



Long-term wild recovery and resilience of green turtles *Chelonia mydas* to various anthropogenic injuries

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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 2 photo-identification databases spanning 14 yr, we identified 105 injured turtles among 7233 sightings (709 individuals). Thirteen turtles with 19 injuries had multiple re-encounters, allowing for estimation of healing durations. Average healing times were for propeller strikes: 527 d; fishing line entanglements: 538.5 d; and for injuries of unknown causes: 560.2 d, with severe injuries taking 600 d and minor injuries 491 d to recover. Recovery trajectories in wild green turtles were slower than those reported for other marine megafauna. Long-term resightings of 5 individuals confirmed survival after recovery from severe injuries; these turtles remained detectable for an additional 106 to 2264 d, after which monitoring was discontinued. Approximately 10.5% of injured turtles suffered recurring injuries from propeller strikes, emphasizing the need for targeted conservation measures, including go-slow zones, recreational fishing regulations, and 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 research highlights the value of long-term monitoring, supported by citizen scientists, in assessing sublethal impacts and guiding mitigation for marine megafauna.

KEY WORDS: Natural recovery · Propeller strike · Fishing line entanglement · Anthropogenic disturbance · Photo ID · Citizen science · Foraging habitat · Sea turtle

1. INTRODUCTION

Marine megafauna inhabiting coastal ecosystems are increasingly exposed to numerous anthropogenic threats, including vessel traffic, fishing activity, pollution, and coastal development (Womersley et al. 2021, Ferreira et al. 2023). These threats directly impact marine turtles (Putman et al. 2020, Serra et al. 2023,

Duquesne & Fournier 2025) and constitute a conservation concern. Green turtles *Chelonia mydas* have recently been downgraded from Endangered to Least Concern on the IUCN Red List (Wallace & Broderick 2025). However, despite signs of population recovery at the global scale that motivated this status downgrade, current population sizes remain far below historical levels, and the species continues to face ongo-

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ing anthropogenic threats. Green turtles forage predominantly in shallow seagrass meadows and coral reef habitats (Hazel et al. 2007, Shimada et al. 2017), environments that overlap extensively with human coastal activity. Exhibiting strong site fidelity, ranging from years to more than a decade (Siegwalt et al. 2020, Fong et al. 2025), green turtles are particularly vulnerable to anthropogenic pressures in these coastal ecosystems and have a high likelihood of repeated exposure to localized anthropogenic threats, particularly in 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), hopper dredging (e.g. Goldberg et al. 2015), 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. P. Work et al. 2010, T. Work et al. 2015, Godoy & Stockin 2018, Foley et al. 2019, Li et al. 2022). Although marine turtles are frequently observed in the wild with mild to severe injuries (Work et al. 2010, Archibald & James 2018, Ataman et al. 2021, Papafitsoros et al. 2021, Franchini et al. 2023, Fong et al. 2025), long-term continuous field records documenting their natural recovery trajectories remain exceedingly scarce. As a result, it is unknown whether the rate and trajectory of marine turtle recovery from anthropogenic threats as measured in individuals undergoing medical treatment and rehabilitation in conservation and veterinary centers—the current source of our recovery and survival data—properly represents 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 & 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, finding 34 of 535 captured turtles with at least 1 boat strike injury and healing times ranging from 174 to 723 d, with only 4 individuals exhibiting a full recovery. More recently, Balensiefer et al. (2024) tracked the recovery of a sin-

gle juvenile green turtle across 6 recaptures over 2 yr in Santa Catarina, Brazil, documenting a 728 d period from a partially healed wound to complete recovery. The data obtained by these capture—mark—recapture studies demonstrate 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 quantitatively characterizing recovery rates of wild injured marine turtles requires long-term monitoring with representative mark—resight data. A compelling example of this methodology is provided by McGregor et al. (2019), who documented the first case of natural wound healing in a reef manta ray *Mobula alfredi* through a 15 yr 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. Complementing in-water surveys with photo observations by citizen scientists allows for increased opportunities to observe wound repair in wild turtles.

In this study, we examined injury-healing cases of green turtles—from minor carapace lacerations to severe propeller strike wounds and flipper amputations—based on repeated *in situ* observations at Liuqiu Island, Taiwan, a key foraging hotspot facing multiple anthropogenic pressures (Fong et al. 2025). Using 14 yr of compiled photographic records (2010–2024), we provide the first comprehensive estimates of natural healing times and recovery trajectories for green turtles by injury type, cause, and severity, including cases of turtles with recurring injuries (multiple unique injuries over time).

2. MATERIALS AND METHODS

2.1. 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 2 databases: (1) the citizen science projects maintained by TurtleSpot Taiwan (see Hoh et al. 2022, Fong et al. 2025), covering 3024 occurrences from 16 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

2 yr systematic in-water survey dataset (C. L. Fong et al. unpubl. data) covering 4192 occurrences at 2 dive sites (Lobster Cave and Dafu-Houshi Reef), conducted quarterly from October 2020 to November 2022.

2.2. 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) based on an established photo-ID database of Liuqi 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 4 criteria: (1) cause (i.e. propeller strike, fishing line entanglement, unknown), (2) location (e.g. carapace, flipper, eye), (3) severity (minor or severe), and (4) healing stage (i.e. fresh, partially healed, healed), following criteria adapted from Work et al. (2010), Phu & Palaniappan (2019), Ataman et al. (2021), and NMFS (2022).

Observed injuries were categorized into 7 distinct types: amputation, carapace laceration, carapace fracture, abrasion, entanglement, carapace deformity, and flipper laceration (Fig. 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 would prevent a full return to the pre-injury state. 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.

2.3. 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 (Fig. 2). For individuals with multiple distinct wounds, each injury was assessed independently and recorded as a separate injury occurrence. To examine whether injury characteristics influenced recovery duration, we performed non-parametric comparisons of healing time (measured in days) across 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) in RStudio (version 2024.04.01+748; Posit Team 2025).

To estimate healing rate, we used the 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 (e.g. the width of a specific lateral scute or 2 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. S1 in the Supplement at www.int-res.com/articles/suppl/esr01472_supp.pdf). The healing rate of each injury between 2 consecutive time points was calculated using the formula:

$$y = \frac{\left[\left(1 - \frac{a_2}{a_0} \right) \times 100 \right] - \left[\left(1 - \frac{a_1}{a_0} \right) \times 100 \right]}{t_2 - t_1} \quad (1)$$

where y is the relative healing rate (percentage reduction in wound surface area per day) over the time interval $t_2 - t_1$, a_0 is the initial wound surface area at the first sighting (Day 0) or the earliest measurable sighting, and a_2 and a_1 are the wound surface areas at time points t_2 and t_1 , respectively. This formula is a simplified version of the one used by Womersley et al. (2021), as all reference scales for our surface area determination were standardized to 1 during measurement. The sighting date of a measurable wound



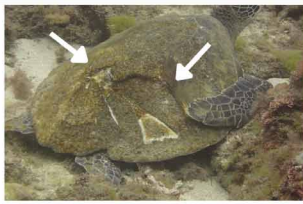



Injury type	Description	Severity	Photographic example
Amputation	Partial or total removal of an appendage, including front and rear flipper.	Minor < 25% of flipper loss.	
		Major ≥ 25% of flipper loss.	
Carapace laceration	Linear cuts produced by a sharp object, often appearing as one or more parallel, evenly spaced incisions.	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.	

Fig. 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)

being regarded as healed was used as the healed date, and the wound surface area was recorded as 0. The recovery trajectories of individuals with at least 3 measurable time points were plotted using the 'Tidy-

verse' package (Wickham et al. 2019) in RStudio and refined with Affinity Designer (version 1.10.5). All data are presented as mean ± SD unless otherwise indicated.



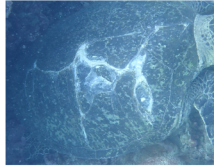









	Entanglement	Abrasion	Carapace laceration	Carapace fracture
Partially healed	 Acute ligature wound	 Necrosis tissue on the scales	 Fractures showing signs of regrowth	 Carapace wound healing with epidermal proliferation
	 Necrosis tissue	 Necrosis tissue on the carapace	 Fractures showing signs of regrowth	 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

Fig. 2. Criterion and representative images used to determine the healing stages of 4 common injury types (entanglement, abrasion, carapace 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, carapace laceration partially healed [lower]); Yoko Nozawa (carapace laceration partially healed [upper]); Yeng-Hsun Huang (carapace laceration healed, carapace fracture healed)

3. RESULTS

3.1. 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 yr monitoring period, from which we were able to identify 790 unique individuals. Of these, 13.3% ($n = 105$), including 104 green turtles and 1 hawksbill turtle *Eretmochelys imbricata*, 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 (10.5%), of which 10 were injured twice and 1 was injured 3 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 (2 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, 8 (7.6%) were partially healed, 7 (6.7%) were recently injured (fresh), and 6 (5.7%) were found dead with the previously observed injuries presumed to be the cause. Injury causes were grouped into severity classes, and the observed final condition of injured turtles is shown in Fig. 3.

3.2. Healing times by injury causes and severity

Of the 105 injured turtles observed, 6 were found dead. Among the remaining 99 individuals, 93 (93.9%) were resighted at least once during the study period, compared to 74.7% of non-injured turtles ($n = 685$). Of the few injured turtles that were not resighted, only 1 exhibited a fresh injury (fishing line entanglement),

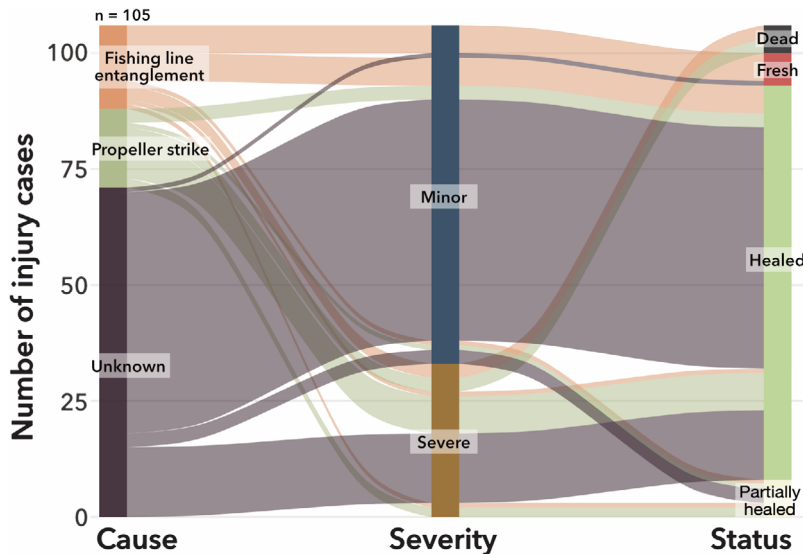


Fig. 3. Sankey diagram illustrating the flow of injury causes by severity classes to the final status for injured turtles ($n = 105$) observed *in situ*. The width of each band is proportional to the number of injuries: left nodes represent injury causes (propeller strike, fishing line entanglement, unknown), middle nodes represent severity (minor, severe), and right nodes represent the last observed condition of turtles regarding the injuries (healed, partially healed, fresh, dead)

while the others were already considered healed at their single sighting. However, only 13 individuals (12.4%) had multiple post-injury sightings suitable for estimating healing times. Six (46.2%) of these bore more than 1 trackable wound, yielding a total of 19 wounds for recovery-timeline analysis. Injuries caused by propeller strikes ($n = 11$) fell into 2 types: carapace laceration ($n = 9$) and carapace fracture ($n = 2$), which required 274 to 860 d (527 ± 215.6 d) to heal. Two turtles retained lasting carapace deformation after healing from propeller strikes. The first (TW01G0059) suffered a severe carapace fracture that healed after 1 yr (388 d) but left a permanent kyphosis bulge and apparent rear flipper paralysis (Fig. 4A; Table S1). The second turtle (TW01G0111) incurred 2 separate injuries 21 mo (651 d) apart: a carapace fracture that healed after about 630 d and carapace lacerations that healed after 371 d (Fig. 4B,C; Table S1). The first carapace fracture of TW01G0111 is potentially visually consistent with a shark bite wound (e.g. Denkinger et al. 2013, Aoki et al. 2023); however, due to the rarity of shark species known to attack marine turtles (e.g. *Galeocerdo cuvier*, *Carcharodon carcharias*, and *Carcharhinus leucas*) within the waters of Liuqiu Island and Taiwan in general (Ebert et al. 2013) and the lack of a conclusive bite pattern (semi-circular pattern), we therefore categorized this injury as propeller strike. Both turtles exhibited site fidelity during and following the healing period, being resighted multiple times up to 2652 and 2623 d after injury, respectively, with

resightings of the latter individual occurring at 6 unique sites around the island, suggesting a broad home range.

Turtles with fishing line entanglements ($n = 2$) took 450 to 627 d (538.5 ± 125.2 d) for their front flipper to progress through entanglement, swelling, necrosis, auto-amputation, and healing. Turtle TW01G0048 (Fig. 5) was first observed entangled in a fishing line that later constricted its right front flipper, causing swelling and loss of function. By Day 627, the flipper had auto-amputated and healed without inflammation. Subsequent resightings over the following years showed normal swimming and foraging behavior, indicating it had functionally adapted to the loss of its flipper.

Injuries of unknown causes ($n = 5$, from 4 individuals) included carapace abrasions ($n = 3$) and facial abrasions near the eyes ($n = 2$), with healing times ranging from 193 to 968 d (560.2 ± 293.3 d; Table S1). Observed healing times by injury cause and severity are shown in Fig. 6A. Minor wounds ($n = 11$) healed over 193 to 968 d (491 ± 240 d). Severe wounds ($n = 8$) took 371 to 860 d to fully heal (600 ± 190 d). Despite apparent differences in healing time among severity levels, Kruskal-Wallis tests detected no significant differences 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 ($\chi^2 = 0.019$, $df = 3$, $p = 0.999$).

3.3. Healing rate and recovery trajectory

The reduction in surface area of wounds was measurable in 8 injuries incurred by 5 individuals. Injuries included abrasion ($n = 1$), carapace lacerations ($n = 5$), and carapace fractures ($n = 2$). Severity of each injury was categorized as minor ($n = 2$) or severe ($n = 6$). Healing rates ranged from 0.08 to 1.53% d^{-1} (mean: $0.38 \pm 0.48\%$, $n = 20$; Table S2). Most injuries ($n = 5$) had a higher healing rate during the early stages (Table S2) but declined over time (Fig. 6B). Minor injuries achieved 50% closure within 300 d; notable exceptions, such as Turtle TW01G0047 (propeller-induced facial laceration), progressed to full recovery earlier than this (i.e. Day 275), showing substantial variability in recovery times among the observed individuals. Several severe injuries ($n = 4$) remained



Fig. 4. 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 movement of the rear flippers. The carapace experienced depression, gradually lifted, and resulted in a permanent kyphosis bulge after healing. Images courtesy of Huai Su (Days 0, 216, 1172) and Ying-Hsiu Liao (Day 2481). (B) Carapace fracture of turtle TW01G0111 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 (Days 0, 70, 695) and Huai Su (Day 316). (C) Turtle TW01G0111 experienced a second carapace laceration 651 d 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)

less than 50% healed even after 375 d. The slowest observed recovery (TW01G0162) took approximately 725 d to reach the 50% closure threshold, which included the regrowth of surface scutes.

4. DISCUSSION

4.1. Recovery success and healing times of injured marine turtles

Our current understanding of the fate of marine turtles in response to anthropogenic injuries is largely based on data available from rescue and/or rehabili-

tation centers. While these centers are of vital importance to the conservation of marine megafauna, recovery and survival rate data obtained are confounded by the support received, such as medical treatment, feeding, and protection from subsequent injuries, and may not properly reflect the healing trajectory and fate of individuals in the wild. However, these data do provide an important benchmark against which *in situ* studies can be compared. Long-term records (approximately 20 yr) of rehabilitation centers in Florida (USA) showed that anthropogenic injuries had a significant impact on marine turtle survival and fate. During this time, over half (55.3%; 1047 of 1700 individuals) of the marine turtles died during



Fig. 5. Healing progression and subsequent sightings of green turtle TW01G0048 following a 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 (Days 182, 627, 1149, 1776), Jiun-Shian Li (Day 488), and Shang-Ping Liu (Day 1993)

rehabilitation, 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). However, recovery rates appear 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 re-

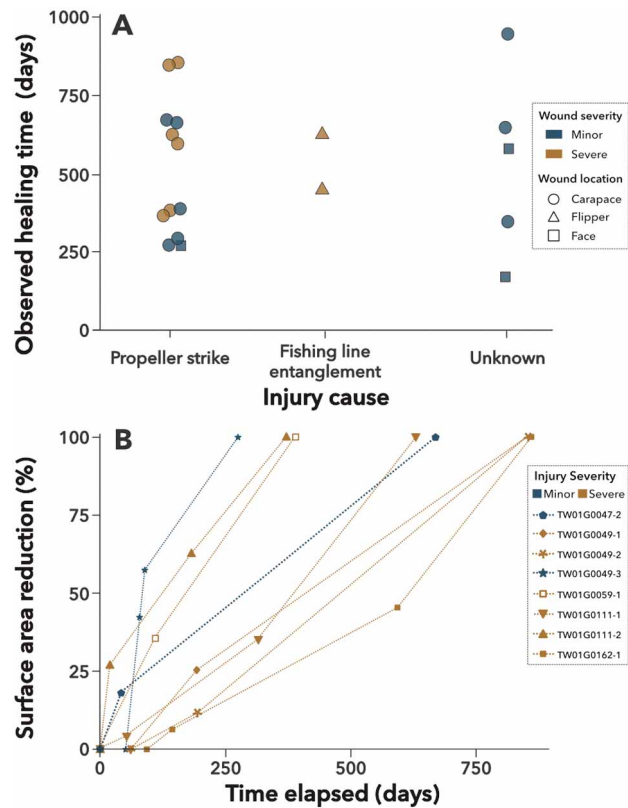


Fig. 6. Healing times and recovery trajectories. Symbols represent the injury cause: circles indicate propeller strikes, triangles indicate fishing line entanglements, and squares indicate unknown causes. Colors indicate wound severity: blue for minor wounds, brown for severe. (A) Observed healing times 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

leased (Baker et al. 2015). Individuals suffering from head trauma had a higher release rate, with 72.4% (21 of 29) of rehabilitated individuals released after a few days to 8 mo (Franchini et al. 2023). The recovery success rates for turtles admitted to rehabilitation centers are lower than those observed in wild populations, likely 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. Further confounding rehabilitation center success and release rates is the practice of euthanizing for animal welfare reasons, artificially decreasing recovery success and release data.

Eighty percent of injured individuals showed complete recovery, and an additional 7.6% showed signs of partial recovery. This finding aligns with previous observations in nesting loggerhead turtles *Caretta caretta* in southeastern Florida, USA, where 24% (107

of 450) of examined individuals had at least 1 external injury, 88% of which were fully healed and 9% were partially healed (Ataman et al. 2021). However, the high recovery rate observed in our study may slightly overestimate the actual recovery potential, as severely injured turtles that died without being detected by divers were likely unrecorded. Nevertheless, injured turtles showed a relatively higher resighting rate than non-injured turtles (93.9 vs. 74.7%), with only 6 turtles of the 105 recorded injured turtles having died. These findings suggest that undetected mortality among injured turtles was likely limited in Liuqiu, Taiwan.

Healing times based on in-water sightings of injured green turtles averaged around 1.5 yr, ranging from approximately 491 d for minor to approximately 600 d for severe injuries. Whether due to fishing line entanglement (average: 538.5 d), propeller strikes (527 d), or unidentified causes (560.2 d), our data show that while wild recovery rates are high, the healing process still takes a considerable amount of time. Healing times for propeller strikes in capture–mark–recapture studies in individuals with similar severity to those in our study by Phu & Palaniappan (2019) and Balensiefer et al. (2024) ranged from 181 to 728 d, similar to the 274–860 d we observed. In contrast, superficial wounds caused by biopsy sampling in juvenile green turtles showed rapid healing during the initial stages (within 100 d) but required at least 176 d or up to 488 d to become fully healed and unnoticeable in the wild (Andrews et al. 2021). This comparison highlights that while even minor lesions may take >1 yr to fully heal externally, traumatic injuries sustained in the wild typically delay recovery and can result in lasting disfigurement or functional impairment.

Healing time is not the only metric that affects marine turtle health. Injured individuals with open lesions are at higher risk of infection (Fichi et al. 2016, De Oliveira et al. 2021) and those with non-lesion injuries, such as flipper constriction or amputation, have compromised feeding efficiency and diving behavior (Franchini et al. 2020) during the healing process. Furthermore, the prolonged period of pain endured prior to auto-amputation or carapace scute regrowth, along with the lasting deformities or paralysis that may remain after wound closure, could have unknown long-term welfare costs despite survival.

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 remain vital interventions to substantially shorten healing times. A juvenile green turtle with severe carapace lacerations and coelomic-cavity exposure underwent surgical

carapace reconstruction and was released after only 120 d (da Bôaviagem Freire et al. 2021). Similarly, loggerhead turtles with severe skull fractures healed in about 2–10 mo after surgical curettage and plant-based dressings, and individuals with severely entangled flippers recovered within 1–3 mo without amputation (Franchini et al. 2016, 2020). In addition to surgical care and nutritional support, stable conditions of rehabilitation centers (e.g. constant temperature, salinity, and possibly filtered water) may also speed up wound closure relative to fluctuating conditions in the natural environment. These cases demonstrate that intensive care can significantly accelerate recovery and are important in the effort to protect marine turtles; however, as the number of individuals that make it to rehabilitation centers is minimal compared to those that incur injuries (Willette et al. 2023), it remains important to properly understand wild healing to better interpret the impacts of anthropogenic threats.

4.2. Comparative wound healing of wild marine megafauna

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 d and complete healing of severe lesions by 170 d (Womersley et al. 2021), while reef manta rays showed a steady reduction in laceration size, with 95% closure within 295 d (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-Ponzzone et al. (2020), who observed complete healing between 21 and 147 d. In contrast, marine turtles require a longer time to heal after injuries, often taking 1–2 yr 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.

4.3. Conservation implications

Anthropogenic injuries to marine turtles are of direct conservation concern, and detailing the real-

world causes, recovery rates, and resulting survival trajectories is vital to our understanding and protecting these ecologically and culturally important species. In determining these, we are further able to identify underlying causes and work towards both localized and large-scale mitigation.

In our study, fishing line entanglement (17.1%) and propeller strikes (15.2%), together accounted for approximately one-third of all injuries observed in wild turtles. Similarly, stranding records from Liuqiu Island indicate that entanglement in fishing lines and gear and propeller strikes or boat collisions pose the greatest individual threats to marine turtles. While year-to-year variations were observed—such as 2019, with 42.8% (6 out of 14) of dead stranded turtles exhibiting carapace damage from propeller impacts (Li et al. 2022)—long-term trends (2017–2022) identified fishing line, hook, or gear entanglement (30%) to be higher than that of boat strikes (25%; Li 2022).

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, around 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 an opportunity 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 (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 S2) experienced secondary injuries, and at least 3 of these cases involved propeller strikes as the cause for both injuries. Our results therefore provide strong support for 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 to substantially reduce the main causes of human-induced marine turtle injuries around the island.

Entanglement injuries pose an additional concern, as turtles cannot remove the fishing lines themselves and the nylon material persists in the marine environment, causing progressive damage that may lead to flipper necrosis, septicemia, and amputation. Mitiga-

ting turtle fishing line entanglement remains a more difficult challenge locally and globally (Battisti et al. 2019). On Liuqiu Island, although fishing exclusion zones (established in 2000) and a ban on gillnet fishing within 3 nautical miles of the island (established in 2013) have likely reduced bycatch and ghost fishing nets, the issue of thin fishing lines and fishhooks harming marine life remains an ongoing issue. Our data 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.

It is important also to consider that injury recovery as measured by wound healing is not the final stage in the recovery or impact of injury on an individual turtle. Injuries causing deformation or disability (i.e. loss of a flipper) may have potential limitations to migration, feeding, mating, or, in females, nesting success (Ataman et al. 2021). While the functional impact of these injuries remains poorly studied and unclear, recent work suggests that marine turtles may be resilient. A recent study on loggerhead turtles in Cabo Verde found no significant differences in clutch size or hatchling success between females with partial (85% of individuals) or complete (15% of individuals) amputations and those without amputated limbs (Marco et al. 2024). However, while these data suggest that individuals with at least partial limb retention can maintain reproductive success, the number of individuals with failed nesting attempts or that fail to nest, mate, or migrate effectively remains unknown and represents an important next step for future research on the long-term consequences of severe injuries.

Long-term observations of a subset of 5 individuals following their full recovery from severe injuries showed consistent behavioral adaptations in the wild for at least 106 to 2264 d (mean \pm SD: 948.7 ± 765 d). This group includes 2 front flipper amputation survivors (TW01G0048: 1366 d; TW01G0429: 106 d) and 3 individuals with permanent carapace deformities (TW01G0049: 620 d; TW01G0059: 2264 d; TW01G0111: 516 d after healing from the first injury before a secondary injury, and a further 820 d after healing from the secondary injury). These observations demonstrate that even severely injured turtles can survive for multiple years and maintain normal foraging and site fidelity behaviors in the wild. Such outcomes provide encouraging evidence that, with sufficient

recovery and appropriate release conditions, rehabilitated turtles with permanent physical impairments may also achieve long-term survival post-release.

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.

Data availability. Data and the codes are available via the GitHub repository (<https://github.com/TurtleSpot-Taiwan/green-turtle-wild-recovery>).

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