative, rather than active participation. This low proportion of contributors may also stem from logistical barriers associated with data collection, as accessing turtles in their natural habitats typically requires SCUBA diving or snorkeling, which may limit broader involvement.

Despite strategies developed to increase public participation (Martin & MacDonald, 2020; Tang et al., 2019; Wald et al., 2016), recruitment and retention of citizen scientists remains an ongoing challenge that limits the efficacy and usefulness of many existing projects. To maintain recruitment, TurtleSpot Taiwan actively engages the public through in-person workshops, educational outreach events, and online interactions, such as inviting citizen scientists to name the turtles they reported and providing feedback and photo-ID results to sighting posts. These initiatives likely contributed to the good number of recruitments of new participants, with nearly two-thirds of participants each year being newcomers. However, our analysis on participant retention revealed that most participants (52%) contributed only once and only a small proportion (12.4%) contributed more than five reports. Correlation analysis indicated that participants with multiple contributions tended to remain active in TurtleSpot Taiwan for longer periods. For instance, 70% of those contributing more than five reports demonstrated retention of over one year. Similar patterns were also identified in other studies, where most contributors participated only once and with minimal effort, while a relatively small percentage of contributors showed higher activity (Sauermann & Franzoni, 2015; Seymour & Haklay, 2017). Meanwhile, although 52% of participants were single-time contributors, this ratio is still lower compared to other environmental CS projects, where single-time contributors often account for higher proportions (e.g., 72%; Seymour and Haklay (2017)). To increase participation and retention levels, conducting surveys or interviews to understand the motivations of citizen scientists (Land-Zandstra et al., 2021), providing more regular updates on the project's progress, and implementing a system of milestones to encourage sustained engagement can be further integrated into the current project framework. Additionally, a more detailed evaluation on the engagement of group members could distinguish between active participants and passive supporters. Their interaction with community through metrics such as comments, reactions (likes, shares), or attendance at educational outreach events or workshops can be further explore in future studies to understand patterns of involvement and develop strategies to convert passive supporters into active contributors.

2.5.4. Conservation implications

Our analyses found that nearly 10% of sightings included observations of at least one category of injury. This high frequency of injured turtles could be due to human prejudice, as citizen scientists are more prone to report rare and charismatic species or events (Deacon et al., 2023; Snäll et al., 2011), leading to over-reporting of injured turtles; however, it also suggests increased human activity and tourism (Chen, 2015), may be stressing local foraging aggregations, similar to the effect seen in other regions (Papafitsoros et al., 2021). These data suggest that a comprehensive management plan is urgently needed, including measures to reduce boat speeds in hotspot areas and strict regulations on coastal human activity (e.g., rock fishing, sewage treatment, and coastal construction) to benefit these flagship species and the broader marine ecosystem.

Conservation efforts can make use of crowdsourced data to complement field-based research by covering a larger geographic area while engaging a broader public in conservation efforts. However, achieving high-quality spatial data requires substantial resource investment, including building strong community partnerships (Brown et al., 2018). Working toward a community contributory approach in the main foraging grounds (e.g., Liuqiu Island, Kenting, and Green Island), where local participants are actively involved in data collection, analysis, or decision-making, should be the conservation focus moving forward. The present crowdsourced conservation platform can further develop for international collaboration projects studying global marine turtle foraging grounds or contribute to the Internet of Turtle, a web-based photo-ID system with a worldwide database (Lesile et al., 2016). Our study provides evidence that this citizen science platform is important in providing reliable, long-term global monitoring data for tracking changes in marine turtle aggregations and foraging grounds, enabling adaptive management strategies that can respond effectively to global climate change issues.

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Tables

Table 2-1. Number of injury-related sightings and turtle individuals at each location in Taiwan.

Location	**Total injury-related sightings**	**Unique individuals with injury-related sighting**	**Injury related sightings at each location (%)**
Liuqiu Island	334	98	11.04
Kenting	8	5	3.35
Northeastern coast	4	1	5.26
Green Island	4	3	2.20
Kinmen	2	2	28.57
Orchid Island	2	2	8.00
Penghu	2	1	6.90
Dongsha	1	1	100.00
Yilan	1	1	25.00

Figures

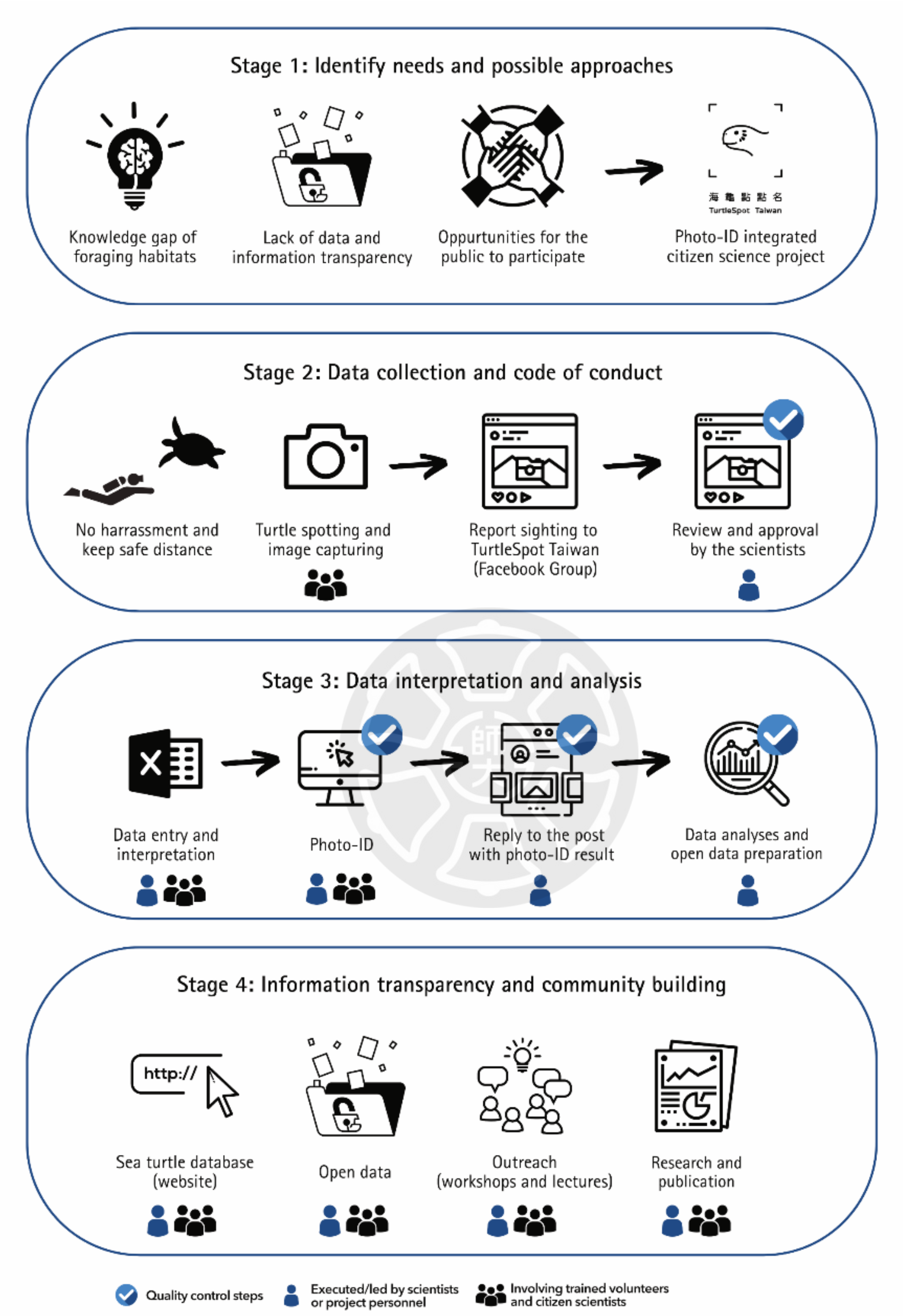


Figure 2-1. Overview of TurtleSpot Taiwan: needs identification, data collection, analysis, and community building.

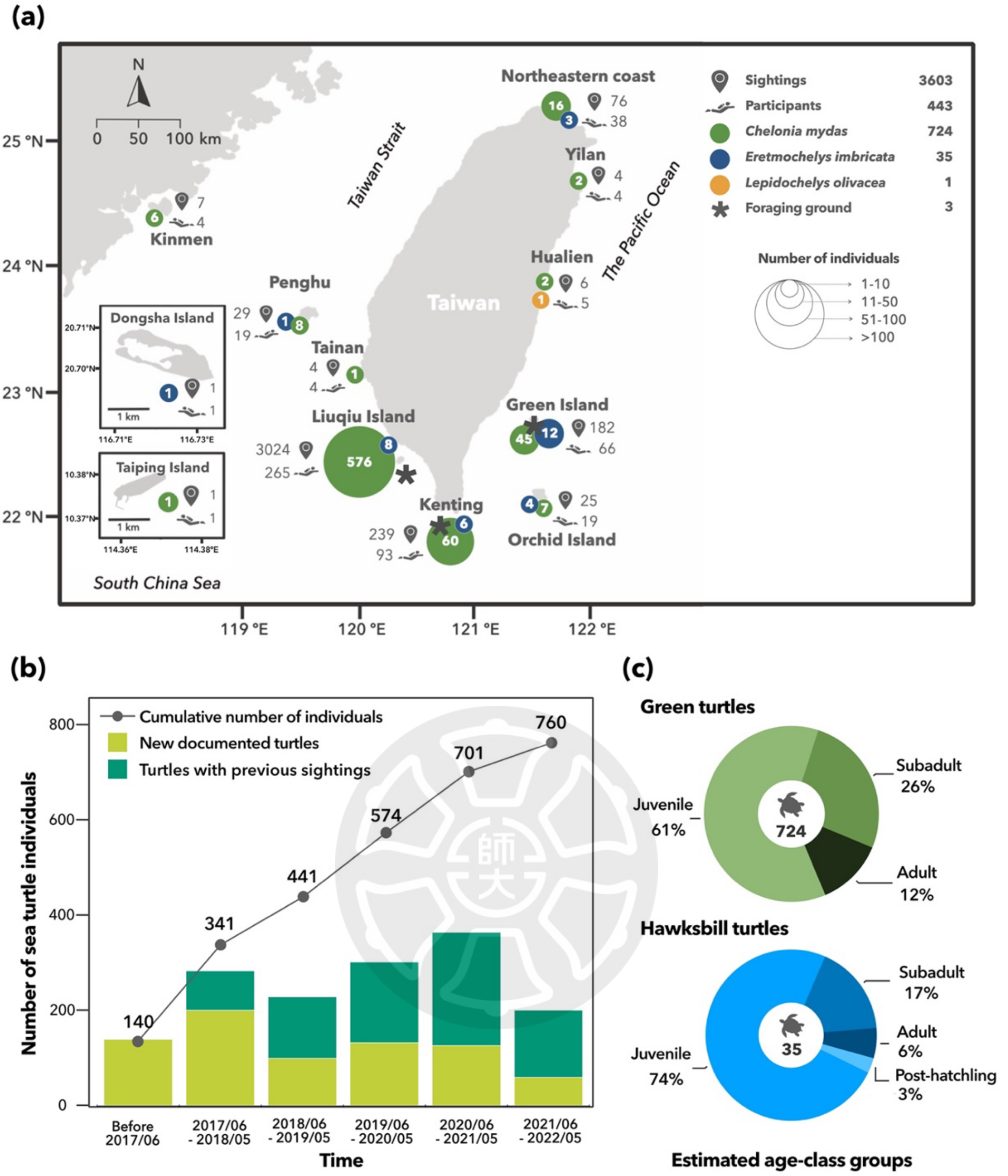


Figure 2-2. Distribution of documented turtles around Taiwan, their annual population trends, and demographic structure.

(a) Spatial distribution of sightings (pin marker symbol), participants (diver symbol), and documented turtles (circle). The color and size of the circle represent the species and the number of individuals, respectively. (b) Annual variations in numbers of marine turtle individuals and line chart showing the cumulative number of recorded turtles. (c) The proportion of estimated age-class groups of green and hawksbill turtles.

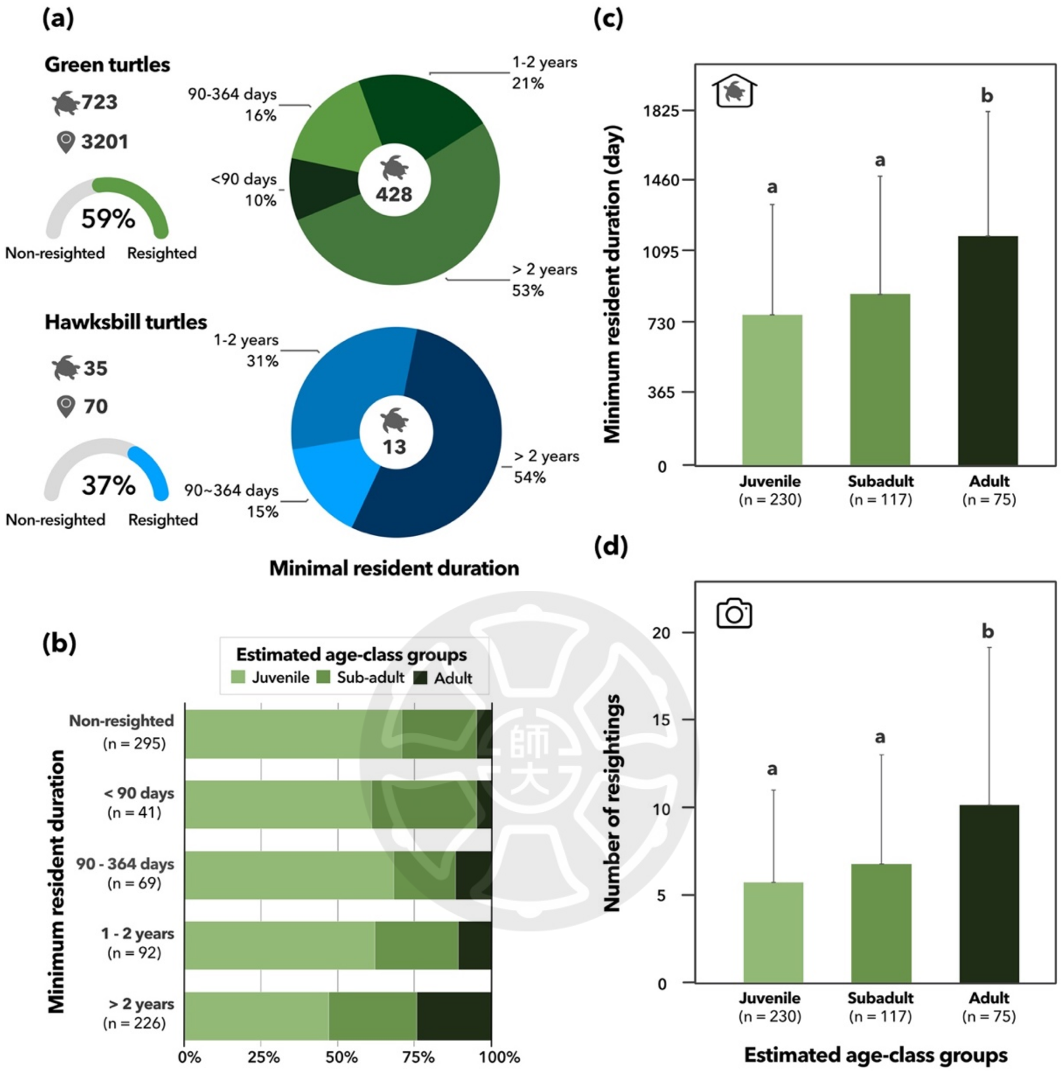


Figure 2-3.The minimum resident duration (MRD) and demographic structure of turtles.

(a) MRD of green and hawksbill turtles by MRD groups. (b) The percentage of green turtles in estimated age-class groups with different MRD. (c) Mean (+SD) of MRD across estimated age-classes of green turtles. a and b denote different groupings identified from post-hoc SNK tests following One-Way ANOVA. (d) Mean (+SD) of number of resightings per individual across estimated age-class groups of green turtles.

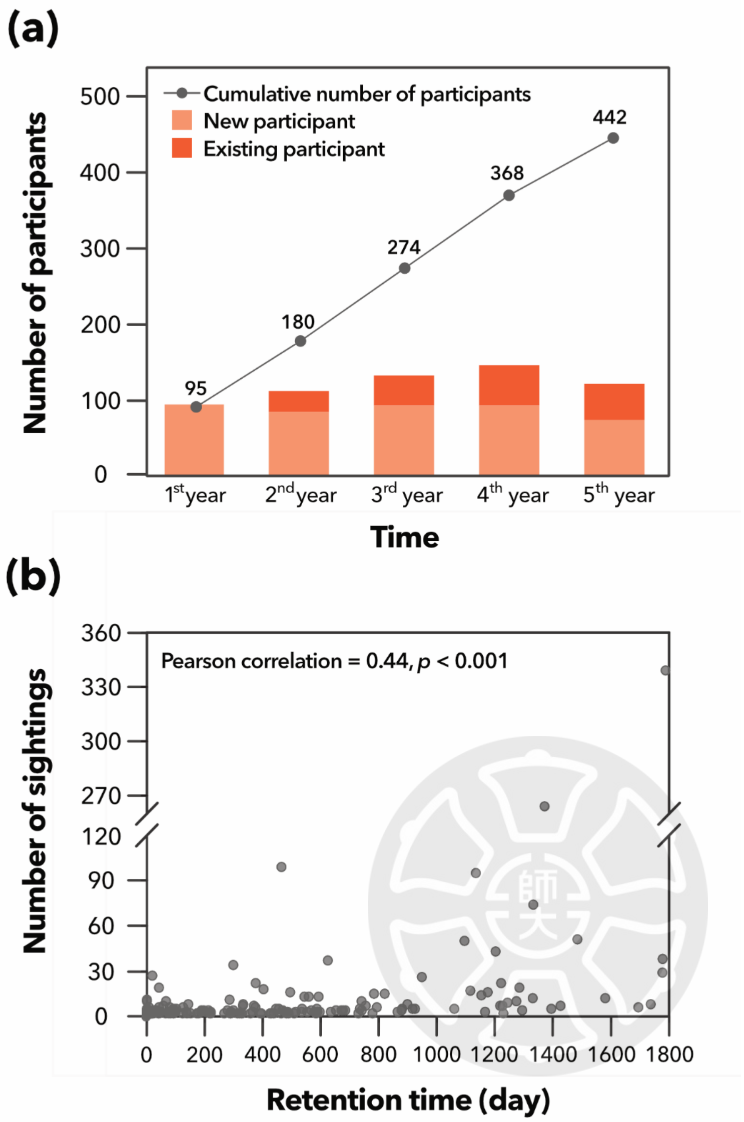


Figure 2-4. Citizen scientists' participation in TurtleSpot Taiwan.

(a) Bar charts showing the annual number of participants between June 2017 and May 2022 and line chart showing the cumulative number of participants. (b) Scatter plots between the number of sightings contributed by each participant and their retention time.

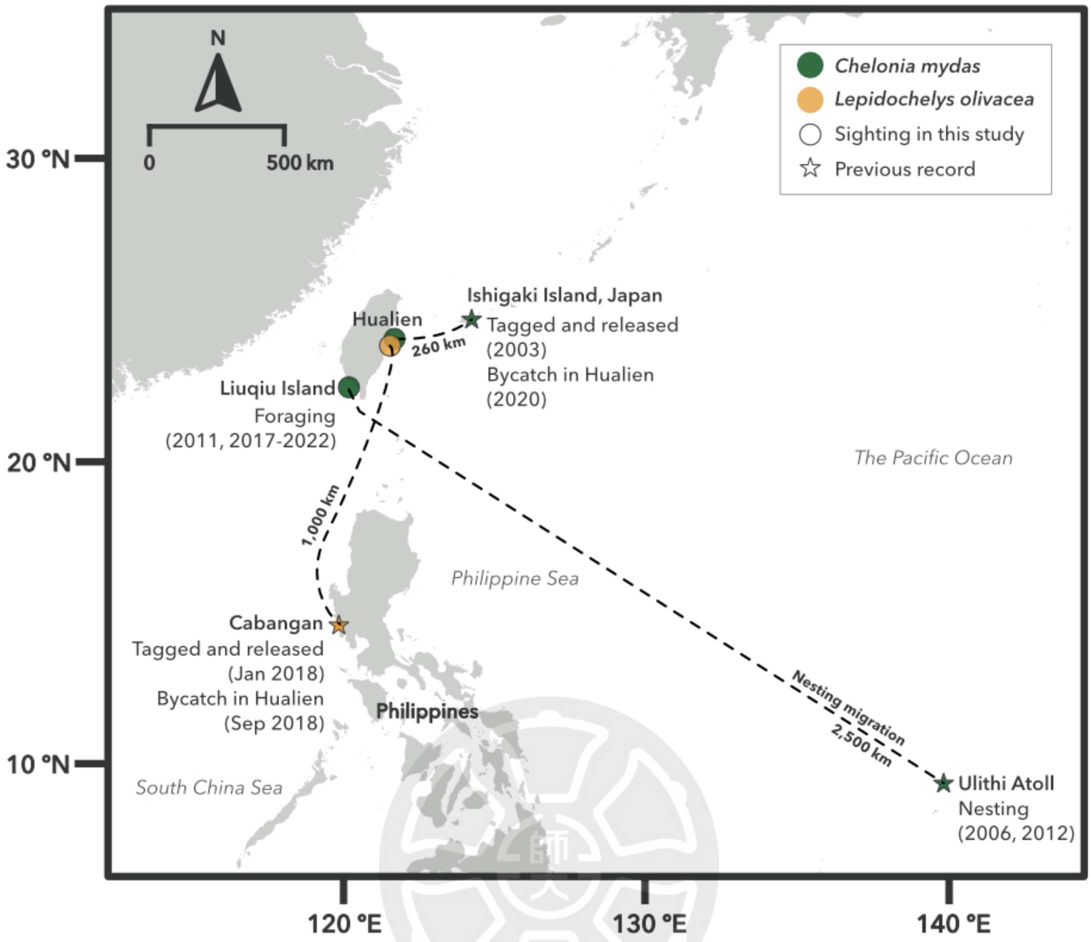


Figure 2-5. Connectivity of marine turtle foraging grounds and nesting sites identified through flipper tag recoveries.

Colors indicate the species of turtle individuals and shapes indicate the location of the sighting and tagging history.

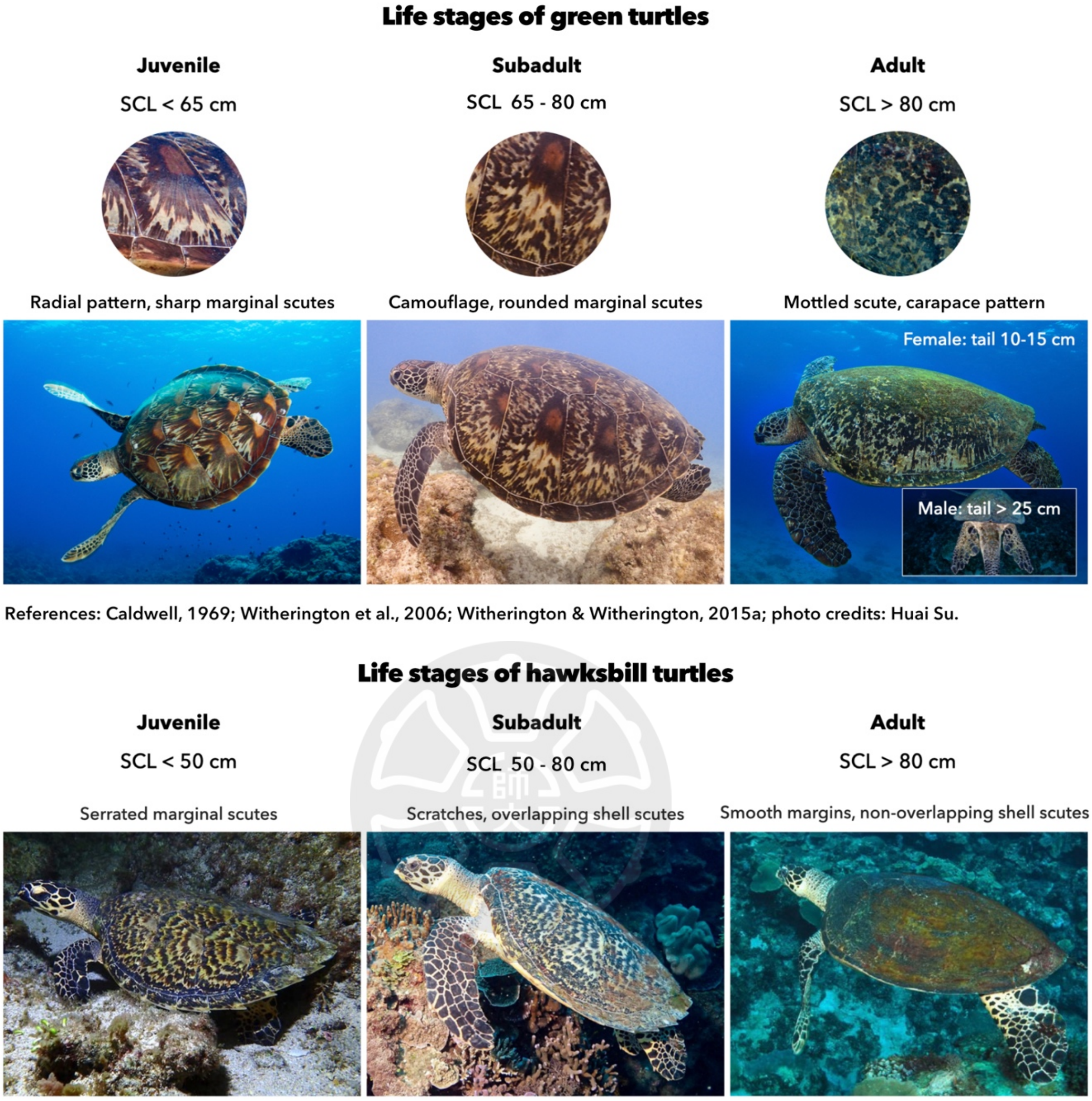
Supplementary Materials

Table

Table S2-1. Participant levels of citizen scientists

Engagement		
Sightings/per participants	**Number of participants**	**Contributed to total sightings (%)**
1	233	10 %
2 – 5	154	18.7 %
6 – 50	49	31.6 %
> 50	6	39.7 %
Retention		
Duration	**Number of participants**	
1 day	271	
2 days – 1 year	88	
> 1 year – 2 years	39	
> 2 years – 3 years	17	
> 3 years – 4 years	20	
> 4 years	7	

Figures



References: Caldwell, 1969; Witherington et al., 2006; Witherington & Witherington, 2015a; photo credits: Huai Su.

References: Avens et al., 2021; Meylan & Redlow, 2006; Wood et al., 2017; photo credits: Kuen-Tian Chen, Chi-Ching Huang and Liou-Yuan Yu (from left to right).

Fig. S2-1. Carapace patterns and estimated straight carapace length (SCL) of green and hawksbill turtles at different life stages. Photo credits: Huai Su, Kuen-Tian Chen, Chi-Ching Huang and Liou-Yuan Yu.

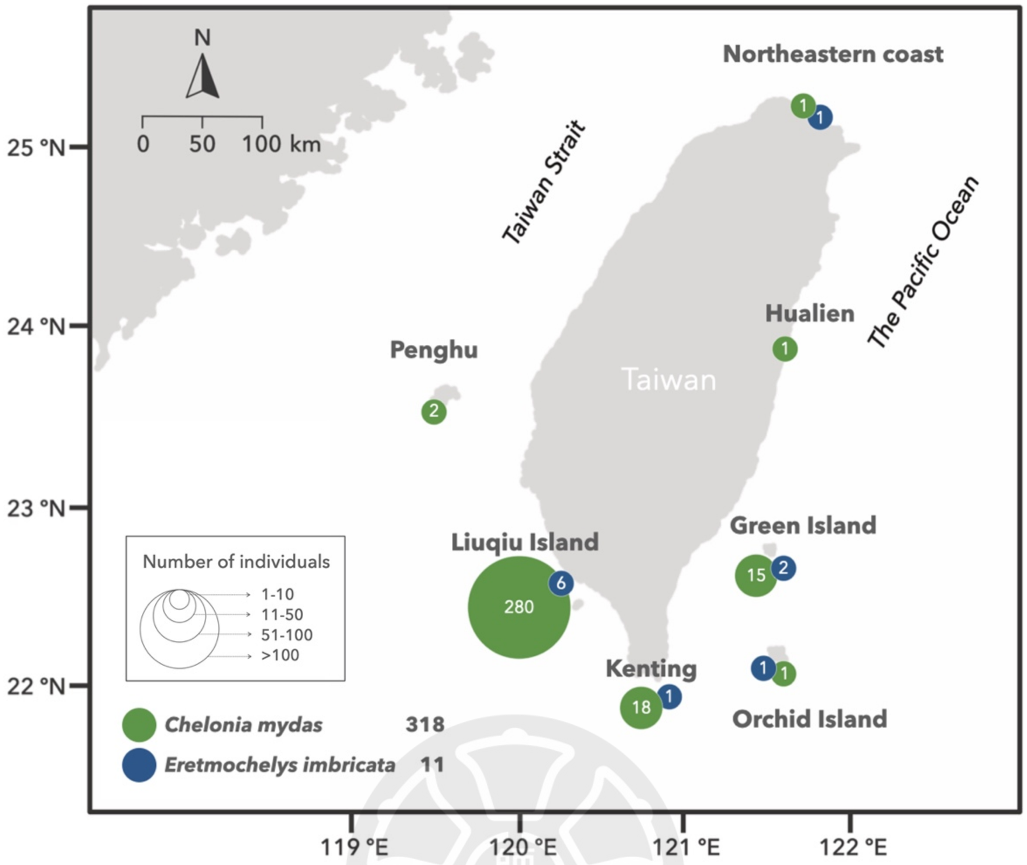


Fig. S2-2. Distribution of resident marine turtles around Taiwan. The color and size of the circles indicate the species and the number of individuals at each site.

CHAPTER 3

Generating Representative Mark-Resight Data and Applying a Standardized Site Fidelity Index to Study Green Turtle Foraging Aggregations

3.1. Abstract

Determining population dynamics and site fidelity of marine turtles in foraging habitats is crucial for effective conservation management, yet few in-water survey designs highlight the importance of statistically robust mark-resight aggregation data. We conducted a two-year, multiple-event snorkel survey with photo-ID to collect mark-resight data on 398 green turtles at two adjacent reef sites on Liuqiu Island, Taiwan. We demonstrated that multiple-event surveys (3 consecutive days every three months; each survey comprising ~1 hour observations in the morning and afternoon of the same day) yield over 95% sampling coverage and a nearly two-fold higher resighting rate than single-event surveys (single ~1 hour survey every three months). Turtle counts differed between tide cycles; flood and high tides had the most sightings, while flood and ebb tides yielded more unique individuals. These results show the need to consider tidal timing when designing surveys. The majority (65.4%) of sighted turtles were juveniles, and 8.5% showed partially-healed or fully-healed injuries. Applying the Standardized Site Fidelity Index (SSFI) to turtles in Liuqiu Island identified Low- and High-SSFI groups. Low-SSFI groups had a higher proportion of adult-sized individuals (12.1% vs. 3.9% in High-SSFI), consistent with an ontogenetic expansion of home range. Of the observed turtles, 7.2% of Low Fidelity turtles and 9.9% of High Fidelity turtles bore visible injuries. SSFI metrics and open-access datasets enable the inter-

study comparisons of site-fidelity patterns across turtle foraging aggregations. However, differences in survey design and sampling frequency can influence the resulting SSFI values, and should therefore be carefully considered in the interpretive context.

3.2. Introduction

Migratory marine species, such as marine mammals, turtles, seabirds, and sharks, exhibit wide geographic distribution and regularly move between distinct areas for feeding, reproduction, and other specific needs (Lascelles et al., 2014). For instance, marine turtles occupy specific ontogenetic habitats during immature stages and later transition to separate breeding and foraging grounds as adults (Musick & Limpus, 2017). Such migratory behaviors foster varying degrees of site fidelity, defined as the tendency to repeatedly return or remain in a particular area for a period of time. Site fidelity benefits these animals through familiarity with resources and environmental conditions (DeSimone & Cohen, 2023). Understanding population status and site fidelity is crucial to studying a migratory animals' movement patterns in relation to their life history and for implementing effective conservation actions.

Numerous studies have highlighted marine turtles exhibiting site fidelity to foraging grounds; however, site fidelity reported among these studies currently often relies on qualitative descriptions that lack methodological consistency (Table. 3-1). Satellite tracking and long-term capture-mark-recapture (CMR) data have shown that green, loggerhead, hawksbill, and flatback turtles, display "strong fidelity" to specific foraging sites, returning to previously used areas after migrating up to 10,000 km between breeding and foraging grounds (Shimada et al., 2020). Stable isotope analysis of turtle tissue supports these observations, revealing consistency in diet and site use over time (Hancock et al., 2018; Shimada et al., 2014). However, species-specific patterns are inconsistent among sites studied: At Aldabra Atoll, Seychelles, Sanchez et al. (2024a) found “lower site fidelity” in green turtles compared to hawksbill turtles, evidenced by lower recaptured rates and a tendency to avoid specific sites, while Araujo et al. (2019) fount “strong site fidelity” in green turtles in Oslob, Philippines, with individuals showing extended residency of over six years based on consistent resighting via photo identification (photo-ID). These differing qualitative results underscore the challenges in defining and measuring site fidelity, which often stems from variations in approaches and adopted definitions, with some studies focusing on pattern-oriented metrics (e.g., returning to previous sites) and others emphasizing process-oriented metrics (e.g., retention within site; Picardi et al., 2023).

To address the lack of standardized methods to quantify site fidelity, Tschopp et al. (2018) developed the Standardized Site Fidelity Index (SSFI) using simulated scenarios and photo-ID data from dolphins. This index combines common indicators, such as permanence (the proportion of time an individual is observed) and periodicity (the frequency of an individual’s recurrence), to measure site fidelity at individual and population levels and, thus, provides a means to compare different populations. Simulation and empirical (real dolphin photo-ID data) tests showed that the SSFI outperforms separate residency and sighting frequency indices, more accurately reflecting Gower distances and individual similarity patterns (Huesca-Domínguez et al., 2024). Currently, the SSFI has been applied to several marine species, including sperm whales, dolphins, and catsharks (Ferreira et al., 2022; Johnson et al., 2024; Pouey-Santalou et al., 2024), but has not yet been used to study marine turtles.

In-water surveys using the photo-ID technique, whether conducted via snorkel or SCUBA diving, provide a minimally invasive, cost-effective alternative to the traditional CMR method for collecting mark-resight data (Carpentier et al., 2016; Schofield et al., 2008). While in-water surveys are essential for assessing site fidelity and population structure in foraging turtles, limited attention has been given to establishing statistically representative sampling effort. In many studies, the sampling frequency is only briefly described and often determined by local topography and logistical constraints, without thorough evaluation of whether the collected data are truly representative. For instance, strip transects were used to survey coastal seagrass foraging sites in the Egyptian Red Sea (Mancini et al., 2015) ; in Belize, turtle counts were collected from one-hour snorkel transects conducted by teams of six to eight participants spread across the reef edge (Strindberg et al., 2016) ; in the Pacific Islands, two SCUBA divers were towed by boat for 50 minutes along a 2.2 km transect (Becker et al., 2019); and Su et al. (2015) carried out intensive snorkel and SCUBA surveys at several sites on Liuqiu Island, Taiwan. The reported variation in data collection methods across studies is problematic for proper comparison or synthesis of obtained data.

Further complicating the data collection process, marine turtles show diurnal and tidal behavior variations (Brooks et al., 2009; Hounslow et al., 2023; Pillans et al., 2021), often visiting shallow waters during high tides. If not accounted for in data acquisition methodology, these differences may confound results and therefore misrepresent actual marine turtle patterns. Together this highlights the need to establish an adequate and representative sampling frequency and timing (i.e., survey intensity and temporal coverage to include different tidal cycles) to accurately account for temporal variability in site fidelity and population assessments in order to obtain statistically representative and comparable data.

The green turtle, *Chelonia mydas*, is listed as Endangered on the IUCN Red List (Seminoff, 2023) and is distributed throughout the NW Pacific region (Ng et al., 2024). In Taiwan, Liuqiu Island served as a crucial foraging ground, hosting hundreds of individuals within the coastal water year-round (Fong et al., 2025) which attract millions of tourists a year for turtle-watching. While green turtles can be observed year round at this island, we currently lack quantitative data on their population trends and site fidelity, both of which are essential for effective marine turtle conservation and management strategies.

This study applies snorkel-based surveys with photo-ID techniques to collect mark-resight data on foraging green turtles. It is the first study to establish and apply a statistically representative framework for in-water data collection of marine turtle site fidelity and population structure with representative spatial and temporal coverage, and demonstrating its efficacy and importance on quantifying site fidelity and population size/structure of marine turtles. Additionally, this study presents the first application of SFFI to marine turtles, providing a quantitative approach for assessing site fidelity and facilitating comparisons with foraging turtle populations in other regions.

3.3. Materials & Methods

3.3.1. Study area and in-water survey design

Liuqiu Island (Fig. 3-1a), located in southwestern Taiwan, is a green turtle foraging hotspot characterized by an algae-dominated coral reef substrate. The sea surface temperature ranges from 20.3 to 28.5°C annually, with a mean temperature of 27.7°C (Central Weather Bureau, 2023). Liuqiu Island experiences a mixed semidiurnal tide cycle, with tidal differences of ca. 1.2 to 1.5 meters during spring tides. In-water surveys were conducted at two sites, Lobster Cave and Dafu-Houshi Reef (Dafu), over three consecutive days every three months from October 2020 through November 2022 (9 sample time points; 53 total in-water surveys). Each survey day included two snorkel sessions—one in the morning and one in the afternoon— to cover different combination of tidal phases, including ebb (lowering tides), flood (rising), high (peak level) and low tides (lowest level). Each snorkel survey was conducted by at least two swimmers working in a paired buddy system, snorkeling parallel to the coastline while capturing images (i.e., left and right facial profiles and whole-body photographs) of encountered turtles. Survey duration averaged 74 mins at Lobster Cave (range: 20 to 120 mins) and 86 mins at Dafu (30 to 141 mins). Surveys were carried out only under calm sea conditions (Beaufort Sea state < 3 and swell < 1 m) to ensure swimmer safety and data quality.

3.2.2. Determining representative snorkel surveys

To examine the effect of sampling efforts on data representativeness, we compared sampling coverage (SC) of mark-resight data under two survey designs: (1) Single-event surveys – one snorkel session every three months; and (2) Multiple-event surveys – two daily snorkel sessions over three consecutive days every three months. Data for the single-survey design were extracted from the first snorkel session of each multiple-event survey period. SC was analyzed using iNEXT Online (Chao et al. 2016), primarily developed for estimating species diversity through rarefaction (interpolation) and prediction (extrapolation) of sampling curves of species richness (Chao et al. 2014). We adapted the model by treating each identified turtle as a distinct "species" and sighting counts as the number of detections.

SC of the observed sample of size *n* is estimated as

$$\hat{C}(n) = 1 - \frac{f_1}{n}\left[\frac{(n-1)\,f_1}{(n-1)\,f_1 + 2\,f_2}\right]$$

where f_1 is the number of singletons (individuals observed only once), f_2 is the number of doubletons in the sample (individuals observed only twice), and *n* is the total number of sightings. Values of $\hat{C}(n)$ close to 1 (e.g., ≥ 0.95) indicate that most individuals in the population have likely been detected, signifying representative sampling, whereas lower SC values suggest that additional sampling is needed for more comprehensive coverage.

In addition to SC determination, cumulative running means and standard deviations of number of turtles identified per snorkel were plotted over the entire 25-month sampling period. As the number of snorkels increased, fluctuations in the running mean of number of turtles identified per snorkel will gradually decline, indicating a sample size with improved accuracy and reduced sampling bias. This also lowered the probability of chance results (i.e., unrepresentative data) (see Wang et al., 2017). The minimum number of snorkels required for representative sampling can be determined as the point when the cumulative mean and standard deviations stabilized in the cumulative sampling plot.

To examine variation in the number of turtle individuals identified per snorkel per hour across tidal cycles and between sites, a two-way ANOVA (tidal cycle × sites) was conducted using SigmaPlot 11 (Graffiti LLC). Data were square-root transformed to achieve normality and homogeneity of variances. A Student-Newman-Keuls (SNK) post hoc test was performed to compare significant differences between groups.

3.2.3. Photo identification, age-class estimation, and body condition

After each snorkel survey, photographs of individual turtles were initially sorted, and partial sightings were manually identified by those who conducted the snorkels, matching unique facial scute patterns to a catalog of known turtle profiles for each site (catalog created from identified turtles in the surveys). Left facial profiles of turtles observed at both sites were printed out and organized into photo albums for easier comparison. A consistent verifier (first author) then reviewed all the manual photo-ID results and identified any unidentified sightings with the HotSpotter software (Crall et al., 2013). During the query process, the overall facial scutes (area of interest) were manually selected as a ‘chip’ for analysis by adding two digital reference points at horizontally and vertically opposing positions on the imported image. The software then automatically compared this ‘chip’ to those in the existing image database established with HotSpotter. Detailed operational procedures for this method are described in Dunbar et al. (2021). If no match was found and the image quality met the criteria for a valid query, the chip was assigned a new turtle ID and recorded as a newly identified individual. Left facial profiles were prioritized during the identification of individuals because the established left facial photo-ID database is more complete than that of the right facial. If a sighted turtle lacked a left facial profile, and the provided photographs (i.e., right facial profile or whole-body) were unidentifiable to a known individual, it was not included in the data as a valid sighting.

Age-class estimation was based on visual assessments of body size and carapace color patterns from both in-field observations and photographic records, as described by Fong et al. (2025). Individuals were categorized as juvenile, subadult, or adult-sized turtles. Individuals who lacked estimated size information were recorded as having unknown life stages. The external body condition of each individual turtle was assessed during surveys and from images to identify visible abnormalities, including injuries to the carapace or body, deformities such as humped or abnormal carapace (potentially from past trauma), missing or damaged flippers, and/or signs of fishing line entanglement. Individuals showing any of these conditions were classified as injured.

3.2.4. Site fidelity

We used the SSFI developed by Tschopp et al. (2018), which was calculated based on the indicators of permanence (*IT*) and periodicity (*It*) and defined as:

$$SSFI = \frac{2}{\frac{1}{IT} + \frac{1}{It}}$$

Permanence (*IT*) is the proportion of time an individual was present in the study area, measured as the time between the first capture and last recapture (F_i), over the sampling period (F):

$$IT_i = \frac{F_i}{F}$$

Here, F_i of each individual was calculated as the total number of days between an individual's first and latest sightings, following the definition of the minimum residency duration (MRD) described by Hanna et al. (2021).

Periodicity (*It*) is the recurrence of an individual, determined by the inverse of the average time between successive recaptures:

$$It_i = \left(\frac{F_i}{\sum_{j=1}^{T} c_{ij} - 1}\right)^{-1}$$

where c_{ij} indicates a sight (1) or an absence to sight (0) of an individual *i* on the sampling occasion *j*, and *T* is the number of sampling occasions.

Since SSFI is calculated as a fraction, its values can be affected by the sampling frequency and the selected time unit (e.g., day, month, or sampling interval). To standardize comparisons across other open-access photo-ID datasets, we used 'day' as the unit for SSFI calculation. Since Lobster Cave and Dafu are adjacent foraging areas, we pooled photo-ID records from both sites to calculate each individual's SSFI as a single measure for Liuqiu Island (for calculations of SSFI, see Supplementary Formula

3-1). Turtles sighted at every sampling event achieved the study’s maximum SSFI of 0.127, whereas those seen only once scored 0, indicating no detectable site fidelity. A Pearson correlation coefficient analysis was conducted to examine the correlation between the SSFI of each individual and their sighting counts and MRD.

We performed one dimensional hierarchical clustering of individual SSFI values in R using the “hclust1d” package (Nowakowski, 2023) with Euclidean distance as the dissimilarity measure and Ward’s method as the clustering algorithm (Ward, 1963). Because only SSFI is used for agglomerative hierarchical clustering (AHC) analysis, the dissimilarity between each pair of individuals equals the absolute difference in their SSFI values. To determine the optimal number of clusters, we computed silhouette analysis with the “cluster” package (Maechler, 2018). The silhouette coefficient measures how well each observation fits within its assigned cluster relative to others, with values ranging from -1 to 1, where higher values indicate more coherent and well-separated clusters. This AHC and silhouette validation approach has proven effective for identifying distinct fidelity groups in cetacean populations with a combination of site fidelity indicators (Courtin et al., 2023; Haughey et al., 2020; Passadore et al., 2018; Zanardo et al., 2016).

To study whether variation in age class and external injury influence site fidelity patterns, we assessed associations between SSFI groups and either (1) age class (juvenile, subadult and adult-sized) or (2) external injury (wounds absent or present) using Pearson's Chi-squared test and Fishers Exact Test (where sample sizes were < 5). All analyses were performed using “stats” package in R.

Besides SSFI groups, we also evaluated differences in SSFI values across age-class groups and between injury presence using non-parametric tests, as the data did not meet assumptions of normality and homoscedasticity. Turtles (n = 5) whose estimated age class was unknown were excluded from this analysis. Differences among age groups (Juvenile, Subadult, Adult) were tested with a Kruskal-Wallis test. If significant, post-hoc pairwise comparisons used Wilcoxon tests with Benjamini-Hochberg correction to control false discoveries. To examine the effect of injury observation (With vs. Without) on SSFI values, we performed a Wilcoxon rank sum test. All analyses were conducted in R using base functions and the “ggplot2”, “dplyr”, and “stats” packages.

To compare site fidelity of green turtles across different studies, we analyzed three other open-access green turtle sighting databases: (1) opportunistic citizen science data from TurtleSpot Taiwan collected across multiple sites in Liuqiu Island (same location as the present study) from 2017 to 2022 (hereafter referred to as Liuqiu-TS; Fong et al., 2025); (2) monthly presence-absence records compiled from citizen scientists and researchers across the Maldives from 2016 to 2019 (Hudgins et al., 2023); and (3) researcher-led in-water surveys conducted at Oslob, Philippines, from 2012 to 2018, though the sampling frequency was not specified (Araujo et al., 2019). To standardize SSFI comparisons across marine turtle studies, we used days as the time unit for all SSFI calculations. SSFI values were compared across datasets using the Kruskal-Wallis test, followed by pairwise Wilcoxon tests with Benjamini-Hochberg correction when significant.

3.3. Results

3.3.1. Determining representative snorkel surveys

A total of 4,192 turtle sightings were collected from both sites (Lobster Cave n = 1,829; Dafu n = 2,363). Of these, 92% (3,846) were valid for photo-ID, identifying 398 unique individuals (Lobster Cave n = 161, Dafu n = 217, both sites n = 20). After removing duplicate sightings of the same individual within the same snorkel survey, a total of 3,085 unique sightings were used for analysis. The number of turtles sighted per snorkel ranged from 1 – 66 (Lobster Cave) and 1 – 78 (Dafu) (Fig. 3-1d).

The number of turtles recorded per multiple-event survey (combining Dafu and Lobster cave) ranged from 75 (August 2021) to 253 (February 2022), with a mean of 168.78 (SD = 58.54) across the nine sampling periods (Oct 2020 – Nov 2022; Fig. S3-1). Counts were initially low in October 2020 (n = 81), rose to near average level before declining in August 2021 (n = 75), and thereafter rising again toward the long-term mean.

The iNEXT analysis indicated that multiple-event surveys provided greater sampling coverage (SC) compared to single-event surveys (Fig. 3-1b). SC increased from single- to multiple-event surveys at both Lobster Cave (0.65 and 0.96, respectively) and Dafu (0.70 and 0.98, respectively). By combining sightings from both sites, multiple-event surveys (n = 105 snorkels) yielded 3,846 valid sightings and 398 individuals, with a resighting rate of 82.9%. In comparison, single-event surveys (n = 18 snorkels) resulted in 483 valid sightings, 214 individuals, and a resighting rate of 43.5%. This represents an 8-fold increase in sightings, 1.86 times more individuals, and a nearly 2-fold higher resighting rate (Table 3-2).

The cumulative running means and standard deviations of individuals sighted in each survey stabilized after approximately 35 snorkels at both sites (Fig. 3-1c). The cumulative number of newly identified individuals reached a breakpoint at 35 snorkels, after which the increase was nearly asymptotic (Fig. 3-1d), indicating that fewer new individuals were being recorded in the latter stages of the study.

3.3.2. Age-class structure and abundance with tides

Among the 393 green turtles with estimated age-class information, 65.4% (n = 257) were juveniles, 26.7% (n = 105) were subadults, and only 7.9% (n = 31) were adult-sized (Fig. S3-2a). The proportion of juveniles was higher at Dafu (73.4%, 160/217) than at Lobster Cave (51.9%, 84/156), while adults are more common at Lobster Cave (12.3%, 20/156) than at Dafu (4.6%, 10/217). Overall, 8.5% (34/398) showed injuries or bore scars. At Lobster Cave, the injury rate was 12.4% (n = 20), and at Dafu 5.1% (n = 11). Among turtles observed at both sites, 15% (n =3) had injuries (Fig. S3-2b).

Both sites had significantly higher turtle counts during flooding and high tides than during ebb tides ($p < 0.05$; post hoc SNK tests: High = Flood = Low > Ebb = Low). No differences were observed between low tides and other tidal cycles (Fig. 3-2a; Table S3). Although most individuals were sighted at various tidal periods, some individuals were only observed during specific tides, particularly during ebb tides (Fig. 3-2b). The fewest unique individuals were seen during low tides (Fig. 3-2b).

3.3.3. Individual detection patterns and site fidelity metrics

Individual sighting counts ranged from 1 to 34 per survey (mean = 7.74). Only 4.5% (n = 18 turtles) were observed in every multiple-event survey (individual sighting counts ranging from 12 to 34). For MRD analysis, 18% of green turtles were sighted only once (n = 69) or twice (n = 2) in different surveys on the same day (MRD = 0). Most (82%, n = 327) were resighted on different days (Fig. 3-3a), with 27% (n = 109) of resightings within one year (1–364 days), 39% (n = 156) within two years, and 16% (n = 62) in more than two years (> 730 days), covering nearly the entire study period (Fig. 3-3b). The mean SSFI was 0.024 ± 0.0205 (SD), with values ranging from 0 to

0.0827 (Fig. 3-3c). SSFI showed significant positive correlations with both sighting counts (Pearson correlation coefficient = 0.85, $p < 0.001$) and MRD (Pearson correlation coefficient = 0.62, $p < 0.001$) (Fig. S3-3).

AHC analysis of SSFI values identified two distinct clusters (silhouette score: 0.625, Fig. S3-4a): (1) Low Fidelity group: 49% of turtles (n = 195); SSFI mean ± SD SSFI: 0.007 ± 0.007; range: 0 – 0.021, and (2) High Fidelity group: 51% (n = 203); SSFI mean ± SD SSFI: 0.0416 ± 0.0137; range: 0.0212 – 0.0827 (Fig. S3-4b). Age-class distributions differed between fidelity groups ($\chi^2 = 9.68$, df = 2, $p < 0.05$): juveniles occupied a relatively higher proportion in both Low Fidelity (60.8%) and High Fidelity groups (77.6%), but adult-sized turtles were significantly more common in the Low Fidelity group (12.1%) than the High Fidelity group (3.9%) (Fig. S3-5). Injury status did not differ significantly between fidelity groups—7.2% of Low Fidelity turtles and 9.9% of High Fidelity turtles bore visible injuries (Fig. S3-5). However, injury rates varied strongly with age class (Fisher's exact $p < 0.05$): adults were more likely to be injured (22.6%), followed by subadults (12.4%), then juveniles (5.4%).

We examined whether biological characteristics (age-class and injury observation) were associated with variation in SSFI. The Kruskal-Wallis test revealed a significant difference in SSFI across age classes ($\chi^2 = 18.652$, $df = 3$, $p < 0.001$). Post-hoc pairwise Wilcoxon tests showed that adult-sized turtles had significantly higher SSFI values than both juveniles ($p < 0.001$) and subadults ($p < 0.05$), while no significant difference was found between juveniles and subadults (Fig. 3-4a). In contrast, no statistically significant difference in SSFI values was found between turtles with and without injury observations, as assessed by the Wilcoxon rank sum test (W = 5109.5, $p = 0.090$; Fig. 3-4b).

Resighted rates of the present study were higher (82%), had fewer individuals at SSFI = 0, had a more even distribution, and relatively middle to high SSFI (SSFI range: 0 – 0.08) than that of those we calculated from published data from other studies in Liuqiu-TS (skewed towards low SSFI; distribution 0 – 0.06), Maldives (middle SSFI; 0 – 0.06), and Oslob (high SSFI; 0 – 0.5). See Fig. 3-3d, Fig. S3-6, and Table S3-4. SSFI values varied significantly across the four datasets, as indicated by the Kruskal-Wallis test ($\chi^2 = 169.71$, $df = 3$, $p < 0.001$). Post-hoc pairwise Wilcoxon rank sum tests with Benjamini-Hochberg correction revealed that SSFI values of Liuqiu were significantly higher than Liuqiu-TS ($p < 0.001$) and Maldives ($p < 0.001$), but not significantly different from Oslob. Liuqiu-TS, Maldives, and Oslob also differed significantly from one another ($p < 0.001$; Fig. 3-5).

3.4. Discussion

3.4.1. Conducting representative snorkel-based surveys

Effective monitoring of marine populations requires methods that account for imperfect detectability to avoid biased estimates (Katsanevakis et al., 2012). Insufficient data can undermine the reliability of ecological models (Simmonds et al., 2020) and may reduce the accuracy of key metrics. In this study, multiple-event surveys achieved over 97% sampling coverage in contrast to single-event surveys, which had 65 to 70%. This approach improved individual detection and provided a more representative estimate of individual diversity. Moreover, multiple-event surveys captured 3.5 times more resighted individuals than single-event surveys (330 in 398 vs. 93 in 214), offering a stronger foundation for assessing site fidelity and residency duration. In contrast, relying on a single snorkel survey per season (or once every three months) risks underestimating the numbers of aggregation and misrepresenting residency pattern. We recommend multiple-event surveys on consecutive days each season or at set intervals, as this approach is not only more logistically feasible, especially for remote study sites, but also ensures more representative data. Sampling efforts should be tailored to local conditions, as representative sample sizes, sampling frequencies, and strategies may vary due to local environmental factors (e.g., tidal influences, benthic features) and/or logistical constraints (e.g., available personnel, photo-ID processing time).

Survey counts in October 2020 and August 2021 were lower than expected, and these anomalous counts are ascribed to weather conditions and COVID-19, respectively. Persistent inclement weather in October 2020 forced a reduced snorkel effort due to safety concerns, resulting in only four and five surveys being conducted for each site, respectively, rather than the six planned surveys. Likewise, a COVID-19 level 3 health alert in Taiwan from mid-May to the end of July 2021 prohibited all water activities, leaving in the previously heavily human-influenced waters of the study sites absent of human disturbance for a uniquely prolonged period. During this period the turtles may have become accustomed to the human-free conditions, potentially resulting in them becoming more skittish and reclusive when water access was opened again to humans just prior to the mid-August 2021 surveys (personal observations).

Tides significantly influence the number of turtles encountered during snorkels, with higher counts observed during flood and high tides than during ebb tides. This pattern is consistent with turtle tracking studies, which have shown that both flatback and green turtles in Australia rest in the deeper offshore water zones and then move into shallower near-shore water zones to forage when high tides make them accessible (Hounslow et al., 2023; Pillans et al., 2021). In our study, fewer unique individuals were recorded during low tides, suggesting that turtles frequenting the survey sites during low tides tend to remain present across multiple tidal phases. In contrast, flood, high, and ebb tides brought in more less frequently recorded or unique individuals, likely reflecting tide-driven movements between foraging and resting areas. These findings highlight the importance of considering tidal influences when designing in-water surveys to ensure comprehensive population assessments.

3.4.2. Comparative site fidelity across different datasets and foraging grounds

The SSFI is a standardized methodology allowing quantitative population-level comparison of site fidelity within and among studies (Ferreira et al., 2022; Tschopp et al., 2018). In our dataset, SSFI was strongly positively correlated (0.85) with sighting count and moderately with MRD (0.62), indicating SSFI better reflects how often individuals return to a site rather than how long they remain there. AHC identified two distinct SSFI clusters in our data; however, the Low Fidelity group actually exhibited two different behavioral types: individuals sighted only once or twice on the same day (ca. 36.4%, n = 71; MRD: 0, SSFI: 0), and those that made occasional return visits (ca. 63.6%, n = 124; sighting: 2 – 9, MRD: 1 – 765, SSFI: 0.00261 – 0.02103).

Adults were more abundant in the Low Fidelity group and had a significant higher SSFI than juveniles and subadults, which aligns with an ontogenetic expansion of space use. For example, in Australia, average 50% kernel utilization distribution (KUD) areas (i.e., the core space used by an individual) increased from 0.29 km^2 in juveniles to 0.47 km^2 in subadults to 0.57 km^2 in adults (Pillans et al., 2022). Larger home ranges naturally reduce the probability of detecting a turtle at any single location. Further, various environmental factors, such as seasonal changes (i.e., over-wintering) (Broderick et al., 2007; Fukuoka et al., 2019), food availability (Siegwalt et al., 2020), or predation risk (Lamont et al., 2015; Smulders et al., 2023), and intrinsic traits, such as behavioral tendencies (van Overveld & Matthysen, 2010) or ontogenetic shift in foraging behavior among immature turtles (Hays et al., 2021) are all likely to shape variations in site fidelity. Individuals exhibiting lower fidelity in the present study are likely a reflection of their larger home ranges and innate foraging movements, which reduces the likelihood of repeated detection at fixed snorkel sites. However, such lower detectability does not necessary imply shorter residency, as these turtles may still remain within the broader study area but outside the spatial coverage of our surveys.

By applying a standardized and representative survey design, we minimized biases from opportunistic observations (e.g., observer preferences; (Goldstein et al., 2024) or overreporting of rare individuals (Bird et al., 2014), generating an SSFI distribution that more faithfully represents true site-fidelity patterns, together vital for informed management. Although the present study and Liuqiu-TS dataset both cover the same location (Liuqiu Island, Taiwan), this SSFI distribution in this study (Liuqiu) was more even, whereas the Liuqiu-TS citizen science dataset were skewed toward low fidelity. SSFI values from the Maldives fall largely in the moderate to high range, consistent with the minimal temporary emigration and infrequent movement between atolls documented by Hudgins et al. (2023). The overall high SSFI values from Oslob were driven by exceptionally high resighting frequency of a subgroup of individuals, where 22% of 82 turtles were encountered over 130 times and two individuals were recorded over 500 times (527 and 670 sightings) within their respective residency periods of 1,521 and 1,611 days (Araujo et al., 2019). These results emphasize that site fidelity may be site-specific, and accurate assessment of local fidelity patterns requires representative spatiotemporal coverage.

While the SSFI values in Oslob appeared higher than those in Liuqiu in both range and mean, the statistical comparisons did not detect a significant difference between the two. Instead, both Liuqiu and Oslob were statistically grouped due to their similarly high SSFI values, both significantly higher than those of Liuqiu-TS and the Maldives. This suggests that although Oslob may show stronger site fidelity anecdotally (e.g., due to extremely high sighting frequency), the broader and more even distribution of SSFI values in Liuqiu contributes to comparable overall site fidelity levels.

Although the SSFI provides a standardized scale of 0 to 1 for comparing site fidelity at population level, direct numerical comparisons between datasets or across studies should be interpreted with caution. Differences in survey duration and sampling frequency can influence SSFI values, and such comparisons may require consistent survey designs or appropriate corrections to account for sampling bias. In this study, we combined clustering analysis, statistical groupings, and distributional analysis to interpret SSFI values within and across fidelity groups. This approach enables a more ecologically informed understanding of site fidelity, as statistical groupings on SSFI values reflect central tendencies but may overlook behavioral extremes that are ecologically meaningful. Rather than relying on absolute SSFI values alone, our interpretation emphasizes the importance of contextualizing fidelity metrics in relation to sampling design, data structure, and the ecological characteristics of the study site.

3.5. Conclusions

This study provides a methodological framework for collecting representative mark-resight data to evaluate population trends and site fidelity in marine turtles. An extended survey effort and ensuring known confounding factors affecting marine turtle habits (i.e., tidal cycles) were shown to improve the resolution of SSFI results, leading to a more accurate description of marine turtle site fidelity. This approach fills a methodological gap of previous studies (e.g., single time point and/or opportunistic surveys), which often overlooked sampling representativeness and thus underestimated the numbers of aggregation, residency, and site fidelity, leading to misdirection of conservation efforts. Although photo-ID cannot match the fine-scale movement and near-continuous tracking afforded by satellite telemetry, it scales to much larger sample sizes and is a cost-effective means to cover longer temporal periods. Further research to improve our understanding of green turtles' habitat use and residency patterns could integrate satellite or acoustic tracking with photo-identified individuals to quantify and compare their home ranges and movement patterns, assessing how environmental and intrinsic factors shape their site use. The present study accumulated an extensive, structured mark-resight dataset spanning two years, providing a valuable foundation for future population modeling, including estimation of apparent survival, temporary emigration, and sighting probability, under a capture-mark-recapture framework analysis of marine turtles. Lastly, we encourage the broader application of SSFI in marine turtle research, alongside open-access data sharing, to facilitate interstudy comparisons and improve consistency in site fidelity assessments. These efforts will ultimately enhance our understanding of population ecology and strengthen conservation strategies for marine turtles.

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Tables

Table 3-1. Overview of Definitions and Metrics Used to Assess Site Fidelity in Marine Turtle Studies.

Study Reference	Method	Definition of Site Fidelity (Description)	Metrics Used (Resolution)
Sanchez et al. (2024a)	CMR	Frequently returned to a site more often than expected under random movement.	Numerical
Palaniappan and Hamid (2017)	CMR	Repeated use of specific dive sites (recapture)	Nominal
Bechhofer and Henderson (2018)	CMR	Repeated use of specific dive sites (recapture)	Nominal
Avens et al. (2003)	CMR and radio telemetry	Repeated use of specific areas	Homing behavior and recapture rate (Nominal and Numerical)
Schofield et al. (2010)	GPS tracking	Return to the same foraging areas after breeding seasons in consecutive years	Foraging site home range with kernel analysis (Nominal)
Shimada et al. (2020)	GPS tracking	Return to the foraging sites they had used previously after breeding	Foraging site home range with kernel analysis (Nominal)
Chambault et al. (2020)	GPS tracking	Tracking duration (mean ± SD: 136 ± 104 days) and the small home ranges (mean ± SD: 0.18 ± 0.25 km2)	Foraging site home range with kernel analysis (Nominal)
González Carman et al. (2016)	GPS tracking	Return to the same foraging areas after overwintering and stay there for extended periods.	Foraging site home range with state-space model and kernel analysis (Nominal)
Siegwalt et al. (2020)	GPS tracking and CMR	Long-term residency (> 2 years) and restricted space use within specific developmental areas	Estimated residency times (Numerical); foraging site home range with kernel analysis (Nominal)
Godley et al. (2003)	GPS tracking and CMR	Distances of movement range	Categorical and nominal
Chevis et al. (2017)	Passive acoustic telemetry tracking	Residency within the specific foraging areas	Categorical
Araujo et al. (2019)	Mark-resight data	Being resighted consistently during study period	Nominal
Neves-Ferreira et al. (2023)	Mark-resight data	Sighting frequency, resighted rate and residency	Numerical
Thomson et al. (2012)	Stable isotope analysis, animal-borne video and CMR dataset	Frequency of recapture and the tendency returns to the same feeding sites over time	Nominal
Hancock et al. (2018)	Stable isotopes	Remain specific areas linked to diet for several months	Nominal
Sanchez et al. (2024b)	Stable isotopes	Isotopic differences in prey at a fine spatial scale (1 km) suggest strong turtle foraging site fidelity	Nominal
Tucker et al. (2014)	Stable isotopes and GPS tracking	Return to the same foraging areas after breeding seasons in different years	Distances between track termini in different year (Numerical)

Table 3-2. Comparison of sampling effort and turtle recapture outcomes between single-event and multiple-event surveys at Lobster Cave and Dafu.

Method	**Information about sampling efforts**				
	Duration (days)	**Sites**	**Sightings**	**Sightings valid for photo-ID**	**Individuals in each survey (mean ± SD)**
Single-event surveys	763	Lobster Cave	192	176	7.46 ± 10.29
		Dafu	332	307	17.14 ± 20.75
Multiple-event surveys	765	Lobster Cave	1828	1683	24.85 ± 14.82
		Dafu	2363	2163	33.91 ± 21.59

Method	**Information about turtle individuals**					
	Recorded site	**Number of individuals**	**Individual sight once**	**Individuals with resight**		
				Total	**Intra-annual**	**Inter-annual**
Single-event surveys	Lobster Cave	81	49	32	12	20
	Dafu	129	72	57	21	36
	Both	4	0	4	3	1
Multiple-event surveys	Lobster Cave	161	41	120	39	81
	Dafu	217	27	190	68	122
	Both	20	0	20	5	15

Table 3-3. Two-way ANOVA table of results examining the effects of site and tidal phase on the number of green turtles identified per snorkel. * = $p < 0.05$.

Source of Variation	**DF**	**SS**	**MS**	**F**	**P**
Site	1	0.544	0.544	0.26	0.611
Tide	3	21.864	7.288	3.488	0.019*
Site x Tide	3	0.748	0.249	0.119	0.949
Residual	97	202.7	2.09		
Total	104	226.604	2.179		
SNK tests					
H=F=L > E=L					

Note: H = High tide, F = Flood tide, E = Ebb tide, L = Low tide.

Table 3-4. Comparison of SSFI metrics from four green turtle foraging ground sighting datasets.

SSFI (day)	**Liuqiu**	**Liuqiu-TS**	**Maldives**	**Oslob**
Reference	This study	Fong et al., 2025	Hudgins et al., 2023	Araujo et al., 2019
Duration	Oct 2020 - Nov 2022	Jun 2017 - May 2022	Jan 2016 - Dec 2019	May 2012 - Oct 2018
Number of individuals	398	576	535	82
Resight rate	82.0%	75.9%	61.0%	72.0%
SSFI Range	0 - 0.0827	0 - 0.0614	0 - 0.0612	0 - 0.5178
SSFI Mean ± SD	0.0246 ± 0.0205	0.0078 ± 0.0093	0.0170 ± 0.0183	0.0865 ± 0.1258

Figures

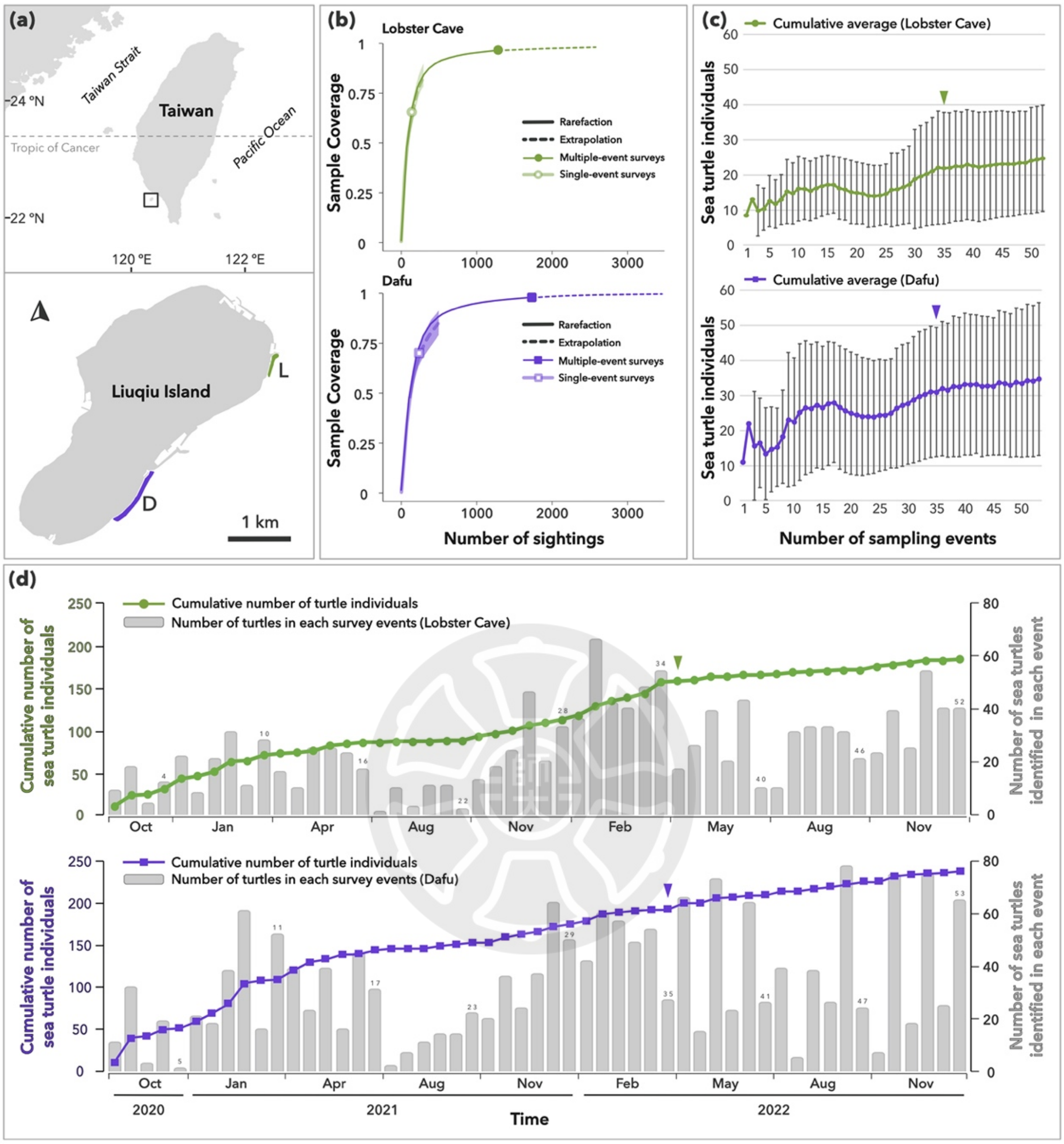

Figure 3-1. Study area, sampling design, and survey effort assessment.

(a) Map of Taiwan and Liuqiu Island (enlarged in 1a lower panel), showing study sites Lobster Cave (L) and Dafu-Houshi Reef (D). (b) Sample coverage (SC) curves for single-event surveys (open symbols) and multiple-event surveys (solid symbols) at Lobster Cave (green) and Dafu (purple). SC estimates the proportion of the total population detected by the survey, with values near 1 indicating that most individuals have been detected. Solid and dashed lines represent rarefaction and extrapolation, respectively. (c) Running mean (±1SD) of turtles identified per snorkel at both sites. (d) Cumulative number of identified turtles (lines) and individuals sighted per survey event (bars) over the study period at both sites. (▼) indicates when the number of sampling events reach 35, at which point the cumulative mean of turtle individuals and cumulative number of turtle individuals started to level off in (c) and (d), respectively. Map was generated in QGIS (version 3.34.9-Prizren) and further refined with Affinity Designer (version 1.10.5).

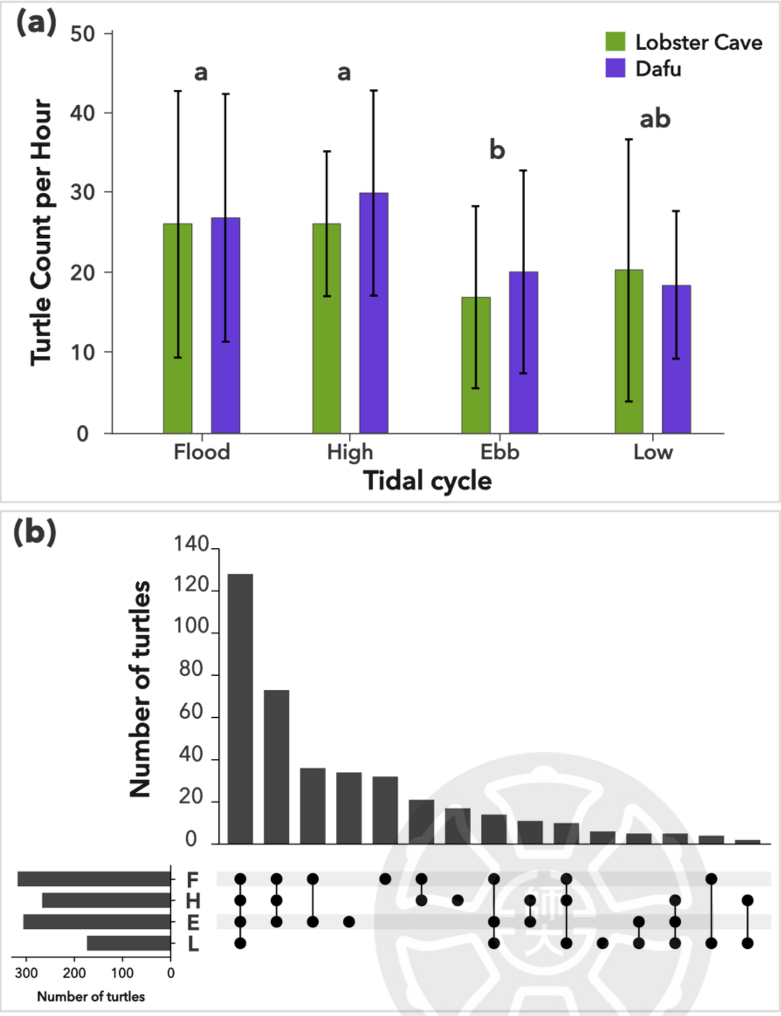

Figure 3-2. Variation on turtle counts and individual sightings among tidal periods.

(a) Mean (±1SD) turtle count per hour at Lobster Cave (green) and Dafu (purple) across tidal cycles. Annotations a, b, and ab indicate significant groupings in pairwise SNK tests ($p < 0.05$). (b) UpSet plot showing the distribution of unique individuals sighted across tidal periods. The bar plot represents the total number of turtles observed, while the intersection matrix indicates individuals sighted across multiple tidal cycles (F: Flood, H: High, E: Ebb, L: Low).

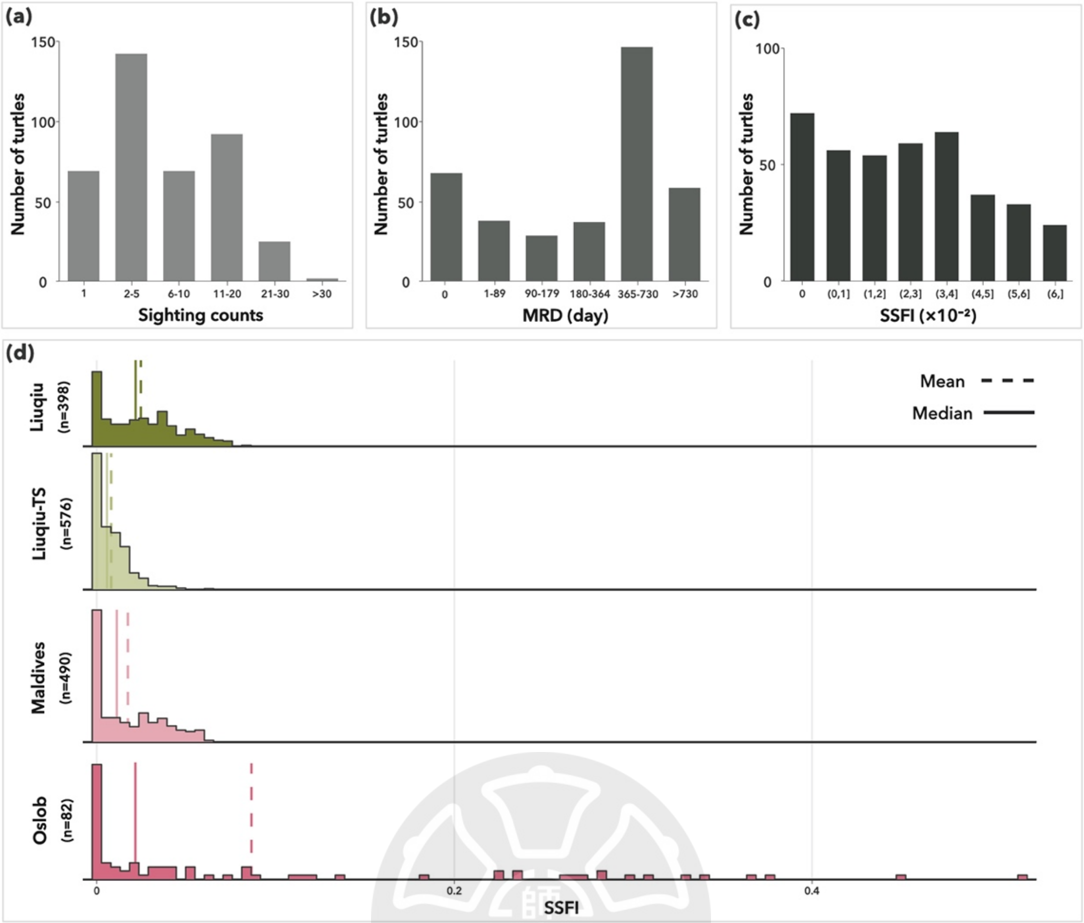

Figure 3-3. Site fidelity metrics and clustering analysis of green turtles across datasets.

(a) Distribution of sighting counts (b) MRD and (c) SSFI values of turtles identified in Liuqiu (this study). (d) Ridge plot of SSFI values for Liuqiu (green), Liuqiu-TS (pale green), Maldives (pink), and Oslob (rose pink) datasets. Dashed lines indicate group means; solid lines indicate medians.

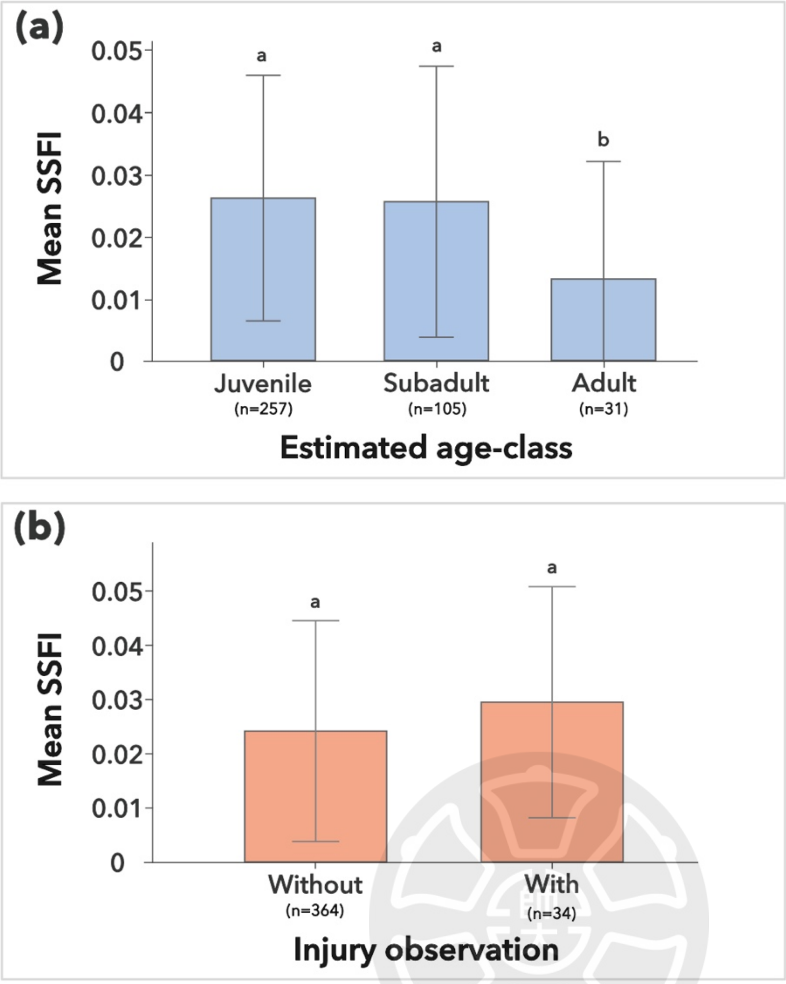

Figure 3-4. Variation in SSFI values in green turtles associated with biological characteristics.

(a) SSFI values across estimated age-classes (juvenile, subadult, and adult). Individuals with unknown age classes were excluded (n = 5). (b) SSFI values between turtles with and without observed external injuries. Bars represent mean SSFI ± standard deviation (SD). Letters in (a) indicate statistically distinguishable groups based on post-hoc pairwise Wilcoxon tests following a significant Kruskal-Wallis test ($p < 0.001$). No significant difference was found in (b) using the Wilcoxon rank sum test. Sample sizes are provided below each bar.

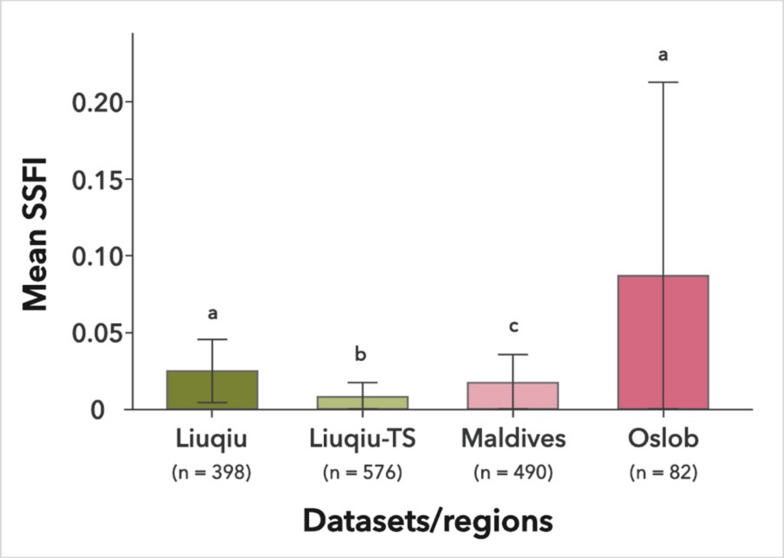

Figure 3-5. Mean SSFI values (± SD) across datasets.

The letters above the bars indicate statistically distinct groups based on post-hoc Wilcoxon tests following a significant Kruskal-Wallis test ($p < 0.001$). Sample sizes are provided below each bar.

Supplementary Materials

Figures

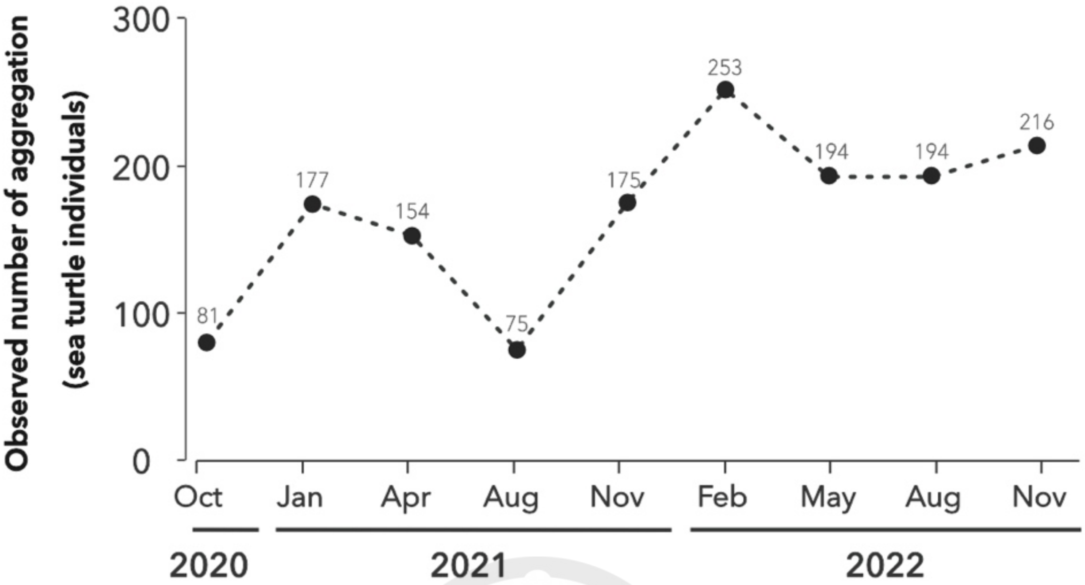

Fig. S3-1. Observed number of aggregations at both sites over time.

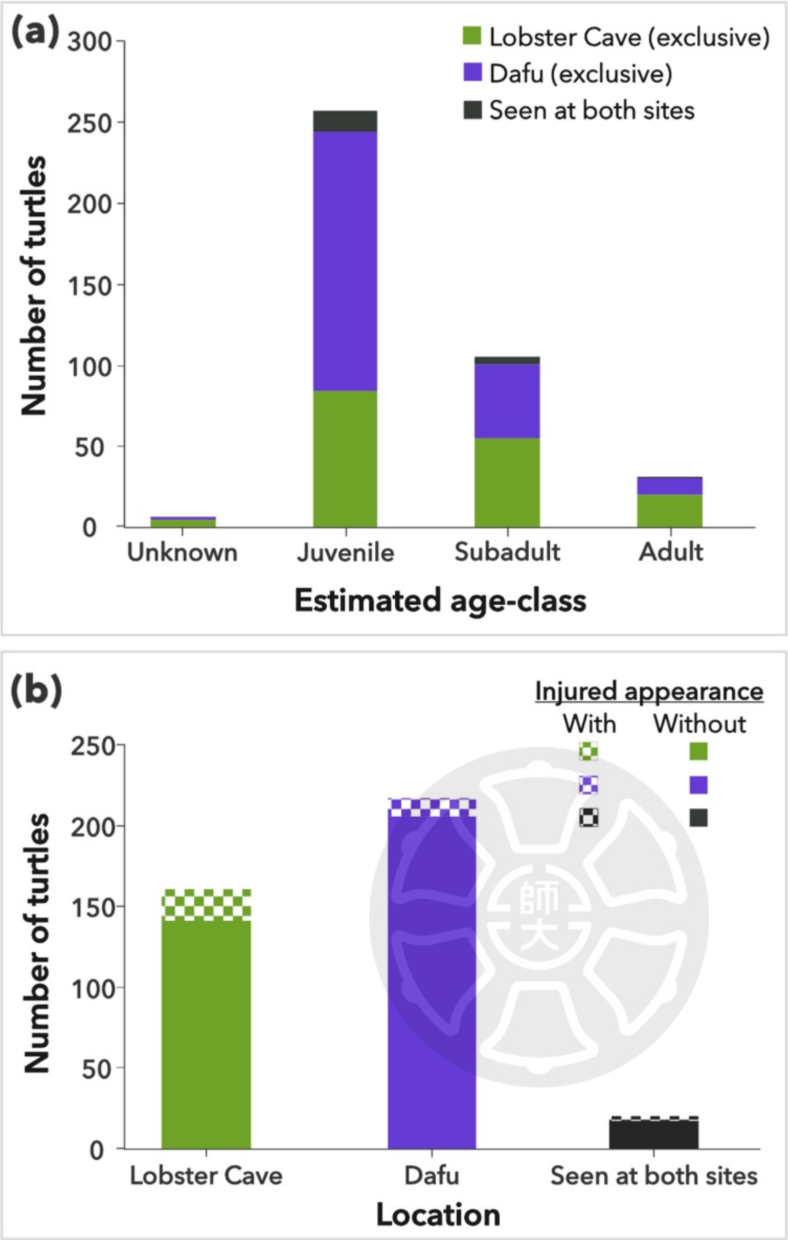

Fig. S3-2. Biological characteristics of green turtles.

(a) Estimated age-class distribution of green turtles. **Colors** represent sighting locations: Lobster Cave (green), Dafu (purple), and individuals seen at both sites (grey). (b) The injury prevalence of green turtles at each site.

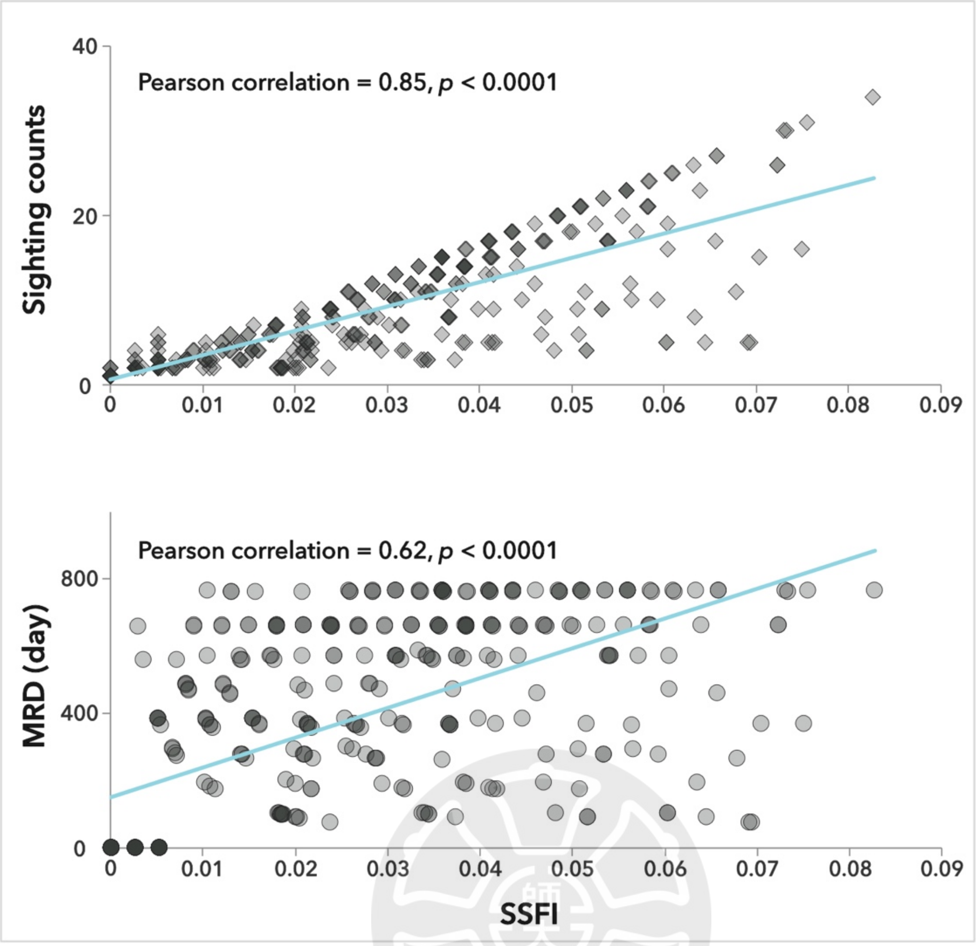

Fig. S3-3. Correlation between the Standardized Site Fidelity Index (SSFI) and sighting counts and minimum residency duration (MRD) of green turtles.

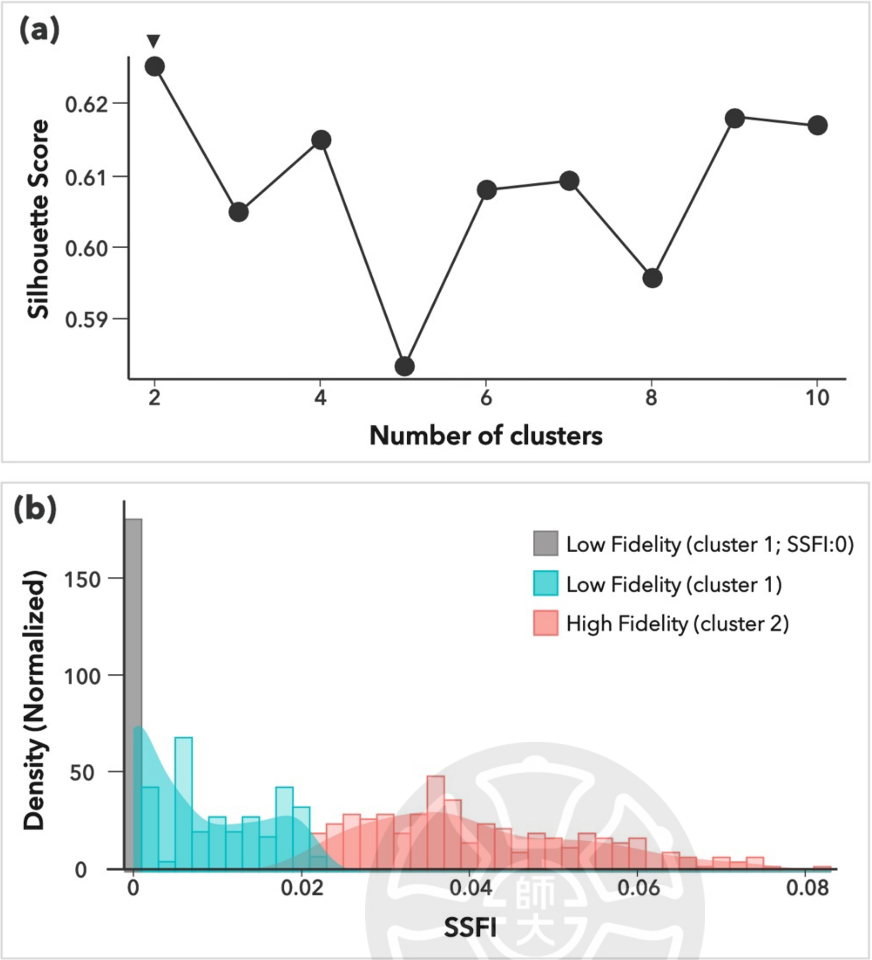

Fig. S3-4. Agglomerative hierarchical clustering (AHC) of green turtles in Liuqiu based on Standardized Site Fidelity Index (SSFI). (a) Silhouette scores for clustering analysis of SSFI values. The highest silhouette score (▼) indicates the optimal number of clusters. (b) Normalized SSFI distributions for the two clusters: "Low Fidelity" (cluster 1; grey [SSFI = 0] and turquoise) and "High Fidelity" (cluster 2; coral). Colors represent group membership, with grey indicating turtles observed only once (SSFI = 0).

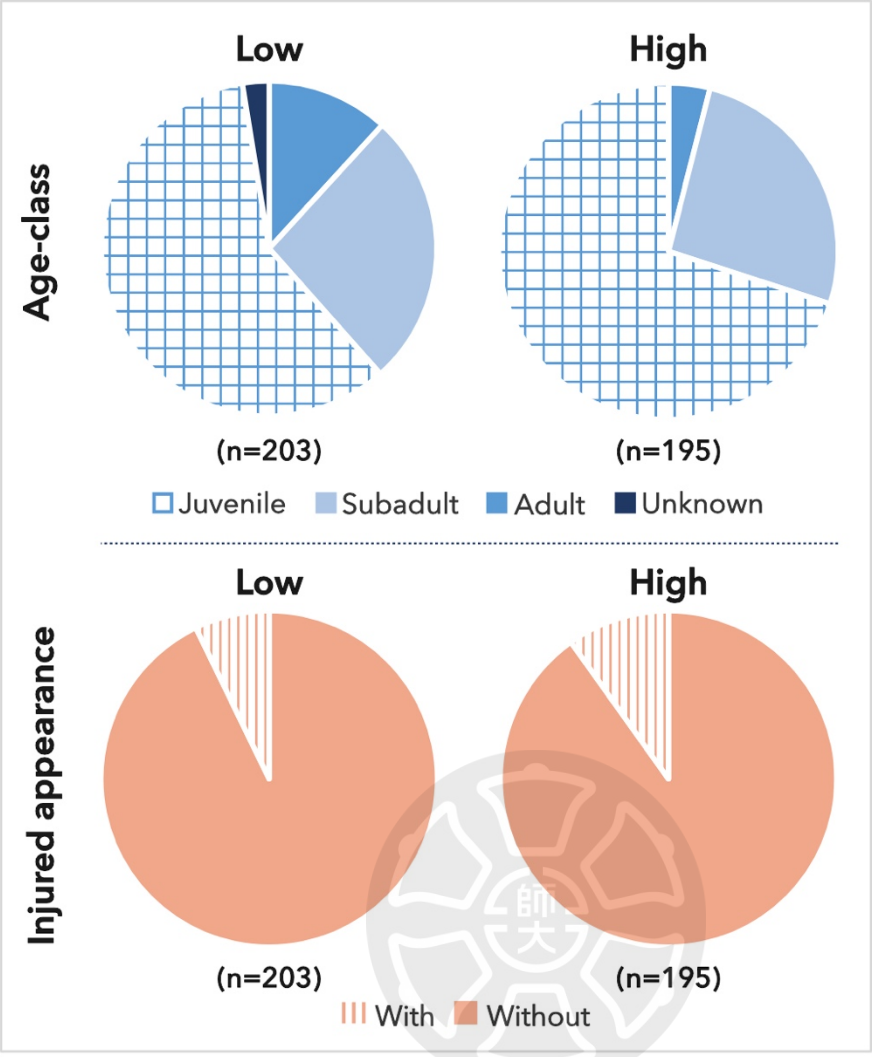

Fig. S3-5. Proportion of green turtles across different age groups (top), and observed occurrence of injuries (bottom) between fidelity groups.

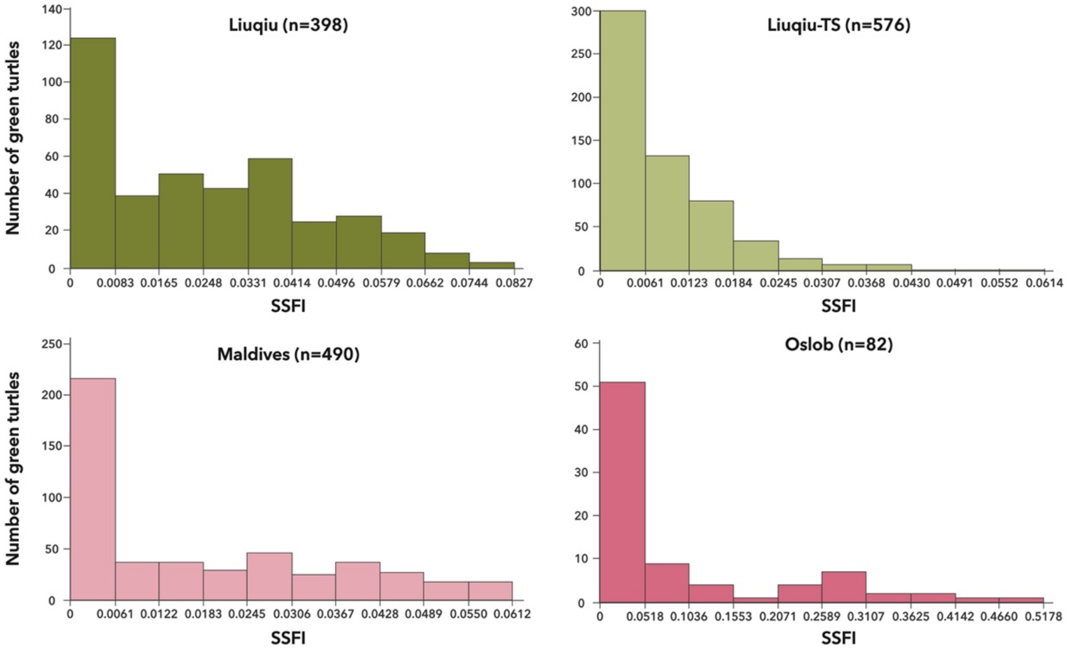

Fig. S3-6. Distribution of SSFI values for green turtles across datasets.

Supplementary Formula 3-1. Calculation of the Standardized Site Fidelity Index (SSFI).

The SSFI integrates two aspects of detection history—duration of presence and regularity of sightings—into a single index between 0 and a study-design maximum. Here, we illustrate the SSFI calculation using two example turtles.

Example 1: Turtle A

A turtle was sighted in every snorkel sampling event (sighting: 53) throughout the entire study (MRD: 765 days).

$$IT_i = \frac{F_i}{F} = 765/765 = 1$$

$$It_i = \left(\frac{F_i}{\sum_{j=1}^{T} c_{ij} - 1}\right)^{-1} = \big(765/(53-1)\big)^{-1} = (765/52)^{-1} = 52/765$$

$$SSFI = \frac{2}{\frac{1}{IT} + \frac{1}{It}} = \frac{2}{\frac{1}{1} + \frac{1}{52/765}} = 2/(1 + 765/52) = 104/817 \approx 0.1273$$

Turtle A, therefore, reaches the maximum SSFI (0.127) obtainable under our survey design.

Example 2. Turtle B

A turtle with 26 sightings and an MRD of 663 days in this study.

$$IT_i = \frac{F_i}{F} = 663/765 \approx 0.8667$$

$$It_i = \left(\frac{F_i}{\sum_{j=1}^{T} c_{ij} - 1}\right)^{-1} = \big(663/(26-1)\big)^{-1} = (663/25)^{-1} = 25/663 \approx 0.03771$$

$$SSFI = \frac{2}{\frac{1}{IT} + \frac{1}{It}} = \frac{2}{\frac{765}{663} + \frac{663}{25}} = 2/(1.1544 + 26.52) = 2/27.6744 \approx 0.0722$$

CHAPTER 4

Injury and resilience: wild recovery of green turtles from various anthropogenic damages

4.1. Abstract

Injuries from human activities are commonly reported in marine turtles worldwide, and efforts to promote recovery through treatment at rehabilitation centers have proven important. However, little is known about the resilience of turtles recovering in the wild without human intervention. Here, we document the natural healing of external injuries in green turtles (*Chelonia mydas*) using repeated in-water photographic sightings from a coastal foraging ground at Liuqiu Island, Taiwan. Drawing from two photo-identification databases spanning 14 years, we identified 105 injured turtles among ca. 7200 sightings (709 individuals). Thirteen turtles with 19 injuries had multiple re-encounters, allowing for estimation of healing durations. Average healing times were 527 days (propeller strikes), 538.5 days (fishing line entanglements), and 560.2 days (injuries of unknown causes), with severe injuries requiring ca. 600 and minor injuries ca. 491 days to heal. Healing trajectories in wild green turtles were slower than those reported for other marine megafauna. Long-term resightings of five individuals confirmed survival after recovering from severe injuries at least 106 to 2264 days, after which monitoring was discontinued. Individuals with recurring injuries were observed, with tracked individuals showing frequent use of nearshore areas near ports, emphasizing the need for targeted conservation measures specific to port areas and by extension regions with high boat traffic. These include go-slow zones, recreational fishing regulations, and increases in public outreach. This

study provides the most extensive evidence of natural injury recovery in marine turtles to date, demonstrating the long recovery durations and impacts of multiple recurring injuries. This highlights the value of long-term monitoring, supported by citizen scientists, in assessing sublethal impacts and guiding mitigation for marine megafauna.

4.2. Introduction

Marine megafauna inhabiting coastal ecosystems are increasingly exposed to numerous anthropogenic threats, including vessel traffic, fishing activity, pollution, and coastal development (Ferreira et al. 2023; Womersley et al. 2021). Green turtles (*C. mydas*), listed as Endangered on the IUCN Red List (Seminoff, 2023), forage predominantly in shallow seagrass beds and reef areas (Hazel et al. 2007; Shimada et al. 2017) and are especially susceptible because individuals often exhibit residency for years to over a decade (Fong et al. 2025; Siegwalt et al. 2020). This long-term habitat use increases their likelihood of repeated exposure to localized anthropogenic threats, particularly in coastal regions with intense fishing and tourism activity.

Anthropogenic causes of marine turtle injury and mortality are diverse, including bycatch (e.g., Cheng et al. 2019), ghost-net entanglement (e.g., Himpson et al. 2023), marine debris entanglement or ingestion (e.g., Orós et al. 2016; Sönmez 2018), hook-and-line gear entanglement (e.g., Dentlinger et al. 2024), vessel collision (e.g., Read et al. 2023), and propeller strike (e.g., Godoy and Stockin 2018; Li et al. 2022; Work et al. 2010; Work et al. 2015). Although marine turtles are frequently observed in the wild with mild to severe injuries (Archibald and James 2018; Ataman et al. 2021; Fong et al. 2025; Franchini et al. 2022; Papafitsoros et al. 2021; Work et al. 2010), long-term continuous field records documenting their natural recovery trajectories remain exceedingly scarce. As a result, it is expected that the rate and trajectory of marine turtle recovery from anthropogenic threats as measured in individuals undergoing medical treatment and rehabilitation underrepresents those experienced by wild individuals.

Determining the causes and mitigating occurrences of anthropogenic sources of injury and mortality, combined with rehabilitation efforts for injured individuals, are of primary importance to marine turtle conservation. However, understanding the resilience of wild marine turtles to single or multiple sub-lethal injuries through determining the rate of and time to recovery is important towards assessing impacts of long-term anthropogenic threats. Phu and Palaniappan (2019) provided one of the earliest field-based observations of wild green turtles recovering from propeller strike injuries through repeated captures in Mabul Island, Sabah, Malaysia; however, only four individuals exhibited a fully recovery, with healing times ranging from 174 to 723 days. More recently, Balensiefer et al. (2024) tracked the recovery of a single juvenile green turtle across six recaptures over two years in Santa Catarina, Brazil, documenting a 728-day period from a partially healed wound to complete recovery. The data obtained by these capture-mark-recapture studies demonstrated the feasibility and importance of long-term field monitoring of marine turtle injury recovery; however, due to their low sample sizes it remains uncertain how representative these values are, emphasizing the need for more comprehensive empirical data on wild recovery outcomes in marine turtles.

Bridging this knowledge gap and properly characterizing wild recovery rates of injured marine turtles requires long-term monitoring with representative mark–resight data. A compelling example is provided by McGregor et al. (2019), who documented the first case of natural wound healing in a reef manta ray (*Mobula alferrdi*) through a 15-year photo-identification (photo-ID) study in Australia. However, the acquisition of these data is both temporally and financially limiting to most conservation and research programs, impeding our understanding of how marine turtles respond to injuries of varying severity in the wild. Leveraging citizen scientists and the comprehensive temporal and spatial data available from underwater photographs of marine turtles in foraging habitats experiencing anthropogenic threats, combined with photo-ID techniques and complementary in-water surveys, provides an opportunity to collect data at a resolution necessary to answer outstanding questions related to wild injury recovery.

In this study, we examined a series of injury-healing cases—from minor carapace lacerations to severe propeller strike wounds to flipper amputations—based on repeated *in situ* observations of green turtles at Liuqiu Island in Taiwan, a known foraging hotspot for green turtles (Fong et al. 2025) that is experiencing numerous concurrent anthropogenic threats and is also a popular coastal tourism destination. These records were compiled from two extensive datasets: a multi-year citizen science photo-ID dataset (Fong et al. 2025; Hoh et al. 2022) and two years of regular in-water surveys (Fong et al. in submission), combining to form 14 years of long-term monitoring (2010 to 2024). Our study provides the first comprehensive estimates of natural healing times and recovery trajectories for green turtles by injury type, cause, and severity. Further, our data captures individuals experiencing recurring injuries (multiple unique injuries over time), reflecting the consistent exposure to multiple anthropogenic threats that marine turtles face within coastal habitats at Liuqiu Island.

4.3. Materials and Methods

4.3.1. Data collection

Turtle sighting records from the coastal areas of Liuqiu Island, Taiwan (22.34172° N, 120.36960° E) were examined for the presence of injuries and injury-healing progression from two databases: (1) the citizen science projects maintained by TurtleSpot Taiwan (See Fong et al. 2025; Hoh et al. 2022), covering 3024 occurrences from 18 dive sites from March 2010 to May 2022, and 17 sporadic sightings of known injured turtles from June 2022 to July 2024; and (2) a two-year systematic in-water survey dataset (Fong et al. in submission) covering 4192 occurrences at two dive sites, conducted quarterly from October 2020 to November 2022.

4.3.2. Evaluation of injury types, causes and severity of injured individuals

Individual injured turtles were identified by their unique facial scale patterns on both sides of their faces (Carpentier et al., 2016) either manually or with HotSpotter facial recognition software (Crall et al. 2013) to support photo-ID analysis based on an established database of Liuqiu turtles. In some cases, distinctive wound patterns were also used as supplementary markers to confirm individual identity. Injury assessment was based on individual turtle sightings documented through photographs or videos. Each occurrence was visually examined to determine the presence of external injuries or signs of healed scars. Injuries were categorized according to four criteria: (1) cause (i.e., propeller strike, fishing line entanglement, unknown), (2) location (e.g., carapace, flipper, face), (3) severity (minor or severe), and (4) healing stage (i.e., fresh, partially healed, healed), following criteria adapted from NMFS (2022), Phu and Palaniappan (2019), Work et al. (2010), and Ataman et al. (2021).

Observed injuries were categorized into seven types: amputation, propeller laceration, carapace fracture, abrasion, entanglement, carapace deformity, and flipper laceration (Table 4-1). Each was scored as minor or major based on wound dimensions and whether it caused permanent structural damage, such as carapace deformity or flipper amputation that prevents a full return to the pre-injury state (Table 4-1). Because lesion morphology can change during healing (e.g., a carapace fracture may later present as an abrasion or deformity, and a fishing-line entanglement may progress to partial amputation), we grouped wounds by their initial cause (i.e., propeller strike, fishing-line entanglement, or unknown) when quantifying recovery timelines.

4.3.3. Measurement of healing progression

Images of injured individuals that had multiple sightings were used to determine the healing process. Injured turtles that were sighted only once were excluded from the analyses. For each injury case, the healing time was estimated as the number of days between the initial sighting (i.e., when the injury was classified as fresh or partially healed) and the subsequent sighting in which the wound was visually determined to be fully healed. Partially healed injuries were characterized by early signs of tissue regeneration such as granulation or scar tissue, or residual necrotic material, showing some regrowth along the edge of the wound. Fully healed injuries were characterized by complete wound closure, no necrosis or inflammation, and full regeneration of scutes or soft tissue, along with surface keratinization and remodeling (Table 4-2). For individuals with multiple distinct wounds, each injury was assessed independently. To examine whether injury characteristics influenced recovery duration, we performed non-parametric comparisons of healing time (measured in days) across categories of injury cause, type, anatomical location, and severity. Kruskal-Wallis rank sum tests were applied using base R (kruskal.test function; R version 4.3.3, R Core Team, 2024) through RStudio (version 2024.04.01+748, RStudio Team, 2024).

To estimate healing rate, we used image analysis software SigmaScan Pro version 5.0.0 to measure the surface area of the wound at different time points. Prior to measurement, all injury images from each case were manually reviewed to identify a consistent reference point (ex., the width of a specific lateral scute or two stable spots within the carapace scute pattern) to act as a relative scale bar. The rectangle tool in the image analysis software was used to select and measure the surface area of the wound and was then calibrated against the selected reference feature to ensure consistency across images (Fig. S4-1). The healing rate of each injury between two consecutive time points was calculated using the formula:

$$y_i = \frac{\left(1 - \frac{a_i}{a_0}\right) \cdot 100 - \left(1 - \frac{a_{i-1}}{a_0}\right) \cdot 100}{t_i - t_{i-1}}$$

where y_i is the relative healing rate (percentage reduction in wound surface area per day) over the time interval $t_i - t_{i-1}$, a_0 is the initial wound surface area at the first sighting (Day 0) or the earliest measurable sighting, and a_i and a_{i-1} are the wound surface areas at time point t_i and t_{i-1}, respectively. This formula is a simplified version as that used by Womersley et al. (2021), as all reference scales for surface area determination were standardized to 1 during measurement. The recovery trajectories of individuals with at least three measurable time points were plotted using Tidyverse package in R and refined with Affinity Designer (version 1.10.5).

4.4. Results

4.4.1. Prevalence of external injuries in the marine turtle aggregation at Liuqiu Island

We obtained 7233 occurrences of marine turtles around the waters of Liuqiu Island across the 14-year monitoring period, from which we were able to identify 790 unique individuals. Of these, 13.3% (n = 105; 104 green turtles and one hawksbill) showed evidence of active or healed injuries. Among the injured turtles, the primary causes of injury were fishing line entanglement (n = 18, 17.1%), propeller strike (n = 16, 15.2%), and unknown causes (n = 71, 67.6%). Recurring injuries were documented in 11 individuals, with 10 turtles injured twice, and one injured three times. Most injuries were located on the carapace (n = 52, 49.5%), followed by the flippers (n = 35, 33.3%), head (n = 7, 6.7%), multiple body parts (two of carapace, flippers, or head; n = 10, 9.52%), and the mouth (n = 1, 0.95%). Of the injured turtles, 73 (69.5%) had minor injuries while 32 (30.5%) had severe injuries. At their final sighting (the latest recorded condition), 84 turtles (80%) had fully healed lesions, eight (7.6%) were partially healed, seven (6.7%) were recently injured (fresh), and six (5.7%) were found dead with the previously observed injuries presumed to be the cause. Injury causes are grouped into severity classes, and the observed final condition of injured turtles is shown in Fig. 4-1.

4.4.2. Healing times by injury causes, anatomic location and severity

Of the 105 injured turtles observed, 13 individuals (12.4%; all green turtles) were resighted multiple times post-injury. Six (46.2%) of these bore more than one trackable wound, yielding a total of 19 wounds for recovery-timeline analysis. Injuries caused by propeller strikes (n = 12, from seven individuals) fell into two types: propeller laceration (n = 10) and carapace fracture (n = 2), which required 274 to 860 days (mean ± SD: 527 ± 215.6) to heal, respectively. Some turtles retained lasting deformation of their carapace after the injury had healed. For example, the green turtle TW01G0059 suffered a severe propeller-induced carapace fracture that gradually recovered but left a permanent kyphosis bulge (Fig. 4-2A; Table 4-3)**.** On its earliest sighting (Day 0), an irregular fracture with bone exposure and epibiotic algae was evident on the right posterior scutes. By Day 216 bone regrowth had begun beneath the wound margins, and the wound was considered healed at Day 388 when the encounter sightings showed keratinous sealing and scute regrowth, with a slight dome forming over the former fracture (a further observation on Day 401 supported this determination; Fig. S4-2). When resighted on Day 1172, the “bump up” was more obvious, and neither rear flipper showed any sign of movement during swimming. Seven further resightings of TW01G0059 were made after Day 1172, most recently on July 3, 2024 (Day 2652), resting in the same reef spot as on Day 2481 (Fig. 4-2A), demonstrating its long-term survival after this severe injury.

Turtle TW01G0111 incurred two separate injuries from propeller strikes during our observation period, with a pre-existing but fresh injury of carapace fracture on Day 0 and a second propeller laceration observed on Day 1281 (Fig. 4-2B and 4-2C; Table 4-3). On Day 0, the fracture wound had exposed bone on the left posterior side of the carapace. By Day 70, the bone had bridged, surface scutes began to regrow by Day 316, and the wound was observed to be fully healed on Day 630. As of the next resighting on Day 695, the carapace surface had smoothed over but retained a permanent deformity at the wound site (Fig. 4-2B). About 3.5 years after its first sighting with injury (Day 1281), Turtle TW01G0111 suffered a second propeller strike and left three lacerations on its carapace (Fig. 4-2C). Both the first and second wounds measured over 20 cm in length and about 1 to 2 cm in depth and the third wound was about 10 cm in length and shallower than the first two. By Day 1463 (182 days after second injury observation), early bone bridging was visible. Surface scutes took longer to regenerate, and on Day 1652 (371 days after second injury observation) the lacerations were observed to be healed as the wounds were completely sealed with signs of surface scale regrowth. Sightings on Days 1692 and 1803 (411 and 522 days after second injury observation) showed clearly that the wounds were fully healed with a continuous scute layer. In total, Turtle TW01G0111 has been sighted 43 times and estimated to have a minimum residency duration of 2623 days on Liuqiu Island. These resightings occurred at six different sites along both the east and west shores of Liuqiu Island, including inside the main harbor, suggesting a broad home range.

Turtles with fishing line entanglements (n = 2) took at least 450 to 627 days (mean ± SD: 538.5 ± 125.2) for their front flipper to progress through entanglement, swelling, necrosis, auto-amputation, and healing. On its first sighting, Turtle TW01G0048 (Fig. 4-3) was initially observed entangled by a fishing line attached to a rock-fishing buoy; the observer, a citizen scientist, attempted but was unable to remove the line. By Day 182, the line had constricted the base of its right front flipper, causing visible swelling. A video on Day 475 confirmed that the turtle was not using the injured flipper while swimming. On Day 488, the swelling persisted with suspected ischemic necrosis and by Day 627, the flipper had already auto-amputated but showed no signs of inflammation and was considered as healed. When resighted on Days 1107 and 1149, the turtle appeared to have fully resolved the loss of its flipper with adaptive function and was thereafter resighted feeding on Day 1549. On Day 1776, a new line was observed around the left front flipper and possibly a hook in its mouth. However, in a sighting on Day 1850, the turtle appeared uninjured. On Day 1993 the same turtle was sighted feeding in the surf zone, demonstrating robust recovery and resilience after the severe fishing line entanglement followed by self-amputation.

Injuries of unknown causes (n = 5, form four individuals) were either abrasions on the carapace (n = 3) or those on the facial area near the eyes (n = 2). These were observed healed over 193 to 968 days (mean ± SD: 560.2 ± 293.3; Table 4-3). Observed healing times by injury cause, anatomic location, and severity are shown in Fig. 4-4A. Minor wounds (n = 11) healed over 193 to 968 days, with a mean ± SD of 491 ± 240 days. Severe wounds (n = 8) took at least 371 to 860 days to fully heal, with a mean ± SD of 600 ± 190 days. Despite apparent differences in healing time between severity, statistical test did not find significant differences in healing time were found among groups based on injury cause ($\chi^2 = 0.018$, df = 2, $p = 0.991$), location ($\chi^2 = 4.63$, df = 4, $p = 0.328$), severity ($\chi^2 = 1.15$, df = 1, $p = 0.283$), or wound type ($\chi^2 = 0.019$, df = 3, $p = 0.999$).

4.4.3. Healing rate and recovery trajectory

The reduction in surface area of the wounds was measurable in eight injuries incurred by five individuals. Injuries included abrasion (n = 1), propeller lacerations (n = 5), and carapace fractures (n = 2). Severity of each injury was categorized as minor (n = 2) and severe injuries (n = 6). Healing rates were measured as the as percentage reduction in injury surface area per day and ranged from 0.08% to 1.53% per day (mean ± SD: 0.38 ± 0.49, n = 20; Table 4-3). Most injuries (n = 5) had a higher healing rate during the early stages (Table 4-3) but declined over time (Fig. 4-4B). Minor injuries achieved 50% within 300 days; notable exceptions, such as Turtle TW01G0047 (propeller-induced facial laceration), progressed to full recovery earlier than this (i.e., Day 275), showing a substantial variability in recovery times among the observed individuals. Several severe injuries (n = 4) remained less than 50% healed even after 375 days. The slowest observed recovery (TW01G0162) took approximately 725 days to reach the 50% closure threshold, which included the regrowth of surface scutes.

4.5. Discussion

Anthropogenic injuries are a pervasive threat to marine megafauna globally. Although conservation programs exist to minimize these impacts through medical treatment and rehabilitation (Baker et al. 2015; Gallini et al. 2021), the number of injured individuals that make it to these centers are insignificant compared to those that are left to recover in the wild (Willette et al. 2023). Currently, we know very little about the fate of injured marine megafauna in the wild, including that of marine turtles. This knowledge has importance in our understanding of the impacts of anthropogenic injuries on populations and on their conservation.

Here, we present the first comprehensive and long-term direct in-water observational evidence of injury healing in wild green turtles at a coastal foraging ground in Taiwan. Of the identified individuals, 13.3% exhibited external injuries or healed scars and 80% of these turtles were later observed with fully healed wounds. The healing times of injuries were prolonged, averaging 491 days for minor injuries and 600 days for severe injuries, with some cases exceeding 860 days. Several individuals survived serious trauma—such as propeller strikes or amputation caused by fishing line entanglement—and were able to adapt their behaviors and remain resident in the area after recovering. Recurring injuries in some individuals highlight the ongoing risk of human activities in nearshore habitats and the need for targeted mitigation. Opportunistic in-water sightings may introduce bias, particularly toward injured individuals, as citizen scientists tend to report unusual or visually striking cases (Deacon et al., 2023; Snäll et al., 2011). This observational bias, combined with the irregular observation intervals, could result in an overrepresentation of injury rates and an overestimation of healing times. Nonetheless, this limitation is unavoidable with *in situ* observation of marine megafauna. However, given the temporal (n = 14 years) coverage and injury observations (n = 105) observed in our study, our results provide foundational information that describes the potential for wild marine turtles to heal and provides a template for expected healing and recovery trajectories for wild individuals observed in the future.

4.5.1. Recovery success and healing times of injured marine turtles

Wild marine turtles exhibited a strong capacity to recover from the injuries at their foraging site. In this study, 80% (n = 84 of 105) of injured individuals showed complete recovery, and an additional 7.6% (8 of 105) showed signs of partial recovery. This finding aligns with previous observations in nesting loggerhead turtles in southeastern Florida, USA, where 24% (107 of 450) of examined individuals had at least one or more external injuries, 88% of which were fully healed and 9% were partially healed (Ataman et al., 2021).

Long-term records (ca. 20 years) of rehabilitation centers in Florida, however, showed that anthropogenic injuries had a significant impact on marine turtle survival and fate. During this time, over half (55.3%; 1,047 of 1,700 individuals) of the marine turtles died during rehabilitation, only 36.8% (626 individuals) healed to a point where they could be released, and 1.5% (27 individuals) remained in captivity permanently due to severe injuries (Baker et al., 2015). Recovery rates appear, however, to be injury specific. Stranded marine turtles had a substantially lower recovery and release rate, with data from Queensland, Australia, showing that only 26% were ever healthy enough to be released (Baker et al., 2015). Individuals suffering from head trauma had a higher release rate from rehabilitation center, with 72.4% (21 of 29) of rehabilitated individuals recovered after treatment and were released after a period ranging from a few days to 8 months (Franchini et al., 2022). The recovery success rates for turtles admitted to rehabilitation centers are not directly comparable to those observed in wild populations, due to the severity of their injuries and the fact that these stranded turtles could not survive independently in their natural habitat, resulting in their stranding and subsequent admission to the rehabilitation facility. Additionally, euthanizing animals in rehabilitation centers for animal welfare reasons may contribute to the decreased success rate of releasing individuals back into the wild.

In our study, healing times based on in-water sightings averaged around 1.5 years, ranging from ~491 days for minor to ~600 days for severe injuries, with similar durations across different causes (fishing line entanglement: 538.5 days; propeller strikes: 527 days; unidentified causes: 560.2 days) These values align with healing times reported in other capture-mark-recapture studies, such as Phu and Palaniappan (2019) and Balensiefer et al. (2024), which documented recovery periods of 181 to 728 days for propeller injuries—comparable to our observed range of 274 to 860 days. It is important to note that healing time itself is not the only metric that affects marine turtle health, longevity, and reproductive output, all of which are important impacts of an initial injury. During the healing process, individuals may be at risk of infection (Fichi et al. 2016; De Oliveira et al. 2021) and flipper constriction or amputation may compromise feeding efficiency and diving behavior (Franchini et al. 2020). As such, it is important to note that healing time is a representation of a marine turtle's resilience to the initial trauma, but the presence of the trauma itself can have secondary impacts. This emphasizes the importance of mitigating the sources of trauma for the protection and conservation of marine turtles.

While our study provides evidence of wild turtle recovery and survival following minor to severe injuries from anthropogenic causes, direct human intervention and rehabilitation practices are still important conservation tools. Freire et al. (2021) reported a juvenile green turtle with severe propeller lacerations exposing the coelomic cavity, was recovered and released after 120 days in rescue center, following surgical carapace reconstruction and intensive care. However, lacking pre-release images or documentation of scute regrowth, it is difficult to directly compare the recovery time with those in our study. Franchini et al. (2016) treated three loggerhead turtles with skull fractures and brain exposure using surgical curettage and a plant-based wound dressing. The wounds closed within 66 to 85 days, and one turtle with neurological deficits fully recovered after ca. 10 months of rehabilitation. Moreover, Franchini et al. (2020) demonstrated that among severely entangled flippers in loggerhead turtles (n = 14), only two required amputations, while the rest recovered fully within 1 to 3 months with a combination treatment of surgical curettage, antibiotics, and plant-based wound dressing. These cases demonstrate that intensive care can substantially speed up recovery. In addition to surgical care and nutritional support, these rapid recoveries were likely aided by the stable conditions of rehabilitation centers (e.g., constant temperature, salinity, and possibly filtered water), in contrast to fluctuating conditions in the natural environment that may prolong healing.

Although the rate of healing in reptiles is temperature-dependent, the common garter snake healed significantly faster in higher ambient temperatures (Smith & Barker, 1988). On Liuqiu Island, the sea surface temperature averages 27.7 ± 2.3 °C (Central Weather Bureau, 2023), indicating a moderate and biologically stable thermal environment. This range is unlikely to cause thermal stress or cold-stunning but may still influence healing rates slightly, with potentially faster recovery during warmer periods. However, current data are insufficient to examine this variation, as healing observations in the wild are limited in number, irregular in timing, and rarely coincide with detailed environmental measurements such as water temperature at the time of injury or recovery.

Compared to marine turtles, other marine megafauna species exhibit far more rapid wound healing following anthropogenic injuries. Whale sharks (*Rhincodon typus*) were found to achieve 90% surface-area closure within 35 days and complete healing of severe lesions by 170 days (Womersley et al., 2021), while reef manta rays (*M. alfredi*) showed a steady reduction in laceration size with 95% closure within 295 days (McGregor et al., 2019). Recent studies have found that cetaceans have evolved unique genetic adaptations and specialized immune cells that modulate inflammation and facilitate skin wound healing (Kang et al. 2024; Su et al. 2025), potentially accounting for observations of increased wound healing rates in common dolphins (*Delphinus delphis*), such as those by Olaya-Ponzone et al. (2020) which observed complete healing between 21 to 147 days. In contrast, marine turtles require a longer time to heal after injuries, often taking 1–2 years to regrow both carapace and scutes, which could be due to their lower metabolic rates. This significant difference underscores the challenges of carapace regeneration and the long duration required for complete recovery in chelonians.

4.5.2. Conservation implication

The identified causes of injuries, namely fishing line entanglement and propeller strikes, can result in both permanent carapace deformity or disability (loss of flipper) after recovery. A hull strike injury to a green turtle (TW01G0059) impacted its spinal cord, resulting in a "bump up" carapace and impairing its ability to move its hind limbs. This secondary impact of the primary injury may further compromise its ability to crawl properly and, if female, to build a nest successfully (Ataman et al. 2021). Threats from fishing line entanglement are serious, as turtles cannot actively remove the lines independently and the nylon fishing line won't break down naturally, incurring a continued harm that could later lead to necrosis, septicemia, and amputation.

Most sightings of injured turtles with trackable healing progression were concentrated in nearshore waters (<5 m depth), often close to ports (Fig. 4-5). This spatial clustering highlights the importance of implementing targeted conservation measures to reduce the risk of vessel strikes. Several prevention measures for propeller strikes have been proposed and examined, but most have been found to be ineffective. For example, propeller guards are only slightly helpful when the boat is at idle speed (i.e., when the motor is in gear but operating at its lowest speed, ca. of 7 km h^{-1}) but are completely ineffective at planing speed (Work et al., 2010) when most turtle impacts occur. Speed reduction is therefore considered the most effective measure, limiting boat speed (e.g., 4 km h^{-1}; 2 knots) within foraging areas so that turtles have the capacity to swim away from the threat (Hazel et al., 2007). Speed reduction has been found to reduce cetacean injury and death, with speed limitations for large ships (i.e., > 300 gross registered tons) of 10 knots (ca. 18 km h^{-1}) decreasing death in both blue and humpback whales by 11–13% and 9–10%, respectively (Rockwood et al. 2020). This rate of reduction would have important impacts on marine turtle injuries, as nearly half of the healed turtles in our study (46.2%, 6 out of 13; Table 4-3) experienced secondary injuries, and at least three of these cases involved propeller strikes as the cause for both injuries. Our results therefore provide strong evidence that establishing "go-slow" zones at foraging hotspots around Liuqiu Island and implementing a strict vessel speed limit (less than 6 knots) when entering and exiting the harbor can substantially reduce the main causes of human-induced marine turtle injuries around the island.

Mitigating turtle fishing line entanglement remains a more difficult challenge locally and globally (Battisti et al. 2019). On Liuqiu Island, although fishing exclusion zones have been established since 2000 and a ban on gillnet fishing within three nautical miles of the island established in 2013 likely reduced bycatch and ghost fishing nets, the issue of thin fishing lines and fishhooks harming marine life remains an ongoing issues. Stranding records from Liuqiu Island indicate that entanglement in fishing line and gear poses a more significant risk than propeller strike and boat collisions. In 2019, 42.8% (6 out of 14) of dead stranded turtles found on Liuqiu Island exhibited carapace damage from propeller impacts (Li et al. 2022). Yet when data from 2017 to 2022 were aggregated, more stranded turtles were affected by fishing line, hook, or gear entanglement (30%) than by propeller strikes (25%; Li 2022). Our data also show that discarded recreational fishing lines were responsible for severe injuries, but to date these remain unregulated. Tackling this issue will require targeted public outreach and community engagement, the installation of recycling bins and signs at popular fishing spots, and the promotion of biodegradable fishing line, if available, to minimize long-term hazards.

Long-term observations of a subset of five individuals recovered from severe injuries showed ongoing evidence of their adapted behavior and survival in the wild for at least 106 to 2,264 days (mean ± SD: 948.7 ± 765 days) after complete recovery. This group includes two front flipper amputation survivors (TW01G0048: 1,366 days; TW01G0429: 106 days) and three individuals with permanent carapace deformities (TW01G0049: 620 days; TW01G0059: 2,264 days; TW01G0111: 516 days after healing from the first injury before a secondary injury, and a further 820 days after healing from the secondary injury). These post-recovery survival times greatly exceed the 8 to 387 days (155 ± 95 days) reported in a satellite-tracking study on post-release rehabilitated marine turtles, despite nearly 20% (5 of 26) of the deaths being linked to other anthropogenic factors (Robinson et al., 2021). Our findings reveal the remarkable resilience of wild-recovered turtles and strengthen the case for releasing rehabilitated individuals back into their natural habitats. However, despite our findings that wild turtle recovery does occur, as long as anthropogenic threats persist within their foraging and migratory waters, injuries to marine turtles from boat propellers, hulls, and fishing gear remain a substantial conservation concern requiring immediate and locally-adapted solutions.

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Tables

Table 4-1. Injury type and severity classification of green turtle injuries from external visual assessment in-water and using encounter photographs.

Images (top to bottom): courtesy of Huai Su (1–5), Shih-Ting Liu (6), and Chian-Shiun Hu (7).

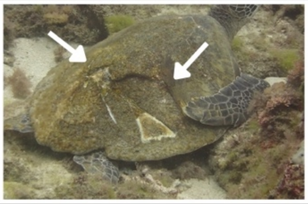
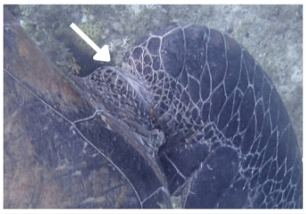
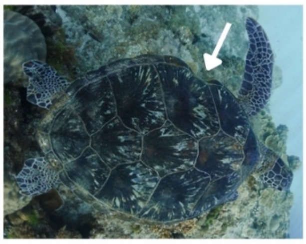
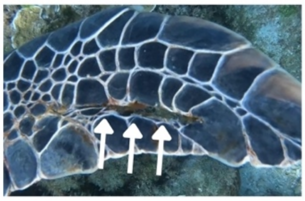
Injury type	Description	Severity	Photographic example
Amputation	Partial or total removal of an appendage, including front and rear flipper.	**Minor** < 25% of flipper loss.	
		Major ≥ 25% of flipper loss.	
Propeller laceration	Linear cuts produced by a sharp object, often appearing as one or more parallel, evenly spaced incisions, often on carapace.	**Minor** Superficial slice <1 cm depth and < 5cm length.	
		Major Slice ≥ 1 cm depth with underlying tissue or bone visible and/or scute fractured.	
Carapace fracture	Irregular crack resulting from a blunt collision with a vessel, skeg, or heavy object.	**Minor** Thin or shallow crack < 5 cm and no bone exposed.	
		Major ≥ 5 cm and bone or tissue exposed, or shell segment unstable.	
Abrasion	Scraped keratin; white or pink dermis visible; often on scutes or plastron.	**Minor** < 25 cm^2.	
		Major ≥ 25 cm^2.	
Entanglement	Fishing line, gear or rope present and attached to the animal.	**Minor** Superficial line mark or hook attached.	
		Major Deep constriction. Causing swelling, necrosis or amputation.	
Carapace deformity	Irregular or asymmetric shell edge.	**Minor** Indentation ≤ 25 % of perimeter or confined to marginal scutes	
		Major Indentation ≥ 25% shell perimeter and reach to the lateral scute.	
Flipper laceration	A linear cut, notch, or incision on the margins or surface of a flipper.	**Minor** Incision that does not impair flipper movements.	
		Major ≥ 5 cm length with tissue/bone exposure or impaired function.	

Table 4-2. Criterion and representative images used to determine the healing stages of four common injury types (entanglement, abrasion, propeller laceration, and carapace fracture) observed in green turtles.

Injuries were categorized as partially healed (tissue regeneration evident at wound margins), or completely healed (sealed wound, full regrowth of scutes or skin). Images illustrate each injury type at different healing stages to guide standardized classification. Image credits: Huai Su (entanglement, abrasion partially healed, carapace fracture partially healed); Chia-Ling Fong (abrasion healed, propeller laceration partially healed [lower]); Yoko Nozawa (propeller laceration partially healed [upper]); Yeng Hsun Huang (propeller laceration healed, carapace fracture healed).

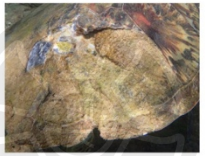
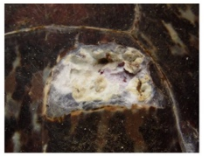
	Entanglement	**Abrasion**	**Propeller laceration**	**Carapace fracture**
Partially healed	 Acute ligature wound	 Necrosis tissue on the scales	 Fractures showing signs of regrowth	 Carapace wound healing with epidermal proliferation
	 Necrosis tissue	 Necrosis tissue on the carapace	 Fractures showing signs of regrowth	 Carapace wound healing with epidermal proliferation
Healed	 Wound closure	 Regrowth of the affected scales	 Full regrowth of the affected scutes	 Full regrowth of the affected scutes

Table 4-3. Summary of observed injuries in green turtles with estimated healing times.

Each entry includes the turtle ID, inferred cause, injury type, location, severity classification, and healing time (in days). Healing time is estimated based on repeated sightings, representing the interval from the first observation of an injury to the point at which when external healing was visually confirmed.

Injury No.	Turtle ID	Note	Cause	Injury Type	Location	Severity	Days of observation from injured to healed
1	TW01G0047	1st wound	Unknown	Abrasion	Carapace	Minor	369
2	TW01G0047	2nd wound	Unknown	Abrasion	Carapace	Minor	669
3	TW01G0048	1st wound	Fishing line entanglement	Entanglement, amputation	Right front flipper	Severe	627
4	TW01G0049	1st wound	Propeller strike	Propeller laceration	Carapace	Severe	619
5	TW01G0049	2nd wound	Propeller strike	Propeller laceration	Carapace	Severe	852
6	TW01G0049	2nd wound	Propeller strike	Propeller laceration	Right face	Minor	275
7	TW01G0058	1st wound	Propeller strike	Propeller laceration	Carapace	Minor	317
8	TW01G0059	1st wound	Propeller strike	Carapace fracture	Carapace	Severe	388
9	TW01G0106	1st wound	Propeller strike	Propeller laceration	Carapace	Minor	393
10	TW01G0106	2nd wound	Propeller strike	Propeller laceration	Carapace	Minor	677
11	TW01G0111	1st wound	Propeller strike	Carapace fracture	Carapace	Severe	630
12	TW01G0111	2nd wound	Propeller strike	Propeller laceration	Carapace	Severe	371
13	TW01G0120	1st wound	Propeller strike	Propeller laceration	Carapace	Minor	668
14	TW01G0120	2nd wound	Propeller strike	Propeller laceration	Carapace	Minor	274
15	TW01G0162	1st wound	Propeller strike	Propeller laceration	Carapace	Severe	860
16	TW01G0218	2nd wound	Unknown	Abrasion	Left eye	Minor	602
17	TW01G0294	1st wound	Unknown	Abrasion	Carapace	Minor	968
18	TW01G0429	1st wound	Fishing line entanglement	Entanglement, amputation	Right front flipper	Severe	450
19	TW01G0514	1st wound	Unknown	Abrasion	Eye	Minor	193

Table 4-3. Summary of relative healing rates (% per day) for injured green turtles based on the reduction in wound surface area between consecutive observations. **Injury Label** corresponds to injuries shown in the recovery trajectories (Fig. 4-5). **Injury No.** refers to the identifiers in Table 4-2, which provide information on injury type, location, cause, and severity. **Interval** indicates the number of days between two measurable observations, with day values referenced to the initial sighting of the injury.

Injury Label	Injury No.	Interval	Healing Rate (%/day)
TW01G0047-2	2	Day 0–42	0.43
		Day 42–669	0.13
TW01G0049-1	5	Day 61–193	0.19
		Day 193–852	0.11
TW01G0049-2	5	Day 61–193	0.09
		Day 193–852	0.13
TW01G0049-3	6	Day 51–79	1.51
		Day 79–89	1.53
		Day 89–275	0.23
TW01G0059-1	8	Day 0–111	0.32
		Day 111–388	0.23
TW01G0111-1	11	Day 0–52	0.08
		Day 52–316	0.12
		Day 316–630	0.21
TW01G0111-2	12	Day 0–19	1.41
		Day 19–182	0.22
		Day 182–371	0.20
TW01G0162-1	15	Day 93–144	0.13
		Day 144–593	0.09
		Day 593–860	0.20

Figures

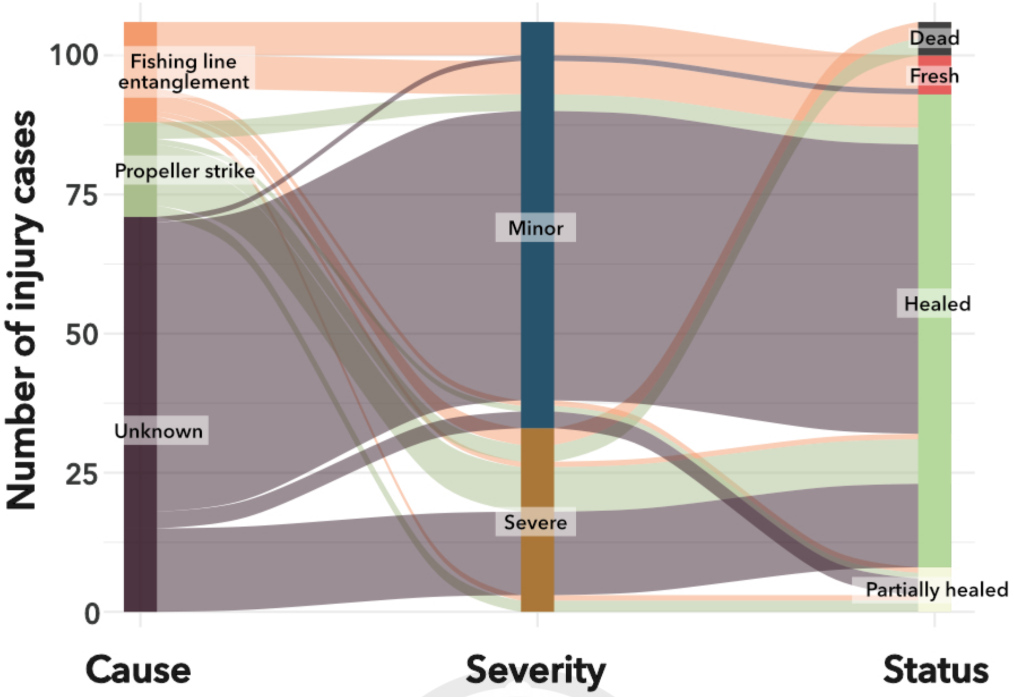


Figure 4-1. Sankey diagram illustrating the flow of injury causes through severity classes to the final status for injured turtles observed *in situ*.

The width of each band is proportional to the number of injuries: left nodes represent injury causes (propeller strike, fishing line entanglement, unknown), middle nodes represent severity (minor, severe), and right nodes represent the last observed condition of turtles regarding its injury (healed, partially healed, fresh, dead).

Figure 4-2. The natural healing progressions of injured green turtles with severe injuries caused by propeller strikes.

A: Turtle TW01G0059 had a carapace fracture and spinal cord injury that impaired the movement of rear flippers. Its carapace experienced depression, gradually lifted, and resulted in a permanent kyphosis bulge after healing. Images courtesy of Huai Su (Day 0, 216, 1172) and Ying-Hsiu Liao (Day 2481). B: Turtle TW01G0111's carapace fracture exposed underlying bone on Day 0. By Day 70, initial bone bridging had sealed the fracture, while complete scute regrowth and surface remodeling took longer. Images courtesy of Yeng-Hsun Huang (Day 0, 70, 695) and Huai Su (Day 316). C: Turtle TW01G0111 experienced a second propeller laceration 651 days after the initial fracture had healed. By Day 182, bone bridging had sealed the laceration, and new scutes had begun to grow. By Days 411 and 522 the wounds were completely closed, with a continuous shell surface. The healing point for this injury was considered to be Day 371. Images courtesy of Arwen Lin (Day 0), Chia-Chen Tsai (Day 182), Yeng-Hsun Huang (Day 411), and Cheng-Yu Chao (Day 522).

Figure 4-3. Healing progression and subsequent sightings of green turtle TW01G0048 following fishing line entanglement that resulted in flipper amputation.

The yellow asterisks indicate a fishing line entanglement. The white arrows indicate lacerations. Images courtesy of Po-Han Hsu (Day 0), Huai Su (Day 182, 627, 1149, 1776), Jiun-Shian Li (Day 488), and Shang-Ping Liu (Day 1993).

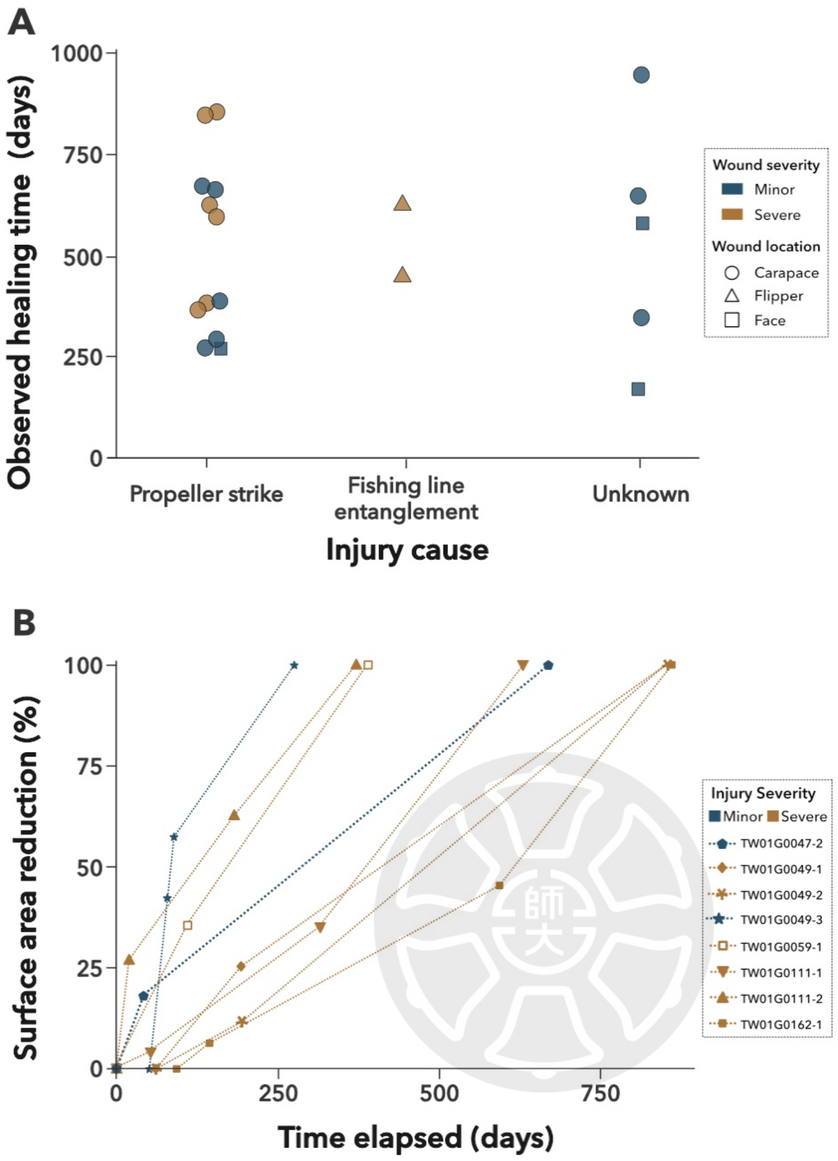


Figure 4-4. Healing times and recovery trajectories.

Symbols indicate the injury location: circles indicate carapace, triangles indicate flipper, and squares indicate wounds on the face. Colors indicate wound severity: blue for minor wounds, brown for severe. (A) Observed healing times for green turtle wounds by injury cause and severity. Each point indicates the number of days from injury to the last sighting of complete healing. (B) Recovery trajectories based on surface area reduction of wounds.

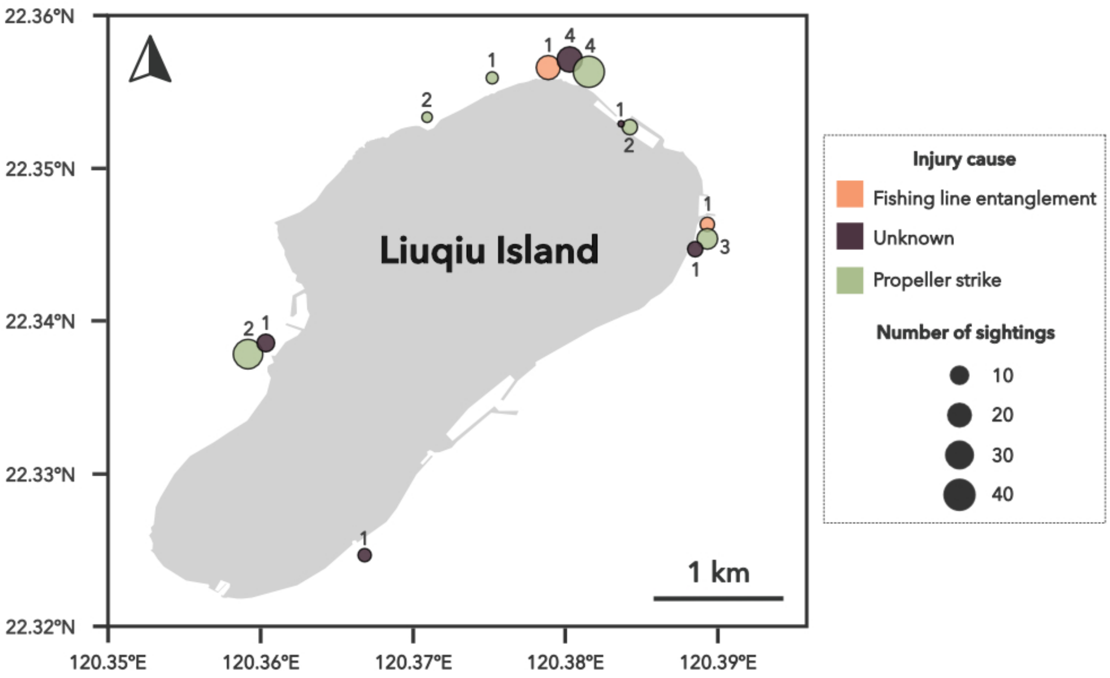


Figure 4-5. Distribution of injured turtles with trackable healing times around Liuqiu Island.

Each point marks a sighting location of individuals whose injury recovery was monitored over time. Colors indicate injury causes: green (propeller strike), orange (fishing line entanglement), and purple (unknown cause). Circle sizes indicate the number of sightings per cause at each site. Labels (e.g., 1) next to circles indicate the number of injured turtles per cause at each site.

Supplementary Materials

Figure

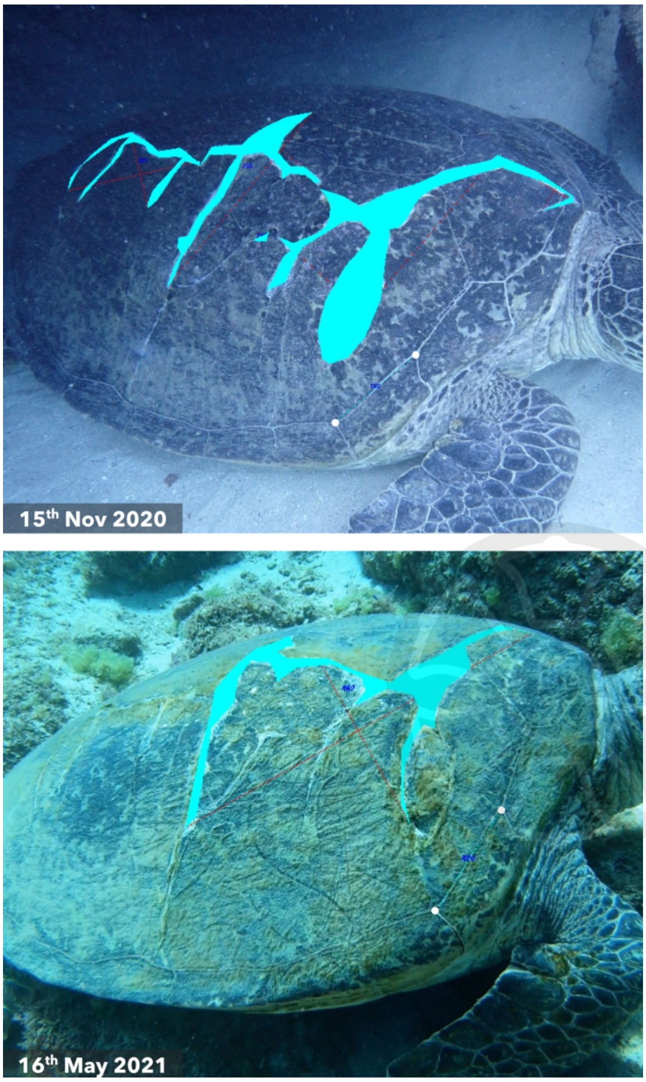


Fig. S4-1. Example of wound-area measurement protocol in SigmaScan Pro. The blue polygon outlines the selected wound surface, and the blue line between white dots indicates the pixel-based reference scale used to standardize measurements. Images courtesy of Arwen Lin (15th Nov 2020) and Chia-Chen Tsai (16th May 2021).

Fig. S4-2. Keratinous sealing and scute regrowth of injured green turtle TW01G0059. Images courtesy of Chi-An Sung (Day 388) and Yeungs Ting (Day 401).

CHAPTER 5

General discussion

5.1. Summary and conservation implications

Conservation of marine turtles requires an integrative approach that covers all life stages from different aspects, such as nesting populations, hatchlings, foraging populations, stranded turtle rescue, and rehabilitation. While most research and conservation efforts in Taiwan have focused on nesting beaches and rehabilitation centers, this dissertation addressed a critical gap by focusing on population ecology on foraging green turtle (*Chelonia mydas*) in coastal waters. By combining crowdsourced data and systematic in-water surveys, this research provides a better understanding of their spatial distribution, demographic structure, habitat connectivity, residency patterns, and resilience under anthropogenic threats in Taiwan.

Foraging grounds are vital for maintaining populations, in order for individuals to restore energy, enhance population growth, and support successful breeding migrations (Chatzimentor et al., 2021). Conducting in-water research in foraging grounds offers valuable insights into demographic population structure and spatial use, but also presents unique logistical and methodological challenges. To overcome these challenges, we explored two complementary approaches: opportunistic data contributed by citizen scientists and statistically representative data obtained through systematic in-water snorkel surveys. Crowdsourcing reports of marine turtle sightings enables broad geographic and temporal coverage that would be logistically challenging for research teams to achieve alone. However, variations in sampling efforts and observer bias can affect data reliability. For instance, citizen scientists may disproportionately report rare events such as injury incidents, while underreporting individuals frequently encountered, as noted in Chapters 2 and 3. In contrast, surveys conducted or led by research teams can implement standardized protocols, thereby improving data consistency and enabling robust ecological modeling, albeit within more constrained spatial and temporal scopes. Importantly, this does not imply that the citizen science approach is inferior. Even researcher-led surveys may lack an optimal sampling design (Hoffmann et al., 2019). Depending on the study's objectives, designing systematic surveys with consistent sampling efforts at key monitoring sites, coupled with participation from trained citizen scientists, can help address spatial gaps or observer bias. When citizen science is well-integrated, citizen science data can provide a reliable complement to traditional survey methods (Harvey et al., 2018; Krabbenhoft & Kashian, 2020).

Currently, the inconsistent use of the term ‘site fidelity’ and the lack of standardized metrics, including quantitative descriptions, hinders advanced analysis and cross-study comparisons. The application of a Standardized Site Fidelity Index (SSFI) in this study provided a quantitative framework for evaluating residency patterns among foraging turtles. However, further methodological refinement is needed. For example, combining SSFI with other fidelity metrics (e.g., residency duration, resighting rate, or sighting frequency) may offer a more robust basis for clustering analyses like AHC. Additionally, exploring normalization procedures or effort-based corrections would help address the strong influence of sighting or survey frequency, which can inflate or deflate SSFI values and compromise comparisons across studies with differing survey designs. Furthermore, clustering SSFI values enables the identification of distinct fidelity groups, allowing for the estimation of the proportion of local aggregation that repeatedly utilizes the same foraging area over multiple years.

Long-term monitoring and collaborative efforts between scientists and citizen scientists, combined with contributions to open photo-ID data, it becomes possible to define critical foraging hotspots globally more effectively. These definitions can go beyond identifying areas with a higher number of local aggregations, also by incorporating residency patterns to pinpoint key foraging hotspots that support long-term use by foraging populations. As current models predicting of shifting foraging hotspots under the impact of climate change heavily rely on species occurrence records (Duquesne & Fournier, 2025) and thermal vulnerability assessments of foraging grounds using compiled satellite tracking data (Goudarzi et al., 2024), integrating global photo-ID datasets and residency pattern information, if available in the future, could refine these projections and contribute to more ecologically realistic conservation strategies.

The *in situ* observation of injury healing progression in Chapter 4 represents one of the few comprehensive datasets of its kind globally, and such monitoring would not be possible without the sustained involvement of citizen scientists. Recovery from fishing line entanglement, propeller strikes, and unknown causes was observed over months to years, providing solid evidence that certain injuries can heal in the wild without intervention and exhibit strong resilience despite permanent dysfunction of flippers or carapace deformity. However, the cases of repaid recovery from rescue centers (Franchini et al., 2016; Franchini et al., 2022; Freire et al., 2021) demonstrates the potential role of rescue and rehabilitation in supporting turtle survival and recovery. In Taiwan, intervention efforts are currently limited to the stranded, floating, or bycatch individuals. Therefore, developing (1) clear criteria to guide decisions on whether an injured turtle should remain in the wild or be rescued and transferred to a rehabilitation center, and (2) handling protocols and training for safely disentangling or capturing wild individuals in need of intervention, should be considered as important topics for future discussion on conservation measures.

Although marine turtles are listed as protected species in Taiwan, the direct use, killing, or harassment of individuals is strictly prohibited. The high prevalence of injuries and recurring injuries observed in wild populations, as noted in Chapters 2 and 4, and the stranding records (Li, 2022; Li et al., 2022), all indicate that anthropogenic threats remain persistent pressures in the coastal foraging habitats. Authorities such as the Ocean Conservation Administration, local county or town governments, and the National Park Service should take more active roles in promoting conservation measures and enforcing regulations, including go-slow zones for vessels, fishing restrictions in critical foraging sites, improvements in sewage management, and visitor control. Notably, marine turtle foraging grounds in Taiwan are predominantly degraded coral reef ecosystems, now dominated by algae, particularly on Liuqiu Island.

Although protective measures are necessary and urgently need to reduce human-related threats to green turtles on Liuqiu Island, it is also important to recognize that increasing turtle abundance can pose challenges to their foraging habitats (Heithaus et al., 2014). Research has shown that intensive turtle grazing can reduce seagrass biomass, hinder regrowth, and alter community structure, especially in shallow and disturbed habitats (Christianen et al., 2014). Similar concerns have been raised in the Dongsha Atoll, a Taiwanese atoll in the South China Sea, where green turtle activity was associated with significant seagrass decline, raising questions about ecosystem-level feedbacks (Hsu et al., 2024). On Liuqiu Island, a small intertidal seagrass patch in the Duzaiping area that once supported abundant seagrass growth has been largely degraded in recent years. Experimental exclusion studies by Wu (2025) demonstrated that seagrass growth was significantly higher in the turtle-exclusion plots, suggesting potential grazing pressure in this area. However, there is currently insufficient evidence to establish a direct causal link between turtle foraging to the seagrass decline in Liuqiu Island, as multiple factors such as wave exposure, typhoon, nutrient availability, and substrate type, and anthropogenic disturbance can also affect seagrass resilience and recovery (Unsworth et al., 2015; see examples in Fig. 4).

A similar but more complex situation have been observed on Liuqiu Island's coral reefs throughout the duration of this study. While green turtles can help sustain reef health through grazing on turf algae (Goatley et al., 2012), increased turtle aggregation over the past decade (Fong et al., 2025) has not been accompanied by improved reef conditions. On the contrary, live coral cover dropped from 30-50% before 2015 to as low as 6-12% by 2021-2023 (Taiwan Control Yuan Report, 2024). The degradation and loss of coral reefs is likely driven by increased tourism activity for turtle watching and the resulting influx of new residents working in the tourism sector. Natural factors also play a role, including coral bleaching due to warming, and typhoon-driven sediment and runoff from the main island of Taiwan.

Today, although Liuqiu Island is a coral reef island, this description merely reflects a geological state rather than an ecological one; although the entire island was built by coral reefs, today the ecological community is nearly void of corals or a semblance of a coral reef community. Divers often say that "there are only green turtles, there is nothing else in the water around Liuqiu Island." These interactions highlight a potential conservation dilemma: efforts to protect and restore green turtle populations must also consider the carrying capacity and resilience of their foraging habitats. Leveraging marine turtles as umbrella species may offer an entry point for establishing marine protected areas to protect the critical foraging habitats at the ecosystem level and to benefit reef-associated biodiversity.

5.2. Future direction

This dissertation addresses several knowledge gaps in the study of green turtles at foraging grounds in Taiwan, including the lack of a baseline on foraging populations, the absence of a standardized in-water photo-ID survey design, and a limited understanding of residency patterns, emerging threats, and turtle resilience. Based on the findings presented herein, several future research directions are recommended to further advance our understanding of foraging turtle populations in Taiwan and the broader Northwest Pacific region.

To improve TurtleSpot Taiwan, future efforts should focus on standardizing observer effort to make the interpretation and estimation of turtle sighting data more reliable. For example, including information about sampling effort, encounter rate, and whether sightings were incidental or targeted. This data can enhance the "structured" aspect of current semi-structured citizen science data. Questionnaires on participant motivations and expectations toward the project can also inform strategies to improve user experience, foster long-term engagement, and align outreach with contributors' values and goals. More automated processes for data entry, interpretation, and photo-ID can reduce the time project coordinators (or co-founders) spend on repetitive tasks, thereby improving the efficiency and sustainability of the program.

Expand standardized in-water surveys to additional foraging areas like Kenting, Green Island, and the northeastern coast to obtain reliable and methodologically consistent data. Complementing these efforts with long-term citizen science datasets to enhance detectability and temporal resolution, and to help establish a robust nationwide photo-ID database for further analysis. This will aid in identifying both ecological and anthropogenic factors that influence the distribution and population dynamics of foraging turtles around Taiwan. Applying population modeling approaches (e.g., Pollock’s Robust Design) will also enable estimation of demographic parameters (such as survival, temporary emigration, and population size) and support projections of future trends.

SSFI analysis revealed clusters of low- and high-fidelity individuals, but the ecological or behavioral drivers of this variation remain unknown. Biologging on a subset of known turtles (identified via photo-ID) could help elucidate how individuals with different fidelity levels utilize habitats, and further examine how environmental factors (e.g., season, habitat type, tidal cycles) and intrinsic traits (e.g., age class, personality) influence site fidelity patterns.

Habitat connectivity between Taiwan and neighboring countries, including Japan, the Philippines, and Micronesia has been partially confirmed through tag recoveries (Fong et al., 2025), satellite tracking, and genetic evidence (Ng et al., 2018; Ng et al., 2024) based on a limited number of individuals. However, the post-emigration movement of short-term resident turtles remains largely unknown. More satellite tracking of foraging individuals is needed to assess their connection to neighboring countries. Meanwhile, expanding population genetic studies could reveal links between foraging turtles in Taiwan and their nesting origins, helping clarify Taiwan’s role as a foraging hub supporting multiple genetic stocks in this region.

Last but not least, explore historical information about foraging populations and habitats of marine turtles in Taiwan, for example, by collecting local knowledge from older residents (when still possible), archived media, and historical records. Oral histories and community-based questionnaires with elderly fishers and coastal residents may offer valuable insights into how foraging turtle abundance, distribution, and human-turtle interactions. It can help reconstruct how the ecological and socio-cultural context of turtle populations has changed over the past 30 to 50 years and their connections to wider environmental and human-driven transformations. Where available, historical specimens from museums or stranded individuals may also provide DNA for retrospective population genetics analyses. Combined with contemporary genetic data, these potentially could illuminate changes in population structure over time and inform predictions about future connectivity, resilience, and conservation priorities.

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Appendix

Published papers from this dissertation

The following peer-reviewed publications are based on the research conducted for this dissertation:

1. **Fong, C.-L.**, Hoh, D.Z., Su, H., Chen, P.-Y., Tsai, C.-C., Tseng, K.W.H., Huang, H.-C., Wu, J.-Y., Nozawa, Y., & Chan, B.K.K. (2025). Crowdsourcing conservation: Unveiling Taiwan’s sea turtle foraging grounds, emerging threats, and residency with broad societal engagement. *BMC Ecology and Evolution*, *25*, Article 27. https://doi.org/10.1186/s12862-025-02354-2

2. Hoh, D. Z., **Fong, C.-L.**, Su, H., Chen, P., Tsai, C.-C., Tseng, K. W. H., & Liu, M. J. Y. (2022). A dataset of sea turtle occurrences around the Taiwan coast. *Biodiversity Data Journal*, *10*, Article e90196. https://doi.org/10.3897/BDJ.10.e90196

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BMC Ecology and Evolution

RESEARCH **Open Access**

Crowdsourcing conservation: unveiling Taiwan's sea turtle foraging grounds, emerging threats, and residency with broad societal engagement

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Abstract

Background Determining sea turtle foraging grounds, emerging threats, and population status are essential for conservation management. Crowdsourced science is a recently recognized approach that enables internet-based data collection, providing important contributions to scientific goals while also benefiting society and public education. This study is based on the published dataset from TurtleSpot Taiwan (2017–2022) with the aim to leverage crowdsourced data to determine sea turtle foraging grounds, emerging threats, demography, and residency patterns in Taiwan.

Results We identified three green turtle (*Chelonia mydas*) foraging grounds in Taiwan (Liuqiu Island, Kenting, and Green Island), defined as sites with > 100 sightings and > 50 individuals. Among all sites, Liuqiu Island contributed 77% of the total sightings, suggesting this island is a hotspot. Emerging threats to foraging aggregations of sea turtles in Taiwan were evident from the reported sightings, with ~ 10% of the total sightings involving turtles with fishing line entanglement, ingested debris, missing flippers, or injuries. Most of these sightings occurred in Liuqiu Island, indicating a significant level of human-turtle disturbance. Residency patterns identified from sighting data showed that 43.4% of individuals stayed in the same area for one or more years, with adult-sized turtle residency greater than that of immature turtles.

Conclusions Taiwan supports healthy foraging grounds for green turtles, where adults often stay for more than one year and with dynamic populations of younger individuals. However, despite a certain number of foraging green turtles observed in Liuqiu Island, many of these turtles displayed injuries. This high population density combined with increased injury frequency suggests that a comprehensive management plan for turtle foraging grounds is urgently needed, including measures to reduce boat speeds in hotspot areas and strict regulations on coastal human activity.

Keywords Photo-identification, *Chelonia mydas*, *Eretmochelys imbricata*, Citizen science, Foraging habitat, Demography

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Background

As migratory megafauna, sea turtles have a complex life cycle requiring unique life stage-dependent nesting and foraging habitats (i.e., hatchling, juvenile, sub-adult, and adult) [1]. Historically, sea turtle research and conservation efforts have focused on nesting habitats, while their foraging habitats are less understood [2, 3]. Determining the distribution of and the population dynamics within key foraging habitats has been recognized as a global research priority for sea turtle conservation [4], ecology, and conservation management. Despite significant progress in addressing these knowledge gaps, progress remains limited by a bias towards specific questions, species, and regions, highlighting the need for greater engagement with social sciences and a broader range of contributors [5].

Five of the world's seven sea turtle species – green (*Chelonia mydas*), hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*), olive ridley (*Lepidochelys olivacea*) and leatherback (*Dermochelys coriacea*) – have been recorded in the East Asia region [6]. Among these species, green and hawksbill turtles are the two most common species historically observed in the waters of Taiwan. Many studies have attempted to identify potential foraging grounds for green and hawksbill turtles in East Asia through various methods, including historical records, bycatch, mark-recapture studies, stable isotope analysis, and satellite tracking [7–10]; however, crucial information such as demography and residency of local aggregations remain lacking. This gap is understandable as both measures require direct in-water surveys and long-term mark-recapture studies, both of which are logistically challenging given the necessary person-hours and financial investments to provide the required resolution of data. Properly moderated citizen science and crowdsourced data collection projects can offer a way to alleviate these logistical hurdles and thereby address the standing knowledge gaps on both local and global scales.

Citizen science (CS) broadly refers to the engagement of the general public in scientific research and has existed for centuries in various forms [11] but has in recent decades expanded dramatically in both scope and application [12]. The current use of crowdsourced data through CS has proven powerful in generating ecological knowledge [13], improving conservation science, and enhancing environmental protection [14]. Crowdsourced science, a subset of CS that utilizing internet connectivity to recruit large groups of volunteers who would otherwise be disconnected for the purpose of problem-solving scientific projects, has the potential to expand societal participation and reduce associated costs of acquiring data [15].

While providing opportunities for increased data collection, including higher temporal and spatial resolution, with minimized logistical limitations to the researcher, CS and crowdsourced conservation projects have their own sets of challenges. These challenges include improving participant engagement and retention, establishing comprehensive project evaluations, and developing better communication strategies [16], while also mitigating potential challenges in data quality, and data coverage [17]. For crowdsourced science to provide data in both the quantity and quality needed for scientific purposes, it is necessary for projects to include standardized data collection protocols, means of quality-assurance, engaging community involvement (co-creation), and venues to share data and knowledge with the public [13, 18].

Photographic identification (photo-ID) methods that use unique body patterns for individual identification provide an innovative avenue for researchers and citizen scientists to study animals in their native habitats [19]. The distinctive facial and flipper scale patterns of sea turtles have been validated as reliable natural markers for studying their in-water biology and ecology [20–23]. The recent availability of digital platforms, affordable underwater cameras, and photo-ID software (e.g., I3S, HotSpotter, Internet of Turtles) facilitated the emergence of photo-ID CS projects to reveal the population status of foraging turtles [24–27].

TurtleSpot Taiwan is a crowdsourced conservation project launched in June 2017 on social media platform (https://www.facebook.com/groups/turtlespotintw; Facebook, Meta) with the dual aim of collecting sighting reports of sea turtles for identifying foraging grounds in Taiwan and providing a portal for public education. Engaging over 20,000 group members, TurtleSpot Taiwan's key innovations were establishing a publicly accessible sea turtle photo-ID database website (https://turtlespottw.org/) that allows users to search and provide optional functions for users to identify their documented/photographed turtles. This database has standardized data collection protocols to enhance data quality, and employs numerous interactive measures to foster community engagement and enhance societal engagement.

Hoh and Fong [28] and Hoh et al. [29] previously published occurrence open-access datasets from TurtleSpot Taiwan data between 2017 and 2022, along with metadata and data collection methodology. Here we provide the first analysis of these datasets and identify the foraging grounds, emerging threats, demography, and residency of sea turtles in Taiwan. To examine the effectiveness and scope of crowdsourced conservation, we further analyzed citizen scientist participation and retention trends over five years of TurtleSpot Taiwan's implementation.

Methods

Sea turtle sighting and distribution in Taiwan

A total of 760 sea turtle individuals were identified and documented on the photo-ID database of TurtleSpot Taiwan, including *C. mydas* ($n = 724$), *E. imbricata* ($n = 35$), and *L. olivacea* ($n = 1$). To study the diversity and abundance of different species of sea turtles around Taiwan, density distribution maps for all sea turtle sightings, individual turtles and participating citizen scientists were generated in R using mapdata (version 2.3.1), sf and ggplot2 [30–32], and modified with Affinity Designer (version 1.10.5).

Foraging grounds, demographic structure and residency of green and hawksbill turtles

Foraging grounds were identified as areas that have received a high number of sightings (> 100 sightings) and a stable number of local aggregations (> 50 individuals) over the monitored period. This study focused on evaluating foraging grounds, demographic structure and residency for green and hawksbill, as these species are the two most common sea turtles in Taiwan.

To determine the demographic structure of sea turtles, turtle body size was visually estimated from whole-body photographs and categorized into different life history stages (post-hatchling, juvenile, subadult, or adult), combined with the carapace color pattern and marginal scute roundness characteristics and descriptions provided by the reporters. Turtles that lacked a whole-body image and estimated size information were recorded as life stage 'unknown'. We used previously published straight carapace length (SCL) measurements and carapace characteristics to categorize all sighted turtles into putative age classes as follows: For green turtles, post-hatchling SCL of 10 to 20 cm, juvenile SCL < 65 cm with sunburst patterns on each scute, subadult SCL of 65 to 90 cm with camouflage patterns on each scute, and adult SCL > 95 cm with variously light and dark spotting on the carapace [33–35]. For hawksbill turtles, post-hatchling SCL of 8 to 22 cm, juvenile SCL of 23 to 50 cm, subadult SCL of 50 to 80 cm, and adult SCL > 80 cm [36–38]. For olive ridley turtles, adult SCL from 53 to 79 cm, with a median size of 60 cm at sexual maturity [39]. The identification of sex in adult-sized turtles was limited to males, defined as individuals having tail lengths exceeding 25 cm (visually longer than the rear flippers) [40]. Since it is not possible to definitively determine the sex and sexual maturity of sea turtles with short tails, turtles with tail lengths of 10 to 15 cm (visually shorter than rear flippers) or with no visible tail were classified as sex unknown.

To examine the residency of the sea turtles, minimum residency duration (MRD) of green and hawksbill turtles was calculated and plotted separately. The MRD for each turtle was estimated based on total duration (days) between the earliest and latest recorded sighting [25]. Individuals who stayed in the same area for more than 365 days (1 year) were considered residents. To study variations of MRD and number of sightings among estimated age-class groups (i.e., juvenile, subadult, or adult-sized), only green turtles were included due to low sample sizes for other species. Variations in MRD and the number of sightings per individual across different estimated age-class groups were examined using One-Way Analysis of Variance (One-Way ANOVA; factor: estimated age-class groups) in SigmaPlot 11 (Graffiti LLC). The dataset included 428 green turtle individuals from six areas: Northeastern coast, Penghu, Green Island, Liuqiu Island, Kenting, and Hualien. The MRD values passed the equal variance test ($p = 0.509$) without requiring transformations. The number of sightings per individuals were square root transformed twice and passed the equal variance test ($p = 0.118$).

Participation and retention of citizen scientists

The publicly accessible TurtleSpot photo-ID database website houses information and images of documented turtles, featuring a filter function that enables users to search using keywords (e.g., number of the post-ocular scutes, morphological features, location, species, age-class, turtle ID number, or turtle name). This allows citizen scientists to browse through the image database to manually identify the turtles they photographed. To assess citizen science participation, we counted the number of citizen scientists who attempted to identify the turtles they sighted at the individual level, using the photo-ID database website or other means. Regardless of identification accuracy, these attempts were used as an indicator of the involvement level of citizen scientists.

The number of new and retained citizen scientists from previous years was analyzed for each year from 2017 to 2022 to assess the recruitment and retention trends of TurtleSpot Taiwan. Retention of citizen scientists was calculated as the total duration (in days), including both the first and the last sightings reported by an individual to the Facebook Group. A Pearson correlation coefficient analysis was conducted to examine the correlation between the number of sightings contributed by each participant and their retention time, visualized with a scatter plot in SigmaPlot 11. To avoid bias, sightings directly provided by citizen scientists to us without posting to the Facebook Group were excluded from the above analysis.

Results

Distribution of foraging grounds and demographics of sea turtles

The majority of the sea turtle individuals identified from sightings were from Liuqiu Island (76.7%, $n = 584$

identified from 3,024 sightings), followed by Kenting (8.7%, *n* = 66 identified from 239 sightings) and Green Island (7.5%, *n* = 57 identified from 182 sightings), all of which serve as foraging grounds for green turtles (Fig. 1a). We observed a steady increase in the number of unique individuals recorded over time, with an average of 127 (range: 60 to 201) new individuals recorded each year (Fig. 1b), resulting in a total of 760 individuals as of May 2022. For the estimated age-class groups of *C. mydas*, 61.3% (*n* = 444) of documented turtles were juveniles, 26.2% (*n* = 190) were subadults, and 12.4% (*n* = 90) were adults (Fig. 1c). Among the adult-sized green turtles, 33 individuals were identified as males. For *E. imbricata*, 74.3% (*n* = 26) were juveniles, 17.1% (*n* = 6) were subadults, and 5.7% (*n* = 2) were adults (one identified male), with one individual identified as a post-hatchling (Fig. 1c).

In addition to identifying turtle foraging grounds, sighting data highlighted emerging threats to foraging aggregations of sea turtles in Taiwan, such as boat strikes, propeller injuries, and marine debris. Nearly 10% (*n* = 358) of total sightings involved turtles with fishing line entanglement or with ingested debris (i.e., plastic bags, fishing lines and ropes) observed protruding from the anus (1.5%, *n* = 53), missing flippers or injuries to flippers (3.2%, *n* = 116), or carapace injuries (5.3%, *n* = 189). There were 114 injury-related turtles, comprising 106 green turtles (346 sightings), 8 hawksbill turtles (10 sightings) and two sightings for which neither species nor individual was identified. Most of these sightings (93.3%, *n* = 334) were from 98 turtle individuals and occurred at Liuqiu Island (Table 1), indicating a significant level of human-turtle interaction in this area.

Minimum Resident Duration (MRD) of sea turtles

A total of 723 green turtles (sightings *n* = 3,201) and 35 hawksbill turtles (sightings *n* = 70) were included in MRD analysis after excluding records with incomplete date information (*n* = 5). Of these, 295 green and 22 hawksbill turtles were categorized as "non-resighted" because they were only sighted once (green *n* = 287; hawksbill *n* = 22) or only had multiple same-day sightings (green *n* = 8). The resighting rates of green and hawksbill turtles were 59.2% (*n* = 428) and 37.1% (*n* = 13), respectively, with the number of re-sightings per individual ranging from 2 to 47 (mean: 4.56, SD: 6.47). Among resighted green turtles (*n* = 428), 74.3% (*n* = 318) stayed in the same area for one or more years (i.e., resident turtle), and 25.7% (*n* = 110) stayed for less than one year (Fig. 2a). Resident green turtles (MRD ≥ one year) were mainly distributed in southern Taiwan (Fig. S2) at Liuqiu Island (*n* = 280), Kenting (*n* = 18), and Green Island (*n* = 15). Among resighted hawksbill turtles (*n* = 13), 15.4% (*n* = 2) stayed for less than one year (Fig. 2a) and 84.6% (*n* = 11) were resident turtles, mainly in Liuqiu Island (*n* = 6) (Fig. S2). Juvenile green turtles contributed more than half of the proportion of non-resighted, < 90 days, 90–364 days and 1–2 years groups (Fig. 2b). However, the proportion of turtles with larger body sizes (estimated as subadults and adults) generally increased with longer MRDs. In the > 2 years MRD category, juveniles accounted for 46.9%, while subadults and adult-sized turtles made up 28.8% and 24.3%, respectively (Fig. 2b). Green turtle mean MRD increased with age-class, from juvenile (775 days), subadult (882 days), to adult-sized turtles (1,182 days). Adult-sized turtles had significantly greater MRD than juveniles and subadults (One Way ANOVA, $F_{2,425} = 13.36$, $p < 0.001$, SNK: adults > juveniles = subadults; Fig. 2c). Adult-sized turtles had a significantly higher resighting rate (average 10.12 times per individual) than both juveniles (5.71 times per individual) and subadults (6.75 times per individual) (One way ANOVA, $F_{2,425} = 14.67$, $p < 0.001$, SNK: adults > juveniles = subadults; Fig. 2d).

Additionally, the longest MRD recorded to date was 3,502 days (ID: TW01G0049; 28 sightings), documented in an adult-sized green turtle with carapace injuries and scars, presumably female, from Liuqiu Island. The longest interval between two consecutive sightings was 1,604 days (ID: TW01G0034) documented in a subadult green turtle from Liuqiu Island. This single individual was recorded at a deep boat diving site, which is likely less frequently visited by divers, potentially explaining the extended gap between sightings.

Participation and retention of citizen scientists

From a total of 2,324 sightings contributed by 442 citizen scientists directly to the Facebook group platform, nearly 30% (*n* = 683) of the sightings were manually identified by 99 individual citizen scientists, indicating their engagement beyond mere data contribution. From June 2017 to May 2022, the annual number of turtle reporters ranged from 95 to 148, with an average of 122 ± 20 citizen scientists per year. In each year, about 67% of reporters were new participants (ranging from 61 to 75%), while 33% were retained from the previous years (Fig. 3a). The consistent influx of new participants in each year highlights sustained public interest in the initiative and the project's effectiveness in recruiting contributors. The number of sightings per citizen scientist ranged from 1 to 339, with 52.7% (*n* = 233, including one author) contributing a single sighting, 34.8% (*n* = 154) reporting 2–5 sightings, 11.1% (*n* = 49, including one author) reporting 6–50 sightings, and 1.4% (*n* = 6, including two authors) reporting more than 50 sightings (Table S1). These contributions accounted for 10%, 18.7%, 31.6%, and 39.7% of the total sightings, respectively. Participant retention duration ranged from one day to 1,789 days. Among the citizen scientists, 61.3% (*n* = 271, including one author)

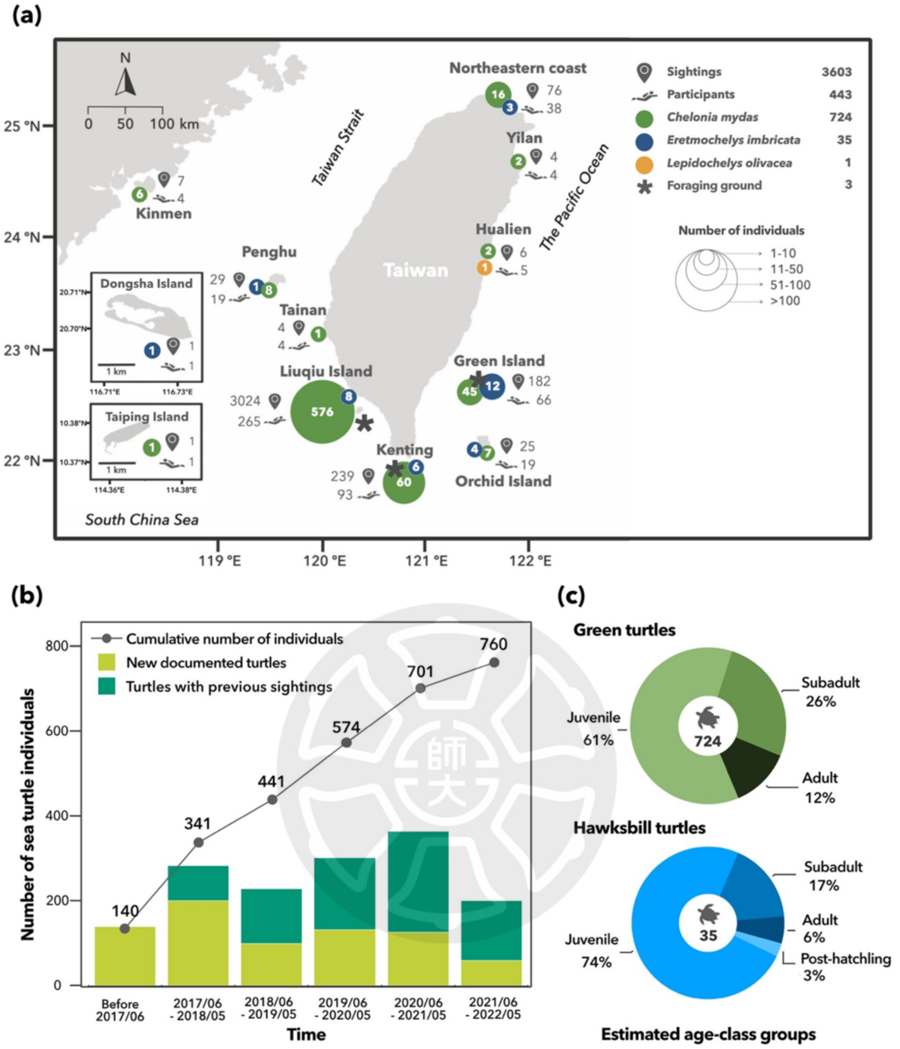

Fig. 1 Distribution of documented turtles around Taiwan, their annual population trends, and demographic structure. (**a**) Spatial distribution of sightings (pin marker symbol), participants (diver symbol), and documented turtles (circle). The color and size of the circle represent the species and the number of individuals, respectively. (**b**) Annual variations in numbers of sea turtle individuals and line chart showing the cumulative number of recorded turtles. (**c**) The proportion of estimated age-class groups of green and hawksbill turtles

Table 1 Number of injury-related sightings and turtle individuals at each location in Taiwan

Location	Total injury-related sightings	Unique individuals with injury-related sighting	Injury related sightings at each location (%)
Liuqiu Island	334	98	11.04
Kenting	8	5	3.35
Northeastern coast	4	1	5.26
Green Island	4	3	2.20
Kinmen	2	2	28.57
Orchid Island	2	2	8.00
Penghu	2	1	6.90
Dongsha	1	1	100.00
Yilan	1	1	25.00

contributed their sightings on a single day, while 19.9% ($n = 88$) contributed within a one-year period (2 days – 1 year), 8.8% ($n = 39$) contributed over 1 to 2 years, 3.8% ($n = 17$) over 2 to 3 years and 4.5% ($n = 20$, including one author) over 3 to 4 years. Lastly, 1.6% ($n = 7$, including two authors) contributed sightings consistently across all five years (Table S1). A significant moderate positive correlation (Pearson correlation coefficient = 0.44, $p < 0.001$) was observed between the number of sightings reported by each participant and their retention time (Fig. 3b).

Discussion

Foraging sea turtles in Taiwan

Direct in-water sighting data showed that Taiwan's coastal waters, especially Liuqiu Island, Green Island, and Kenting, are foraging grounds for green turtles and host a smaller aggregation of hawksbill turtles, represented by individuals of all size groups but dominated by juveniles (61% and 74%, respectively). The foraging grounds of sea turtles surrounding Taiwan exhibit diverse ecological characteristics. Liuqiu Island and Kenting primarily feature fringing reefs, intertidal zones, and small sporadic seagrass beds along their coastlines. Many reefs in these areas are algae-dominated reefs, especially turf algae [41, 42] making them preferable foraging sites for herbivorous green turtles. This dominance of juveniles in foraging grounds is comparable to that of green turtles in the Japanese Kuroshima Islands (79.9% juveniles) and Yaeyama Islands (1995–2003: 88%; 2004–2016: 78%) to the north [43, 44], as well as Malaysian Mabul Island (78.9%) and Semporna (49%) to the south of Taiwan [45, 46]. In the Great Barrier Reef in Australia, foraging grounds typically host a greater mix of life stages, but with juveniles still comprising the majority (approximately 80.5%) [47]. The ratio of juveniles in Taiwan's coastal foraging aggregations (61%) lies in between the values at these other locations. The variation in juvenile dominance among regions may influenced by differences in habitat characteristics and food availability. For example, the foraging habitats in the Great Barrier Reef are coral reef dominated [47], while Kuroshima Islands and Yaeyama Islands feature coral reef habitats mixed with seagrass and algae [43, 44], and Semporna and Mabul Island combines coral reef with seagrass meadows [45, 46, 48, 49]. The foraging grounds in Taiwan are mainly algae-dominated reefs. Variations in food availability among these different habitats may contribute to the differences in the demography of sea turtles across regions. Temporal shifts in food availability can also contribute to different age-class demographics. In Bermuda, a decline in seagrass availability may have driven the emigration of juveniles before maturation, altering the demographic structure of the aggregation [50]. Mortality rates of turtles can also affect the demographic composition of foraging aggregations. For instance, in the Yaeyama Islands, the decline of the sea turtle fishery due to increased conservation awareness led to a 10% rise in the proportion of larger-sized turtles during 2004–2016 compared to earlier periods [44]. Establishing long-term monitoring programs in Taiwan could help track demographic shifts and provide insights into site-specific ecological roles.

Steady increases in newly sighted individuals each year and a high ratio of juvenile turtles suggest a healthy recruitment pattern in these foraging grounds [44]. Our study also found that adult-sized turtles have significantly longer residency durations and higher resighting frequencies than immature turtles. A similar trend of adults having higher residency indices than juveniles and subadult green turtles has been observed in Australian foraging grounds [51]. Lower resighting rates and shorter residency of juveniles and subadults suggest a more dynamic assemblage within these aggregations. Additionally, individual variability in home ranges and core areas [52–54] may influence the resighting probability in photo-ID-based surveys. However, current understanding of their habitat shifts in this region remains limited. Ng et al. [10] tracked four rehabilitated and released immature green turtles: one turtle released from Dongsha migrated to the Philippines over 143 days, while three turtles released from Kenting remained within Taiwanese waters (tracking duration ranging from 124 to 188 days). Two of these turtles returned from their release sites to the areas where they were originally found stranded or bycaught. These findings suggest that immature turtles can have high variability in home ranges or dynamic movement patterns, with some traveling large geographical distances, making them less frequently observed by volunteer turtle watchers.

Our study showed an increasing temporal trend in sea turtle residency over the past decade. Cheng et al. [55] surveyed 432 individual turtles at Liuqiu Island from 2011 to 2017 and found that around 10% remained for more

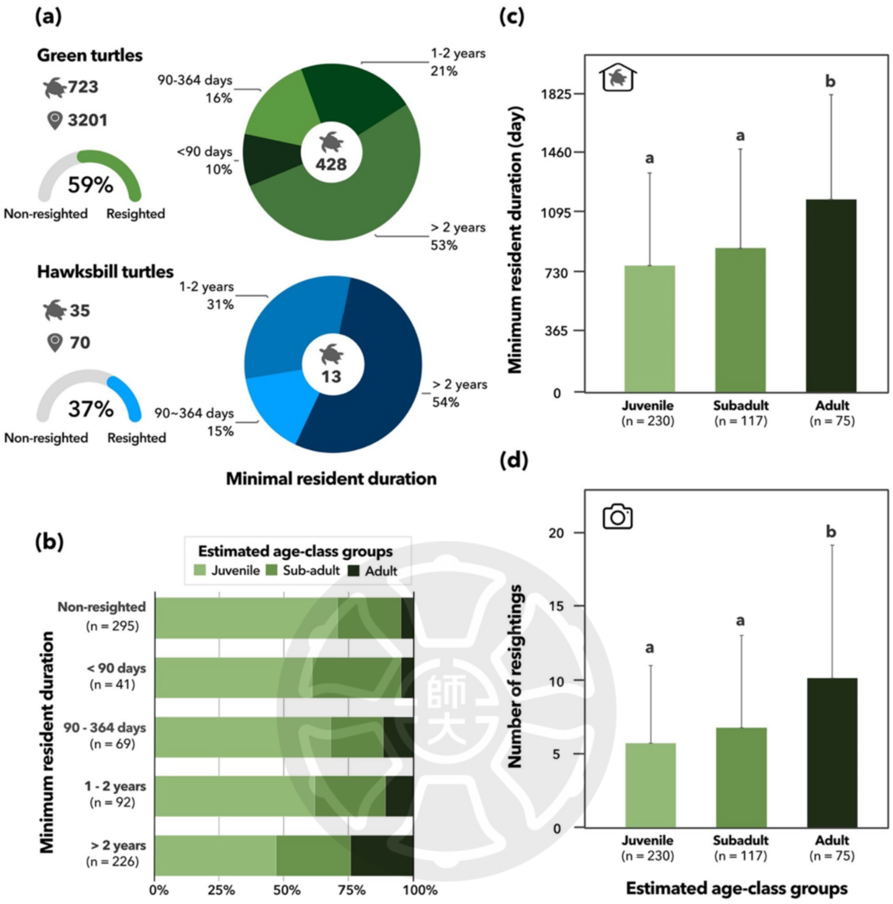

Fig. 2 The minimum resident duration (MRD) and demographic structure of turtles. (**a**) MRD of green and hawksbill turtles by MRD groups. (**b**) The percentage of green turtles in estimated age-class groups with different MRD. (**c**) Mean (+ SD) of MRD across estimated age-classes of green turtles. a and b denote different groupings identified from post-hoc SNK tests following One-Way ANOVA. (**d**) Mean (+ SD) of number of resightings per individual across estimated age-class groups of green turtles

than one year. Our study found that from 2017 to 2022, of 584 identified individuals, 49% stayed for over a year. It is possible that the habitat conditions of Liuqiu Island have become more suitable for foraging turtles since 2017. Two adult-sized turtles (short tail, presumed female) with flipper tags from the Secretariat of the Pacific Regional Environmental Programme (SPREP) were sighted in Liuqiu Island multiple times each between 2017 and 2022 and 2022, respectively, indicating this foraging ground is also utilized by adults following ontogenetic emigration. This suggests that the foraging grounds around Taiwan, particularly Liuqiu Island, support all turtle life stages of turtles and are therefore of heightened conservation importance.

Our study also identified a small number of resident turtles on the northeastern coast of Taiwan which

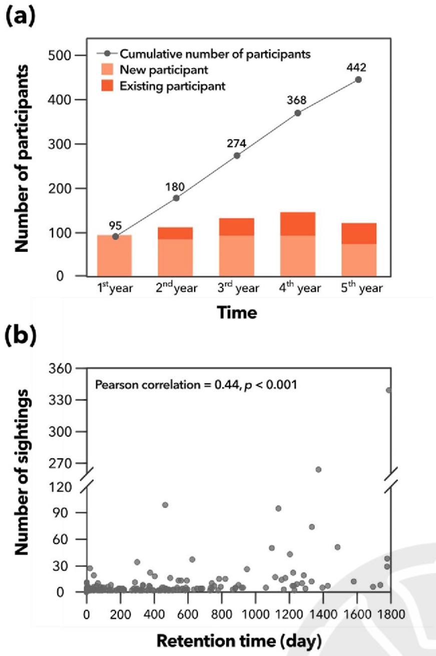

Fig. 3 Citizen scientists' participation in TurtleSpot Taiwan. (**a**) Bar charts showing the annual number of participants between June 2017 and May 2022 and line chart showing the cumulative number of participants. (**b**) Scatter plots between the number of sightings contributed by each participant and their retention time

supports previous suggestions [56] that this area could be a foraging ground for green turtles. The benthic community on the northeastern coast consists mainly of turf algae, macroalgae, and non-reefal coral communities [42], which may contain a high abundance of Rhodophyta and Chlorophyta, the main diet of green turtles in reef ecosystems [57].

One factor to consider is that the foraging grounds identified in this study may be biased toward sites more accessible for diving. For instance, Penghu has a notable number of sea turtles documented through fishing industry bycatch [56] but showed low sightings in our data. This may be due to the high turbidity of Penghu's waters, which likely increased the difficulty of sighting and recording turtles in the area. Potential biases can occur in opportunistic observation databases, such as over-representation of common species [58] and over-sampling of accessible locations [59] due to uneven sampling efforts. However, such bias can be mitigated by applying photo-ID at the individual level in this study, thereby reducing the likelihood of overestimation. In contrast, Liuqiu Island, a popular diving destination with frequent turtle encounters, yielded significantly more sightings. This higher resolution data enabled more reliable estimates of residency and population trends, offering a closer reflection of reality-based population distribution.

Habitat connectivity

Sightings of sea turtles with flipper tags can provide valuable information about their previous foraging grounds or nesting sites, offering insights into habitat connectivity. This project recovered five turtles with flipper tags, three of which had visible tag numbers: An olive ridley turtle (PH1004M/PH1005M) originally tagged and released from Cabangan, Zambales, the Philippines, in January 2018, was found alive (bycatch) in September 2018 along the east coast of Taiwan (Hualien County); a subadult green turtle (KK3 0125) originally tagged and released from Ishigaki Island, Okinawa, Japan, in 2003 was found alive (bycatch) in 2020 along the east coast of Taiwan (Hualien County); a green turtle (R36192; https://turtlespottw.org/turtle-profile/TW01G0082), was an adult nesting female from Ulithi Atoll, Yap State, Federated States of Micronesia, where it nested in 2006 and 2012. Notably, this third turtle was first observed at Liuqiu Island in 2011 and has been frequently seen foraging at the same site from June 2017 to May 2022, indicating that this individual has migrated between Ulithi Atoll and Liuchiu Island (2,500 km apart) at least twice (Fig. 4). In additional, both front flipper tags (R36192/R36191) of this turtle were intact during its first sighting in 2011. By 2017, only one tag (R36192) remained, which was subsequently lost in Feb 2020. The information gleaned from these tagged turtles corroborates previous studies using satellite tracking and molecular techniques, which demonstrated that Yap in the Federated States of Micronesia and Yaeyama of Japan are potential source rookeries for the green turtle foraging aggregations around Taiwan [6, 60]. These observations underscore the importance of understanding sea turtle migratory patterns and habitat use across international boundaries and highlight the scientific significance of the collective efforts of citizen scientists to enhance the conservation of sea turtles.

Operation and maintenance of an extensive crowdsourced conservation network

After seven years of operation (as of 19 August 2024), TurtleSpot Taiwan Facebook Group has more than 21,723 members from diverse sectors of society, including SCUBA and free divers, scientists, schoolteachers, and students, among other members of the general public. Member profile data described a diverse cohort of participants, with a nearly even male-to-female ratio

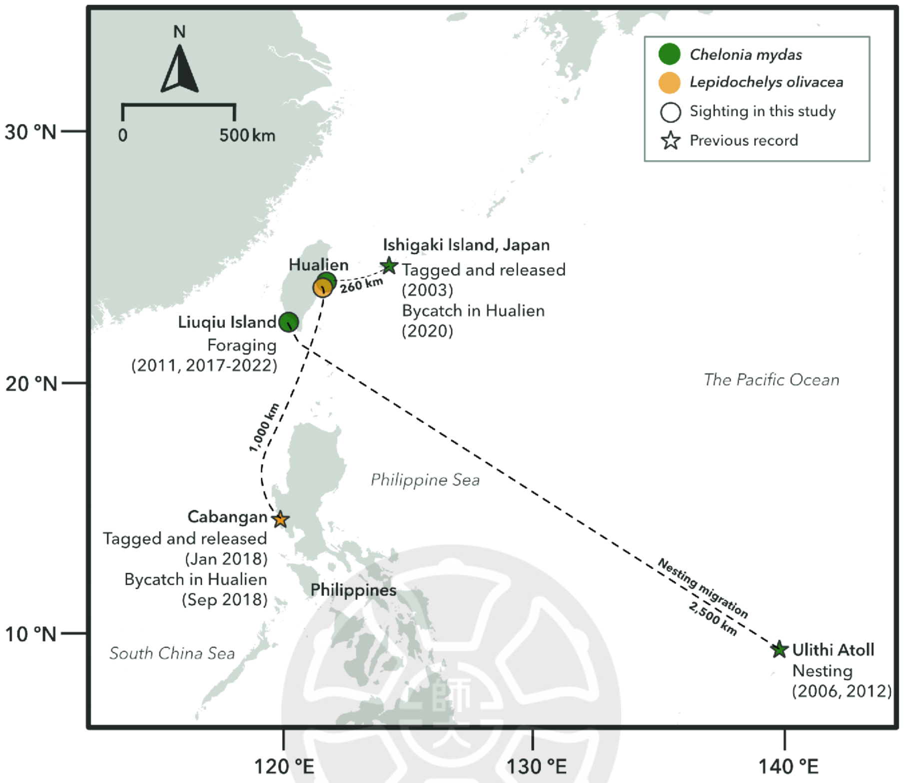

Fig. 4 Connectivity of sea turtle foraging grounds and nesting sites identified through flipper tag recoveries. Colors indicate the species of turtle individuals and shapes indicate the location of the sighting and tagging history

(45% and 55%, respectively), an age range of 13 to +65 years old (majority within the 35–44 range; 39%). However, only about 2% of these members have actively contributed turtle sightings, indicating that much of the engagement represents passive support, such as expressing interest in the initiative, rather than active participation. This low proportion of contributors may also stem from logistical barriers associated with data collection, as accessing turtles in their natural habitats typically requires SCUBA diving or snorkeling, which may limit broader involvement.

Despite strategies developed to increase public participation [61–63], recruitment and retention of citizen scientists remains an ongoing challenge that limits the efficacy and usefulness of many existing projects. To maintain recruitment, TurtleSpot Taiwan actively engages the public through in-person workshops, educational outreach events, and online interactions, such as inviting citizen scientists to name the turtles they reported and providing feedback and photo-ID results to sighting posts. These initiatives likely contributed to the good number of recruitments of new participants, with nearly two-thirds of participants each year being newcomers. However, our analysis on participant retention revealed that most participants (52%) contributed only once and only a small proportion (12.4%) contributed more than five reports. Correlation analysis indicated that participants with multiple contributions tended to remain active in TurtleSpot Taiwan for longer periods. For instance, 70% of those contributing more than five reports demonstrated retention of over one year. Similar patterns were also identified in other studies, where most contributors participated only once and with minimal effort, while a relatively small percentage of contributors showed higher activity [64, 65]. Meanwhile, although 52% of participants were single-time contributors, this ratio is still lower compared to other environmental CS projects, where single-time contributors often account for higher proportions (e.g., 72%; [65]). To increase participation and retention levels, conducting surveys or interviews to understand the motivations of citizen scientists [66], more regular updates on the project's progress, and a system of milestones to encourage sustained engagement can be further integrated into the current project's framework.

Conservation implications

Our analyses found that nearly 10% of sightings included observations of at least one category of injury. These injured turtles could be due to human prejudice, as citizen scientists are more prone to report rare and charismatic species or events [67, 68], leading to over-reporting of injured turtles; however, it also suggests increased human activity and tourism [69] may be stressing local foraging aggregations, similar to the effect seen in other regions [70]. These data suggest that a comprehensive management plan is urgently needed, including measures to reduce boat speeds in hotspot areas and strict regulations on coastal human activity (e.g., rock fishing, sewage treatment, and coastal construction) to benefit these flagship species and the broader marine ecosystem.

Conservation efforts can make use of crowdsourced data to complement field-based research by covering a larger geographic area while engaging a broader public in conservation efforts. However, achieving high-quality spatial data requires substantial resource investment, including building strong community partnerships [71]. Working toward a community contributory approach in the main foraging grounds (e.g., Liuqiu Island, Kenting, Green Island, and the northeastern coast), where local participants are actively involved in data collection, analysis, or decision-making, should be the conservation focus moving forward. The present crowdsourced conservation platform can further develop for international collaboration projects studying global sea turtle foraging grounds or contribute to the Internet of Turtle, a web-based photo-ID system with a worldwide database [72]. Our study provides evidence that this citizen science platform is important in providing reliable, long-term global monitoring data for tracking changes in sea turtle aggregations and foraging grounds, enabling adaptive management strategies that can respond effectively to global climate change issues.

Abbreviations

CS	Citizen science
Photo-ID	Photographic identification
MRD	Minimum resident duration
GBIF	Global Biodiversity Information Facility
SCUBA	Self-Contained Underwater Breathing Apparatus

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12862-025-02354-2.

Supplementary Material 1

Supplementary Material 2

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Author contributions

CLF, DZH, HS, and PYC initiated the CS project and were responsible for the conceptualization, data curation, data analysis, funding acquisition, methodology, and project administration. CCT, KWHT, and HCH contributed to data curation and data analysis. CLF wrote the main manuscript, conducted formal analysis, and prepared figures and tables. JYW contributed to statistical analysis and the preparation of Fig. 4. DZH, YN, and BKKC contributed to the manuscript editing. YN and BKKC provided resources and supervised analysis and manuscript preparation. All authors reviewed and approved the final version of the manuscript.

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Data availability

The sea turtle occurrence dataset is available at the Global Biodiversity Information Facility portal (https://doi.org/10.15468/43z4mj) and with data structure details (https://doi.org/10.3897/BDJ.10.e90196). The analysis data is available via the GitHub repository (https://github.com/TurtleSpot-Taiwan/2024_Fong_5yearsTurtleSpot).

Declarations

Ethics approval and consent to participate

The dataset used for the ecological analysis in this study has been published on GBIF [28], with its structure detailed in [29], contributing to open data framework of this citizen science project. The participants of this citizen science project were provided informed consent to agree to the project's objectives, data collection methods, and potential uses of their contributions. The project was conducted in adherence to the National Wildlife Conservation Act of Taiwan to ensure the ethical treatment of sea turtles. This project has not involved any human participation, human tissue, or human experiments, and there is therefore no need for approval from any ethical issues committee.

Consent for publication
Not applicable.

AI use
AI prompts from Grammarly software (Grammarly, Inc.) were utilized to enhance the writing process, particularly using prompts to improve text grammar.

Competing interests
The authors declare no competing interests.

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Data Paper

A dataset of sea turtle occurrences around the Taiwan coast

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Abstract

Background

We describe a dataset of sea turtle sightings around the coast of Taiwan and its islands (Hoh and Fong 2022). This data collection was initiated by TurtleSpot Taiwan, a citizen-science project that collects sea turtle sighting data. This dataset includes 3,515 sighting data dated from March 2010, except most of the data (n = 3,128; 89%) were collected between June 2017 to December 2021. Sightings were reported by citizen scientists to the Facebook Group of TurtleSpot Taiwan by providing occurrence information. We also requested photos and videos for species identification and to record any physical abnormality of the turtle, if observable. In addition to recording data often associated with an occurrence, TurtleSpot aims to identify each sea turtle up to the individual level using the Photo Identification (Photo ID) method. Hence, if photos of left facial scutes were available, the sighted individual can be identified and given a unique turtle ID. In total, 762 individuals were assigned a turtle ID, comprising 723 Greens (*Chelonia mydas*), 38

Hawksbills (*Eretmochelys imbricata*) and one Olive Ridley (*Lepidochelys olivacea*) turtle. This dataset is now publicly opened in Global Biodiversity Information Facility (GBIF) and available for download. It is hoped that the data may assist in future ecological studies and the development of conservation measures.

New information

This dataset contains 3,515 occurrence records of sea turtles (Cheloniidae) and is currently the largest public dataset of sea turtle sighting records in Taiwan. Post-publication of this dataset to the GBIF platform demonstrated that the number of Green sea turtle *Chelonia mydas* records in Taiwan is one of the largest in the world (last accessed date: 15-10-2022). The data served as the foundation for understanding biogeography and sea turtle ecology in Taiwan's coastal waters.

Keywords

sighting data, citizen science, coastal waters, photo identification

Introduction

People involved in citizen-science programmes have played a major role in contributing occurrence data of diverse organisms worldwide (Global Biodiversity Information Facility 2022, iNaturalist 2022). Following technological advancement, citizens can now report their sightings simply by using a mobile phone with an internet connection to biodiversity-associated citizen science platforms, such as iNaturalist and eBird. In addition, some citizen-science programmes are now incorporated with the use of social media for biodiversity data collection (Liberatore et al. 2018, Oliveira et al. 2021). One of the advantages of using social media platforms is the convenience and great opportunity for the recruitment and retention of volunteers and Facebook is the most widely used (Oliveira et al. 2021). For example, the Taiwan Roadkill Observation Network effectively use the Facebook Group for interactions within the community and collection of information, making it one of the most successful and active citizen-science projects in Taiwan.

Sea turtles are migratory Chelonian species that travel between nesting and foraging sites during their life cycle. In Taiwan, much is known about the nesting ecology (Cheng et al. 2009, King et al. 2013, Cheng et al. 2015, Cheng et al. 2018), owing to the easier accessibility of the nesting sites. Nonetheless, understanding of the foraging population and its ecology is still limited. Recognising the gap, TurtleSpot Taiwan - a community-led citizen-science initiative was founded to collect data with the majority focusing on the sighting of sea turtles underwater. This project started in 2017 and receives sighting reports provided by citizen scientists via the TurtleSpot Facebook Group. In addition to the sighting reports, TurtleSpot aims to develop a database of turtle profiles in Taiwan by identifying each individual turtle using the Photo ID method (Dunbar et al. 2021). We identified sea turtle individuals through their unique facial-scutes patterns and record any distinct characteristics of their physical appearances, such as carapace or limb injury, if available. To encourage continuous reports of the citizen scientists, we allow the sighting reporter to name the turtle if the individual is a new record in our database.

The purpose of preparing the current dataset was to publicly open the data for advancement, especially in the scientific and conservation communities. The data of TurtleSpot Taiwan have allowed a basic understanding in biogeography of foraging sea turtles in Taiwan and some ecological observations of sea turtles in the wild, such as witnessing the recovery of some injured turtles, types of behaviour, intra- and inter-species interactions and physical abnormalities.

Sampling methods

Step description: 1. Data collection: Citizens who encountered sea turtles reported their sightings to us via our Facebook Group. Reporters post a regular post to the Group following our reporting format (Fig. 1) to contribute sighting information including sighting location, date, time, depth, observation method, photographs of the whole body and left- and right faces of the turtle individual.

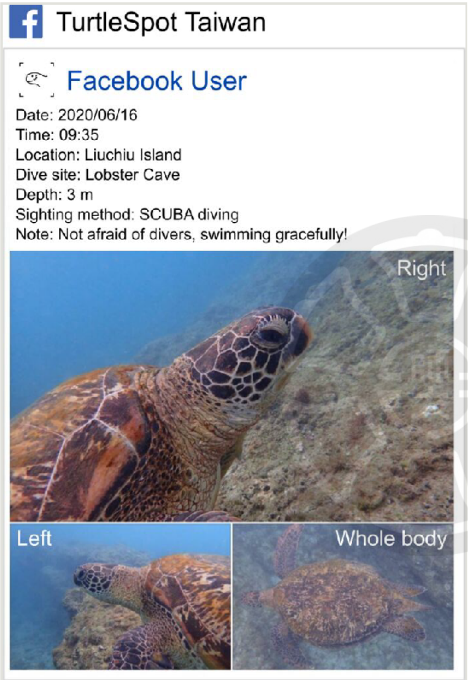
2. Quality control of sighting report received: Each sighting reported to the Group was first checked by the group administration prior to approval. The group administration checked if the post followed the reporting format mentioned above and the sighting provider will be requested to provide any of the missing information unless unavailable. Once the submitted post passed the quality check, the post will be approved by the group administration to be visible in the Facebook Group.

3. Data transcription: Sighting information contained in the post/report was transcribed into Google Sheets as raw data.

4. Determine additional information from the sighting report: We recorded additional information about the occurrence through the sighting reporter’s notes of onsite observation and our identification through the provided photos and videos. Additional information included the biological characteristics of the sighted individual turtle (sex, life stage, behaviour, associated taxa) and physical abnormality of the turtle (e.g. fishing line entanglement, tumour and others).

5. Sea turtle individual identification: If clear photos of the left face of the sighted turtle were provided in the report, we use the Photo Identification (Photo ID) method to identify the turtle individual. Currently, we use two methods to perform Photo ID: (1) compare the facial scute pattern manually and (2) HotSpotter (Crall et al. 2013, Dunbar et al. 2021), open-source software for pattern recognition in wildlife research. Each sea turtle individual was assigned a unique turtle ID. The turtle ID was assigned as follows: Country code, site code, species code and sequence number. For example, in TW01G0082, “TW”, “01”, “G” and “0082” stands for Taiwan, island or county label, green turtle and unique number for the individual, respectively.

6. Open data preparation: The language used in most of the recorded data is Traditional Chinese. Nevertheless, valuable information including sighting location, method, common name and life stages which allowed future data use was translated into English. We converted the occurrence data into Darwin Core Archive standard in Google Sheets, an online spreadsheet tool, using the Darwin Core Archive Assitant Add-on (Salim and Saraiva 2020). Refer to the Data resources section for a detailed description of each column. We then validated the occurrence dataset using the Data Validator developed by GBIF (Global Biodiversity Information Facility 2017). Lastly, we uploaded, stored and published the dataset using The Integrated Publishing Toolkit (IPT) of GBIF installed under the Taiwan Biodiversity Information Facility. The data is then opened on the IPT and GBIF for the public to access.


TurtleSpot Taiwan

Facebook User

Date: 2020/06/16
Time: 09:35
Location: Liuchiu Island
Dive site: Lobster Cave
Depth: 3 m
Sighting method: SCUBA diving
Note: Not afraid of divers, swimming gracefully!

Figure 1. doi

Format of reporting sea turtle sighting to TurtleSpot Taiwan. Facebook icon made by Freepik via Flaticon.

Geographic coverage

Description: Most of the sighting data were from Taiwan and its islands (Fig. 2) and only a few (n = 35) were from other countries which include Indonesia, Philippines, Malaysia, Palau, the Mariana Islands, Japan, Maldives and United States.

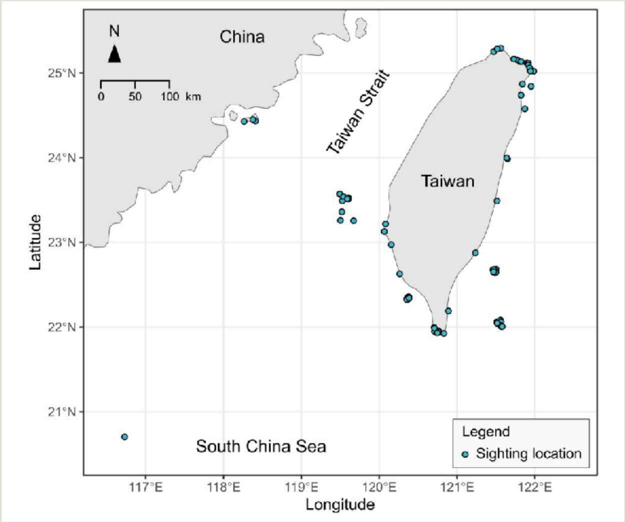


Figure 2. doi

Location of sea turtle sightings in Taiwan. Data outside of Taiwan are not shown. Map was plotted using the R package 'rnaturalearth' (South 2017).

Taxonomic coverage

Description: Four species of sea turtles were recorded in the dataset, including Green turtle (*Chelonia mydas*), Hawksbill (*Eretmochelys imbricata*), Olive Ridley (*Lepidochelys olivacea*) and Kemp's Ridley (*Lepidochelys kempii*). Most of the sea turtle sightings in the dataset were of Green and Hawksbill turtles (97.3% and 2.4%). Occurrences that failed to assign species (n = 11) were recorded as Cheloniidae.

Taxa included:

Rank	**Scientific Name**	**Common Name**
kingdom	Animalia	Animal
phylum	Chordata	
subphylum	Vertebrata	
superclass	Reptilia	
order	Testudines	
suborder	Cryptodira	
superfamily	Chelonioidea	Sea turtle
family	Cheloniidae	

genus	*Chelonia*	
genus	*Eretmochelys*	
genus	*Lepidochelys*	
species	*mydas*	Green
species	*imbricata*	Hawksbill
species	*olivacea*	Olive Ridley
species	*kempii*	Kemp's Ridley

Temporal coverage

Data range: 2010-3-23 - 2021-12-29.

Notes: TurtleSpot was officially founded in June 2017. Hence, most sighting records range from June 2017 to December 2021, comprising about 89% (n = 3,128) of the dataset (Fig. 3). Occasionally, we receive sighting reports dated before June 2017, with the earliest dated 23 March 2010. Sighting reports dated before June 2017 were accepted and recorded if the sighting reporters could provide both photos/videos and occurrence information by following our reporting format as described in the Step description.

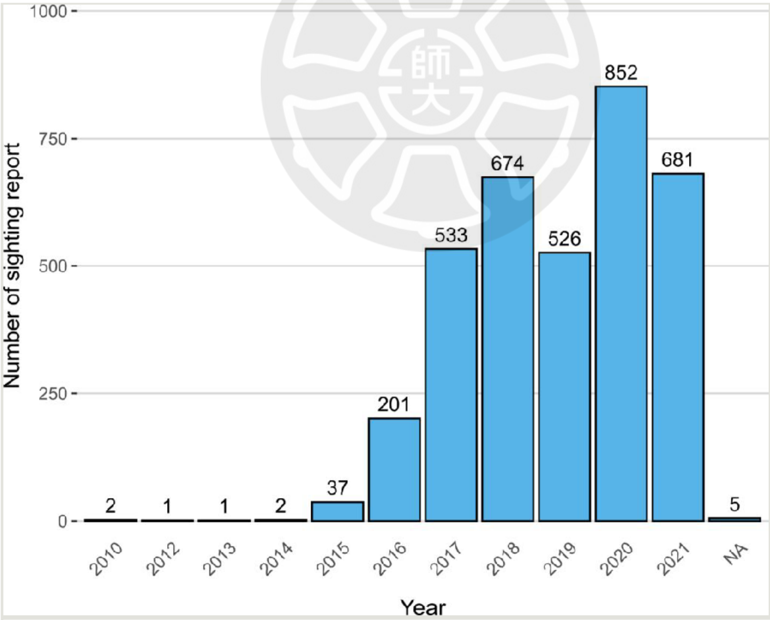


Figure 3. doi

Number of sighting records across the year. 'NA' indicates no sighting year was given.

Usage licence

Usage licence: Other

IP rights notes: The dataset in the current work is licensed under a Creative Commons Attribution (CC-BY) 4.0 Licence. Any image and video accessed through the URL from the dataset are licensed under the Creative Commons Attribution (CC-BY-NC) 4.0 Licence.

Data resources

Data package title: Sea turtle sightings in Taiwan

Resource link: https://doi.org/10.15468/43z4mj

Number of data sets: 1

Data set name: Sea turtle sightings in Taiwan

Data format: Darwin Core Archive

Data format version: 2021-07-15

Description: The dataset contains data of two major categories: data associated with the occurrence and data related to the biological characteristics of the sighted turtle individual. The former category consists of information during the sighting event such as date, time, location, geographical coordinates, observation method and species. The latter category characterised the observed turtle individual using our controlled vocabulary (see Suppl. material 1) during the sighting, including data such as living status, life stage, sex, physical abnormality and associated organism. The data allowed future research studies, such as biogeography, sea turtle foraging ecology that includes habitat use, sex ratio, abnormalities encountered and intra- and interspecies interaction. The data may also potentially guide any policy-making process through the assessment of species conservation status and diversity in the area of occurrences.

Some additional remarks on the dataset:

1. On average, 57 sighting reports were received monthly;

2. More than half (n = 2,235; 63.6%) of the data were provided by citizen scientists. The remaining data (n = 1,280; 36.4%) was records contributed by two of the co-authors as part of the citizen-science programme;

3. So far, only turtle sightings in Taiwan were given a turtle ID.

Data fields were standardised into 46 Darwin Core terms as listed in the following table. The column label and some of the relevant descriptions are written as listed in the List of Darwin Core terms (accessed June 2022; created by the TDWG Darwin Core

Maintenance Group). A more specific description of the column used in the current dataset was also added if applicable.

The dataset is publicly opened in GBIF (see Resource link) and users can download the occurrence dataset in CSV format through the 'Download' section of the dataset page. The dataset can also be downloaded using GBIF API-based tools such as 'rgbif' and 'pygbif' for further analyses.

Column label	**Column description**
occurrenceID	An identifier for the Occurrence (as opposed to a particular digital record of the occurrence).
catalogNumber	An identifier unique for the record within the dataset.
rightsHolder	A person or organisation owning or managing rights over the resource.
recordedBy	Names of the sighting reporter/citizen scientist.
year	The four-digit year in which the Event occurred, according to the Common Era Calendar. Year of sighting.
month	The integer month in which the Event occurred. Month of sighting.
day	The integer day of the month on which the Event occurred. Day of sighting.
eventDate	Sighting date.
eventTime	The time or interval during which an Event occurred.
country	The name of the country in which the Location occurs.
countryCode	The standard code for the country in which the Location occurs.
higherGeography	A list of geographic names less specific than the information captured in the locality term.
locality	Name of the sighting location or dive site.
locationRemarks	More specific location compared to locality, usually the name of the dive site.
decimalLatitude	The geographic latitude (in decimal degrees, using the spatial reference system given in geodeticDatum) of the geographic centre of a Location. Positive values are north of the Equator, negative values are south of it. Legal values lie between -90 and 90, inclusive.
decimalLongitude	The geographic longitude (in decimal degrees, using the spatial reference system given in geodeticDatum) of the geographic centre of a Location. Positive values are east of the Greenwich Meridian, negative values are west of it. Legal values lie between -180 and 180, inclusive.
coordinateUncertaintyInMetres	The horizontal distance (in metres) from the given decimalLatitude and decimalLongitude describing the smallest circle containing the whole of the Location.

georeferenceRemarks	A note stating that our GPS coordinates were estimated from the dive site or sighting location.
geodeticDatum	The ellipsoid, geodetic datum or spatial reference system (SRS) upon which the geographic coordinates given in decimalLatitude and decimalLongitude are based.
verbatimDepth	The original description of the depth below the local surface. This is an estimation provided by the sighting reporter.
samplingProtocol	Sighting method of the Occurrence.
associatedReferences	An URL links to the Facebook post from the sighting reporter in our Facebook Group, which we define as a single Occurrence event. The link may be broken if the sighting reporter decided to delete the post.
basisOfRecord	The specific nature of the data record.
individualCount	Our purpose of preparing this occurrence dataset is to identify each turtle individual. Hence, if a sighting report contains more than one sea turtle, this occurrence record will be duplicated as a new row. Hence, the individual count of each data is only '1'.
kingdom	The full scientific name of the kingdom in which the taxon is classified.
taxonRank	The taxonomic rank of the most specific name in the scientificName.
vernacularName	A common or vernacular name.
scientificName	The full scientific name.
taxonID	An identifier for the set of taxon information (data associated with the Taxon class). We use the URL of species in GBIF Backbone Taxonomy checklist.
behaviour	The behaviour shown by the subject at the time the Occurrence was recorded.
occurrenceRemarks	Condition of the turtle during the sighting (e.g. alive, dead, stranded).
dynamicProperties	Any physical abnormality that was observed (e.g. injury, tumour, debris entanglement).
associatedTaxa	A simple description of association and vernacular name of taxa in which this Occurrence is to each of them.
lifeStage	The age class or life stage of the organism at the time the Occurrence was recorded. Estimated via physical appearence of the sighted turtle.
sex	The sex of the biological individual represented in the Occurrence. Determination of sex is only applicable to adult sea turtles through the size of their tail. Sex determination is successful only when photos/videos of the tail are available.
organismName	A textual name or label assigned to an Organism instance. Mostly named by the citizen scientists.
licence	A legal document giving official permission to do something with the resource. The licence in this column is applied to the text data of this dataset only.

identificationID	Turtle ID. Every identifiable turtle individual has a unique ID.
associatedMedia	An URL links to the website of TurtleSpot Turtle Photo ID database, which show media and information about this particular individual.
identifiedBy	Names of people who identified the turtle individual via Photo-ID method.
informationWithheld	Additional information that exists, but that has not been shared in the given record.
occurrenceStatus	A statement about the presence or absence of a Taxon at a Location. All value is 'present' in the current dataset.
eventRemarks	Notes about the incomplete sighting eventDate.
continent	The name of the continent in which the Location occurs.
county	The full, unabbreviated name of the next smaller administrative region than stateProvince (county, shire, department etc.) in which the Location occurs.
island	The name of the island on or near which the Location occurs.

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Author contributions

DZH, CLF, HS and PC conceived the study; DZH and CLF designed the scientific protocol; CLF, HS and CCT performed most of the individual turtle identification; HS and CCT contributed a substantial amount of data; DZH wrote the paper and prepared figures; DZH, CLF, HS, PC, CCT and KWHT performed data curation; MJYL assisted throughout the data management process; all authors approved the manuscript.

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Supplementary material

Suppl. material 1: Controlled vocabulary describing additional information about the occurrence doi

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Data type: biological
Download file (1.02 kb)