

# Marine Turtle Newsletter

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Mating leatherbacks observed in waters of Costa Rica. See pages 11-12. Photograph: J J. Kiszka

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# Guest Editorial: Demographic Criteria for Downlisting and Delisting Kemp's Ridley Sea Turtle Based on Numbers of Females Nesting in a Season Need Revision

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Under the U.S. Endangered Species Act, the USDOC *et al.* (2020) recovery planning handbook states: "If a review of the plan and its implementation, whether during a 5-year review or other process, shows that the plan is not current (*i.e.*, is no longer being used to guide recovery efforts or does not contain adequate criteria) or that its usefulness is limited, the plan should be modified as discussed in 8.5, Recovery Plan Modifications." Herein, we focus attention on the need for revision of some of the demographic criteria for downlisting and delisting the endangered Kemp's ridley sea turtle (*Lepidochelys kempii*). The following demographic criteria are specified by the second revision of the binational (United States-Mexico) recovery plan for Kemp's ridley (NMFS *et al.* 2011):

## Downlisting

1. A population of at least 10,000 nesting females in a season (as measured by clutch frequency per female per season) distributed at the primary nesting beaches (Rancho Nuevo, Tepehuajes, and Playa Dos) in Mexico is attained. Methodology and capacity to implement and ensure accurate nesting female counts have been developed.
2. Recruitment of at least 300,000 hatchlings to the marine environment per season at the three primary nesting beaches (Rancho Nuevo, Tepehuajes, and Playa Dos) in Mexico is attained to ensure a minimum level of known production through in situ incubation, incubation in corrals, or a combination of both.

## Delisting

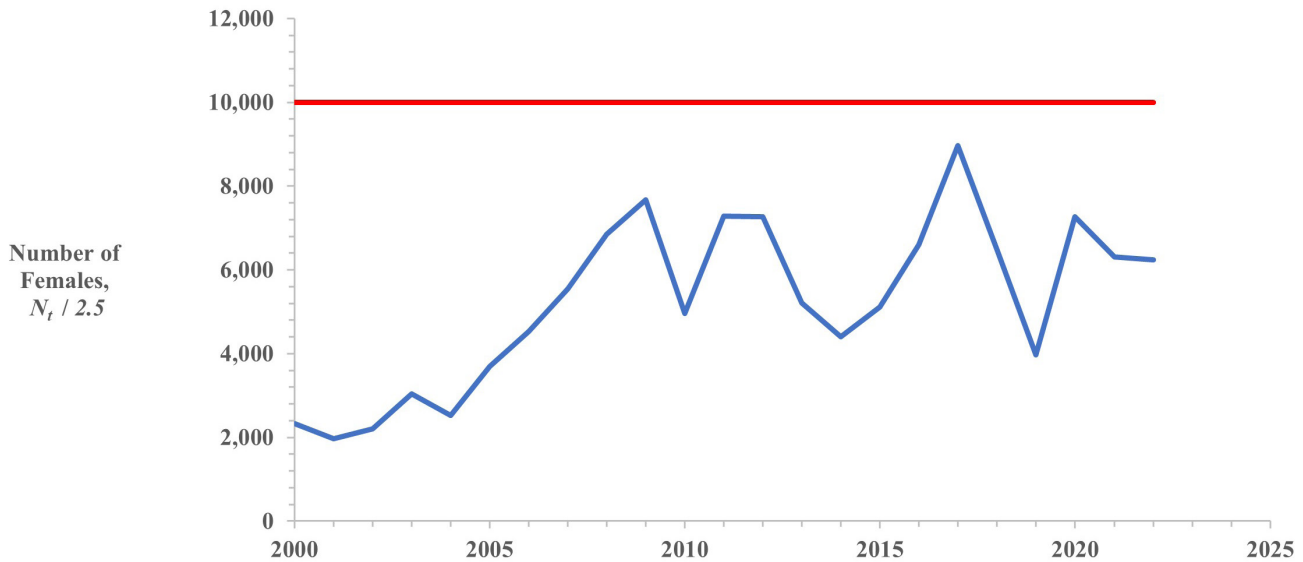
1. An average population of at least 40,000 nesting females per season (as measured by clutch frequency per female per season) over a 6-year period distributed among nesting beaches in Mexico and the U.S. is attained. Methodology and capacity to ensure accurate nesting female counts have been developed and implemented.
2. Ensure average annual recruitment of hatchlings over a 6-year period from in situ nests and beach corrals is sufficient to maintain a population of at least 40,000 nesting females per nesting season distributed among nesting beaches in Mexico and the U.S. into the future. This criterion may rely on massive synchronous nesting events (*i.e.*, arribadas) that will swamp predators as well as rely on supplemental protection in corrals and facilities.

The origin of the recovery plan's (NMFS *et al.* 2011) demographic criteria based on 10,000 and 40,000 females nesting in a season appears to be from Hildebrand (1963). On 18 June 1947, Ingeniero Andrés Herrera discovered Kemp's ridley's primary nesting beach near Rancho Nuevo, Municipio de Aldama, Tamaulipas, Mexico, and on that day he filmed a movie of this species largest ever documented arribada (Carr 1963; Hildebrand 1963). This discovery was made public in 1961, when Hildebrand (1963) screened a copy of Herrera's movie of the arribada at the Austin, TX meeting of the American Society of Ichthyologists and Herpetologists. In

a translation (Caillouet 2010) of Hildebrand (1963), Hildebrand stated: "...I estimated there were at least 10,000 turtles on the beach at a given time and that probably 40,000 individuals nested on that day, between 9 in the morning and 1 in the afternoon." Hildebrand (1963) wisely distinguished "turtles on the beach" from "individuals [that] nested" during the 1947 arribada, but he provided no details regarding how he estimated the numbers that nested.

Using frames from Herrera's film, Bevan *et al.* (2016) estimated the arithmetic mean size of the 1947 arribada to have been 26,916 females that nested. Although they also referred to 26,916 as the number of nests (clutches laid) during the 1947 arribada, we assume that 26,916 nesting females was intended. Bevan *et al.* (2016) stated: "Although the dynamics of arribada nesting have not been well quantified, if the main portion of an arribada represents a steady state in which the same number of turtles are moving onto as well as off of the beach, then we could predict that during this portion of the arribada, approximately 60% would be engaged in the nesting process and 30% would be in transit moving up the beach preparing to nest or returning to the sea." It is unknown whether arithmetic mean Kemp's ridley arribadas larger than 26,916 nesting females occurred prior to or during the 1947 season or before annual monitoring of nesting began in 1966, but none have been documented since annual monitoring began. It is noteworthy that Bevan *et al.* (2016) estimated the range for nesting females in the 1947 arribada to be 15,384-45,760, which is asymmetric around their estimated arithmetic mean.

In 1966, Mexico's Instituto Nacional de Investigaciones Biológicas Pesqueras (INIBP) implemented highly manipulative conservation interventions that protected Kemp's ridley nesters, nests and hatchlings on the beach near Rancho Nuevo (Adams 1966; Márquez-Millán & Garduño-Dionate 2014). In 1978, the National Park Service (NPS *et al.* 1978) implemented an action plan for restoration and enhancement of Kemp's ridley populations near Rancho Nuevo and Padre Island National Seashore, Texas (Caillouet *et al.* 2015b). Márquez-M. (1994) noted that "young" (neophyte) adult female Kemp's ridleys began appearing on the beach near Rancho Nuevo by 1976. He attributed this to Mexico's conservation interventions during 1966-1976, noting that "old" adult females (those remaining from the pre-1966 residual population) disappeared by 1984. We agree with Márquez-M. (1994) that conservation interventions near Rancho Nuevo during 1966-1976 contributed to reversal of the decline in nesting by 1986, because this reversal occurred despite pre-1986 anthropogenic mortality caused by unintended bycatch of neritic life stage Kemp's ridleys in shrimp trawls and natural mortality of all life stages (Carr 1977; Márquez-Millán & Garduño-Dionate 2014; Caillouet *et al.* 2015a; Bevan *et al.* 2016; Wibbels & Bevan 2019). Beginning around the mid-1980s, the suite of manipulative conservation interventions later referred to as rescue, resuscitation, rehabilitation and release



**Figure 1.** Number of Kemp’s ridley females in a season,  $N_t/2.5$ , on the Tamaulipas index beach during 2000–2022, where  $t$  is calendar year; the horizontal red line represents the recovery plan’s (NMFS *et al.* 2011) first demographic criterion for downlisting Kemp’s ridley.

(RRRR) of live-stranded, debilitated Kemp’s ridleys were added, but the contribution of RRRR to Kemp’s ridley population recovery has not been determined (Caillouet *et al.* 2016). The National Research Council (1990) concluded that for sea turtle “juveniles, subadults, and breeders in the coastal waters, the most important human-associated source of mortality is incidental capture in shrimp trawls, which accounts for more deaths than all other human activities combined.” The National Research Council (1990) proposed regulations requiring turtle excluder devices in shrimp trawls. Jenkins (2012) reviewed implementation of those regulations. Putman *et al.* (2023) modeled bycatch of Kemp’s ridley and green sea turtles (*Chelonia mydas*) in recreational fisheries along the southeastern U.S. coasts for years 1996–2017 and estimated it to be greater than the sum of bycatch that occurred in commercial fisheries that used trawls, gillnets and bottom longlines.

Beginning in 1966 and continuing annually since then, numbers of Kemp’s ridley nests, eggs and hatchlings were monitored on the Tamaulipas index beach during each nesting season. Initially, the index beach was limited to the beach segment near Rancho Nuevo only. The index beach was later extended by adding Tepehuajes and Playa Dos beach segments (Márquez-Millán & Garduño-Dionate 2014). Herein  $N_t$  (where  $t$  is calendar year) represents the number of nests on the Tamaulipas index beach during a nesting season, and  $h_t$  represents the total number hatchlings released from the index beach during a nesting season (Caillouet *et al.* 2018; Caillouet 2021; Arendt *et al.* 2023).

The Turtle Expert Working Group (TEWG 1998) estimated the number of nests/female/season on the index beach to be 2.5 as follows:

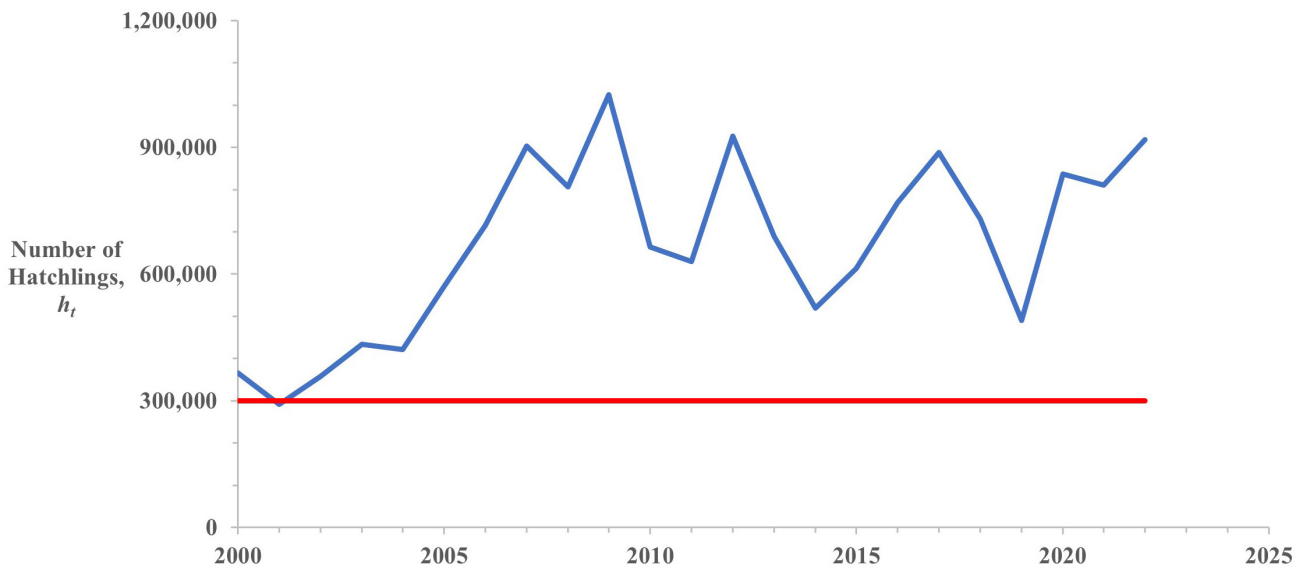
“Nests/female/season were calculated by Rostal (1991) to be 3.075 from a physiological/ultrasonographic study. Pritchard (1990) estimated 2.31 nests/female/season and a recent pit-tag study by Marquez (unpublished data) suggests the mean is 1.8 nests/female/season. We used the mean of means from these studies (2.4 nests/female/season), which we rounded to 2.5 nests/female/season.”

The estimate of 2.5 nests/female/season is accepted in both the current recovery plan (NMFS *et al.* 2011) and the most recent 5-year review of Kemp’s ridley (NMFS & USFWS 2015). We make no claims regarding accuracy of the estimated 2.5 nests/female/season or its application to estimating number of nesters in a season.

Herein we show trends for  $N_t/2.5$  (Fig. 1),  $h_t$  (Fig. 2) and  $h_t/N_t$  (Fig. 3) for years 2000–2022. Although Gladys Porter Zoo’s annual report for 2023 (Burchfield & Adams 2023) was available, data for Rancho Nuevo and Barra Del Tordo (= Playa Dos) beach segments were not included, so  $N_t$  for 2023 could not be calculated. For graphic comparisons with the trends in  $N_t/2.5$  (Fig. 1) and  $h_t$  (Fig. 2) during 2000–2022, we included a horizontal line representing the recovery plan’s (NMFS *et al.* 2011) first demographic criterion for downlisting (10,000 females = 25,000 nests/2.5) and a horizontal line representing its second demographic criterion for downlisting (recruitment of at least 300,000 hatchlings per season), respectively. The first demographic criterion for downlisting has not been attained through 2022 (Fig. 1), while the second criterion for downlisting has been exceeded in each year 2000 and 2002–2022, and it came close to 300,000 at 291,268 in 2001 (Fig. 2). Caillouet (2019) stated: “Given that density dependence appears to have begun reducing the rate of growth of the Kemp’s ridley population around year 2000, I hypothesize that annual numbers of neritic immatures became excessive around that year.” Caillouet (2019) stated further: “If annual numbers of neritic immatures in the population are already excessive and preventing population recovery as defined by NMFS *et al.* (2011), it would seem prudent to begin reducing numbers of neritic immatures by reducing annual numbers of hatchlings released from Tamaulipas beaches.”

Caillouet *et al.* (2018) fitted a logistic model to  $N_t$  over years 1966–2017 and noted that  $N_t$  exhibited multiplicative error around the model-fitted trendline. Two upper asymptotes of the fitted line were 24,306 (which preceded the pre-1986 decline in  $N_t$ ) and 17,434 (which followed the 1986–2009 exponential increase in  $N_t$ ). The exponential increase in  $N_t$  was abruptly interrupted in 2010, the year in which the Deepwater Horizon oil spill occurred in the northern





**Figure 2.** Number of Kemp’s ridley hatchlings,  $h_t$ , released in a season from the Tamaulipas index beach during 2000–2022, where  $t$  is calendar year; the horizontal red line represents the recovery plan’s (NMFS *et al.* 2011) second demographic criterion for downlisting Kemp’s ridley.

Gulf of Mexico off the coast of Louisiana (Caillouet 2014). Divided by 2.5, the pre-1986 and post-2009 asymptotes from Caillouet *et al.* (2018) represent 9,722 and 6,974 adult females, respectively. Arendt *et al.* (2023) developed a Kemp’s ridley population model of changes in age-structure and various demographic rates, based on  $N_t$  and  $h_t$  for years 1947 and 1966–2022; however, they overlooked the arribada of 1,500 nesting females, the largest of seven arribadas observed in 1966 (Chavez *et al.* 1968). Among the conclusions of Arendt *et al.* (2023) were:

1. “Barring changes in demographic rates or survival, the null model nest and hatchlings per nest values predict nesting potential as  $Nests = [(30,000 * hatchlings) / (30,000 * 49.6)]$ . Accordingly, hatchlings released since 2013 may support 17,519 nests (range = 11,780 to 21,298) annually during 2023–2032.”
2. “Kemp’s ridley sea turtle nesting may not achieve 1947 levels by 2048, ...”

Divided by 2.5, 17,519 nests (range 11,780 to 21,298) represent 7,008 females nesting in a season (range 4,712 to 8,519). The observed levels of  $N_t$  during 2013–2022 averaged 15,141 and ranged from 9,932 to 22,415, which equate to 6,056 (range 3,973 to 8,966) females nesting in a season, all of which are below 10,000. It is noteworthy that the highest level of  $N_t$  observed post-1985 (22,415 in 2017) was 5% higher than the highest level of  $N_t$  (21,298) predicted for 2023–2032 by Arendt *et al.* (2023). Post-2009 predictions for  $N_t$  by Arendt *et al.* (2013) suggest that Kemp’s ridleys on the Tamaulipas index beach may not reach the downlisting level of 10,000 females nesting in a season any time soon. The anticipated mean number of females nesting in a season (7,008) during 2023–2032, based on Arendt *et al.* (2023), is 30% lower than 10,000. However, Hays *et al.* (2024) confirmed that the Kemp’s ridley population is not decreasing.

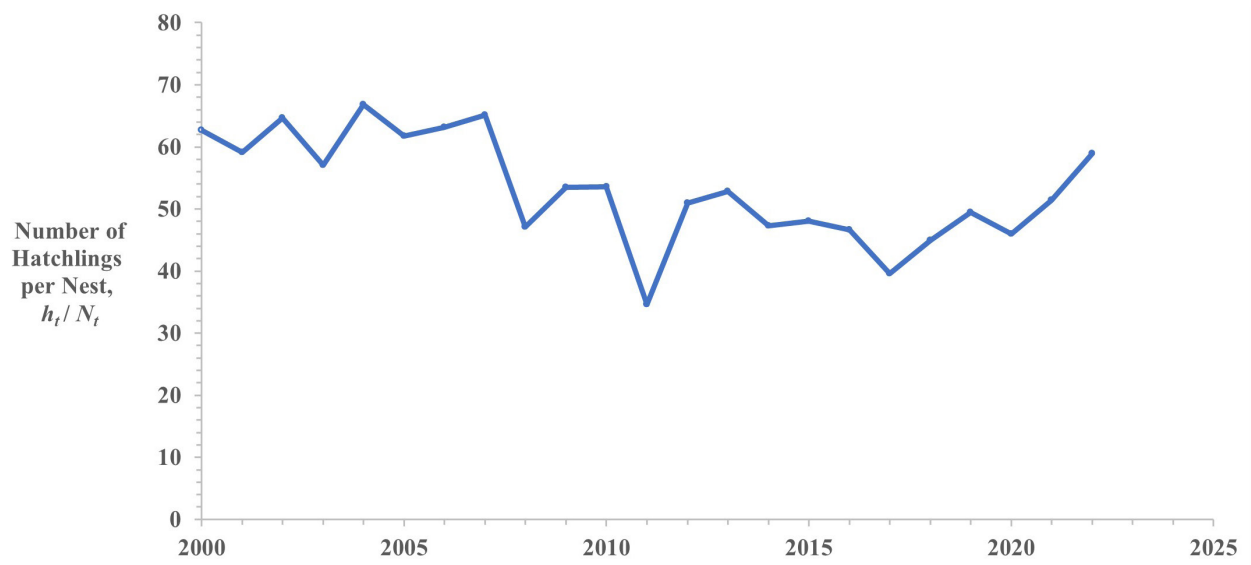
The recovery plan’s (NMFS *et al.* 2011) second criterion for delisting relies “on massive synchronous nesting events (arribadas) that will swamp predators as well as rely on supplemental protection in corrals and facilities.” It therefore is clear that arribada size is

important to fulfillment of this delisting criterion.

We suggest that better criteria for the recovery plan would be ones linked to the original baseline metric for the population, which is the 1947 arribada (Bevan *et al.* 2016). Specifically, we recommend that a 10,000 nesting female arribada during a season be the threshold for downlisting and a 27,000 nesting female arribada during a season be the threshold for delisting. Data on arribadas are more readily available and arribadas are more easily monitored than total nests per season. If our suggested criteria are adapted, it will be necessary to develop a method of estimating the number of females that nest during the largest arribada within each season.

The first downlisting criterion of 10,000 nesting females in a season is not expected to be reached by 2032 or even 2048 (Arendt *et al.* 2023). Yet, from year 2000 onward (except for year 2001) through 2022, the second demographic criterion for downlisting (recruitment of at least 300,000 hatchlings per season) has been exceeded by average hatchling releases of 668,358 per season within a range from 291,268 in 2001 to 1,025,027 in 2009 (Fig. 2). During 2000–2022, there was an initial downward trend in hatchlings released per nest ( $h_t/N_t$ ) followed by an increase in recent years (Fig. 3), but such variation did not prevent hatchling releases from exceeding the recovery plan’s (NMFS *et al.* 2011) downlisting level by 2 or 3 times.

It will be challenging to determine the amount of hatchling recruitment necessary to meet the recovery plan’s (NMFS *et al.* 2011) first demographic criterion for delisting, an average of 40,000 nesting females per season over the 6-year period by 2024. In addition, attainment of an arithmetic average of 40,000 nesting females per season over the 6-year period by 2024 would require at least 216,216 females nesting on beaches in Mexico and the U.S. during years 2023–2024 combined (Table 1). As far as we are aware, no estimates of a 6-year average of Kemp’s ridley females nesting in a season on beaches of Mexico and the U.S. combined have ever been published. It is highly unlikely that 40,000 nesting females per season can be attained by 2024, despite all the reductions in anthropogenic mortality of Kemp’s ridleys that have occurred



**Figure 1.** Number of Kemp’s ridley females in a season,  $N/2.5$ , on the Tamaulipas index beach during 2000-22, where  $t$  is calendar year; the horizontal red line represents the recovery plan’s (NMFS *et al.* 2011) first demographic criterion for downlisting Kemp’s ridley.

since the 1990s, and all the hatchlings that have been released since 1966. NMFS & USFWS (2015) reviewed the threats that have been mitigated and those that have emerged since 2007 (NMFS & USFWS 2007).

The number of females nesting in a season is obviously higher than the number of females nesting in the largest arribada during a nesting season (Bevan *et al.* 2016; Burchfield & Adams 2022). For each nesting season during years 2006-2013, Bevan *et al.* (2016) estimated the percentage that the number of nests in the largest seasonal arribada represented of the total season’s nests; it ranged from 12.82% in 2010 to 32.62% in 2011. Arribada nesting during daytime is characteristic of Kemp’s ridley, although nighttime arribadas are characteristic of its congener species, olive ridley (*Lepidochelys olivacea*), with some nesting during daytime. Data may exist for the 1978 nesting season (and possibly for earlier years) onward, from which graphs of cumulative numbers of nests

over each nesting season could be developed (Jiménez-Quiroz *et al.* 2003; Bevan *et al.* 2016; Burchfield & Adams 2022). Such graphs could be informative by depicting seasonal progress in nestings and the timing and sizes of arribadas over the years. A report by Thane Wibbels and Forrest Collins, found within Burchfield & Adams (2023), describes the use of aerial drones to conduct surveys of adult Kemp’s ridley movements, behavior, courtship and nesting, showing promise that such drone surveys will generate data on the number of nesting females in the largest arribada of a season.

Although the public comment period for the next 5-year review of Kemp’s ridley ended on 30 August 2021 (NMFS & USFWS 2021), we hope that our recommendations can and will be examined and evaluated by that review.

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Year	Nests in a season ( $N_t$ )	Adult females in a season ( $N/2.5$ )
2019	9,932	3,973
2020	18,176	7,270
2021	15,757	6,303
2022	15,594	6,238
2023-2024	540,541 <sup>a</sup>	216,216 <sup>a</sup>
6-yr sums	600,000	240,000
6-yr means	100,000	40,000

**Table 1.** Minimum seasonal sums for Kemp’s ridley nests and adult females on beaches of Mexico and the U.S. over years 2023 and 2024 that would be needed, in combination with available seasonal numbers of nests and adult females over years 2019-2022, to attain an average of 40,000 nesting females per season over the 6-year period ending in 2024. a = estimated.

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# Visualization of Perivitelline Membrane-bound Spermatozoa and Embryonic Cells in Nonviable Leatherback (*Dermochelys coriacea*) and Loggerhead (*Caretta caretta*) Eggs

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Sea turtle eggs that fail to hatch can provide valuable insight into the timing and conditions under which embryonic mortality occurs. Additionally, the study of unhatched, nonviable eggs can improve our understanding of the role of infertility in egg failure. Nest monitoring programs that estimate infertility by observing eggs during nest excavations at the end of incubation are likely to overestimate infertility due to the difficulty of identifying signs of early embryonic development (e.g., egg chalking, embryos, blood islands, embryonic tissues, or germinal disc development) (Parmenter 1980; Blanck & Sawyer 1981; Limpus *et al.* 1984; Wyneken *et al.* 1988; Bell *et al.* 2003; Phillott & Godfrey 2020). In earlier studies, if none of these were found, an egg would be designated as infertile (Bell *et al.* 2003). Recognizing the difference between infertility and early embryonic death is important when studying egg failure, as they have different causes and implications for management and conservation.

The necropsy of unhatched sea turtle eggs typically includes both an external and internal examination. Externally, eggs can be examined for signs of fungal infection, predation, and egg chalking (the whitening of the eggshell). Indications of egg chalking have been used as a sign of fertility, because only fertile eggs will chalk (Blanck & Sawyer 1981). However, not all fertile eggs will appear chalked, because the embryo could die before the chalking process begins or the chalking could fade after embryo death (Miller 1985; Phillott & Parmenter 2007). Internally, eggs are examined for any signs of embryonic development (an embryo, blood islands, other embryonic tissues, or germinal disc development). If an embryo is found, it can be staged based on its morphological characteristics (Miller 1985; Miller *et al.* 2017). However, it is often difficult to stage an embryo or even identify if an embryo is present, because the egg contents continue to incubate in warm conditions until the clutch hatches and the nest is excavated for inventory of the contents (Miller 1996). During the time between egg failure and nest inventory, the egg contents significantly degrade (Bell *et al.* 2003). If an embryo dies early in development, it can be difficult or impossible to identify any clear signs of an embryo with the naked eye (Parmenter 1980; Wyneken *et al.* 1988). Therefore, microscopic examination of unhatched eggs is necessary to more accurately classify an egg as fertile or infertile (Parmenter 1980; Phillott & Godfrey 2020).

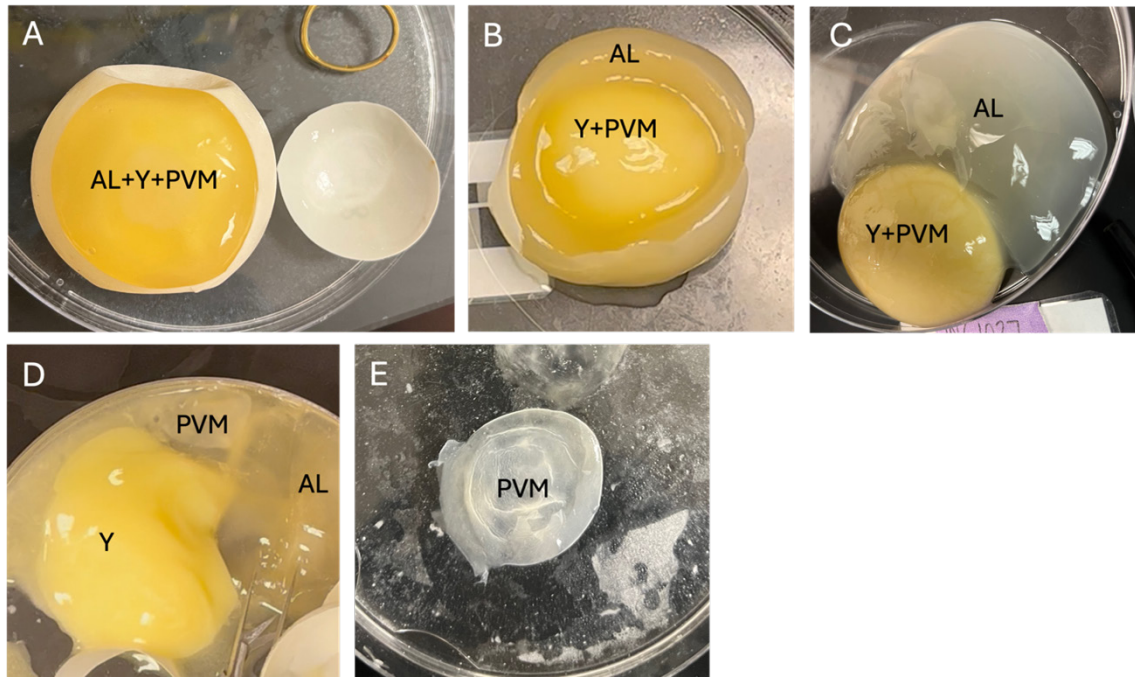
Previous studies that investigated sea turtle fertility have included excavating *in situ* eggs early in incubation to look for egg chalking (Abella *et al.* 2017), monitoring egg chalking in *ex situ* conditions (Rafferty & Reina 2014; Williamson *et al.* 2017a,b; Booth *et al.* 2021) and necropsying eggs if no chalking was detected (Bell *et al.* 2003), and sacrificing eggs that are collected freshly after oviposition to look for embryos (Limpus *et al.*, 1984; Wyneken *et al.* 1988; Miller *et al.* 2003). This last technique is lethal, and the other approaches are invasive as they require working with eggs

that have not degraded in natural nests. Thus, there is a need for methods of fertility assessment that are nonlethal and can be used despite egg degradation.

Fluorescent microscopic approaches for assessing fertilization have been described in birds (Birkhead *et al.* 2008; Croyle *et al.* 2012; 2015), crocodiles (Augustine 2017), and non-marine chelonians (Croyle *et al.* 2016) but have yet to be validated in sea turtles. Here we test this method in unhatched, nonviable eggs from two sea turtle species, the loggerhead (*Caretta caretta*) (n=12 eggs) and leatherback (*Dermochelys coriacea*) (n=43 eggs). Eggs were either collected at or shortly after oviposition and incubated in controlled conditions or were collected from natural nests at the end of incubation during nest inventory. Eggs incubated in controlled conditions were monitored daily for signs of embryonic development (i.e., egg chalking or vascular formation visible during candling). If these were not found within 14 days, eggs were removed from the incubators and necropsied. Unhatched, nonviable eggs from natural nests were collected during routine nest excavations at the end of incubation (58-80 days) and necropsied. During egg necropsy, perivitelline membranes (PVMs) were collected for analysis using fluorescent microscopy.

The approach described here is a modification of the methods of Assersohn *et al.* (2021) and Birkhead *et al.* (2008). PVMs are collected from unhatched eggs and stained with Hoechst 33342, a fluorescent nucleic acid stain that binds to DNA. PVMs are then examined microscopically for the presence of spermatozoa and/or embryonic cells. The collection of PVMs requires tissue forceps, dissection scissors, petri dishes, and 1% phosphate buffered saline (PBS). The eggs were gently washed in water to remove external debris, and then either held in the hand or placed on a stable surface, such as a petri dish with a small ring of clay to prevent rolling. If the original orientation of the egg from its position in the nest is known, keep the egg oriented the same way with the top facing up. The eggshell was cut away beginning in the upper 1/3 of the egg, with care taken to not puncture the yolk. The cut eggshell was removed, and the yolk (with the intact PVM) was separated from the albumen. Next, the PVM was grasped with tissue forceps and an opening was cut in order to evacuate the yolk. The remaining yolk was rinsed from the PVM using 1% PBS, and the PVM was excised from the rest of the egg (Fig. 1). The PVM then was placed as flat as possible on a microscope slide and stained with working solution (1µg/mL) Hoechst 33342 (Thermo Scientific™), using enough to ensure that the entire sample was covered. The slides were covered with a cover slip and left in the dark (in a closed drawer or box) to incubate for at least 10 minutes. The slides were then examined under a compound microscope with the appropriate fluorescent attachments for Hoechst 33342 (maximal excitation at 350 nanometers and maximal emission at 461 nanometers). For this study, an Olympus BX50 compound microscope with a Chroma 69002 ET DAPI/FITC/Texas Red® filter

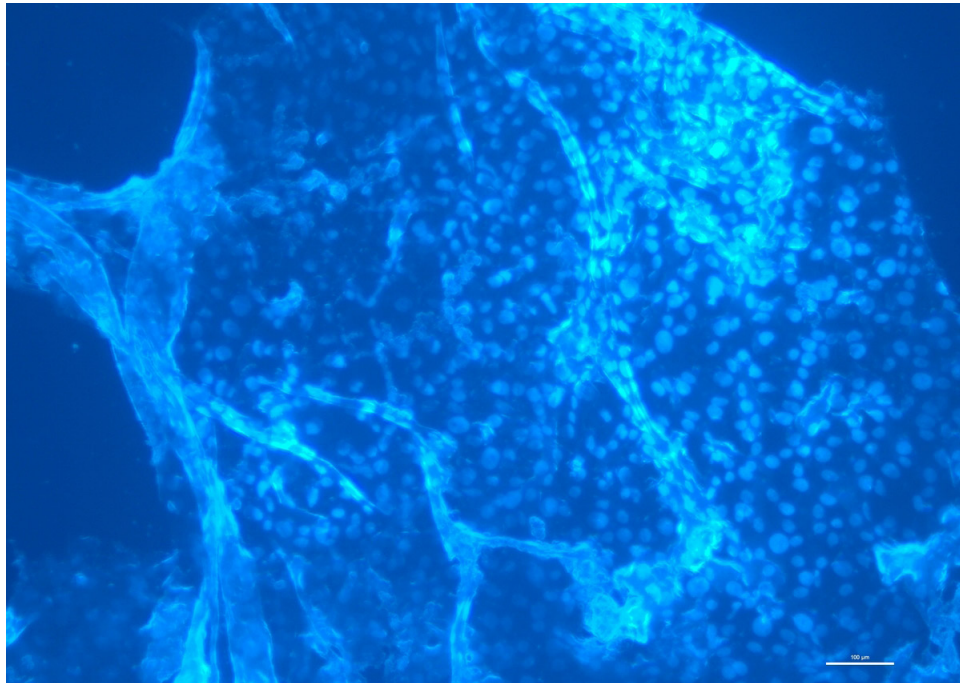




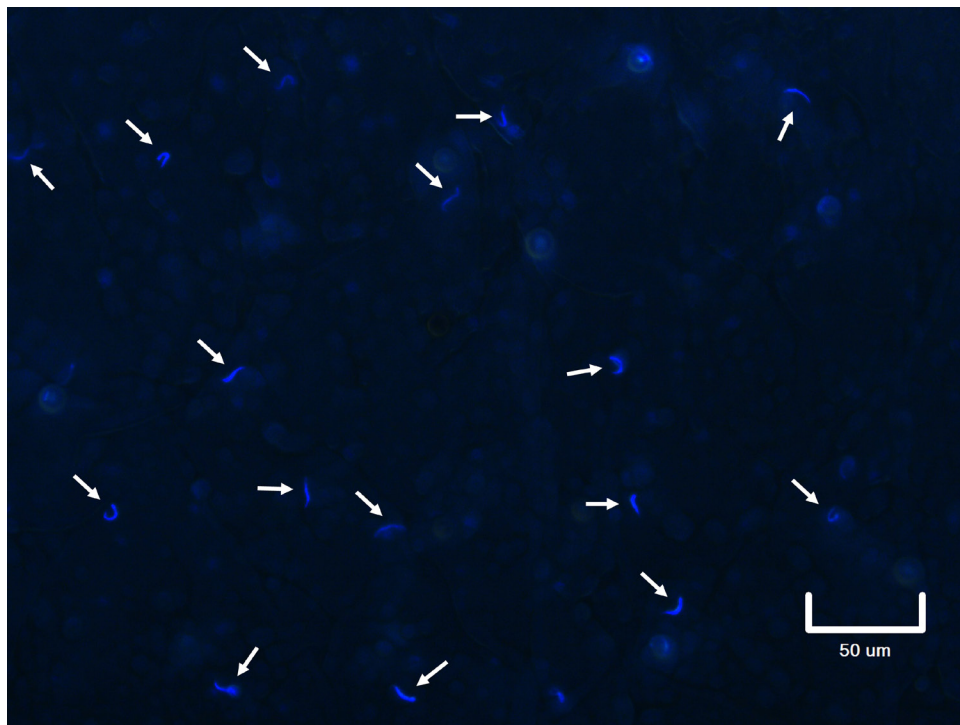
**Figure 1.** Egg necropsy process for perivitelline membrane collection. (AL=albumen, Y=yolk, PVM=perivitelline membrane). A: Eggshell top is removed to expose the egg contents. B and C: Yolk and PVM are separated from albumen. D: The yolk is separated from the PVM. E: A PVM separated from yolk and albumen after rinsing in 1% phosphate buffered saline.

Species	Incubation condition (days of incubation)	Egg storage condition prior to necropsy (storage time in days)	PVM storage condition prior to examination (storage time in days)	Number of eggs
Leatherback	Natural nest (58-59)	Necropsied same day as collection	70% ethanol (7-163)	3
Leatherback	Natural nest (59-80)	Refrigerated at 4°C (1-2)	10% buffered formalin (148-287)	7
Leatherback	Natural nest (59-80)	Refrigerated at 4°C (1-6)	70% ethanol (4-171)	7
Leatherback	Natural nest (71)	Frozen at -18°C (169)	70% ethanol (4-259)	4
Leatherback	Natural nest (78)	Frozen at -18°C (48)	10% buffered formalin (290)	1
Leatherback	Incubator (15)	Necropsied same day as collection	No fixation, examined same day as necropsy	2
Leatherback	Incubator (15-19)	Refrigerated at 4°C (1-2)	No fixation, examined same day as necropsy	2
Leatherback	Incubator (14)	Refrigerated at 4°C (12)	10% buffered formalin (1)	2
Leatherback	Incubator (12)	Frozen at -18°C (315)	10% buffered formalin (9)	2
Loggerhead	Incubator (16)	Frozen at -18°C (238)	No fixation, examined same day as necropsy	1
Loggerhead	Incubator (17-24)	Frozen at -18°C (238-276)	10% buffered formalin (1-12)	4
Loggerhead	Incubator (16-17)	Frozen at -18°C (130-141)	70% ethanol (4-96)	5

**Table 1.** Description of egg and perivitelline membrane (PVM) storage conditions in which embryonic cells were visualized within the PVM. Eggs from the “Incubator” incubation condition were in controlled temperatures (28, 30, or 32°C).



**Figure 2.** Embryonic cells stained with Hoechst 33342 nucleic acid stain as light blue on a perivitelline membrane from a loggerhead egg (100x magnification). Lighter lines of material in this figure are folds in the perivitelline membrane. Scale bar = 100 $\mu$ m.



**Figure 3.** Sperm heads stained with Hoechst 33342 nucleic acid stain on a perivitelline membrane from a leatherback egg (200x magnification). Arrows point to fluorescing sperm heads. Scale bar = 50 $\mu$ m.

Species	Incubation condition (days of incubation)	Egg storage condition prior to necropsy (storage time in days)	PVM storage condition prior to examination (storage time in days)	Number of eggs
Leatherback	Natural nest (60)	Refrigerated at 4°C (1)	70% ethanol (224)	1
Leatherback	Natural nest (71)	Frozen at -18°C (169)	70% ethanol (4)	1
Leatherback	Incubator (14-15)	Necropsied same day as collection	No fixation, examined same day as necropsy	6
Leatherback	Incubator (14)	Necropsied same day as collection	10% buffered formalin (254-354)	4
Leatherback	Incubator (14-15)	Refrigerated at 4°C (2-12)	No fixation, examined same day as necropsy	7
Leatherback	Incubator (14-15)	Refrigerated at 4°C (6)	10% buffered formalin (1-348)	7
Leatherback	Incubator (14)	Refrigerated at 4°C (6)	70% ethanol (218)	1
Loggerhead	Incubator (22)	Frozen at -18°C (4-23)	10% buffered formalin (1)	2

**Table 2.** Description of egg and perivitelline membrane (PVM) storage conditions in which spermatozoa were visualized within the PVM. Eggs from the “Incubator” incubation condition were in controlled temperatures (28, 30, or 32°C). Some leatherback eggs (n=11) had PVMs separated into multiple storage conditions.

set was used, and slides were examined at 100x, 200x, and 400x. The fluorescent stain dyes blastodermal embryonic cells (Fig. 2) and/or the heads of spermatozoa (Fig. 3) in the PVMs. An embryo’s blastodermal cells will be too numerous to count in the PVM of a fertile egg, while an infertile egg will have a uniform background (Barna *et al.* 2020).

This study is the first to validate this PVM analysis approach to identify fertility in sea turtle eggs. Embryonic cells and spermatozoa were identified in nonviable eggs from various incubation and storage conditions (Tables 1 and 2). Therefore, this method can be used with eggs collected shortly after oviposition, degraded eggs in various post-collection storage conditions, and PVMs stored in fixatives (10% buffered formalin or 70% ethanol) for various amounts of time. Phillott & Godfrey (2020) recommend that studies focused on fertility should use eggs that are collected freshly after oviposition since this approach avoids major degradation. However, such studies are not always possible due to logistic or permitting constraints.

Validation of this method in sea turtles provides a valuable tool for studying egg failure because it clarifies the differences between infertility and early embryonic death in unhatched eggs that show no signs of development, including degraded eggs. A deeper understanding of fertility rates of different nests, individual females, populations, and species can be further developed using this technique. Identifying how much infertility contributes to egg failure may inform further studies on reproductive shortcomings, such as causes for ova to fail to be fertilized and changes in fertility rates over time. Alternatively, if infertility is not a major contributor to egg failure, this suggests that investigations into early embryonic mortality are necessary.

Although an improvement, this method of fertility identification remains limited by the level of degradation of the PVM and the

spermatozoa. As they degrade, PVMs become extremely fragile and difficult to recover (Croyle *et al.* 2012), which can limit the number of eggs that can be examined. Additionally, especially in degraded eggs, the absence of spermatozoa could be the result of spermatozoa degradation during incubation, rather than infertility (Croyle *et al.* 2015). It is important to note that if spermatozoa are detected, their presence is not necessarily indicative of the multiple essential processes that must occur to facilitate syngamy (the fusion of two nuclei) (Birkhead & Fletcher 1998; Croyle 2015). Further research is necessary to understand what numbers (or threshold numbers) of spermatozoa are representative of successful fertilization, as this likely varies across species and is usually identified in controlled studies (Birkhead & Fletcher 1998; Liptói *et al.* 2004; Croyle *et al.* 2015). Conservatively, only eggs that are identified to have embryonic cells should be distinguished as fertile when using fluorescent microscopy methods. However, eggs with at least two spermatozoa present on the PVM have been classified as fertile in studies on avian fertility and could be considered as “apparently fertile” (Croyle *et al.* 2015). The presence of spermatozoa indicates successful mating at some point. However, the presence or absence of spermatozoa in sea turtle eggs is not yet a definitive marker for fertility. There is a need for further research on PVM-bound spermatozoa numbers and their relationship to fertility.

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# Leatherback Sea Turtles Mating off the Caribbean Coast of Costa Rica

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The leatherback sea turtle (*Dermochelys coriacea*, Vandelli, 1761), is one of four sea turtle species found along the Caribbean coast of Limón province, Costa Rica. The other species include hawksbill (*Eretmochelys imbricata*), loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) turtles (Sasa et al. 2009). All four sea turtle species utilize various beaches for nesting (Sasa et al. 2009). The breeding season for leatherback sea turtles occurs from February to August, with peak activity in April and May. The main nesting beaches, from north to south, include Tortuguero, Parismina, Pacuare, Laguna Urpiano, Mondonguillo, Moin, Cahuita, Negra, and Gandoca (Fonseca et al. 2012). Globally, the leatherback sea turtle is classified as Vulnerable on the IUCN (International Union for the Conservation of Nature) Red List of Threatened species (Wallace et al. 2013). The primary threats to this species include incidental capture in fishing gears, poaching, and egg collection for human consumption. In the northwestern Atlantic Ocean, the leatherback sea turtle subpopulation is categorized as Endangered and is declining (Wallace et al. 2013). In Costa Rica's Caribbean region, egg poaching for black market sales is the most significant threat to sea turtles (Fonseca & Echeverría 2018). Despite the various threats affecting leatherback sea turtles in the Caribbean Sea region, little is known about their distribution and behavior, particularly at sea.

Here, we report a rare observation of two mating leatherback sea turtles on 06 March 2023, along the southern Caribbean coast of Costa Rica (Fig. 1). This event took place during boat-based surveys conducted to monitor coastal dolphin populations in this region. Initially, a pectoral fin was detected from a distance at 07:34 h. We approached a pair of turtles at a slow speed (<1 knot) and maintained a distance of about 25 m to avoid disturbance from our research vessel. The engine was set to neutral at 7:36 h. The turtles were located outside Punta Cocles (9°40' N and 82°42' W), approximately 3.68 km from the coastline and at a depth of 65 m. The large female and significantly smaller male (Fig. 1A) were actively mating at the surface, with the female frequently moving her pectoral fins and splashing water. The pair separated at 7:41 h, as the female was vigorously trying to separate from the male (Fig. 1B). Shortly after the separation, the male was observed actively swimming, possibly searching for the female. The research vessel left the area at 7:42 h. Another research vessel conducting dolphin surveys also observed a single adult leatherback sea turtle, offshore of Gandoca beach (9° 35' N and 82° 36' W) on the same day (L. May Collado & M. Austin, pers. comm.).

The nearest nesting beaches for leatherback turtles are Negra close to Cahuita National Park, 8.3 km to the northeast, and Gandoca, 17.9 km to the south. Both beaches are located within protected areas under the Costa Rican Sistema Nacional de Areas de Conservación. The events described here have rarely been reported in the Caribbean region, except off Culebra in Puerto Rico (Carr & Carr 1986) and in Matapica beach in Suriname (Godfrey & Barreto

1998). In previous observations (Carr & Carr 1986; Godfrey & Barreto 1998), copulations occurred in waters adjacent to the nesting beach (between 50-400 m), in the present event it is reported in waters more distant from the nesting beach. This provides further evidence of the areas used for mating by leatherback turtles in the coastal waters of the Caribbean region and Costa Rica. Previous research using satellite telemetry revealed that both breeding males and females occur in this region, but this is the first evidence that this species breeds in the coastal waters of the Caribbean coast of Costa Rica (Bond & James 2017). Future studies are needed to evaluate the importance of the coastal waters of the Caribbean coast of Costa Rica for leatherback sea turtles. A better understanding of the co-occurrence between leatherback sea turtles and human activities, particularly fisheries, would also be important to potentially mitigate impacts on this endangered species.

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**Figure 1.** Figure 1. Leatherback sea turtles mating at the surface in the Caribbean waters off Punta Cocles, Limon, Costa Rica. A: Female and male mating at the surface; B: Female emerging out of the water once the male released her (Photographs: Jeremy J. Kiszka).



# First Attempt of Solar-Reliant Towable Transmitters to Track Leatherback Sea Turtles

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Satellite transmitters have been used to track sea turtles for over four decades and can provide high-resolution data on movement, behavior, and environmental variables (Stoneburner 1982; Hays & Hawkes 2018). When considering which technology to use, animal welfare is a priority followed by transmission quality and duration of service (Hawkins 2004; Wilson & McMahon 2006). Piacenza *et al.* (2018) suggested key areas of focus for the improvement of sea turtle satellite tracking device designs, including attachment methods, minimizing hydrodynamic drag, and alternative energy harvesting options.

Leatherback sea turtles (*Dermochelys coriacea*) have a pliable carapace and easily abraded skin, unlike the hard-shelled Cheloniids, making transmitter attachment uniquely challenging. Eckert & Eckert (1986) pioneered satellite tracking leatherback sea turtles, using backpack harness systems, which provide researchers the ability to gain valuable insight into the in-water ecology on this cryptic species (Hughes *et al.* 1998). However, backpack harnesses can physically damage the turtle (Troëng *et al.* 2006), decrease the locomotor travel rate by 16% (Fossette *et al.* 2008), and increase drag coefficients by 91 to 112% (Jones *et al.* 2011). These hydrodynamic impacts, combined with potential restrictions of flipper movement, may result in increased transit times and decreased dive times, likely impacting foraging efficiency (Fossette *et al.* 2008). For these reasons, along with the development of new technologies, the United States National Oceanic and Atmospheric Administration (NOAA) has stated that they do not use or endorse the use of backpack harness systems for modern leatherback satellite tracking (NMFS 2008).

Platform terminal transmitters (PTT) mounted directly to the medial ridge of the carapace (Fossette *et al.* 2008) result in less impact on contact tissues, providing a preferential configuration compared to harness-attached PTTs (Hamelin & James 2018). However, the ridges found on the leatherbacks' carapace enhance the animal's hydrodynamic performance (Bang *et al.* 2016). When tested in a lab, directly attached PTTs increased the drag coefficient on leatherback models by up to 3% (Jones *et al.* 2011). Additionally, the direct attachment of PTTs necessitates drilling up to four holes through the carapace (Byrne *et al.* 2009). Despite these liabilities, directly mounted PTTs offer a considerable reduction in drag and potential for tissue damage relative to harness techniques.

A third approach to tracking leatherbacks is the use of towable pop-up satellite transmitter (PSAT) tags attached by a tether (Morreale *et al.* 1996). This method has been used successfully to continuously track leatherbacks over long distances and extended periods (up to 10,000 km and over 240 days) (Bailey *et al.* 2012; Roe *et al.* 2014; Robinson *et al.* 2016; Sasso *et al.* 2021; Rider *et al.* 2022). Towable PSATs have been estimated to increase the drag of an adult leatherback by 1.5-2.8%, which is comparable to

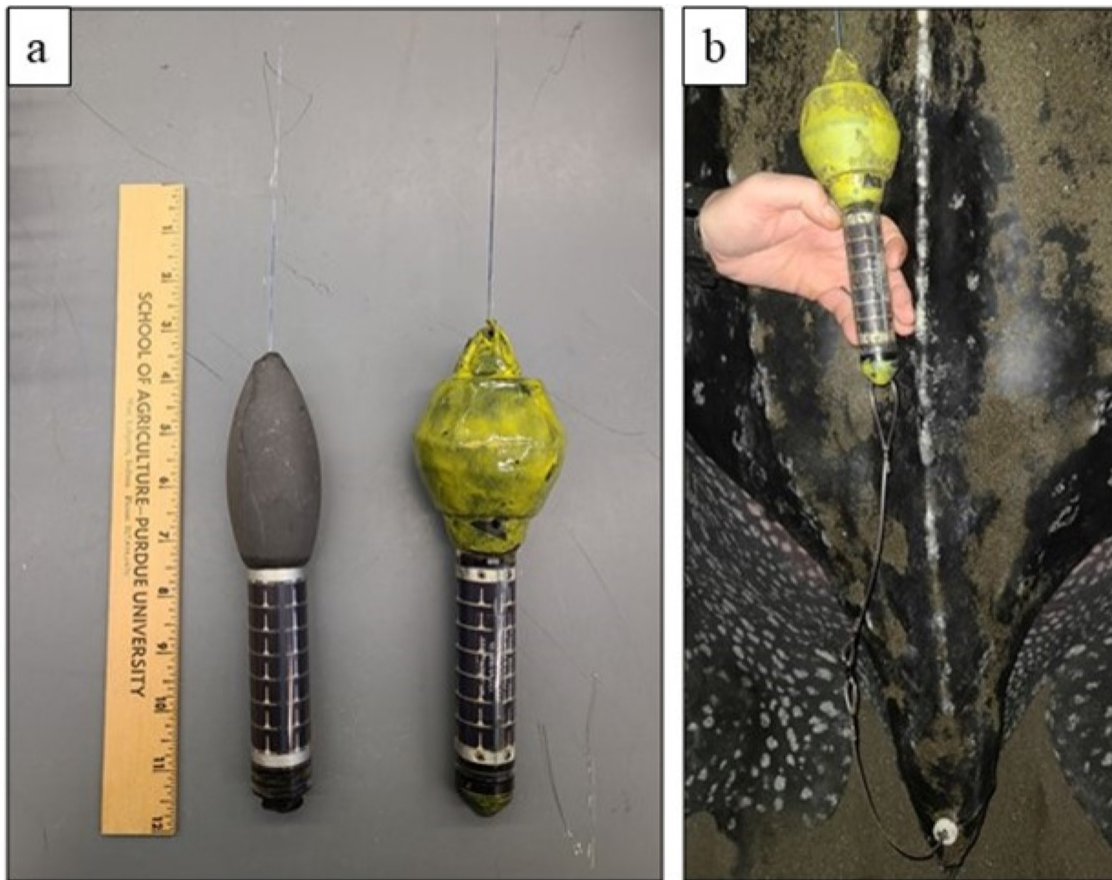
that of directly mounted PTTs (Jones *et al.* 2014). However, the attachment method for towable tags only requires a single small hole to be drilled in the overhanging rear margin of the carapace (pygal process), thereby minimizing handling effort and time, and decreasing tissue damage and potential sites of infection.

Despite these advantages, consideration should be given to the potential of entanglement and a higher probability of loss during movement, mating, or due to 'predatory nipping' of the tags. Furthermore, if the turtle returns to nest with the tag still attached, the tag may fall into the nest cavity or interfere with the rear flippers during nesting and lead to an abandoned nest. It remains unclear if the advantages of towable PSATs outweigh these risks. Further exploration of towable PSATs and their design is needed to compare their utility to that of directly mounted PTTs on leatherbacks.

Alternative energy harvesting remains the area of sea turtle satellite tracking with the most potential for technology development. Advances in this area could increase transmitter longevity (Piacenza *et al.* 2018) and decrease environmental contamination from non-recovered transmitters if batteries are excluded (Mrozik *et al.* 2021). Shafer & Morgan (2014) proposed capitalizing on pressure cycles from repeat dives or harvesting kinetic energy from drag to increase the longevity of PTTs. While these methods remain largely untested, Mansfield *et al.* (2012, 2021) has demonstrated solar-generated PTTs as an effective method of satellite tracking sea turtles. To the best of our knowledge, there has been no such attempt to incorporate solar energy harvesting into towable PSATs on leatherback sea turtles.

In January 2023, we used solar-reliant towable PSATs to further explore the post-nesting movements and migratory behavior of leatherback sea turtles nesting on Bioko Island, Equatorial Guinea. Bioko Island has the second-largest number of nesting leatherback encounters in the Gulf of Guinea, a region that includes the world's largest leatherback rookery (Witt *et al.* 2009; Honarvar *et al.* 2016). Understanding the spatiotemporal behaviors of leatherbacks in the region may provide additional insight into the connectivity of nesting habitats and help explain nesting trends (Garzon *et al.* 2023). Here, we report on negative results following the deployment of Desert Star Systems (DSS) SeaTag-MOD PSATs, configured as solar-reliant towable transmitters, on leatherbacks nesting on Bioko Island.

Six SeaTag-MOD modular PSATs (Desert Star Systems, Marina, CA, USA) were adapted for use as towable real-time satellite transmitters to be deployed on leatherbacks nesting on Bioko Island, Equatorial Guinea. We chose these tags because, at the time of purchase, they were the only PSATs on the commercial market manufactured to function for an extended duration on solar power. Furthermore, these tags incorporate a low-profile float, and include depth, accelerometer, magnetometer, and temperature sensors that are advertised to withstand depths of up to 2 km (approximately



**Figure 1.** (a) Desert Star Systems Sea-MOD transmitters before (left) and after (right) additional buoyancy and an antifouling agent were added. (b) Transmitters were towed by a tether attached to the pygal process of leatherback sea turtles.

twice as deep as the deepest known leatherback depths). To ensure an upright posture of the tag when the turtle surfaced to breathe, we supplemented the buoyancy with a small amount of syntactic foam resistant to crushing at depths exceeding 1 km. We omitted the optional battery and timed-release section of each transmitter, reducing the transmitter weight by 55 g and the length by 100 mm (originally 163 g and 275 mm, total); resulting in tags that rely solely on a solar-powered capacitor for energy. We applied an anti-fouling agent (PropSpeed, Auckland, New Zealand) to each transmitter to prevent the loss of solar functions due to biofouling (Fig. 1) (Robinson *et al.* 2016). We included corrodible in-line crimps on the lanyard to release the transmitter, crimps, and swivel within approximately one year (Belskis *et al.* 2010).

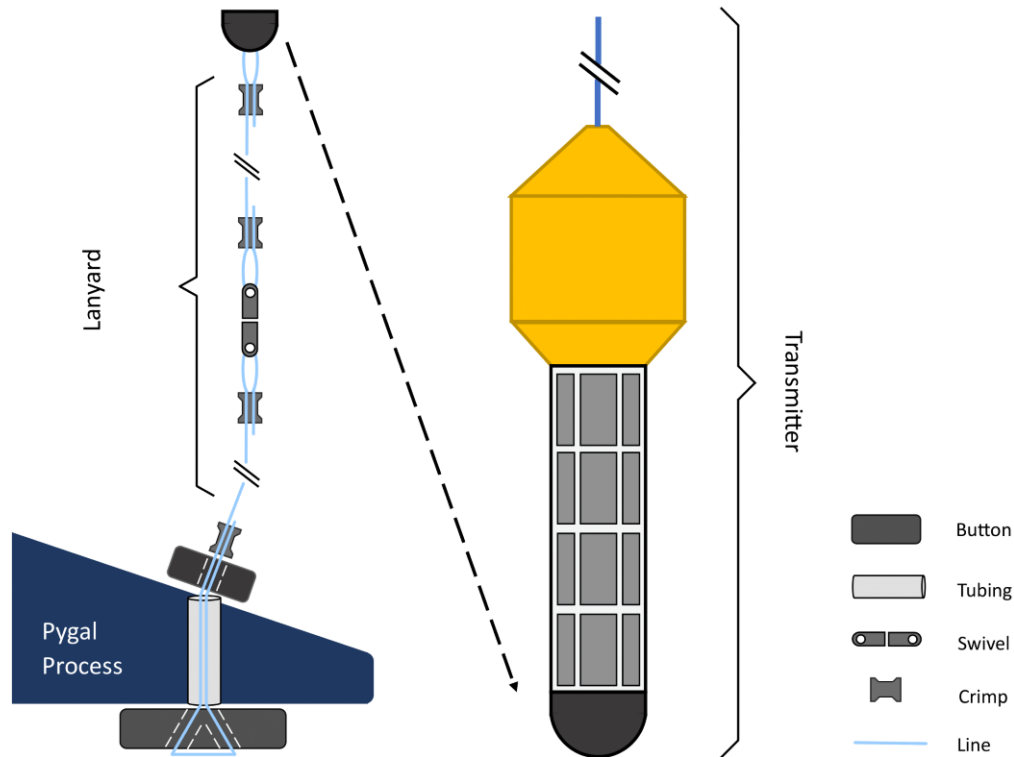
Transmitters were programmed in DSS' SeaDock (2.5.0.17793) software. The mission type was set to PSAT with real-time tracking, sensor sampling interval was set at four minutes, and release conditions were set to 14 days at a constant depth, crush depth exceeded, or mission end/release date. The mission end date was programmed as 15 August 2028, well after the expected transmitter release dates. The transmission function of each transmitter was checked using a TSUR-400 hand-held receiver (Telonics, Inc. Mesa, AZ, USA) during programming, after arrival on Bioko Island, and again at the field site.

Leatherbacks nest predominantly on the southeastern beaches of Bioko Island, with their primary nesting season occurring from November to March (Tomás *et al.* 2010; Honarvar *et al.* 2016). Two teams of two to three people conducted nighttime visual surveys

between spatial coordinates of 3.240234 °N, 8.601610 °E and 3.232639 °N, 8.614697 °E throughout January 2023. This stretch of shoreline consists of a black sand beach with relatively low wave energy and little offshore obstruction (Honarvar *et al.* 2016).

Teams of four to six people conducted leatherback processing and data collection on the nesting beach. Following deposition of the first eggs, half of the team measured the curved carapace length (CCL) and curved carapace width (CCW), recorded the GPS location of the nest (GPSMAP 65s; Garmin, Olathe, KS, USA), and scanned for a passive integrated transponder (PIT) tag. If no PIT tag was detected, a new tag (Avid Identification Systems Inc, Norco, CA, USA) was placed in the right shoulder. Simultaneously, other team members conducted ultrasound examinations of the oviducts (Edge Life Technologies, Miami, FL, USA). Six nesting females were selected for transmitter attachment based on the following criteria: 1) no external evidence of recent injury or disease (*e.g.*, no missing limbs, major lesions, or heavy epibiota); 2) ultrasound examination showed fewer than 30 vitellogenic follicles in each ovary (in an effort to identify turtles depositing their last clutch for the season); and 3) the presence of a complete pygal process with appropriate anatomy to attach the transmitter.

For tether attachment, we followed protocols described by Robinson *et al.* (2016) (Fig. 2). Following the completion of egg deposition, a 5 mm hole was drilled approximately 3-6 cm from the distal end of the pygal process. Silicone surgical tubing was inserted into the hole and trimmed flush to the carapace, to prevent the lanyard from abrading the carapace (Hamelin & James 2018).



**Figure 2.** A diagram of the tether assemblage used to attach Desert Star Systems Sea-MOD transmitter to the pygal process of leatherback sea turtles (Modified from Robinson et al. 2016). Tethers were made from a 200 lb. fluorocarbon leader with a swivel in the middle to prevent coiling of the line. Loops were held together by corrodible crimps which, allowing release of the assemblage from the turtle after approximately one year.

The drill bit, surgical tubing, and pygal process were disinfected using 4% betadine antiseptic solution. Predrilled Delrin buttons were placed on the dorsal and ventral surfaces of the carapace to distribute the force of the lanyard. A 200 lb. test Diamond Presentation 100% Fluorocarbon leader (Momoi Fishing Manufacturing, Co. Ltd., Aiko, Japan) with a diameter of 1.56 mm tether line was passed through the dorsal Delrin button and the surgical tubing, looped through the ventral Delrin button, then brought back up through the surgical tubing and dorsal Delrin button, where it was secured using a corrodible crimp (mini double-barrel copper sleeve, inner dimension of 1.6 mm). An approximately 20cm length of line was terminated in a loop with a size 4 wind-on swivel rated for 240 lb (SPRO Sports Professionals, Kennesaw, GA, USA) using another corrodible crimp. The satellite tag was similarly affixed to the swivel via another ~20 cm length of line to yield a total lanyard length of approximately 40 cm. This length was sufficient to allow the transmitter to break the water's surface when the turtle breathed, yet short enough to negate the possibility of front flipper entanglement. Total attachment time was recorded for each transmitter. Averages are reported as mean  $\pm$ SE, unless stated otherwise.

The attachment process lasted an average of 21  $\pm$ 3 min (range 14-37, Table 1). The average CCL of the tagged turtles was 154  $\pm$ 2 cm (range 150-159) and CCW was 116  $\pm$ 3 cm (range 104-123). Turtle #01 returned to the beach without nesting on 22 January 2023 (14 days after the initial transmitter attachment) and there was no injury to the turtle, nor damage or biofouling of the transmitter observed. On 30 January 2023, local community members observed another turtle with one of our transmitters attached, nesting on the

beach. The tag ID was not recorded, so the turtle's identity remains unknown, but no injury to the turtle, abnormal nesting behavior, or damage/fouling of the tag was reported.

We monitored Argos for transmissions for one year following the completion of tag deployments. During this period, we received a total of 94 transmissions from the six deployed transmitters, averaging 16  $\pm$ 3 messages per tag (range 8-24). The average number of days between transmitter attachment and the cessation of messages was 20  $\pm$ 4 days (range 10-34). Transmitters on turtles #01 and #04 each provided a single dive histogram; however, the depth sensor on turtle #04 was deemed nonfunctional, based on the interpretation of the data received. Messages received from turtles #02 and #05 relayed little-to-no usable data. Eight satellite locations were recorded from turtles #03 (n=1), #04 (n=2), and #06 (n=5). The Euclidian distances from the nesting locations to the last received locations were 10.6, 11.7, and 21.4 km for turtles #03, #04, and #06, respectively. The total distances recorded were 10.6, 81.4, and 120.1 km for turtles #03, #04, and #06, respectively. All these data were likely transmitted before the turtles embarked on a migration. As of 11 February 2024, we have not retrieved any of the transmitters.

While PSATs are generally useful for the broad-scale collection of data from some marine species (Thorstad et al. 2013) and DSS SeaTag-MODs have been successful in several cases (Goetz et al. 2017; Pohlot & Ehrhardt 2018; Doukakis et al. 2020), the tags and configuration used in this study did not yield sufficient data on the post-nesting migratory movements of leatherbacks to be useful. In reviewing the literature, we found our results were not unique. Stewart et al. (2016) reported little success using DSS SeaTag-



Leatherback ID	CCL	CCW	Attachment Time	Attachment Date	Last Transmission Received	Total Messages Received	Total Locations Received
#01	157	112	37	1/10/2023	1/24/2023	17	0
#02	152	121	21	1/12/2023	2/4/2023	9	0
#03	150	116	22	1/15/2023	1/25/2023	8	1
#04	158	119	17	1/16/2023	2/14/2023	24	2
#05	159	123	14	1/20/2023	2/23/2023	13	0
#06	149	104	17	1/22/2023	2/3/2023	23	5

**Table 1.** A summary of tag attachments and transmissions. CCL: Curved Carapace Length (cm). CCW: Curved Carapace Width (cm). Attachment Time: duration between drilling the hole in the carapace and finishing the attachment process (min). Dates are shown as MM/DD/YYYY.

MODs to document the movements of oceanic manta rays (*Manta birostris*), with only two of the four deployed DSS tags reporting data (lasting 7-28 days) and they similarly received few location estimates. Over a 16-year period, Lutcavage *et al.* (2015) deployed various models of PSATs from different manufacturers on bluefin tuna (*Thunnus thynnus*) and Atlantic bigeye (*Thunnus obesus*), including nine DSS SeaTag-MODs. Eight of the nine DSS tags reported some data, but none reported for the full 12-month term they were programmed for, and the attachment durations averaged 19 days. The short attachment period was attributed to the nose cone shearing due to pin breakage during high-force acceleration; DSS reports that the tags have been strengthened to address this issue (Lutcavage *et al.* 2015). Of the eight tags that reported data, only three produced usable data, which the authors attributed, in part, to DSS's Argos transmission protocol. PSAT failure from leaking is a documented concern, especially with species that make deep and frequent dives (Musyl *et al.* 2011). This may be one reason for the nonreporting PSATs in our study, as leatherbacks dive repetitively (Sale *et al.* 2006) and to depths exceeding 1 km, although dives to this depth are thought to be uncommon and should not be exaggerated (Eckert *et al.* 1989). Increasing the strength of the housing and/or potting material to withstand the forces of repeated deep dives may be an effective approach to addressing this issue.

The low number of messages and locations in this study could also be attributed to the timing of transmissions when tags broke the surface of the water. When these DSS tags are set to real-time tracking, they transmit each time the capacitor reaches a set voltage limit, regardless of the location of the tag in the water column. It is likely that when attached to sea turtles, many transmissions get sent while the tag's antenna is submerged underwater, preventing transmissions from reaching the satellites. The transmission discharges the capacitor to below the set voltage limit and the capacitor must be recharged before another transmission can be sent. Thus, when the turtle is at the surface breathing, the tag must recharge before the first transmission can be sent. While the transmitters can be programmed to transmit only when the tag is in a vertical position, this is likely an uncommon scenario as the transmitter is dragged behind the leatherback, which may maintain forward momentum while surfacing to breathe or be surfacing in a current. Alternately, the incorporation of a salt-water switch into the design of DSS SeaTag-MODs could be tied to satellite transmission signaling, which would allow capacitor charge to be conserved until the antenna is clear of the water, thereby increasing opportunities

for successful satellite communications.

Despite the efforts made to attach the transmitters to leatherbacks during their last nesting event of the season, we documented two occurrences of tagged turtles returning to the beach. The first turtle tagged, turtle #01, returned to the beach without nesting, with the transmitter attached. We attributed this to an incorrect image depth setting of ~9 cm during the ultrasound examination of turtle #01, preventing visualization of developing follicles deeper than 9cm. This was attributed to user error, as this was our first in-field use of a new ultrasound unit and user interface. The second tagged leatherback that returned was observed on the beach after the research team had departed the field and was not definitively identified.

Researchers should make every effort to minimize the risk of negative impacts of research activities on study animals, especially when studying endangered populations. For example, prolonged or repeated stressors, extended restraint, pain, and increases in hydrodynamic drag, may negatively impact individual animals. Cumulatively, these impacts on the most reproductively important adults in a population (nesting female leatherbacks in this case), could potentially hinder population stability or recovery (Romero *et al.* 2015). Handling sea turtles is known to increase levels of stress hormones and stress-related behaviors (Gregory & Schmid 2001; Hunt *et al.* 2016; Mills 2022). While we were able to attach transmitters in an average of 21 min, which is less than NOAA's recommended maximum of two hours (NMFS 2008), we suggest that continued efforts are warranted to improve attachment methods and reduce handling time.

Little to no useful geolocation data were collected through this effort, thus we are unable to assert that solar powered towable PSATs are a preferred method of satellite tracking leatherbacks, especially when compared to some battery powered towable PSATs, which have recorded leatherback migratory distances up to 10,000 km, and for periods exceeding 200 d (Robinson *et al.* 2016). However, it is our opinion that fundamental technological failures could be resolved with further effort, and we encourage continued development to explore the feasibility of solar-powered Argos transmitters for this species. Continued efforts to advance tag technology, such as alternative energy harvesting, improved energy management, and satellite transmission efficacy, have the potential to decrease the drawbacks of instrumentation and lead to improved understanding of the long-term migratory behaviors of leatherback sea turtles.

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# First Records of Hawksbill Sea Turtle (*Eretmochelys imbricata*) Connectivity Between the Galápagos Islands and Continental Ecuador

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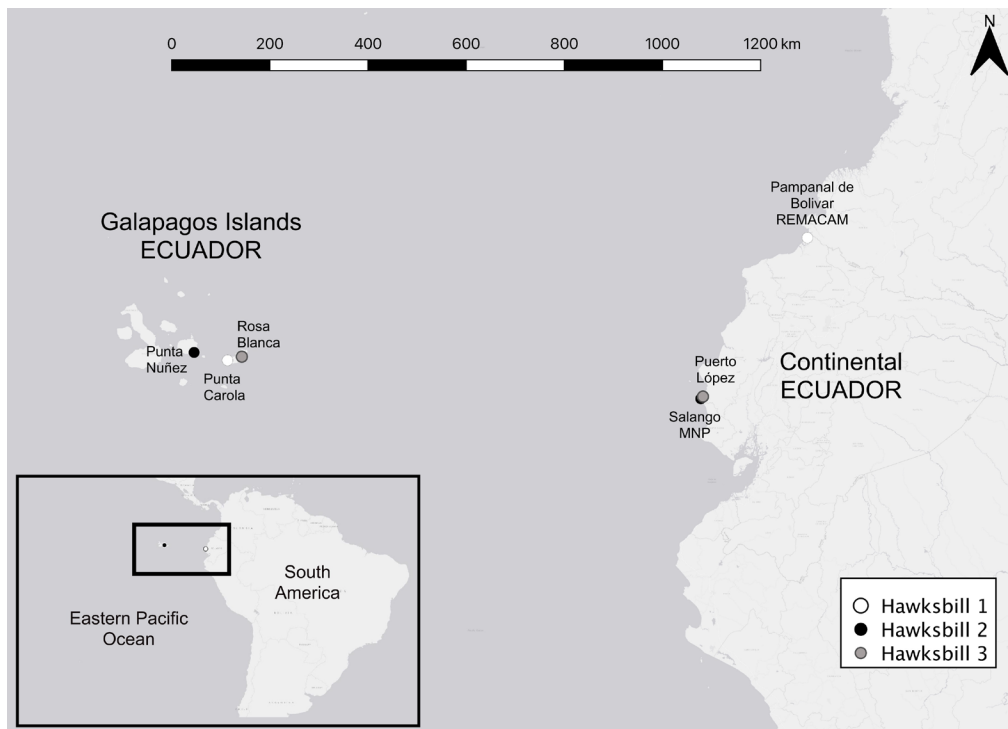
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Ecuador hosts the southernmost nesting sites for hawksbill sea turtles (*Eretmochelys imbricata*) in the Eastern Pacific Ocean (EPO). Hawksbills are a highly threatened species whose populations are particularly vulnerable in the EPO (Gaos et al. 2010, 2018; Rguez-Barón et al. 2019). Ecuador consists of both mainland (herein referred to as Continental Ecuador) and insular land masses, with the latter including the Galápagos Islands, an archipelago of volcanic islands covering approximately 8,000 km<sup>2</sup> and located approximately 900 km west of Continental Ecuador (Mestanza-Ramón, et al. 2019; Fig. 1).

Consistent hawksbill nesting in Ecuador has been documented in two areas along Continental Ecuador (Gaos et al. 2010, 2017a), and although a single hawksbill hatchling was encountered on the Galápagos Islands in 2015 (Gaos et al. 2018; J.P. Muñoz pers. obs.), no confirmed records of nesting by the species exist for the archipelago. In contrast, foraging by juveniles, and to a lesser extent adults, has been documented in several areas along both Continental Ecuador and the Galápagos Islands (Zárate et al. 2015; Alarcón et al. 2016; Gaos et al. 2018).

Post-nesting hawksbills equipped with satellite telemetry tags by Equilibrio Azul (EA) at Machalilla National Park (MNP) on Continental Ecuador have been recorded undertaking limited migrations (<300km) to foraging grounds located along the country's southern coast, including to mangrove estuaries in the Gulf of Guayaquil and Jambeli Archipelago (Gaos et al. 2012a, 2012b). Records of migrations for juvenile hawksbills are rare in Ecuador and other parts of the EPO, with turtles in this life stage typically remaining within geographically restricted home ranges for extended periods (Carrión-Cortez et al. 2013; Miranda et al. 2019). There is no information available for the movement of adult male hawksbills in Ecuador, but preliminary information from Pacific Nicaragua suggests reproductively mature males do not migrate (A.R. Gaos pers. obs.; FFI-Nicaragua unpublished data).

Genetic studies indicate that nesting hawksbills in Ecuador represent a distinct management unit that is demographically isolated from populations in other parts of the EPO (Gaos et al. 2016). Genetic studies also suggest that EPO hawksbills use feeding grounds in the vicinity of their natal beaches (Gaos et al. 2017b).



**Figure 1.** Map of locations where Hawksbill 1 (white dot), Hawksbill 2 (black dot) and Hawksbill 3 (grey dot) were captured and recaptured. Hawksbill 1 was tagged at Punta Carola (San Cristobal Island) in Galápagos and recaptured in Pampanal de Bolívar (REMACAM: Reserva Ecológica Manglares Cayapas Mantaje) in Continental Ecuador. Hawksbill 2 was tagged at Punta Nuñez (Santa Cruz Island) in Galápagos and recaptured in Salango (MNP: Machalilla National Park) in Continental Ecuador. Hawksbill 3 was tagged at Rosa Blanca (San Cristobal Island) in Galápagos and recaptured in Puerto López in Continental Ecuador.

Hawksbill number	Tags	Date		Elapsed time (yrs)	Sex	Curved carapace length (cm)			Weight (kg)			Location		Distance travelled (km)
		Capture	Recapture			Capture	Recapture	Change	Capture	Recapture	Change	Capture	Recapture	
1	JC268; JC269	24-Jun-14	14-Ago-2015	1,3	Female	70.0	70.0	0.0	38	-	-	Punta Carola, Galapagos Islands	Pampanal de Bolivar (REMACAM), Continental Ecuador	1224.1
2	BA624; ME35; ME36	18-Jun-04	3-Feb-17	12,6	Male	38.1	83.4	45.3	12	60	48	Punta Nuñez, Galapagos Islands	Salango (MNP), Continental Ecuador	1046.9
3	EA020; EA021	22-Jan-20	27-Aug-23	3,5	Not identified	60	62.1	2.1	35	-	-	Rosa Blanca, Galapagos Islands	La Poza, Puerto López, Continental Ecuador	953.76

**Table 1.** Capture and recapture data on the three hawksbills included in this study, including size (CCL: Curved Carapace Length), weight (kg), location, growth, distanced travelled (straight line measurement). Dash indicates no data available. MNP: Machalilla National Park. REMACAM: Manglares Cayapas-Mataje Ecological Reserve.

Combined results from satellite telemetry and genetic studies suggest the species rarely, if ever, undertake long-distance migrations in the EPO (Gaos *et al.* 2018; Gaos *et al.* 2017b; Gaos *et al.* 2016). Despite nearly a decade of flipper tagging efforts of adult and juvenile hawksbill turtles at multiple locations in Continental Ecuador and the Galápagos Islands, a flipper tag from Ecuador has never been registered in another country of the EPO, and vice versa. Similarly, flipper tag returns have not been previously documented between disparate nesting and foraging grounds in Ecuador.

This report discusses the first capture-recapture events of three hawksbill turtles, including one male, one female and one juvenile, all of which were originally tagged in the Galápagos Islands and subsequently encountered in Continental Ecuador. The hawksbill records were obtained from three different sources: ongoing and prior in-water monitoring efforts in Continental Ecuador and the Galápagos Islands, reports from local fishers and environmental authorities in Continental Ecuador and reports from the EA citizen-science photo-identification project, Foto-ID.

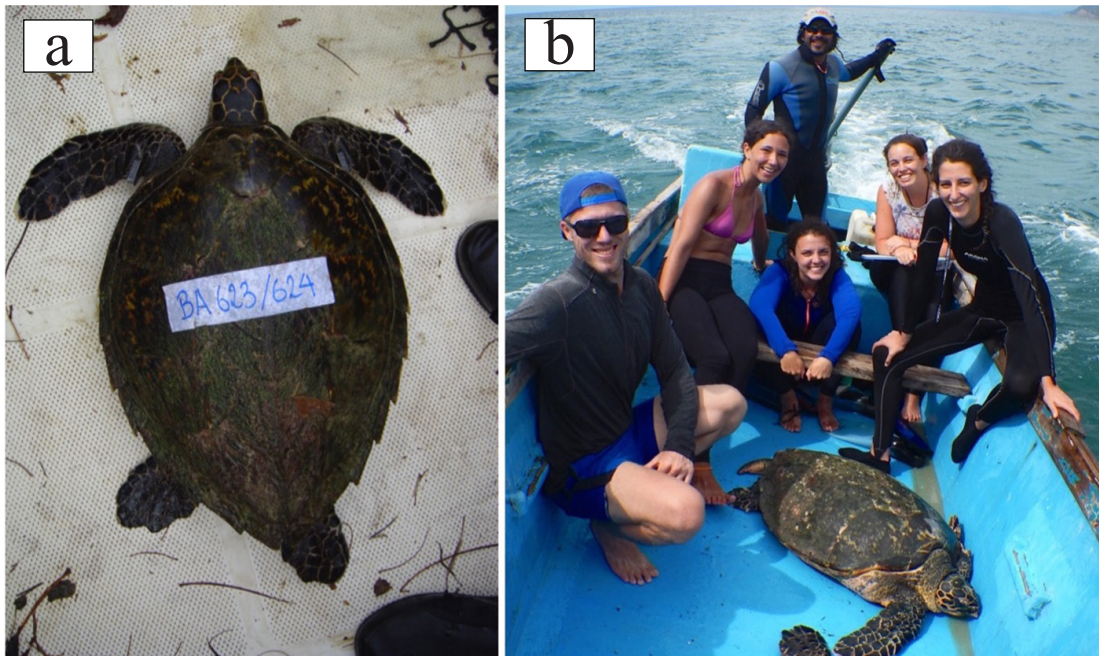
Along Continental Ecuador, monthly in-water censuses of hawksbill turtles are carried out by EA in collaboration with the

Eastern Pacific Hawksbill Initiative (ICAPO), with a focus on surveying nearshore habitats of MNP and surrounding areas. The surveys are conducted by at least three observers, snorkeling in defined transects, and in an attempt to observe and capture hawksbills using free-diving techniques. Similar in-water surveys are conducted by an ongoing project in the Galápagos Islands led by the group Proyecto Tortuga Negra - Galápagos Science Center (PTN-GSC). PTN-GSC surveys primarily occur on the island of San Cristobal but are undertaken opportunistically in other parts of the archipelago. Additionally, although focused on green turtles (*Chelonia mydas*), a past project in the Galápagos Islands led by the Charles Darwin Foundation (CDF) included in-water monitoring using tangle-nets around Santa Cruz Island, during which hawksbill turtles were occasionally captured (Zárate *et al.* 2015). Finally, the EA Foto-ID project consists of a citizen-science program where people get involved in sea turtle research by reporting any encounters with turtles with photographs, videos and the location and date of the encounter. The objective is to identify individuals using the information in the images through photo-identification using recognition of scales or other visual means such as flipper tags.



**Figure 2.** Photographs of Hawksbill 1 when first captured by PTN-GSC at Punta Carola, Galápagos Islands (a), and when recaptured by a local fisherman at Pampanal de Bolivar, Continental Ecuador (b). Photos by Juan Pablo Muñoz/PTN-GSC (a), and MAATE (b).





**Figure 3.** Photographs of Hawksbill 2 when captured as a juvenile by CDF in the Galápagos Islands (a), and when captured by EA as an adult (b) in Continental Ecuador. Photos by Patricia Zárate/CDF (a) and Felipe Vallejo/Equilibrio Azul (b).

During the initial capture events of all hawksbills, morphometric measurements were taken and Inconel (Style 681, National Band & Tag, Newport, KY, USA) flipper tags were applied to the trailing edge of both front flippers. Curved carapace length (CCL) was measured for all captured turtles using a flexible measuring tape, and, when feasible, weight was calculated using a portable scale.

The first record of connectivity came from a turtle (herein referred to as Hawksbill 1) originally tagged by GSC on 24 June 2014 in Punta Carola, San Cristobal Island, Galápagos Islands (Fig. 2a). The turtle measured 70 cm CCL and weighed 38 kg. Based on the turtle's size and lack of an elongated tail, it was determined to

be a putative female (Table 1). Hawksbill 1 was recaptured on 14 August 2015 when it became incidentally entangled in a gillnet of a fisher in the Manglares Cayapas Mantaje Ecological Reserve (REMACAM) in Continental Ecuador (Fig. 2b). Observing the tag on the flipper, the fisher held the turtle and provided it to members of Ecuador's Ministry of Environment, Water and Ecological Transition (MAATE). The turtle had no CCL change at recapture and no weight information was collected. MAATE personnel reported the turtle and relevant data to EA. The time between capture events was approximately 1.3 years, and the straight-line distance between the two capture sites was 1,224.1 km.



**Figure 4.** Photographs of Hawksbill 3 when captured in Galapagos in 2020 (a) and when recaptured through the Equilibrio Azules Photo-ID project in Puerto López, Continental Ecuador in 2023 (b). Photos by Juan Pablo Muñoz from Galapagos Science Center (a) and Sebastián Hernández during a session with his freediving school in Puerto López, Continental Ecuador (b). Highlighted in red is one of the tags when the turtle was encountered by the citizen-science project.



The second record of connectivity came from a turtle (herein referred to as Hawksbill 2) originally tagged by CDF on 18 June 2004 in Punta Nuñez, Santa Cruz Island, Galápagos Islands (Fig. 3a). The turtle measured 38.1 cm CCL and weighed 12 kg. Hawksbill 2 was recaptured on 3 February 2017 during a monthly survey carried out by EA at Salango Island (MNP) in Continental Ecuador (Fig. 3b). The time between capture events was approximately 12.6 years, and the straight-line distance between the two capture sites was 1,046.9 km. The turtle measured 83.4 cm CCL at the time of recapture and 60 kg, increasing by 45.3 cm and 48 kg between capture events. The turtle was confirmed as a male during the recapture as a result of its elongated tail and increased size (Fig.3b).

The third record of connectivity came from a turtle (herein referred to as Hawksbill 3) originally tagged by GSC on 22 January 2020, in Rosa Blanca, San Cristobal Island, Galápagos Islands (Fig 4a). This turtle was observed on 27 August 2023 by a free-diving instructor in Puerto López who registered the turtle using photos, videos and the number of one flipper tag to the Foto-ID project. One month later, on 29 September 2023 the turtle was recaptured during EA's monthly surveys in the same place in Puerto López where it was reported to Foto-ID. The time between capture events was 3.5 years, and the straight-line distance between the two sites was 953.76 km. The turtle was a juvenile when first captured, measuring 60 cm CCL, and when recaptured measured 62.1 cm CCL, representing an increase in size of 2.1cm. The location of recapture is one of EA's monthly monitoring sites adjacent to the main index nesting beach of the area within MNP, and this turtle had not been observed prior to this event, suggesting a recent recruitment to the reef.

These results provide the first records of hawksbill turtle connectivity between the Galápagos Islands and Continental Ecuador, as well as the first records of tag returns from different monitoring programs within the country as a result of a citizen-science project. To our knowledge, these findings also represent the longest migrations for hawksbill turtles documented in the EPO to date (Gaos *et al.* 2012a), as well as the longest recapture timeframe of an individual hawksbill in this ocean region. In the case of Hawksbill 2 and 3, considering the turtles were juveniles when first captured, the migration registered represents a developmental migration and for Hawksbill 1, an actual migration.

Given hawksbill turtles have never been documented nesting in the Galápagos Islands, despite monitoring at nesting beaches around the archipelago (Zárate *et al.* 2013), it is likely that these turtles originated from nesting beaches on Continental Ecuador, dispersing to the Galápagos Islands as post-hatchlings, where they settled to forage and grow. The movements to Continental Ecuador could be the first leg of a round-trip migration to nest, demonstrated by Hawksbill 1, and to copulate for developmental migration, demonstrated by Hawksbill 2. Alternatively, one or both turtles could have made permanent shifts to habitats in Continental Ecuador at some point prior to recapture. Of note is that REMACAM is a mangrove estuary, coinciding with habitat preferences for adult hawksbills in several countries of the EPO (Gaos *et al.* 2012a,b; 2018) and MNP, including the adjacent Puerto López is a reef and the main nesting area in the country.

**Acknowledgements.** The results obtained in this study are thanks to the collaboration of different researchers and NGOs working together to learn about Eastern Pacific hawksbills and support their conservation. The data obtained are part of ongoing

hawksbill studies undertaken by EA and the ICAPO network (Research Permit from the Ministry of Environment of Ecuador, Contrato Marco: MAE-DNB-CM-2016-0053) since 2016, with the aim of quantifying hawksbill juvenile recruitment to reefs to measure the success of more than ten years of nest protection efforts. Additionally, the data are supported by the ongoing sea turtle research undertaken by the Proyecto Tortuga Negra - GSC (Galápagos Science Center -Universidad San Francisco de Quito) in the Galápagos. These results are also thanks to prior tagging efforts by Patricia Zárate, the CDF and colleagues and to the collaboration and sharing of tagging information and data by all the involved. The collaboration with the MAATE, Machalilla National Park and park rangers from the REMACAM has been essential in this work and for the conservation of this species, and we thank them all. Finally, these results highlight the importance of research through citizen science programs such as the EA Foto-ID project, where important information can be obtained and the public can be directly involved in research and conservation. We especially thank Sebastián Hernández from the "Vamos al Agua" Freediving School for this important report and for continually collaborating with the project. We also thank and highlight the financial support given by the National Fish and Wildlife Foundation, NFWF, to Equilibrio Azul and ICAPO's ongoing projects and the help provided by WildAid to the Foto-ID project

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# From Puerto Rico to Venezuela: A Twenty-Five-Year Long Distance Recapture of a Hawksbill Turtle (*Eretmochelys imbricata*)

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On September 25, 2023, a hawksbill turtle (*Eretmochelys imbricata*), bearing Inconel tags (X7113, X7114) on its front flippers, was captured during in-water surveys in front of the nesting beach, Los Garzos, Gulf of Paria, Venezuela (Balladares *et al.* 2019; Fig 1). The recovered tags were in good condition (Fig 2). At the time of capture, the turtle's curved carapace length (CCL) was 76 cm and its tail extended beyond the carapace, suggesting it was an adult male (Van Dam & Diez, 1998, Fig 3 & 4). The animal received new Inconel tag (V014M, V015M) on its front flippers.

This turtle had been originally tagged 25 years earlier, on 16 September 1998 during in-water surveys by personnel from Proyecto Carey-Isla de Mona in the feeding grounds of Monito Island (near Mona Island, Diez & Van Dam 2002; Fig 1). At the time of original capture, the turtle measured 30.4 cm CCL and weighed 2.3 kg. According to Diez & Van Dam (2002), this animal was considered a juvenile with undetermined sex due to its size (Fig 5).

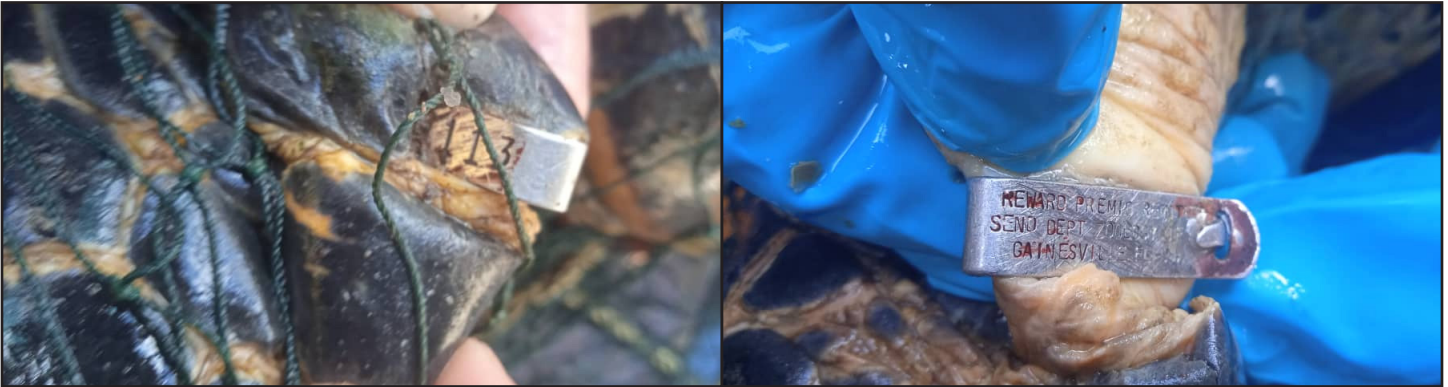
The time interval between the tagged date on this turtle in Puerto Rico and when it was found in Venezuela was 25 years, which indicates that the turtle survived for more than two decades bearing the tags and reached its sexual maturity within that time (Van Dam & Diez 1998; Diez & Van Dam 2002). This current report not only confirms the connectivity between different areas in the Caribbean for the hawksbill migrations (Velez-Zuazo *et al.* 2008), but also is the oldest long distance tag recapture for a hawksbill turtle tagged at Monito Island and a record Inconel tag retention duration (Van Dam & Diez 1999). This type of information reinforces the importance of collaborative regional conservation networks.

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Figure 1. Geographic locations of Monito Island (Puerto Rico) and Los Garzos (Venezuela).





**Figure 2.** Condition of the 25 year old Inconel tag on a hawksbill turtle encountered during an in-water study in Venezuela after being initially tagged in Puerto Rico.



**Figure 3.** Recapture of the tagged adult hawksbill turtle with 76 cm curved carapace length in Venezuela.



**Figure 4.** Elongated tail of the adult hawksbill turtle encountered during an in-water study in Venezuela.

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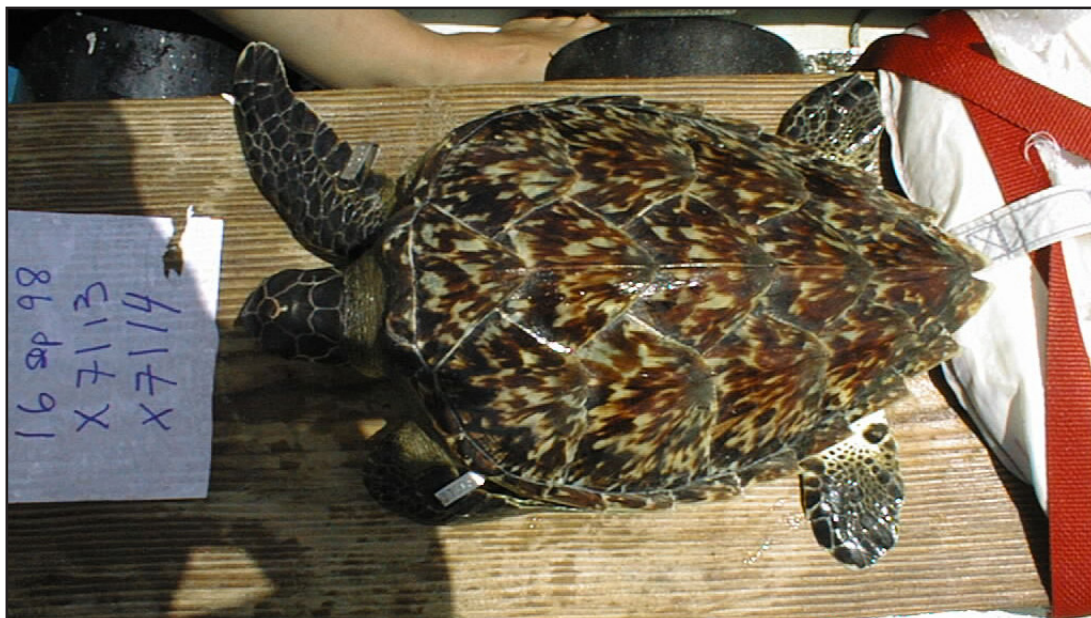
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**Figure 5.** Hawksbill turtle with 30.4 cm curved carapace length when it was first captured in 1998 and given Inconel tags on front flippers



# Running out of Sand: Sea Turtle Nesting Activity on Félicité Island, Seychelles

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The Seychelles are home to one of five regional populations of hawksbill turtles with more than 1,000 females nesting annually (Mortimer 2000) with a distinct nesting period from October until March. Green turtles are also known to nest in the Seychelles, but nesting density in the granitic inner islands is significantly lower compared to the coralline outer islands (Salm 1976). Félicité Island, located in the inner islands of the Seychelles, and its nearby marine park Ile Coco Marine Park are renowned for their hawksbill turtle population. Six Senses Zil Pasyon resort was established on the privately owned island in October 2016, occupying one third of the island. The island harbors five sandy beaches, of which four are easily accessible. The fifth beach (Anse Takamaka) is located at the southwestern side of the island and is difficult to reach due to challenging terrain.

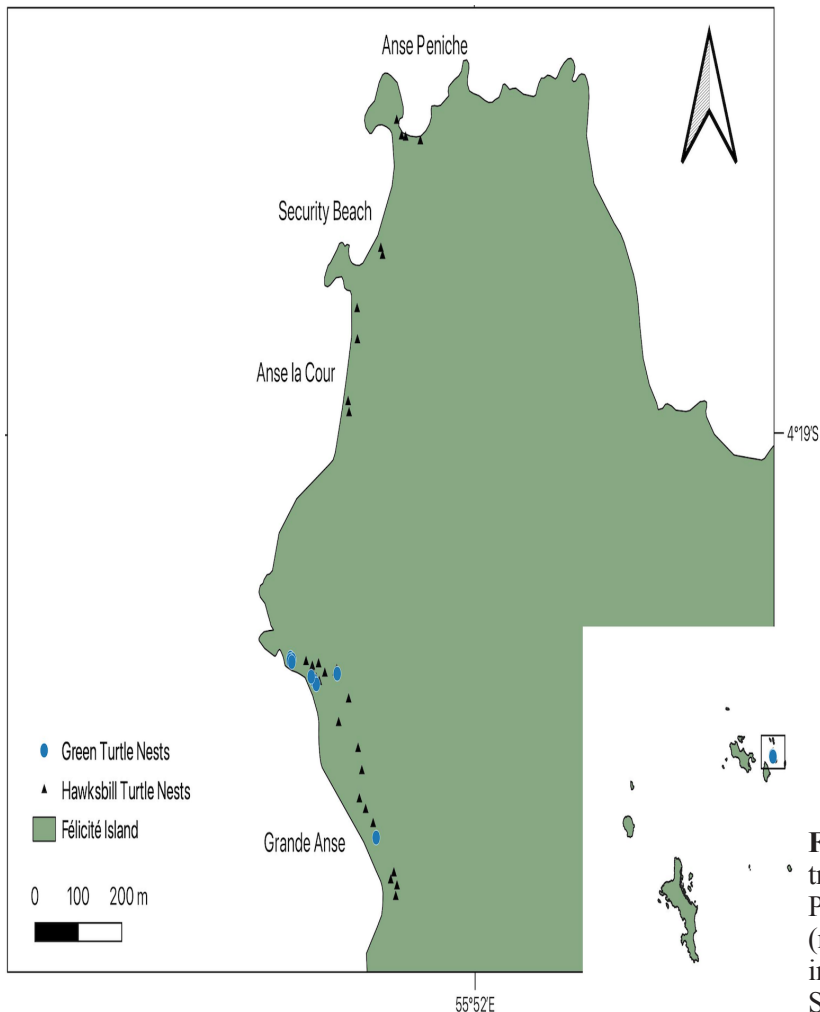
In December 2021 the Olive Ridley Project partnered with Six Senses Zil Pasyon to establish a monitoring and conservation program to ensure long-term data collection and protection for nesting turtles on the islands. The partnership was established in the middle of the hawksbill turtle nesting season, therefore data

collected from the 2021/2022 period is incomplete and this paper will exclusively focus on data from the 2022/2023 season.

Daily patrols, on the four main beaches (Fig. 1), were carried out between April 2022 and April 2023 to record any nesting attempts and true nests. GPS location, species, and track width were recorded for each nest and false crawl. If the turtle was encountered whilst laying eggs, photographs for the identification of the nesting female were taken. Photo identification, a non-invasive mark-recapture method (Gonzalo *et al.* 2016), allowed for the identification of individual females, clutches per female per season and an estimate of the length of interesting intervals.

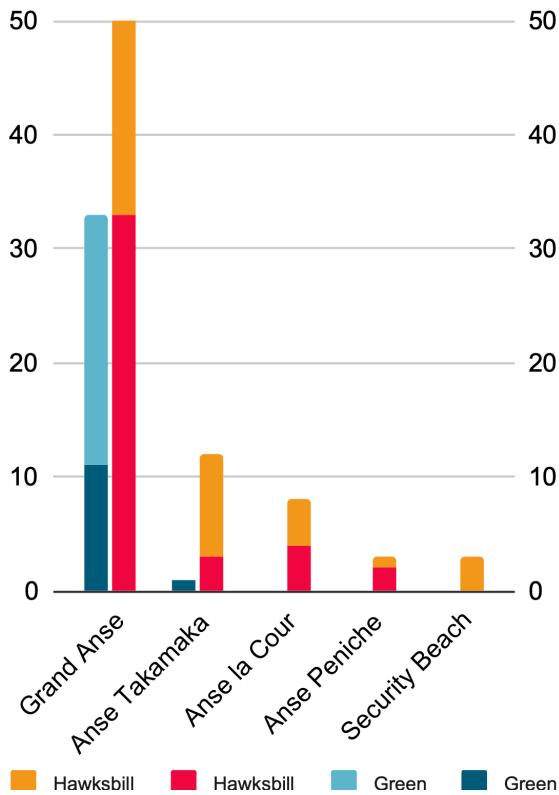
Nest excavations were carried out 48-72 hours after emergence to ensure all hatchlings had the chance to emerge by themselves before recording clutch size, depth of egg chamber, the estimated developmental stage of unhatched eggs and releasing any trapped hatchlings.

During the reporting period 87 false crawls and 51 true nests were recorded on all five beaches on Félicité Island (Fig. 2). The majority of the nesting activity was recorded on Grand Anse, the



**Figure 1.** Map showing the location and number of true nests on the four beaches on Félicité Island: Anse Peniche (n = 4), Security Beach (n = 2), Anse la Cour (n = 4), and Grande Anse (n = 30) on Félicité Island in Seychelles. Made with QGIS 2021. Seychelles Shapefile: <https://data.humdata.org/dataset/cod-ab-syc>





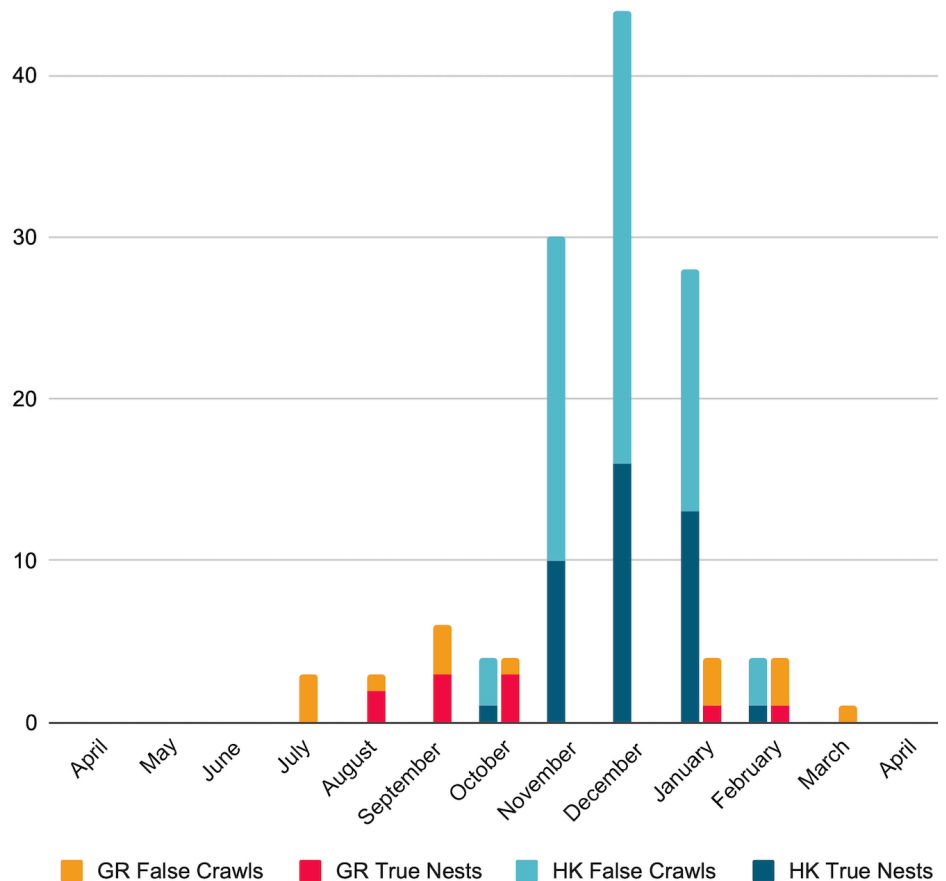
**Figure 2.** Sea turtle nesting activity per beach on Félicité Island from April 2022 to April 2023. GR = green turtle, HK = hawksbill turtle.

longest beach on the island. Hawksbill nesting activity reached its peak from October to February (Fig. 3), with the highest number of nests recorded in December ( $n=16$ ) (Fig. 3). Of 41 hawksbill nests laid during this season, 30 were laid on Grand Anse. The mean track size recorded for hawksbill turtles was 78 cm ( $\pm 7$  SD,  $n=73$ ). Nesting activity by green turtles was comparatively low with a peak in nesting observed between July and September 2022, with a total of eight true nests and seven false crawls. During a second smaller wave of green turtle nesting activity in January and February 2023, eight false crawls were observed, and two nests were laid (Fig. 3). Mean track width for green turtles was 122 cm ( $\pm 13$  SD,  $n=14$ ). Measuring tracks width aids species identification and serves as a proxy for estimates of the individuals body size and nest characteristics.

Median egg chamber depth for green turtles (105 cm  $\pm 14.3$  SD) was deeper than for hawksbill turtle nests (45 cm  $\pm 13.8$  SD), but the incubation time was similar for both species throughout the season (Table 1). Median incubation time from April 2022 to April 2023 was similar for both species with 62 days for green turtles and 64 days for hawksbill turtles (Table 1).

Clutch size was recorded for 88% of nests ( $n = 44$ ), while clutch size remained unclear in the remaining 12% due to full or partial clutches being lost to predation by crabs. Mean clutch size for hawksbill turtles was 160.6 eggs ( $\pm 23.5$  SD,  $n=38$ ), which was significantly larger compared to 137.3 for green turtles ( $\pm 17.6$  SD,  $n=6$ ; t-test,  $p<0.005$ ).

Hatching success, the percentage of eggs within a nest that hatched, was 80.1% for green turtles ( $\pm 35.5$  SD,  $n = 7$ ) and 76.2%



**Figure 3.** Temporal distribution of sea turtle nesting activity on Félicité Island from April 2022 to April 2023. GR = green turtle, HK = hawksbill turtle.

	Median depth to top of egg cavity (cm)	Median depth to bottom of egg cavity (cm)	Median Incubation in days
Green	89 ±20.3 SD, n=7	105 ±14.3 SD, n=7	62 ±19.0 SD, n=6
Hawksbill	30.5 ±11.5 SD, n=40	45 ±13.8 SD, n=40	64 ±12.9 SD, n=36

**Table 1.** Egg chamber depth and incubation time of green and hawksbill turtle nests on Félicité Island during the 2022/2023 season.

for hawksbill turtles on average ( $\pm 30.1$  SD,  $n=36$ ). Twelve of the hawksbill turtle nests had to be relocated due to immediate threat by beach erosion. Nests were relocated to the eastern side of Grand Anse, the only area not affected by erosion during this period. Four hawksbill turtle nests had 0% hatching success due to complete predation by ghost crabs (*Ocypode spp.*), out of which two were relocated and two remained *in situ*. Predation was observed in all relocated nests with a range of 17 up to 167 predated eggs per clutch. Relocated nests had 58.9% average hatching success ( $\pm 33.7$  SD,  $n=12$ ) compared to 74.9% for non-relocated nests ( $\pm 31.8$  SD,  $n=15$ ) on Grand Anse, including completely predated nests. When nests with 100% predation were excluded, average hatching success for relocated nests was 72% ( $\pm 19$  SD,  $n=10$ ), compared to 86.5% ( $\pm 10$  SD,  $n=13$ ) for *in situ* nests on Grand Anse.

Sea turtles in Seychelles have been legally protected by the Wild Animals Birds and Protection Act since 1994 (Burt *et al.* 2015). Records from the inner islands Cousin and Cousine indicated increasing hawksbill nest numbers since 1999 and 2006 respectively (Allen *et al.* 2010; Gane *et al.* 2020), with numbers of up to 256 individual females emerging to nest per season. D'Arros Island in the outer islands of the Seychelles hosts 277-318 hawksbill nests per year according to Mortimer *et al.* (2011a). In our study, a lower number of hawksbill turtle nests were recorded on Félicité than in the aforementioned studies. This is mainly attributed to two factors: Firstly, Anse Takamaka, a beach on the eastern side of Félicité, was monitored only *ad hoc* due to its remote and highly inaccessible location. Nesting activity on this beach is potentially high as previously unrecorded sea turtle tracks were observed during each *ad hoc* site visit. Additionally, the beach offers completely undisturbed nesting habitat, as it is not frequently visited by either resort guests or outside operators. Secondly, Félicité offers sparse nesting space in general. The sandy beaches on the island all together span less than 750 m in length at their greatest extent and are extremely dynamic, undergoing drastic transformations with the changes in the monsoon season. This change results in complete erosion of nesting areas especially on the main beach of Grand Anse and coincides with the beginning of the hawksbill turtle nesting season. The erosion makes the majority of the beach inaccessible for turtles and causes the loss or inundation of previously laid nests. Due to the severe erosion, the suitability of the island's beaches for nesting are questionable in the future in the face of increasing environmental challenges, including sea level rise (Fish *et al.* 2008). Mitigation measures such as construction setback regulations, which are promising on other turtle nesting beaches (Fish *et al.* 2008) are unlikely to prove successful on Félicité, because the main limiting factor is natural granite boulders. Lastly, since Cousin has been identified as one of the most important hawksbill nesting spots in the region and has been managed as a nature reserve (Allen *et al.* 2010), it is to be expected

that the number of hawksbill turtle nests in this location are higher than on other less protected islands such as Félicité.

For green sea turtles, Burt *et al.* (2015) reported an average of 13.5 nests per year on the inner island of Curieuse, which is located only 17 km away from Félicité; this level is similar to the 10 nests reported in this study. This contrasts with an average of 65-120 nests per year reported on the outer island of D'Arros (Mortimer *et al.* 2011a), and even more so to the increase from 2,000-3,000 to over 15,600 green turtle nests per year has been observed in the Aldabra atoll in the outer islands (Mortimer *et al.* 2011b). These numbers may be attributed to the intense protection of the species since 1968 (Mortimer *et al.* 2022). The example of Cousin Island and Aldabra illustrates how effective protection of the area led to increasing sea turtle populations, both for hawksbills as well as for green turtles.

No previous data are available to comment on a trend in nest numbers for either hawksbill or green turtles on Félicité, therefore we recommend continuation of nest monitoring to compare the development to that observed on other islands in the Seychelles. Additionally, the expansion of the nearby Ile Coco Marine Park to include Félicité Island would be beneficial to increase the number of nests on the island. The inclusion of the island in the Marine Park will reduce the number of outside visitors that are currently visiting the public beaches, and therefore reduce disturbance of nesting sea turtles. In addition, this could serve as the starting point for a collaborative coral restoration initiative with the Seychelles Parks and Gardens Authority. The restoration of the deteriorated reef structure has the potential to mitigate beach erosion and provide vital protection for nesting habitats.

Green turtle nests on Félicité are deeper compared to those reported in the literature for example from Australia and Taiwan (see for example Bustard *et al.* 1968; Chen & Cheng 1995). Published literature values on egg chamber depth of green turtles in Seychelles is available only from Ascension Island, located in the outer islands. The author reported a mean egg chamber depth at the bottom of 85 cm ( $\pm 18.8$  SD, Mortimer 1990). The mean depth at the bottom during this study is markedly deeper at 102 cm ( $\pm 14$  SD). Egg chamber depth on Félicité was measured during nest excavations, 58-71 days after the nest was laid. Given the significant amount of movement of materials along the coast by longshore drift it is possible that additional sand accumulated on top of the egg chambers resulting in an increased depth measurement. This effect might be more significant on Félicité than in the other study locations.

Besides beach erosion, predation by crabs is a severe threat to sea turtle nests on Félicité Island. Especially on the main nesting beach of Grand Anse, high crab densities are observed and a total of five nests were completely predated. This resulted in a high standard deviation for the average recorded hatching success for green turtles as well as hawksbill turtles. Relocation zones might

lead to a clustering of nests in one area and the resulting high nest density may lead to an increase in predation risk (for example, see Leighton *et al.* 2011). In the future the establishment of further relocation zones as well as the development of predator protection measures should be considered.

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Non-nesting crawl (false crawl or half moon crawl) on a North Carolina beach made by a loggerhead sea turtle. Photo by M. Godfrey

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