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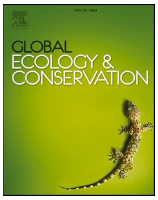

Nesting population trend of the leatherback sea turtle in Bocas del Toro province and Comarca Ngäbe-Buglé, Panama for the period 2002–2022

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ABSTRACT

Sea turtle biologists have made sustained efforts to understand the global status of leatherback sea turtle populations. However, despite progress in assessments, demographics, and ecology, key uncertainties persist in tracking leatherback population trends. Trend analyses have historically focused on nesting beaches, with nest counts providing a widely used index for population abundance. Here, we analysed 20 years of annual nest abundance at four main nesting beaches (Soropta, Bluff, Playa Larga and Chiriquí) in Bocas del Toro province and the Comarca Ngäbe-Buglé, Panama, which constitute the largest nesting leatherback sea turtle population in Central America. We conducted daily nest counts during the leatherback season. We standardized the Soropta nest counts, as the survey extent varied over time. We calculated catch per unit effort (CPUE) to account for sampling effort differences. We used the Information-Theoretic approach for model selection, based on Akaike's Information Criterion correction for small sample sizes, using linear regression to assess population trends and discrete rate of population growth (λ). Soropta exhibited a positive nesting trend (8.9 % year^{-1}; λ = 1.089; 1.076 – 1.10 95 % CI). Bluff (-8.8 % year^{-1}; λ = 0.911; 0.892–0.930 95 % CI) and Playa Larga (- 8.3 % year^{-1}; λ = 0.917; 0.9045–0.930 % CI) indicated declining nesting populations, while Chiriquí had a stable population (λ =0.993; 0.982–1.004 95 % CI). For CPUE, the data yielded a stable population for all beaches combined (λ = 0.997; 0.995 – 0.999 95 % CI). Overall, distinct nesting trends were observed at each leatherback sea turtle nesting beach. Given that females from different nesting sites mix at shared foraging grounds, this suggests that local factors may be influencing beach-specific nesting trends. The delicate balance of leatherback nesting in Bocas del Toro archipelago, along with its critical importance within the Western Caribbean, makes continuous monitoring and conservation efforts essential in this region, as well as increased protection from governmental agencies.

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1. Introduction

Sea turtle biologists have made numerous and substantial efforts to understand the global status of sea turtle populations in general (e.g. Bjorndal et al., 1999; Witherington et al., 2009; Mazaris et al., 2017; Fonseca et al., 2023) and, in particular, of the leatherback turtle (*Dermochelys coriacea*) (e.g. Pritchard, 1982; Spotila et al., 1996; Dutton et al., 2005; Stewart et al., 2011; SWOT, XVIII, 2022). These studies address significant knowledge gaps that existed (and still exist) regarding the ecology and population dynamics of this marine megafauna species, laying the groundwork for future global management and conservation strategies. Despite all these efforts, the listing status on the IUCN Red List have undergone repeated changes in leatherback global population (Northwest Atlantic Leatherback Working Group, 2019), this seems to be a reflection of the uncertainties that still remain in the analysis of leatherback population trends.

The highest estimate of the global leatherback population size to date was based on an extrapolation of aerial surveys along the Pacific coast of Mexico, calculating around 115,000 adult females (Pritchard, 1982). Spotila et al. (1996) used this estimation as a reference, incorporated data from 28 beaches worldwide and lowered the estimate by one-third (34,500 nesting females) in just under two decades. This sharp decline in less than one generation played a crucial role in classifying their status as critically endangered in the global Red List assessment for the leatherback global status (Sarti Martinez, 2000). Subsequently, to enhance the quality of estimates, nesting female abundance data were updated by adding new rookeries and performing the assessment for each of the subpopulations or Regional Management Units for the first time (Wallace et al., 2013; RMUs; Wallace et al., 2010, 2023). This evaluation resulted in the global leatherback status being elevated from critically endangered to vulnerable in just 13 years, primarily driven by positive data from the Northwest and Southeast Atlantic RMUs (Turtle Expert Working Group (TEWG), 2007). Despite this apparent improvement, declines in nest counts and nesting females were later detected on beaches in the Wider Caribbean Region previously considered stable and robust (such as French Guiana; Turtle Expert Working Group (TEWG), 2007). This situation led the Wider Caribbean Sea Turtle Conservation Network (WIDECAST) to conduct a new regional analysis, confirming the negative trend in nesting activity on almost all studied beaches and prompting, once again, a change from least concern to endangered in the Red List status for the Northwest Atlantic RMU in 2019 (NALWG, 2018). Divergences between trend assessments were mostly attributed to different approaches, for example, previous analyses included inconsistent data, mostly before the 1990s (NALWG, 2018; SWOT XVIII, 2022). In a recent analysis of time-series around the world, leatherback turtles were still identified as a species of high concern due to several population declines (Hays et al., 2024). All this highlights the importance of improving monitoring efforts and ensuring a consistent and complete spatiotemporal coverage of nesting activity to enhance the reliability of nesting population trends.

Historically, scientists have used nesting beaches for analyses of sea turtle population abundance and trends as nesting females, clutches and hatchlings are more accessible than all other life stages. Ideally, would be directly based on the number of detected nesting females (e.g. Broderick et al., 2006; Marcovaldi and Chaloupka, 2007; Pfaller et al., 2013; Bourjea et al., 2015). However, the inherent difficulty in detecting a large portion of the nesting events on a beach (especially in high-abundance or isolated nesting beaches), makes the nests laid the most widely used relative index of population abundance (e.g., Carr et al., 1978; Meylan, 1982; Troëng and Rankin, 2005; Witherington et al., 2009; Casale and Tucker, 2017; Restrepo et al., 2023). Nest counts play a crucial role in generating estimates of abundance and trend assessments due to their ease of access and replicability; however, this method does have limitations. For instance, the relationship between the number of clutches on a beach and sea turtle population abundance is conditioned by a series of key demographic parameters, such as fecundity, clutch frequency, breeding probability (or remigration interval) or dispersal probabilities (National Research Council, 2010). A leatherback nesting population may lay in a wide spatial range of beaches and remote locations, thus, assessing these demographic rates over relevant spatiotemporal scales is extremely challenging. For instance, the total number of clutches laid in a season is directly related to clutch frequency, or the number of clutches laid per individual, which can vary annually (Broderick et al., 2003) and across individuals (Santidrián-Tomillo et al., 2009). Calculating this index, even on beaches with extensive monitoring efforts and high rates of nesting female capture-recapture, can be challenging (Rivalan et al., 2006). Additionally, the time span between two nesting seasons for an adult female, or remigration interval, varies between individuals and depends on how quickly she can accumulate the necessary nutrients, and consequently, on the productivity of their foraging areas (Bjorndal, 1985; Saba et al., 2007; Evans et al., 2021). This variability causes the interval between nesting and non-nesting females to vary annually. To mitigate the effects of reproductive parameter variations on the total number of clutches laid (and by extension, nesting females) and obtain a trend reflecting the population's status, at least 20 years of robust and consistent monitoring are needed (Bjorndal et al., 2005; Witherington et al., 2009; Piacenza et al., 2019; Whiting et al., 2020). With all this, the number of breeding females only represents a portion of the population, leaving in the shadows the status and effects of environmental and anthropogenic impacts that individuals in other stages of the lifecycle may experience (Ceriani et al., 2019). In this context, although declines in leatherbacks' nesting activity have historically been attributed to threats, such as fisheries bycatch (e.g., Wallace et al., 2013a), beach erosion (Chevallier et al., 2023), or illegal harvesting (Santidrian-Tomillo et al., 2008) and increases to direct conservation efforts (Dutton et al., 2005), underlying factors, such as multi-decadal natural variations or changes in remigration intervals or environmental stochasticity (e.g., Hays, 2000; Bjorndal and Bolten, 2010; Pfaller et al.2013; Piacenza et al., 2016) are gaining increasing prominence. Despite the challenges of using nest counts as a population index, they remain a relatively easier option to monitor population status.

The presence of leatherback sea turtles in the Bocas del Toro province and Comarca Ngäbe-Buglé, one of five indigenous administrative provinces in Panama (Bocas del Toro and la Comarca hereafter), was poorly studied until the late 20th century; but once monitoring commenced the significance of these rookeries for the population of Central America and the North Atlantic was quickly identified (e.g., Carr, 1982; Meylan et al., 1985; Troëng et al., 2004; Ordoñez et al., 2007; Meylan et al., 2013), and only occurred with significant efforts by numerous local and international organizations, as well as the Ngäbe indigenous community. Leatherback turtles switch between Bocas del Toro and la Comarca nesting beaches and others of the southwest Caribbean, such as Costa Rican or Colombian rookeries, based on capture-mark-recapture (CMR) programs (Ordoñez et al., 2007; Troëng et al., 2007; STC unpubl. data 2013–2024). This led to the conception of these nesting aggregations of leatherback turtles as a single metapopulation (Troëng et al., 2004; Chacón-Chaverri and Eckert, 2007).

For centuries, sea turtles in Central Caribbean America have been harvested for their meat, shells, and eggs, both from nesting beaches and in open water; leatherback turtles of Bocas del Toro and la Comarca are no exception. Although leatherback meat is less desirable compared to other species of sea turtles, illegal egg harvest, and the killing of nesting females (solely for egg extraction) have exerted constant pressure on leatherback populations. Despite being a deeply rooted practice, there was a turning point that changed the situation in la Comarca. Faced with the concerning decline in the number of hawksbill turtles (*Eretmochelys imbricata*) observed on their beaches, the indigenous community initiated in 2003 a long-term monitoring project in collaboration with the Sea Turtle Conservancy (formerly Caribbean Conservation Corporation) for the protection of sea turtles in the Comarca, which resulted in the temporary cessation of sea turtle and clutch extraction. This measure, still in effect today, applies to Playa Chiriquí, where several thousand leatherback nests are documented annually, more than any other beach in Caribbean Central America (Ordoñez et al., 2007; Meylan et al., 2013). The other beaches included in this study (Soropta, Bluff, and Playa Larga) located in Bocas del Toro, are not protected by this initiative. The initiation of monitoring on these beaches led to a sharp decline in leatherback killings; however, during and after the COVID-19 lockdown, an increase in illegal egg harvest was recorded (STC unpubl. data). Given the importance of the Bocas del Toro and la Comarca leatherback sea turtles for the entire Northwest Atlantic (NWA), the continuous analysis and evaluation of population trends are essential for their proper monitoring and the design of potential conservation. Here, we present 20 years of leatherback sea turtle nest abundance and trend analysis of four beaches and discuss the potential effects of anthropogenic impacts, environmental variations, or conservation efforts on the population.

2. Methods

2.1. Study area

Bocas del Toro province (Soropta, Bluff, and Playa Larga beaches) and Comarca Ngäbe-Buglé (Chiriquí beach) are two adjacent areas located on Panama's northwest Caribbean coast (Fig. 1). Nesting sites are confined to the mainland and the northernmost beaches of the archipelago, situated away from the freshwater inputs of Chiriquí Lagoon (Fig. 1). All four beaches are high-energy erosive beaches, associated with tropical rainforest vegetation and the leatherback nesting activity is among the highest in the region.

Soropta, the closest beach to the Costa Rican border and located in the San San-Pond Sak wetlands (Ramsar, 2020), is a black sand beach bordered by the Changuinola river mouth and Cauro Point. The monitored strip, which comprises the most suitable nesting area for leatherbacks along the shoreline, is located between the Changuinola river mouth (9.27526°N, 82.26177°W) and the point at which the wide sandy beach narrows (9.25390°N, 82.23534°W), giving way to lush vegetation. Soropta has experienced a reduction in its expanse over the years due to flooding and changes in the Changuinola river mouth, resulting in a monitored stretch of beach of 12 km in 2002, 8 km from 2003 to 2008, and 6.5 km from 2009 to 2022 (Table 1*)*.

Playa Larga (9.32531°N, 82.13229°W) in Isla Bastimentos National Marine Park and Bluff in Reserva Municipal Playa Bluff at Colón Island (9.419°N, 82.256°W), both located in different islands of the archipelago, are white sand beaches with lengths of 4.3 km and 4.8 km respectively, monitored from end to end. Bluff is located near the urban core of Bocas del Toro town, being the most affected by tourism-related impacts, dog predation and sand extraction.

Chiriquí, a 24 km white sand beach in the westernmost part of the Comarca and located in the Wetland of international importance Damani Guariviara, is one of the most important nesting sites of leatherback and hawksbill turtles in Central America and the Caribbean region (Ordoñez et al., 2007; Meylan et al., 2013). This beach is limited by the two stable river mouths of Rio Caña (9.00433°N, 81.42443°W) in the north and Rio Chiriquí (8.50541°N, 81.34162°W) in the south.

2.2. Nest surveys

The methodology followed on all study beaches was standardized for accuracy and consistency of the data. Nest surveys were conducted by personnel trained by Sea Turtle Conservancy, including workers of the Ngäbe Indigenous community with years of experience, national and international research assistants, volunteers, or field coordinators. The research and monitoring program of Soropta and Playa Larga was initiated by Endangered Wildlife Trust (2002–2012).

Nest surveys were conducted daily during the leatherback nesting season, in the early morning, by walking along the entire length of the monitored beach. To facilitate monitoring and achieve a finer scale of spatial distribution of the nests, each beach was divided into 100 m sections (except for Chiriquí, which was divided into 500 m sections), using marked poles easily spotted by observers. During the survey, all fresh tracks from the previous night were recorded from each section. Each track was visually inspected to identify the species, determine if it represented a clutch or a false crawl (an emergence without egg deposition), and then marked to avoid double-counting.

Importantly, all nest surveys inherently involve a certain degree of surveyor error, both in the identification of species and in differentiating between clutches and false crawls (Whiting et al., 2020). Distinguishing between species based on tracks can be challenging depending on the turtle species involved and the physical characteristics of the beach (Schroeder and Murphy, 1999). However, in the context of this study, this source of error is most likely minimal. All the beaches are sandy, retaining detailed printed tracks, and are primarily used by leatherback and hawksbill turtles, species whose tracks are easily distinguishable. Green turtles

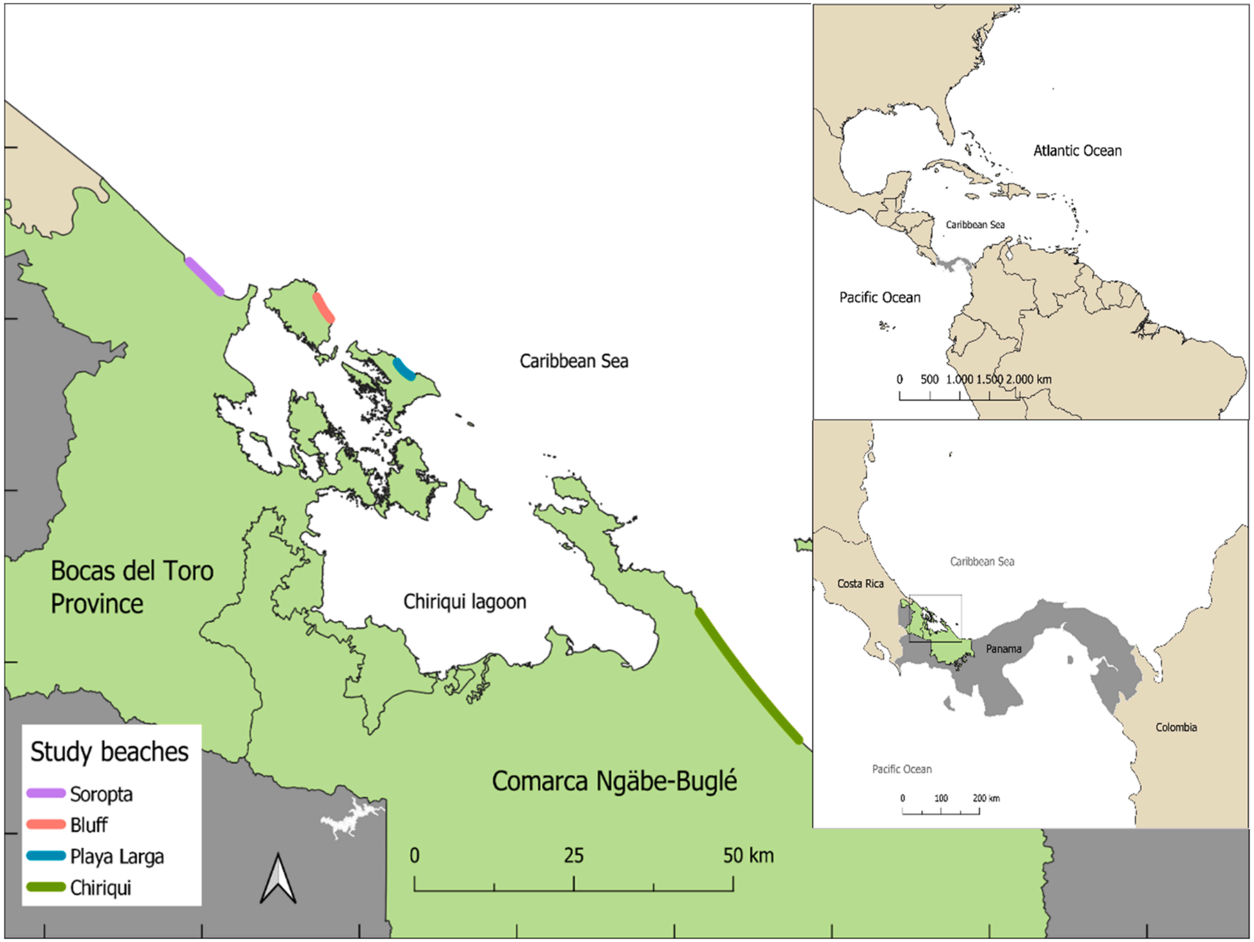

Fig. 1. Map of the Bocas del Toro region indicating the location of the four monitored beaches in this study, Soropta, Bluff, Playa Larga, and Chiriquí.

Table 1

Leatherback Nests model selection for linear model exploring relationships. Note: AICc= Akaike's Information Criterion corrected for small sample size, ΔAICc= difference in AICc from the top ranked model.

Beach	Timeseries	Survey Extent (km)	*r*	95 % CI	*Λ*	95 % CI	AICc	AICc Intercept Only	ΔAICc (M1-M0)	Notes
Soropta (standardized)	2002 – 2022	12 (2002), 8 (2003–2008), 6.5 (2009–2022)	0.08526	0.0618 - 0.109	1.0890	1.07602–1.1014	15.96	42.48	−26.53	Increasing 8.9 % year^{-1}
Chiriquí	2004 – 2022	24	−0.00677	−0.0301–0.0166	0.9932	0.9823–1.00430	8.81	6.38	2.44	Cannot distinguish Lambda from 1 (stable pop)
Playa Larga	2003 – 2022	4.3	−0.08637	−0.116 - −0.0569	0.9173	0.9045–0.9302	21.52	41.36	−19.8	Decreasing 8.3 % year^{-1}
Bluff	2011 – 2022	4.8	−0.09292	−0.140 - −0.0454	0.9113	0.8920–0.9309	8.07	17.18	−9.104	Decreasing 8.8 % year^{-1}
All Beaches Combined	2002 – 2022	12–39.6	0.06572	0.0118 - 0.120	1.0679	1.0408–1.0958	50.80	54.24	−3.443	Increasing 6.8 % year^{-1}

(*Chelonia mydas*) and loggerheads (*Caretta caretta*) nest at the sites occasionally. Leatherback turtle nests are characterized by their large size, the substantial volume of scattered sand, and the turtles' tendency to crawl over the camouflaged area. To distinguish between a nesting attempt and a successful clutch, evidence such as the amount of displaced sand, the presence of a body pit or abandoned chamber, and the presence of returning loops (orientation circles) was assessed.

We analysed the leatherback nesting timeseries for the four beaches, Soropta, Bluff, Playa Larga, and Chiriqui from 2002 to 2022. Soropta has been surveyed consistently since 2002; the other nesting beaches were added to the survey later, with Playa Larga in 2003, Chiriquí in 2004, and Bluff in 2011. We summed the total number of nests counted each year. In addition, we also had data on the number of survey days and the survey extent (km) conducted each year. The survey days varied annually (Table 1). The survey extent for Bluff, Chiriquí, and Playa Larga was consistent across years; however, for Soropta beach, we standardized the total nests counts by the minimum of the survey extent as:

$$Nests\_standardized_i = \sum_{j=0}^{n\ days} Nests * \left(\frac{\min(SurveyExtent)}{SurveyExtent_i}\right) \tag{1}$$

where the minimum survey extent was 6.5 km. This normalized all nesting surveys for Soropta to the smallest survey extent over the survey period.

We controlled for differences in sampling effort by calculating catch per unit effort (CPUE) as:

$$CPUE_i = \frac{\sum_{j=0}^{ndays} Nests}{Survey\ Days_i * SurveyExtent_i} \tag{2}$$

where, the total number of nests is summed, then divided by the total number of survey days in year *i* multiplied the total survey extent for year *i*.

2.2.1. Statistical analysis

We statistically evaluated the timeseries for each nesting beach and all beaches combined to estimate the population trend over time (i.e. the nesting beach was increasing, decreasing or stable) and to estimate the population growth rate annually (λ). We used the information-theoretic approach for model selection, based on Akaike's Information Criterion correction for small sample sizes (AICc; Burnham and Anderson, 2002; Johnson Omland, 2004). The information-theoretic approach is advantageous as it evaluates the strength of evidence to support model selection as well as the fit of the models to the data, regardless of exogenous factors that can influence the evaluation of statistical relationships using traditional null-hypothesis tests, i.e. sample size (Johnson, 1999; Burnham and Anderson, 2002; Johnson and Omland, 2004).

We used a linear model (LM) to test for a population trend in the four nesting beaches and all beaches combined. For all nesting beaches, we log-transformed nest track counts using the natural log. For Soropta, we used the survey extent-standardized nest counts

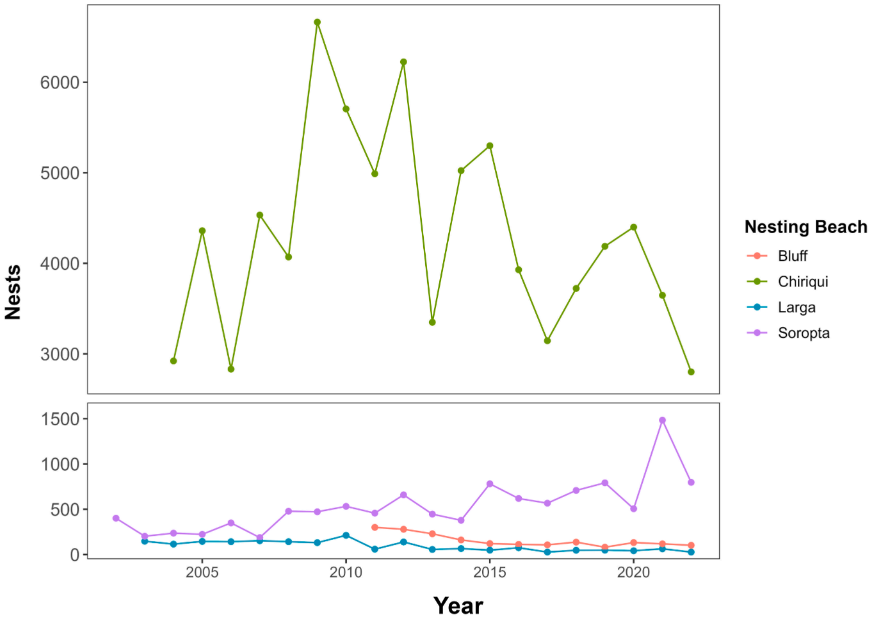

Fig. 2. Leatherback sea turtle nesting observations from Bluff, Chiriquí, Playa Larga, and Soropta nesting beaches from 2002 – 2022. Note that y-axis of top and bottom panels are different for better visualization of each time-series.

(Eq. 1). We evaluated if the residuals conformed to the assumptions of a LM by examining a scatterplot of the fitted values and residuals, histograms of residuals, and quantile-quantile (qq) plot, and there were no major departures (Zuur et al., 2009). In addition, we evaluated the fits of the LM, a candidate generalized LMs (with a gamma distribution), generalized least squares with temporal covariance structures (i.e. compound symmetry, autoregressive moving average, auto-regressive type 1) to account for potential autocorrelation in the time series, and generalized additive models for both ln-nests and CPUE. We also explored log-transforming the CPUE data, but the model fit to the data was worse than for the raw untransformed CPUE data. In all, the LM for both ln-nests and CPUE for each of the beaches had the best model fits (based on AICc), and so we present further on linear regression methods. For the model selection, we used the global linear model:

$$Ln(Nests) = \beta_0 + \beta_1 \times Year + \varepsilon_i \tag{3}$$

where β_0 is the intercept, β_1 is the slope, and the residual error is $\varepsilon_i \sim N(0, \sigma2)$ of each observation *i*. We used the same model to evaluate CPUE. We used this model to compare to an intercept-only model, functioning as the null model, to test for no change in the nesting population over time. We visually assessed model fit and adherence to assumptions using residuals from the models in the confidence set. In this case, β_1 is the only explanatory variable in the model and can be interpreted as the instantaneous population growth rate (r). We then exponentiated the slope (r) to calculate the discrete rate of population growth (λ). We also calculate the standard error (SE) of the slope estimate and the 95 % confidence intervals for both r and λ. We performed all analyses in R version 4.1.2 (R Development Core Team 2018) and R Studio version 2021.09.2 (R Studio, Inc.).

3. Results

Across a 20-year period, important differences across the nesting beaches emerged for leatherback sea turtle nesting from the four nesting beaches. Chiriquí, which has the largest nesting survey area and the largest nesting population – several orders of magnitude larger than the other beaches – has the greatest interannual variability (Fig. 2). When controlling for changes in survey effort, both over survey extent and total number of survey days, the nesting beach trends across all beaches have more similar trends and variability (Fig. 3).

For the linear regression analysis of the total number of nest tracks, we found that the regression models with year had better fit to the data than the intercept-only “null” models and were > 2 ΔAICc (Table 1). This suggested that for all the nesting beaches, year was an important predictor of nest tracks. Only Soropta had a positive nesting trend, with a discrete population trend, $\lambda = 1.089$ (1.076 – 1.10 95 % CI; Table 1). Chiriquí had an estimated $\lambda = 0.993$, but the 95 % CI was 0.982 – 1.0043. Here the confidence interval encompassed 1.0, which indicated that statistically the trend could not be distinguished from 1.0, which indicated a stable population. Playa Larga and Bluff beaches both had $\lambda < 1$ and 95 % CI’s wholly < 1.0, which indicated strong evidence of declining nesting populations (Fig. 4). We combined the nesting beach data for all nesting beaches, but given differences in survey effort over time, calculating a collective lambda from nest track counts was not appropriate.

For the linear regression of CPUE, we found similar trends compared to the nesting data (Table 2). The regression models with year

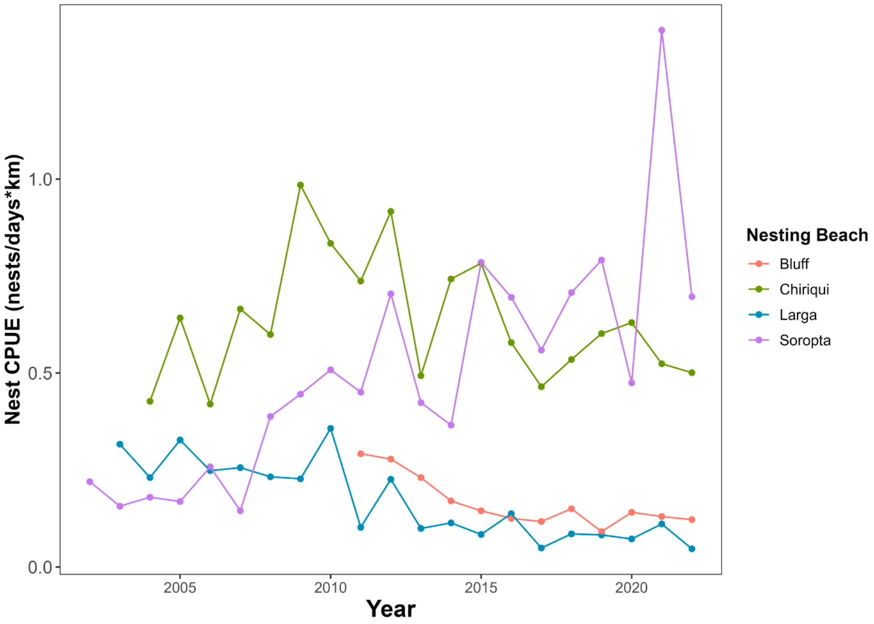

Fig. 3. Leatherback sea turtle nest monitoring catch per unit effort (CPUE) from Bluff, Chiriquí, Playa Larga, and Soropta nesting beaches from 2002 – 2022.

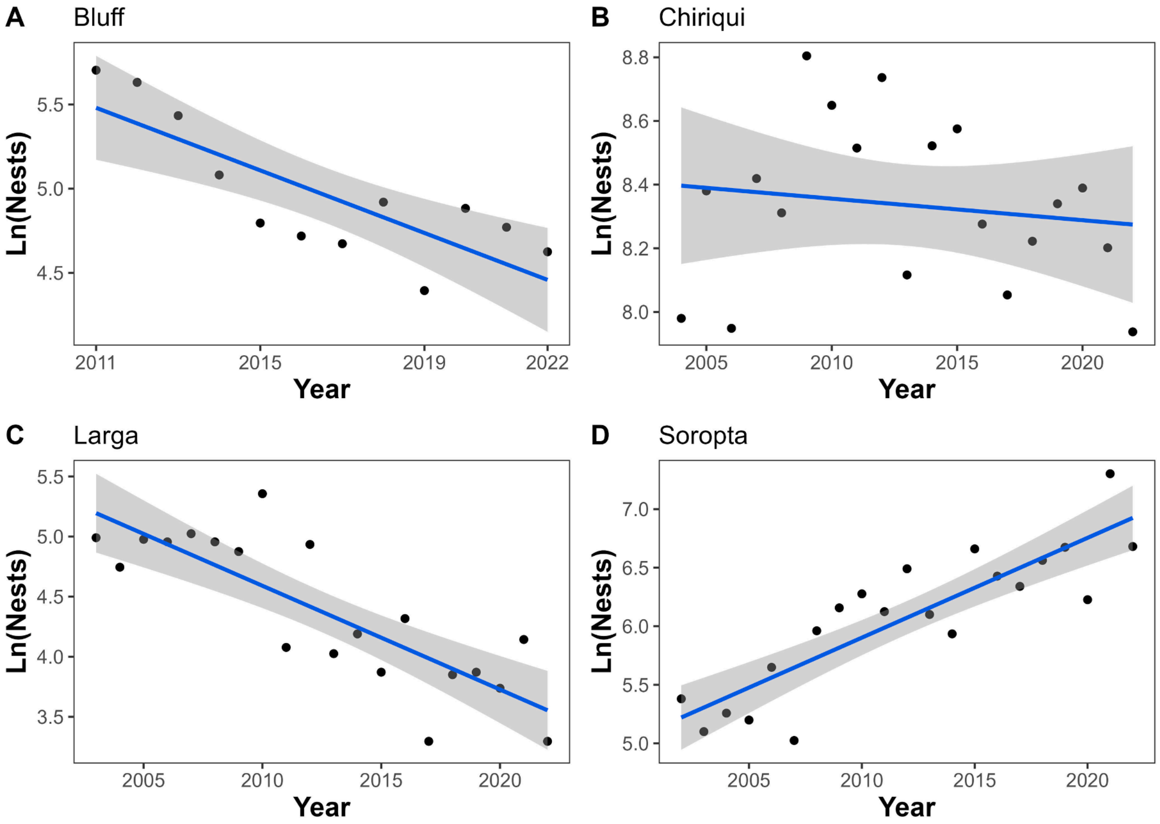

Fig. 4. Linear regression of ln-transformed nest tracks from Bluff, Chiriquí, Playa Larga, and Soropta nesting beaches from 2002 – 2022. Survey extent varied for Soropta, and nests were standardized to the minimum survey extent. The blue line is the linear regression predicted trend and the gray shaded area is the 95 % confidence interval.

had better fits to the intercept-only “null” models, and were > 2 ΔAICc, except for all beaches combined, where ΔAICc < 2 (Table 1). This suggested that for all the nesting beaches separately, year was an important predictor of nest tracks, except for all beaches combined. This was likely due to opposing trends for Soropta and the other beaches. Soropta had an increasing nesting population, while Chiriquí, Playa Larga, and Bluff were all decreasing over time (Fig. 5). Chiriquí had a 95 % CI for λ (= 0.996) that encompassed declining and increasing trends (0.989 – 1.0026), which suggested it could not be distinguished from a stable population. As CPUE accounts for differences in effort across the nesting beaches, we conducted a linear regression on the combined data (Fig. 6). Here, we estimated $\lambda = 0.997$ (95 % CI 0.995 – 0.999), but as the model selection could not disregard the intercept-only model, it may better be regarded as a stable population trend, when controlling for survey effort.

4. Discussion

According to Eckert and Eckert (2019) there are only six beaches left in the Northwest Atlantic with more than 1000 leatherback crawls per year: Cayenne in French Guiana; Grand Riviere, Matura, and Fishing Pond in Trinidad; and Chiriquí and Playa Armila in Panama. The stocks they belong to—Guianas-Trinidad and Western Caribbean—both show a negative trend in different time periods. The once-large and abundant Guianas-Trinidad stock is experiencing a significant decline, initially due to the collapse of Awala-Yalimapo (French Guiana) and Surinamese beaches, more recently from the decrease in Cayenne (French Guiana) and the steady decline at Matura Beach (Trinidad) (NWALWG, 2018).

Ocean-based threats for the NWA leatherback sea turtle subpopulation, such as longline fisheries in high-seas (e.g. Fossette et al., 2014; Stewart et al., 2016), fixed fishing gear in Canadian coastal foraging areas (e.g Hamelin et al., 2017), gillnets placed in inter-nesting areas (e.g. Lum, 2006; Eckert, 2013), maritime traffic (e.g. Foley et al., 2019), or plastic pollution (e.g. Emonnot et al., 2023), are scattered throughout the Atlantic basin; overlapping with breeding, foraging, nesting grounds, and their corridors, thus affecting various portions of the life cycle (Eckert and Hart, 2021). Evans et al. (2021), using satellite-tracked leatherback turtles from Panamanian and Costa Rican nesting beaches, identified the Gulf of Mexico (GoM) and North Atlantic Ocean (NAO) as important high-use habitats for Bocas and la Comarca sea turtles, mostly sharing these feeding and reproductive areas. We might expect that changes in these areas, both negative and positive, would influence the survival rates and good nutritional status of individuals, and would be reflected equally across different nesting beaches. However, the observed trends present quite different scenarios, suggesting the existence of local circumstances that appear to dominate the nesting abundance dynamic of some beaches. Demographic variables,

Table 2

Leatherback Nesting CPUE model selection for linear model exploring relationships. Note: r = instantaneous population growth rate (nests • ~day^{-1}), λ = annual population growth rate (nests • yr^{-1}), AICc= Akaike's Information Criterion corrected for small sample size, ΔAICc= difference in AICc from the top-ranked model.

Beach	Survey Period	Survey Extent (km)	r	95 % CI	λ	95 % CI	AICc	AICc Intercept Only	ΔAICc (M1-M0)	Notes
Soropta (standardized)	2002 – 2022	12 (2002), 8 (2003–2008), 6.5 (2009–2022)	0.0310	0.02413–0.05178	1.039	1.032–1.046	−6.36	12.05	−18.41	Increasing 3.9 % year•km•survey day^{-1}
Chiriquí	2004 – 2022	24	−0.00428	−0.0188–0.01026	0.996	0.989–1.0026	−9.18	−11.60	2.42	Lambda ~ 1 (stable)
Playa Larga	2003 – 2022	4.3	−0.0141	−0.0186 - −0.00958	0.986	0.984–0.988	−53.51	−31.94	−21.59	Decreasing 1.4 % year•km•survey day^{-1}
Bluff	2011 – 2022	4.8	−0.0147	−0.0221 - −0.00735	0.985	0.982–0.989	−36.60	−27.18	−9.42	Decreasing 1.5 % year•km•survey day^{-1}
All Beaches Combined	2002 – 2022	12 – 39.6	−0.00294	−0.00753–0.00166	0.997	0.995–0.999	−52.65	−53.50	0.85	Lambda ~ 1 (stable)

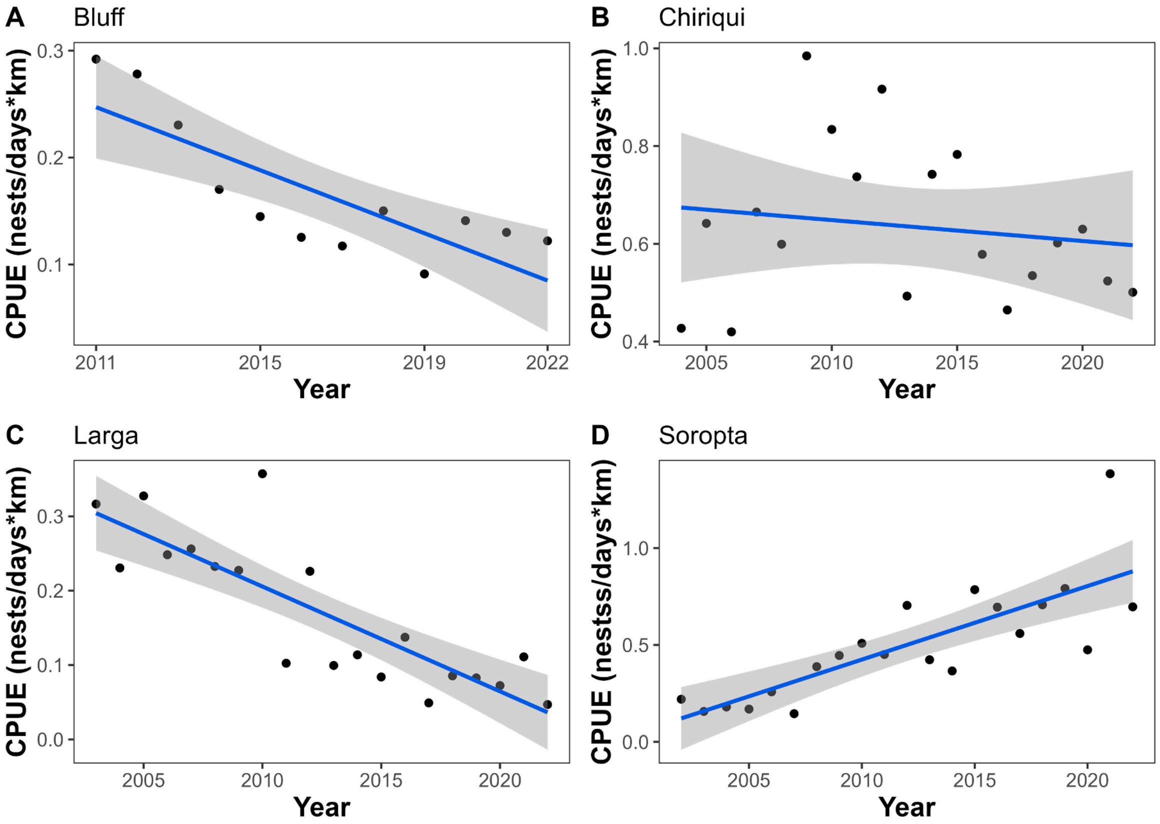

Fig. 5. Linear regression of catch per unit effort from Bluff, Chiriquí, Playa Larga, and Soropta nesting beaches from 2002 – 2022. The blue line is the linear regression predicted trend and the gray shaded area is the 95 % confidence interval.

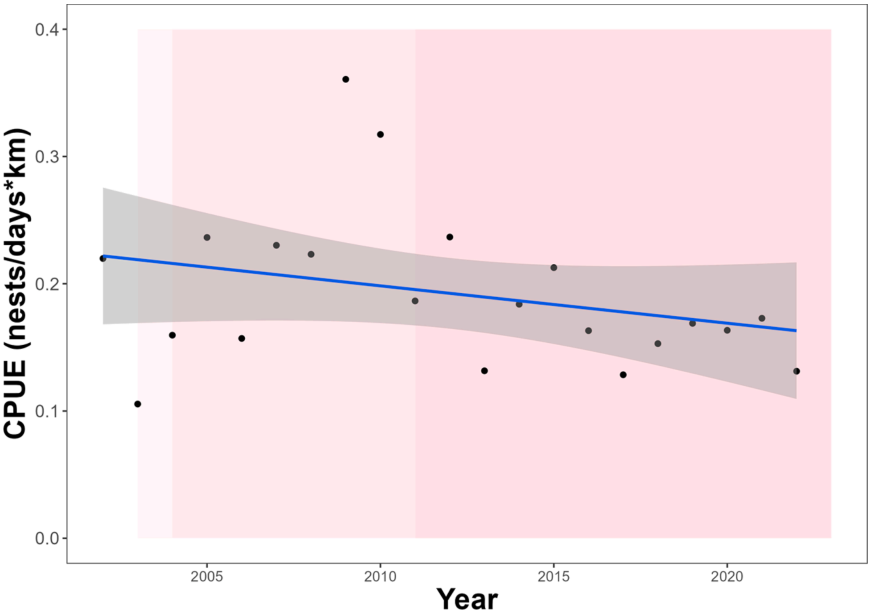

Fig. 6. Catch per unit effort (accounting for days and survey extent surveyed) for all nesting beaches combined. Pink shaded areas indicate when nesting beaches were added to the survey: Soropta began in 2003, Larga in 2003, Chiriquí in 2004, and Bluff in 2011. The blue line is the linear regression predicted trend and the gray shaded area is the 95 % confidence interval.

such as sex ratio and hatchling success, or land-based threats, such as beach erosion, nest loss, poaching of female and eggs, and coastal development, are at least in principle more easily identifiable and quantifiable than those of marine origin. This fact underscores the need to analyse the unique characteristics and circumstances specific of each beach that could explain such differences.

5. Four beaches, three scenarios

Soropta – Soropta has the longest survey record and is the only beach showing a significant positive trend, with an average nest increase of 8.9 % per year according to the linear regression model. This trend has become more pronounced in recent years, with the three highest nest counts recorded in 2019 ($n = 796$), 2021 (1484), and 2022 (792), continuing in 2023 with 1002 nests.

Throughout the study years, the beach has not undergone changes in its physical characteristics that could independently explain the observed increase in number of nests. Furthermore, despite the decrease of survey extent (Table 1), the number of clutches continued to rise, causing the CPUE to surpass the other beaches from 2015 onwards (Fig. 1*B*). Similarly, the declines observed in Bluff and Playa Larga do not seem collectively significant enough to explain Soropta's increase through a dispersal of leatherbacks from these rookeries. Soropta is located near the town of Changuinola and close to the river mouth, potentially making it vulnerable to illegal activities. Between 1999 and 2002, an average of 30 leatherbacks were recorded dead in Soropta per year, a number that plummeted to zero with the start of monitoring in 2002 (Meylan et al., 2013). Taking as an example the approximately 300 nests per year detected between 2002 and 2006 (Fig. 1*A*) and assuming a clutch frequency of 3–6 (Rivalan et al., 2006), a crude nesting population estimation would be around 50–100 individuals per year. Given this approach, the percentage of gravid females killed each season posed a direct and constant pressure of such magnitude that the population recovery was not guaranteed. This resilience suggests the presence of a significant contribution of new nesters or, perhaps, a dispersal of leatherback females from nearby regional rookeries.

The positive effects of conservation efforts focused on protecting clutches may not be observed until the hatchlings from these clutches reach sexual maturity—around 14 years for Atlantic leatherback turtles (Girondot et al., 2021)—and contribute as new nesters to the cohort. Given that our study period was 20 years, the recent positive trend may be the outcome of the synergy of both protecting, nesting females and clutches. If nesting dynamics have been primarily driven by a local factor, such as the killing of nesting females, recovery following its elimination may still mask negative impacts from underlying processes in other habitats or life stages. Only once the Soropta nesting population progresses toward stabilization and reaches a new equilibrium, it may better reflect the dynamics of the Western Caribbean population and thus serve as an indicator of impacts that may be affecting its individuals in more distant habitats.

Bluff and Playa Larga – The nesting trends of these beaches exhibit similar behaviour, both undergoing a decline of 8.8 % and 8.3 % year^{-1}, respectively. The killing of leatherback nesting females was uncommon on these beaches. However, clutch poaching occurred; and although it decreased with the onset of monitoring, conservation efforts have not been translated yet into an increase in the number of nests per season. Bluff was monitored for the last 12 years of the survey period, which may not encompass enough of newly recruited nesters following poaching cessation. However, Playa Larga was monitored for 19 years and theoretically should reflect the first few hatchling cohorts benefitting from nest protection.

Bluff has a high rate of sand renewal, making it the most unstable of the four beaches. A large portion of the sand is lost due to intense waves, recovering during the leatherbacks' nesting months (March – June). However, this cyclical beach erosion occurs later each year, with approximately the first 1.2 km of the beach being devoid of sand until June. This not only implies 25 % less available beach length for leatherback nesting, but also results in a shorter distance between high tide and vegetation along the rest of the beach. The dispersal of these females to other rookeries in search of a more suitable place to lay their clutches could be, at least, one of the reasons behind the observed trend. Previously, changes in coastal dynamics played a crucial role in the decline of leatherback nesting on beaches in the Caribbean basin. For example, in the period 2010–2018, Awala-Yalimapo saw a reduction in beach length by 1 km, experiencing a decline of 40 % of sea turtle nests each year between 2012 and 2017 (NWALWG, 2019; Chevallier et al., 2023). A similar case occurred in Surinam, with a decline of > 90 % of leatherback clutches since the 1990s and intense coastal sand mining activity over the past decade (NWALWG, 2019). While it is true that both the fluctuations in Bluff's beach sand and the decline in leatherback clutches are not as dramatic as in the former cases, this sustained condition over time may be critical. We must wait a few years to see if the beach, monitored since 2011, can overcome this negative trend, reflecting the nest protection efforts made since then.

The Playa Larga nesting population here showed no signs of recovery, even though monitoring spanned 19 years. Its decline is parallel to Bluff, and yet, they do not exhibit the same pattern of beach erosion. Similarly, there is no urban or tourist development that could prevent sea turtles from nesting here, so the existing causes behind the negative trend are not clear. Perhaps, in Playa Larga the observed declines result from more distant spatial and temporal processes, such as neritic or ocean-based impacts. Playa Larga is located within Parque Nacional Marino Isla Bastimentos, an area used as inter-nesting habitat for leatherbacks (Meylan et al., 2013); hence, the gradual decline in nests could be also influenced by females getting trapped in the fishing nets set in these shallow waters.

Chiriquí – Chiriquí has the largest nesting population and based on a 95 % CI encompassing both declining and increasing trends, is the only one that can be considered a stable population. Chiriquí showed a high inter-annual variability in clutch counts over the time series, so we must be cautious when analysing the nesting abundance trends. Leatherbacks exhibit a high annual clutch abundance variability (normally only surpassed by green turtles) (Broderick et al., 2001). The cyclic pattern in breeding probability is associated with climate-driven fluctuations in prey abundance, such as jellyfish (Lilley et al., 2009). The increased environmental unpredictability derived from climate change events may lead to an even higher annual variability in clutch counts in the long term, requiring longer periods for a proper nesting trend assessment.

Chiriquí is the only beach in Bocas del Toro and the Comarca that was considered in the trend analysis conducted for the NWA leatherback turtle status assessment (NALWG, 2018). In that study, trend analyses were conducted based on different geographical areas and periods, being evaluated for an intermediate (1998–2017, 2004–2017 in the case of Chiriquí) and a recent scenario (2008–2017). The results differed slightly, showing a positive and negative trend, respectively, that considering the 95 % CI of the trend, turned out to be non-significant. Our study, which covers more years (2004–2022), aligns with the NALWG (2008–2017) scenario. Even though we considered the population to be stable, we cannot ignore that the current data show a slightly worse scenario than described for 2004–2017 by the Turtle Expert Working Group. Looking at previous NWA sea turtle nesting trends, rookeries, such as Cayenne in French Guiana, experienced a sharp decline in leatherback clutches between 2008 and 2017, after showing an encouraging trend in the early 2010s (NALWG, 2018). Moreover, Tortuguero, which after 50 years of green turtle monitoring and a steadily growing clutch count, saw its trend reversed from 2008 onward (Restrepo et al., 2023); or Florida, where loggerhead annual clutch counts recently entered a decline after following a non-monotonic trend with several turning points spanning over 30 years (Ceriani et al., 2019). Future trend analyses with longer periods will clarify whether Chiriquí's current stability represents ~~in~~ an inflection point that could turn the corner toward either ~~of~~ population decline or recovery, rather than a sustained period of nesting stability.

Conservation efforts for Chiriquí's sea turtles began in the 1990s before the onset of monitoring. Faced with the near disappearance of hawksbill sea turtle nesting after decades of intensive harvesting, residents of the Rio Caña village formed an association to defend the natural resources of the Ngäbe-Buglé, agreeing to limit turtle extractions to once a year. Although these early efforts may seem rudimentary, they served as a foundation for community protection, favouring that, with the arrival of monitoring and total protection in 2003, the number of hunted turtles and raided nests decreased to practically zero.

5.1. All beaches combined

Considering all the nesting beaches together and controlling for differences in survey effort across the beaches, the population trend indicates a stable population (Table 2.). Despite the growth experienced by Soropta in recent years, the high relative weight that Chiriquí still exerts on the leatherback nesting population in this region means that this growth has not yet reached a positive turning point for the overall population in the Bocas del Toro and la Comarca region. Overall, we must holistically consider all monitored nesting beaches, and perhaps even combine into one unified assessment throughout the NWA subpopulation to truly understand the population-level nesting trend.

According to the most recent comprehensive study on sea turtle numbers globally, annual nesting abundance trends for leatherback turtles show clear signs of concern (Hays et al., 2024). In addition to the well-known declining trends at major nesting aggregations (e.g., French Guiana, Trinidad, Suriname), declines have been detected at several other sites, including Indonesia, the U.S. Virgin Islands, and the Caribbean coast of Costa Rica. Futhermore, leatherback nesting populations in the Eastern Pacific and Malaysia are severely depleted (NFSM and USFWS, 2020; Hays et al., 2024). As of today, the cluster of beaches in Bocas del Toro and the Comarca, continues to form one of the most important leatherback nesting aggregations in the NWA. The NWA subpopulation is under a high risk of extinction, especially in light of the Guianas-Trinidad declines, making the stability of these Panamanian rookeries of utmost importance (NMFS and USFWS, 2020).

The Western Caribbean stock consists of numerous leatherback nesting beaches scattered along the Central American coastline. The distributed nesting behavior across a variety of different landscapes and countries, and this form of ecological portfolio effect (Schindler et al., 2015), may somehow shield them from unpredictable or unstable local ecological events. However, it also complicates the management and communication efforts among conservation organizations, local authorities, and government entities. The need for a comprehensive view necessitates an increase in both beach monitoring efforts and communication among organizations to help piece together the big picture of the leatherback population status.

Ethical statement

The work described has not been published previously except in the form of a preprint, an abstract, a published lecture, academic thesis or registered report. See our policy on multiple, redundant or concurrent publication.

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Declaration of Competing Interest

This manuscript is an original work by the authors, which has not been previously published, and is not under consideration for publication elsewhere. The authors do not have financial or any other conflict of interest to declare. All authors have read the manuscript, agreed that the work is ready for submission to a journal, and accepted responsibility for the manuscript's contents. Please contact me should more information be needed.

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Data Availability

Data will be made available on request.

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