Vol. 51: 59–72, 2023
https://doi.org/10.3354/esr01237

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published May 25

Recent decline of green turtle *Chelonia mydas* nesting trend at Tortuguero, Costa Rica

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ABSTRACT: Trends in abundance of different life stages present important opportunities to manage the conservation of threatened species. For marine turtles, most trend assessments are based on long-term monitoring of nesting aggregations, which provides critical information on rookery dynamics across years. Tortuguero, Costa Rica, is the largest nesting colony of the green turtle *Chelonia mydas* in the Atlantic. Here we present an updated trend in annual clutch abundance spanning over 50 yr of monitoring at Tortuguero. We conducted weekly censuses recording clutch counts and used a generalized additive model (GAM) fitted for each monitored nesting season separately to predict daily tallies. We estimated annual clutch count as the sum of these. We modelled the long-term trend in annual clutch numbers with a Bayesian GAM with a cubic regression spline basis, fit to estimated annual clutch counts for 1971–2021. Finally, we examined spatiotemporal patterns in clutch counts along the beach by fitting a GAM with a 2-dimensional spline. Clutch estimates varied across years (78 695 ± 6727 [mean ± SE], range: 7004–186 640 clutches per year), but increased steadily over the first 37 yr. However, growth slowed gradually from 2000 to 2008, when the curve began to trend downwards. Tortuguero remains the largest aggregation of nesting green turtles within the Caribbean. Phenomena occurring across the population's range and at several life history stages influence Tortuguero's nesting trend. Thus, a decreasing trend at Tortuguero may be a warning sign for the Greater Caribbean green turtle metapopulation.

KEY WORDS: Sea turtles · *Chelonia mydas* · Atlantic · Caribbean · Long-term assessment · Population decline · Spatial distribution · Nesting trend

1. INTRODUCTION

Accurately assessing trends in wildlife populations is one of the greatest challenges for the conservation of threatened species (García-Cruz et al. 2015, Whiting et al. 2020). Understanding long-term trends is essential for identifying specific threats and making informed conservation decisions and recovery plans at both local and global scales (Balazs & Chaloupka 2004, Ceriani et al. 2019, Whiting et al. 2020). Marine turtles spend most of their time in oceanic and coastal waters where site access can be a limiting factor in studies based on direct observations (Troëng et al. 2005). Therefore, most assessments of sea turtle population abundance have been based on long-term monitoring of seasonal beach nesting activity of adult females (Chaloupka & Limpus 2001, Whiting et al. 2020). Clutch counts can be systematically obtained and tracked over long time periods (Ceriani et al. 2019), providing a replicable approach for monitoring programs to assess nesting aggregations on a decadal scale (Mazaris et al. 2017, Whiting et al. 2020).

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Though annual clutch numbers are not equal to the number of reproductive females throughout a nesting season (Ceriani et al. 2019), and the number of nesting females every year accounts for only a portion of the reproductively active females in the population (Bjorndal et al. 1999, Seminoff 2004, Casale & Ceriani 2020), numbers of clutches can be a reliable metric for assessing long-term patterns in nesting population abundance (Limpus 1996). Fluctuations in nesting activity (and by extension, number of adult females) reflect ecological processes at both foraging and breeding grounds that contribute to interannual variability in reproductive output, such as the availability of foraging resources and local threats (Ceriani et al. 2019). Nevertheless, clutch counts, if examined over sufficiently long temporal scales, reflect broad population-scale patterns of variability in nesting abundance and reproductive output.

Globally threatened, the green turtle *Chelonia mydas* is one of the most abundant large marine vertebrates in the world (Esteban et al. 2020), and one of the most frequently studied species of marine turtle, with a wide distribution throughout tropical and subtropical waters (Seminoff et al. 2015). Though they present strong natal-site fidelity for breeding, green turtles are highly migratory, with females undertaking long, complex journeys from foraging grounds to reach reproductive areas (Seminoff 2004, Troëng et al. 2005). The behavior and movement of this species is essential to processes of energy and nutrient transport into coastal ecosystems (Vander Zanden et al. 2012, Lovich et al. 2018)). Hence, declining stocks of this species are of great concern. Green turtle abundance is considered a reliable indicator of the health of marine ecosystems, as they constitute an integral part of interspecific interactions as prey, consumers and competitors, and substantially modify the physical structure of foraging habitats (Chaloupka et al. 2008)

It is well established that green sea turtles return to natal rookeries to mate and lay their eggs, and that individual females are faithful to particular nesting sites within the rookery (Carr & Carr 1972). This fidelity to specific breeding sites ensures that individuals mate and reproduce in suitable habitats (Shimada et al. 2021b). Unfortunately, the spatial concentration of nesting sea turtles may increase their vulnerability to exploitation. Nevertheless, it also offers an obvious focal point for the implementation of cost-effective conservation and management measures that seek to halt or reverse ongoing declines in populations (Hamann et al. 2010).

Despite their extensive geographic distribution, several green turtle populations have historically been depleted almost to the point of complete extirpation (Chaloupka 2001, García-Cruz et al. 2015). Though in recent decades several rookeries around the Greater Caribbean have shown an increase in the number of green turtle clutches laid each nesting season (e.g. Blumenthal et al. 2021, FWC 2021, Kauffman 2022), some of the most important nesting populations have steadily declined in the past century at substantial rates (Seminoff 2002). Worldwide, green turtles at various life stages are subject to human exploitation (Balazs & Chaloupka 2004, Senko et al. 2022). The Caribbean, in particular, has a long history of consumptive use of these marine reptiles by human communities (Meylan et al. 2013, Lagueux et al. 2017, Rojas-Cañizales et al. 2020, Mejías-Balsalobre et al. 2021, Pheasey et al. 2021).

Tortuguero nesting beach, Costa Rica, is considered the most important rookery for green sea turtles in the Atlantic Ocean, hosting the largest colony of nesting females in the basin (Seminoff 2002, Troëng & Rankin 2005, Seminoff et al. 2015). Tag-recapture programs have evidenced a wide distribution of adult green turtles marked at Tortuguero throughout foraging sites in Costa Rica and several other countries in the Greater Caribbean (Troëng et al. 2005). Therefore, trends in clutch counts and rookery size at Tortuguero have major implications for recruitment rates of populations on foraging grounds throughout the Greater Caribbean basin. Variations in these population parameters would likely affect the regional status of the species, as well as national classifications (Bjorndal et al. 1999, Seminoff 2004, Seminoff et al. 2015).

Given the divergent trajectories of sea turtle populations worldwide, assessing and reporting nesting trends accurately at various rookeries becomes a necessity to better understand population dynamics at broad scales and to plan effective conservation strategies (Rees et al. 2016, Blumenthal et al. 2021). Therefore, we aimed to (1) present an historical updated trend of green sea turtle annual clutch abundance at Tortuguero based on over 50 yr of monitoring and conservation efforts, (2) describe the spatiotemporal distribution of clutches over the 29.6 km of nesting beach, and (3) discuss management and conservation implications for this population.

2. METHODS

2.1. Study area and monitoring

Tortuguero National Park (TNP) is located on the northern Caribbean coast of Costa Rica in Central

America (Fig. 1). It consists of 29.6 km of dark sand beach adjacent to tropical rain forest. This barrier island is bordered on one side by the Tortuguero river, which meets the Caribbean Sea at 2 points: the Tortuguero river mouth (10.587933° N, 83.523560° W) in the north, and the Jalova lagoon (10.356861° N, 83.390360° W) in the south. For monitoring purposes, we divided the beach into 800 m sectors (half a mile) separated by white painted poles or trees (Fig. 1). Prior to 1999, we recorded total clutch numbers for the entire beach. Starting in 1999, we tallied total clutch numbers per sector. Green turtles *Chelonia mydas* have unmistakable nesting behavior, which leaves behind a set of long track marks, 0.5 m deep craters, and a soft dark spread of sand indicating the presence of freshly laid clutches on the beach (Bjorndal et al. 1999, Troëng & Rankin 2005). From 1971 to 2021 (51 yr), personnel of the Sea Turtle Conservancy (STC) conducted morning censuses during the green turtle nesting season to record nesting activity. Between 1971 and 1985, we conducted approximately weekly censuses to monitor nesting activity on the northernmost 18 km of beach. From 1986 onwards, we established structured weekly censuses spanning the entire 29.6 km of beach at TNP. Censuses were always performed by long-term residents of the local community who had extensive experience identifying green sea turtle nesting activity.

2.2. Annual estimates of clutch abundance

During weekly track censuses, we recorded green turtle nesting activity by counting only tracks indicating clutches laid the previous night, excluding those deposited during the intervening days. For each nesting season, we only included counted data between 15 June and 1 November, which comprised 99.0% of clutches laid at Tortuguero (Troëng & Rankin 2005). Due to logistical difficulties, a few censuses did not include the northernmost 5.4 km in 1995 (n = 3), 1996 (n = 8), 1997 (n = 16) and 1998 (n = 1). We corrected these gaps by adding the proportion of total clutches laid in that section of the beach determined from historic data during the same calendar month (Troëng & Rankin 2005). To account for the shorter 18 km censuses conducted from 1971 to 1985, we performed a linear regression comparing

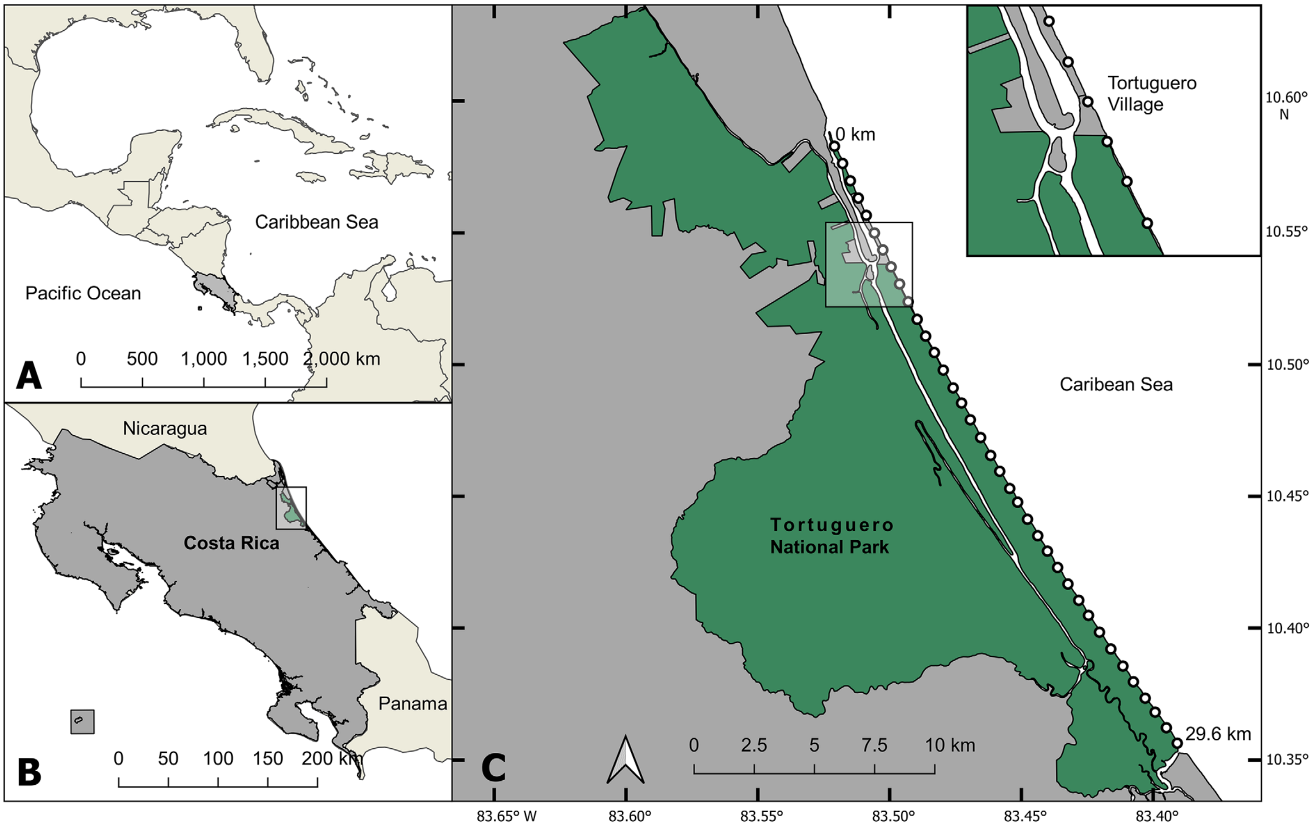

Fig. 1. Study area: (A) Costa Rica in Central America, (B) Tortuguero National Park in Costa Rica, (C) Tortuguero National Park, showing 800 m markers along the nesting beach

clutch counts from the same 18 km to counts from the entire 29.6 km for the period between 1986 and 2021. We used the regression equation to extrapolate the 18 km clutch tally for each year in between 1971 and 1985 to an estimate of the clutch count for the entire 29.6 km (Table A1 & Fig. A1 in the Appendix).

To estimate the total number of clutches laid throughout the nesting season, we fit a generalized additive model (GAM) to clutch count data for each nesting season separately with the mgcv package in R (Wood 2017). This approach was adapted from Bjorndal et al. 1999 and Troëng et al. 2005 with 2 major changes: we did not use artificial end dates, as they did not improve model fit, and we used GAM with uniform weighting, which is shown to produce lower mean absolute error than other nonparametric and parametric models used to estimate annual clutch abundance (Whiting et al. 2014). We selected smooth parameters with restricted maximum likelihood (REML) and did not specify the dimension of the basis function. We allowed the shape of the data for each year to determine the distribution and link function of the best-fitting model, testing each for significant deviance from the nominated distribution, dispersion and outliers using the DHARMa package in R (Hartig 2020). Where multiple GAMs met model assumptions equivalently, we selected the model fit with the lowest conditional Akaike's Information Criterion. We used the selected GAM to predict a daily tally and computed the estimated annual clutch counts as the sum of these.

2.3. Long-term trend

We adopted the methodology of Bjorndal et al. 1999 and Troeng & Ranking 2005 to allow for comparisons of both annual estimates (non-Bayesian approach) and the nesting trend (Bayesian approach) across the 3 studies. Thus, we fit a Bayesian GAM with a cubic regression smoother basis to the estimated annual clutch counts for Tortuguero for the period from 1971 to 2021 using the brms package in R (Bürkner 2017). The model was generated with brms default priors from 5000 iterations with a warmup of 2000, thinning by 5, 3 chains and a tuning parameter of 0.85. We tested the model fit for significant deviance from the normal distribution, dispersion, or outliers with the DHARMa package. We also compared the model fit with 10 random draws from the posterior distribution of the model. The credible interval for the variance parameter did not contain zero, suggesting that a smooth was required to represent the data and that a linear parametric effect would have been inadequate. We used the resulting GAM to generate estimated clutch count values with 95% credible intervals (package emmeans, Lenth 2020) at 100 random time points within the end dates to visualize the long-term trend. Additionally, we calculated the first order derivative of the fitted GAM to identify any changes in the slope of the trend. A first order derivative of zero occurs where the slope of the trend curve changes between positive and negative values, i.e. at the maximum or minimum of the curve.

2.4. Spatio-temporal patterns

During weekly censuses from 1999 to 2021, we counted the turtle clutches laid within every 800 m sector separately. To examine spatio-temporal patterns in clutch deposition, we fit a GAM to these spatially explicit counts using a 2-dimensional spline with census date as day of the year (DOY), assigning continuous counts to every day of the year starting with 1 January as day 1, sector marker in kilometers and the interaction between these as the predictors. We accepted that though our data were autocorrelated, the model would be adequate to describe general spatio-temporal patterns. We used low-rank tensor product interaction, *ti*() in the mgcv package in R (Wood et al. 2016), as the smooth basis and a Tweedie distribution. We manually selected the basis dimension (k) for each predictor by reducing k to counteract unrealistic overfitting (wiggliness) and increasing k to improve diagnostic metrics. Including study year as a random effect did not improve the explanatory power of the model and was therefore not included in the model.

3. RESULTS

3.1. Study area and monitoring

Censuses were conducted with variable frequency in Tortuguero throughout the study period. Prior to 1986, a mean of 14 censuses were conducted per year (range 10 to 18). In subsequent years, this number increased gradually, and by the late 1990s it was standardized to systematically obtain 20 weekly censuses throughout the nesting season (Table A2). Even though nesting activity varied seasonally, it followed similar patterns every year, with low clutch numbers during June, increasing gradually to a peak between mid-August and early September (DOY 230 to 250), after which nesting activity decreased rapidly. For any given nesting season, after mid-October (around DOY 288) the number of newly laid clutches each night was very low (Fig. 2).

3.2. Annual estimates of nesting activity

For annual clutch estimates, we fit a GAM to clutch count data for each nesting season with either a negative binomial (n = 29) or normal (n = 22) distribution (Table A2). Estimates of clutch counts for green turtles *Chelonia mydas* in Tortuguero presented high interannual variability. We estimated a mean (± SE) of 78 695 ± 6727 clutches per year between 1971 and 2021, with a minimum of 7004 clutches in 1979 and a maximum of 186 640 in 2010.

3.3. Long-term trend

Despite high interannual variability in clutch numbers, the green turtle nesting trend at Tortuguero increased steadily over the first 37 yr of the study period. However, after the year 2000, estimated growth in clutch numbers decelerated (Fig. 3), reaching maximum estimated clutch numbers in 2008. Subsequently, the trend curve shifted to a descending trajectory (Fig. 3), evidencing a decrease in estimated clutch numbers laid annually.

3.4. Spatio-temporal patterns

Green turtle nesting occurs at Tortuguero from approximately mid-June (DOY 160) to November (DOY 305) each year. In general, the peak in the nesting activity occurs between the first week of August and mid-September (DOY 220–250) (Fig. 4B). We found that the highest concentration of green turtle clutches was laid between kilometers 10 and 20 approximately. Fewer clutches were laid between kilometers 4 and 5 (the Tortuguero village), or close to the river mouth at both the north (km 0) and south (km 29) ends of the beach (Fig. 4C). DOY (estimated degrees of freedom, edf = 15.57, $F_{3,12427}$ = 645.52,

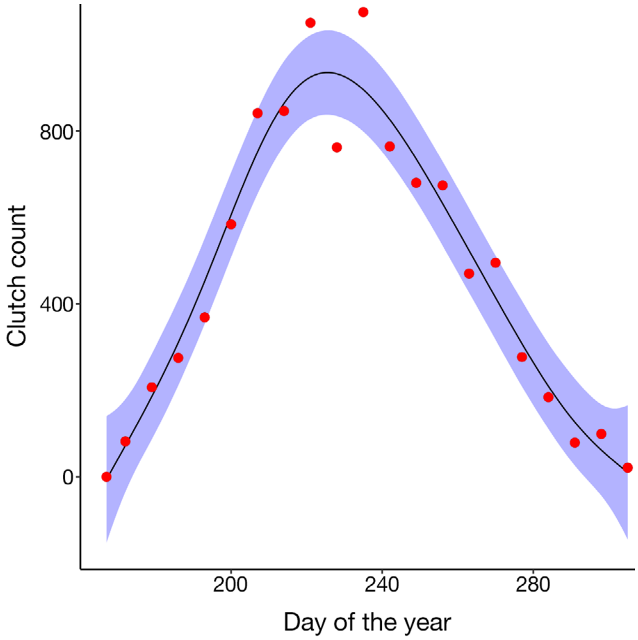

Fig. 2. Fitted GAM (continuous black line) and 95% confidence intervals (shaded area) modeling weekly counts of green turtle clutches from the 2020 nesting season (red dots) collected along the 29.6 km of beach at Tortuguero National Park. Time on the x-axis is presented in day of the year (range: 15 June–1 November)

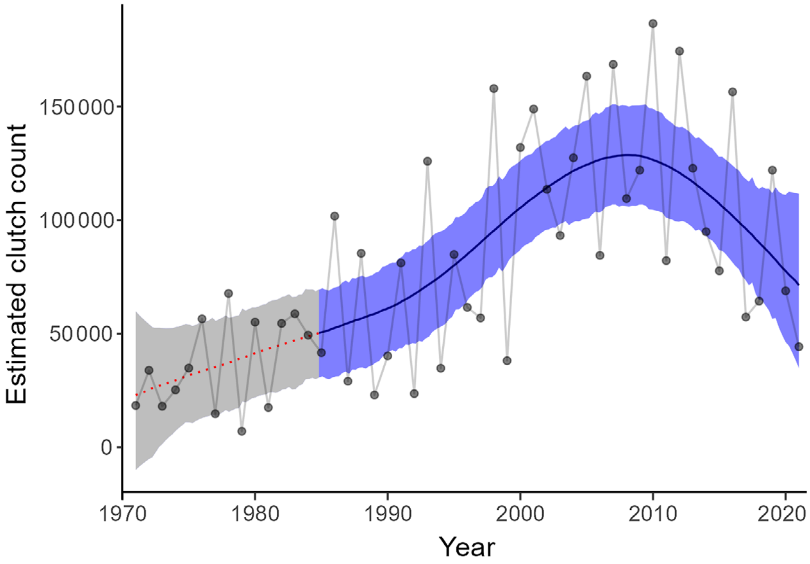

Fig. 3. Trend in the estimated number of clutches laid annually on Tortuguero Beach (red dotted and blue continuous line) and 95% credible intervals (shaded area), predicted from Bayesian GAM at 100 random time points between 1971 and 2021. The GAM was generated from estimated annual clutch counts (grey circles). Estimations prior to 1985 (region of red dotted line and grey area) were extrapolated from a linear model comparing data from 18 and 29.6 km surveys (Table A1, Fig. A1)

$p < 0.0001$), sector (edf = 10.94, $F_{3,12427} = 385.29$, $p < 0.0001$) and their interaction (edf = 11.16, $F_{3,12427} = 27.23$, $p < 0.0001$) all had a significant effect on clutch count, indicating that nesting activity changed spatially over time. The interaction term suggested that at the beginning of the nesting season (DOY 160–200), more clutches were laid in the middle of the beach, and during the peak of the nesting season (DOY 220–260), spatial patterns were less marked. By the end of the nesting season, clutch counts were higher in the northernmost 10 km than the rest of the beach, and the southern end had few or no clutches deposited (Fig. 4A).

4. DISCUSSION

4.1. Study area and monitoring

Tortuguero remains the largest aggregation of nesting green turtles *Chelonia mydas* within the Atlantic Ocean. The nesting population at this rookery was the first sea turtle nesting aggregation to be continuously monitored and studied, constituting the longest ongoing sea turtle conservation program worldwide (Carr & Giovannoli 1957, Bjorndal et al. 1999, Troëng & Rankin 2005, Seminoff et al. 2015). Until recently, reported nesting activity for green turtles at this rookery had demonstrated steady recovery over time following historical overexploitation. Bjorndal et al. (1999) described nesting activity at Tortuguero between 1971 and 1996 as an encouraging upward trend, aided by initiatives of the Costa Rican government to limit the legal harvest of eggs and adult turtles since the 1960s, and the establishment of Tortuguero National Park in 1975. Similarly, Troëng & Rankin (2005) reported a 61% growth in nesting activity between 1986 and 2003, attributing it to increased hatchling production since the mid-60s due to reduction in egg harvesting, combined with a complete ban on legal green turtle fishing in 2002 (La Gaceta 2002). In contrast, and despite the long-term local management and conservation strategies, we found that Tortuguero's nesting trend reached a maximum by 2008 and began to exhibit a gradual decline thereafter.

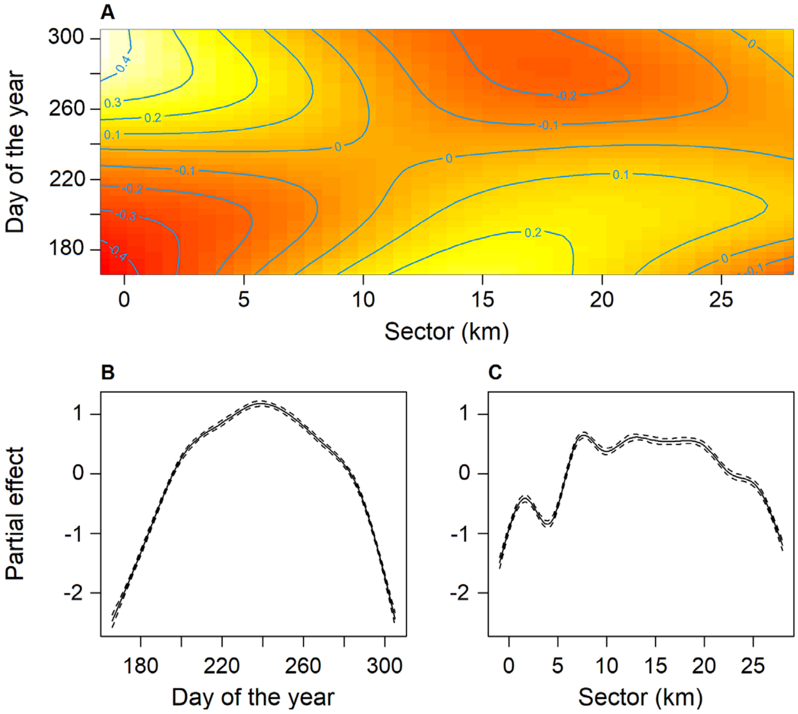

Fig. 4. Plot of component smooth functions in GAM representing (A) the interaction between temporal (day of the year) and spatial (beach sector in km) predictors of clutch count at Tortuguero Beach as contours of the 2-dimensional spline. Contour values and colors represent the influence of the smooth, with redder colors corresponding to negative influence, and yellow colors to positive influence. Partial effects plots of the (B) temporal and (C) spatial components of the GAM are included, showing the largest number of clutches concentrated in the middle of the beach

4.2. Annual estimates of nesting activity

There is considerable interannual variability in sea turtle clutch numbers in many rookeries (Hays et al. 2022). For Tortuguero's nesting population, remigration intervals are estimated at 2 or 3 yr, which regulates the number of nesting females every year (Bjorndal et al. 1999, Troëng et al. 2005, Troëng & Chaloupka 2007). Fluctuations in remigration intervals presumably reflect the need for turtles to attain sufficient reserves and body condition prior to initiating migration and breeding activities. Therefore, the proportion of the population breeding in a particular year is dependent upon conditions at foraging grounds and physiological endogenous mechanisms regulating reproductive function in individuals (Chaloupka & Limpus 2001, Bruno et al. 2020). Since individual green turtle females do not embark on reproductive migrations every nesting season, clutch numbers are an indirect representation of population abundance (Casale & Ceriani 2020). However, monitored over several nesting seasons, clutch counts can be reliable for assessing long-term nesting population trends (Limpus 1996, Seminoff 2004).

Until we know how many egg clutches are laid annually by the average female nesting at Tortuguero, accurate estimates of the size of the Tortuguero nesting population will remain elusive. Carr et al. (1978) estimated numbers of reproductive females at Tortuguero to range from 5723 to 23 142, based on an estimated clutch frequency of 2.8 clutches per female per season. However, Bjorndal et al. (1999) suggested that the mean clutch frequency for Tortuguero green turtles was more likely as high as 6 clutches per year, given high rates of tag loss in the Tortuguero population and the fact that the mark-recapture program used to calculate 2.8 clutches per female was conducted along only a limited section of the Tortuguero beach. Recent studies conducted elsewhere have shown that clutch frequency for green turtles as determined by foot patrols and flipper tagging protocols may underestimate clutch frequency almost by half compared to assessments made implementing remote sensing and telemetry technology (Esteban et al. 2017). Had Carr et al. (1978) used a clutch frequency of 6, their population estimate would only have been 2671 to 10 800. Using 2.8 and 6 as lower and upper limits, Troëng & Rankin (2005) estimated 17 402 to 37 290 females were nesting annually at Tortuguero in the early 2000s. Accurate quantification of clutch frequency of nesting females at Tortuguero requires further investigation.

4.3. Long-term trend

Though there is a long history of green turtle exploitation at Tortuguero (Mejías-Balsalobre et al. 2021, Pheasey et al. 2021, Rojas-Cañizales et al. 2022), we found evidence of an increase in the trend of clutch abundance over the first 3 decades of monitoring. This increment in clutch numbers may partially reflect the success of conservation efforts directed at protecting the beach and preventing turtle poaching (Bjorndal et al. 1999, Troëng & Rankin 2005). These early signs of recovery in the Tortuguero assemblage also came as a consequence of the implementation of the US Endangered Species Act and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 1973, which limited international trade of Tortuguero green turtles (Valverde & Holzwart 2017). These measures significantly reduced harvesting pressure within and outside the USA, a major harvester and importer of green turtle products before the 1970s. Nonetheless, abundance of females on nesting beaches is also a reflection of ecological processes occurring throughout the entire population distribution range (Ceriani et al. 2019). Additionally, it is possible that this initial increase in nesting activity at Tortuguero might have been tied to unexplored life history cycles elsewhere in the Caribbean basin. Given the high variability in interannual clutch numbers and other life history and environmental factors, we do not know whether the recent downward trend will be short or long lived.

Pinpointing the reasons for the recent decline in green turtle nesting activity at Tortuguero is extremely challenging. There are several factors threatening green sea turtles at multiple life stages around the Greater Caribbean. Anthropogenic threats to sea turtle populations are not easily assessed (Rees et al. 2016). Habitat degradation, fisheries bycatch and harvest of eggs and turtles for consumptive use have been identified as the primary factors contributing to the decline of various sea turtle populations globally and in the Caribbean basin (Seminoff et al. 2015, Rees et al. 2016, Lagueux et al. 2017).

Direct capture of sea turtles to meet dietary needs has occurred for centuries (Lagueux et al. 2017, Valverde & Holzwart 2017, Senko et al. 2022). The Caribbean is one of the regions worldwide where this phenomenon is deeply rooted in the collective coastal culture (e.g. Meylan et al. 2013, Lagueux et al. 2017, Barrios-Garrido et al. 2020, Pheasey et al. 2021), and where some of the largest sea turtle fisheries have historically prospered. Harvest rates of legal and illegal fisheries throughout the Caribbean basin were thoroughly detailed by Seminoff et al. (2015). Sea turtle harvest levels relate to social and economic stability of coastal communities (Campbell & Lagueux 2005, Barrios-Garrido et al. 2020). Therefore, control or reduction of poaching has been somewhat challenging to implement.

Despite the long-term conservation efforts made at Tortuguero, poaching of eggs and nesters still occurs at this rookery. Pheasey et al. (2021) quantified poaching levels in Tortuguero from 2006 to 2019 and reported a total of 373 green turtle females poached from the nesting beach. However, Rojas-Cañizales et al. (2022), in characterizing poaching patterns at Tortuguero from 2005 to 2021, estimated a much higher minimum mean of 43.2 green turtles poached annually across the entire beach. Nonetheless, the maximum poached amount could not be ascertained and is thought to be significantly greater. Moreover, key stakeholders from the community expressed that poaching of green turtles in the maritime area of TNP was considerably greater than that occurring onshore, since harpooners traditionally hunt for adult green turtles (both male and female) during the mating and nesting seasons. Unfortunately, in-water poaching rates in this area have not yet been quantified; however, they could be significant (Rojas-Cañizales et al. 2022).

Indigenous communities around the Caribbean have also been reported participating in the green turtle harvest. In the late 1980s in the eastern Guajira in Colombia, local communities were responsible for harvesting at least 5000 turtles per year. Due to adverse conditions in the past decades, local communities in la Guajira are increasingly relying on traditional fisheries for subsistence (Vásquez-Carrillo & Peláez-Ossa 2021). Similarly, it was estimated that between 2005 and 2008, the Venezuelan Wayuú communities captured at least 3402 green turtles each year (Barrios-Garrido et al. 2020). Key stakeholders in the Guajira region in Venezuela stated that marine turtle trade increased between 2003 and 2013, due to the economic crisis in the country (Rojas-Cañizales et al. 2020). In Nicaragua, a legal artisanal green turtle fishery in the Miskito Cays extracted a mean of 8169 green turtles per year between 1991 and 2011, though estimates sometimes exceeded 12 000 turtles harvested in a single year (Lagueux et al. 2014, 2017). The harvest of adults mentioned here may well have impacted the Tortuguero green turtle colony, which we think is currently reflected in our analysis.

Troëng et al. (2005) described migratory corridors used by females on post-nesting migrations, connecting Tortuguero with vulnerable foraging areas around the Caribbean. Tag returns and satellite telemetry studies suggested that seagrass beds in Nicaragua are the major foraging area for adult green turtles nesting at Tortuguero. Thus, the harvest by the Miskito Indigenous and Creole communities in Nicaragua have remained the most significant hindrance for the recovery of this population (Campbell 2003). Bjorndal et al. (1999) highlighted the importance of monitoring the effects of the harvest on population trends. Currently, uncontrolled harvesting of green turtles may represent the biggest threat affecting the Tortuguero population. If current harvest levels do not diminish promptly on a regional scale, it is likely that Tortuguero's population as a whole may be severely affected, declining further as predicted by Campbell (2003) 2 decades ago.

Climatic events such as El Niño Southern Oscillation phenomenon (ENSO) and winter sea surface temperature anomalies correlate with reproductive output of the Tortuguero green turtle population (Solow et al. 2002, Bruno et al. 2020). These warm climate phenomena were linked to increasing nesting activity for green turtles throughout the Great Barrier Reef in Australia and in southeast Asia (Limpus & Nicholls 2000, Chaloupka 2001). Conversely, Bruno et al. (2020) reported that, for green turtles nesting at Tortuguero, fewer females in the Caribbean became reproductively active in the 2 yr period after a warm ENSO event, which is associated with increased rainfall. The high precipitation conditions on foraging grounds might have led to a decrease in seagrass productivity, which comprises a substantial component of green turtles' diet (Bjorndal 1985, Esteban et al. 2020), hindering reproductive output.

Physical variables such as rainfall, temperature, sunlight, and human-altered runoff (Jackson 2001, Waycott et al. 2009) have visible effects on seagrass development, altering water quality, incrementing sedimentation and leading to suboptimal physical characteristics such as increased turbidity or decreased dissolved oxygen, reducing biomass volume and nutritional quality of foraging pastures (Orth et al. 2006, Fourqurean et al. 2019). Moreover, when fewer green turtles graze, seagrass beds grow longer blades that baffle currents, shade the bottom, and start to decompose *in situ* (Jackson et al. 2001). Since 1996, declines have been documented in abundance and extent of some of the main Caribbean seagrass meadows, such as the Bermuda platform, which serve as key developmental habitats for green turtles (Fourqurean et al. 2010). Predominantly herbivorous (Bjorndal 1985), green turtles are especially susceptible to degradation of seagrass foraging areas. Although green turtles can forage on alternate resources (Esteban et al. 2020), significant decline in seagrass beds can be expected to produce changes in their demographics and ecology (Meylan et al. 2022). Therefore, reduction in forage resources over the past few decades might have been a major contributor to declining levels of nesting activity at Tortuguero.

Green turtles spend decades in neritic habitats growing to sexual maturity (Bjorndal et al. 2019). Mean age-at-maturity has been estimated to range from 14 to 50 yr depending on habitat use patterns, foraging behavior and conditions at foraging grounds (Chaloupka et al. 2004, Turner Tomaszewicz et al. 2022). Since the mid-1980s, immature green turtles in developmental habitats around the Greater Caribbean have shown marked declines in abundance (Lagueux et al. 2014). This has been attributed mainly to high harvest rates and possible overexploitation of juveniles in foraging grounds. Though Bjorndal et al. (2005) demonstrated increased abundance of juvenile green turtles at the Bahamas archipelago in the early 1980s, this was quickly followed by a period of significant decline from 1985 to 1994, at an annual rate of 13.1%. Given the slow maturation of this species, declines at key developmental areas (Fourqurean et al. 2010, Bjorndal et al. 2017) may have contributed to the shift in Tortuguero's nesting trend in 2008, but would not have been immediately apparent on the nesting beach (Bjorndal et al. 1999).

On the other hand, the abundance of juvenile green turtles in the Caribbean Netherlands has not shown significant variation in the last decade. Genetic and demographic analyses of this aggregation suggested an increase in the proportion of juvenile green turtles recruited from rapidly recovering rookeries in the northwestern Caribbean, compared to those from the southwest Caribbean (Van der Zee et al. 2019). Tortuguero is by far the largest rookery in the southwestern Caribbean. Thus, the reduction in recruitment rates of smaller juveniles from this region might reflect recent decreasing nesting activity and hatchling productivity at Tortuguero.

Green turtle nesting populations in the North Atlantic are some of the most studied in the world. Despite substantial human impacts on nesting beaches and foraging areas, in recent years some rookeries in this region have shown a recovery in levels of nesting activity (Seminoff et al. 2015). In contrast to Tortuguero, green turtle clutch counts in Florida have increased 80-fold since 1989 (FWC 2021), and the Cayman Islands' population mirrors these trends to a certain degree, albeit on a smaller scale (Blumenthal et al. 2021). Similarly, for 16 beaches spread over 200 km on the Atlantic littoral in Mexico and the Guanahacabibes peninsula in Cuba, annual clutch counts have increased since 2013 (Guzmán-Hernández et al. 2022). In the western Caribbean, the average annual increase in clutch numbers from 1982 to the present was 22% at St. Croix in the US Virgin Islands (Kauffman 2022), and 4.5% at Aves Island between 1979 and 2009, the latter being one of the largest green turtle rookeries in the Caribbean (García-Cruz et al. 2015). Nonetheless, from 2006 to 2009 a reduction in the number of nesters was observed at this rookery (García-Cruz et al. 2015), partially co-occurring with the pattern of estimated clutches seen at Tortuguero from 2008 onwards. A marked reduction in the abundance of nesting green turtles in the Dominican Republic has also been reported, declining from 260 individuals nesting per year in the 1980s to near extirpation (Carreras et al. 2013). Nesting activity has been reported in Cuba (Azanza-Ricardo et al. 2013) and Mexico (Shaver et al. 2020), but insufficient data has been published to assess nesting trends over time.

We acknowledge that fewer clutch censuses were conducted in early years of our study. Though Bjorndal et al. (1999) found that tally census intervals of 2 or 3 wk would have similar outcomes for annual estimates of clutches laid at Tortuguero, coefficients of variation for these estimates were inversely related to census frequency, suggesting that constant and shorter census intervals could reduce variability of clutch estimates. Thus, given the variation in clutch density throughout the nesting season, and that the beach must be censused constantly for the most part of the year to obtain accurate estimates of clutch counts, we increased the frequency of our monitoring activities to 1 census per wk.

4.4. Spatio-temporal patterns

Irrespective of interannual variation in total clutches laid, there appeared to be consistent spatio-temporal patterns in nesting activity over the past 20 yr. Temporally, the peak of the activity occurred between August and September (DOY 213–273). Similar temporal patterns were documented in Tortuguero previously (e.g. Bjorndal et al. 1999, Tiwari et al. 2005). Bjorndal et al. (1999) found that clutch numbers generally peaked around DOY 240 (August 28).

Spatially, green turtle nesting was consistently concentrated in the mid-section of the beach across nesting seasons. Unfortunately, this mid-section of the nesting beach is where there is least surveillance and is presumed to be where most females are harvested without detection (Pheasey et al. 2021, Rojas-Cañizales et al. 2022). The high density of nesting activity towards the north section of the beach at the end of the nesting season may increase the susceptibility of females and eggs to harvesting by the nearby community of San Fransisco (Mejías-Balsalobre et al. 2021, Rojas-Cañizales et al. 2022).

Green turtles display strong nest site fidelity (Bjorndal et al. 1999, Shimada et al. 2021a). At Tortuguero, the locations of consecutive clutches laid by individual females are close together (mean 1.4 km, range 0–7 km), across nesting seasons (Carr & Carr 1972). Long-term site selection by females likely contributes to the consistency of clutch counts in particular sections of the beach. Furthermore, low levels of nesting near the village of Tortuguero (kilometer 4–5), may have resulted from historically unrestricted poaching of nesting females in that section of beach (Carr & Carr 1972, Tiwari et al. 2005). This section of the beach remains prone to harvest of both sea turtles and their eggs (Mejías-Balsalobre et al. 2021, Pheasey et al. 2021, Rojas-Cañizales et al. 2022). Our historical records show that the lower number of nesting turtles in this section of beach was already discernible by the time public lights were introduced in the village in 1986 (data not shown). This suggests that high human activity (including poaching, tourism and general beach usage) in this area is the main culprit for lower nesting activity in this section of beach.

5. CONCLUSION

Tortuguero hosts the largest nesting aggregation of green turtles in the Atlantic Ocean. Long-term conservation efforts have allowed the population to exhibit signs of recovery since the 1970s. Nevertheless, after an initial growth in nesting activity, Tortuguero's green turtle annual nesting trend is now declining. Due to the longevity of green turtles and their broad distribution throughout their life cycle, informing conservation strategies to protect Tortuguero's population is quite difficult. Habitat degradation and unfavorable environmental conditions linked to temperature fluctuations and climate conditions at developmental and foraging grounds can slow growth rates in juvenile turtles, leading to reduced recruitment to adulthood, and longer remigration intervals in adults (Solow et al. 2002, Bjorndal et al. 2017, Bruno et al. 2020). Both conditions could have important effects on the reproductive output of green turtles. Capture of sea turtles by humans at rookeries and foraging grounds constitutes perhaps the primary threat this population faces (Seminoff 2004). Green turtle fisheries remain legal in several countries around the Caribbean, and harvesting levels may present a significant impediment for population recovery. Sea turtle harvest from seagrass meadows, where Tortuguero's green turtles forage, is of particular concern. Though various green turtle rookeries around the Caribbean have shown some degree of recovery in the past 20 yr, the decline in clutches laid at Tortuguero might herald difficult times to come for populations in Florida or elsewhere in the Greater Caribbean, since they all share common developmental and foraging areas.

Effective management strategies rely upon incorporating biophysical and environmental knowledge into resource management and law enforcement (Hamann et al. 2010). Establishing information about Tortuguero's green turtle nesting aggregation over time contributes to the baseline against which to assess potential population recovery. The protection of strategic areas around the Greater Caribbean is essential to attain such recovery. Local as well as international efforts must be made to work closely with communities dependent on green turtle harvest as their primary means of income or protein. Monitoring the abundance and distribution of green turtle clutches at TNP across different nesting seasons can provide information to evaluate population variation over time. Finally, updating nesting population estimates is paramount to informing and engaging key stakeholders to develop comprehensive strategies to protect these endangered populations.

Acknowledgements. Censuses and data collection were conducted by the STC under research permits provided by the Costa Rica government through the Ministry of Environment and Energy and the National System of Protected Areas. We thank personnel of Tortuguero Conservation Area for their support over the many years the STC has worked at this important rookery. Additionally, we acknowledge all those who engaged on endless walks to provide the data to complete this project. We also thank Matthew Godfrey, Tomo Eguchi, Jeanne A. Mortimer and 1 anonymous referee for their input, which helped improve the manuscript. Finally, we extend our gratitude to STC personnel and research assistants for their hard work and dedication over the past 60 yr.

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Appendix

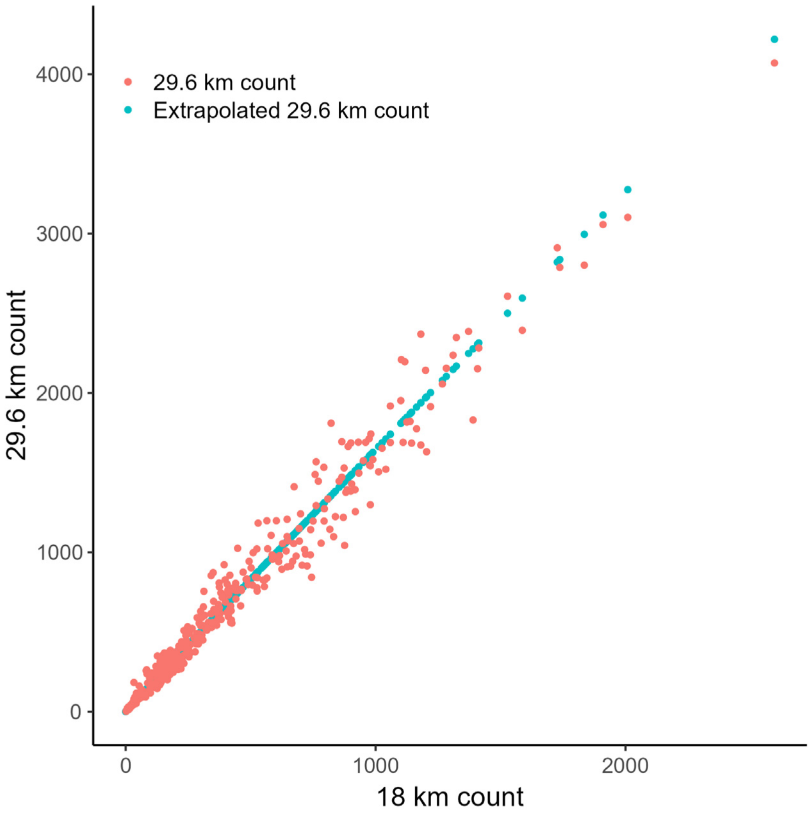

Fig. A1. Scatterplot of clutch counts for 18 km versus 29.6 km. Actual counts from 1986 to 2021 are indicated by red dots, whereas 29.6 km counts extrapolated from 18 km counts using a linear model (1971–1985) are shown by blue dots

Table A1. Linear model of clutch counts for 18 km, compared to 29.6 km surveys (1986-2021). We used the regression equation of the model log(extrapolated 29.6 km count) = 0.987 × log(18 km count) + 0.584 to extra-polate the clutch counts for the entire 29.6 km from the 18 km survey counts for 1971–1985

Term	Estimate	SE	*t* value	p value	Adjusted r^2
Intercept	0.584	0.045	13.108	<0.001	0.976
log(18 km count)	0.a987	0.008	124.413	<0.001	

Table A2. Number of surveys, estimated clutch count, selected distributions, link and basis dimension selected for GAM fits of weekly counts of green turtle clutches applied for each study year. From 1971 to 1985, estimated clutch count was extrapolated using a linear regression (Table A1)

Year	Surveys (n)	Estimated clutch count (29 km)	Distribution	Link	Basis dimension (k)
1971	10	18360			
1972	19	33857			
1973	15	18020			
1974	12	25214			
1975	14	34857			
1976	16	56539			
1977	19	14727			
1978	18	67739			
1979	17	7004			
1980	13	55087			
1981	13	17487			
1982	12	54526			
1983	14	58782			
1984	15	49378			
1985	12	41636			
1986	12	101787	Negative binomial	Log	8
1987	12	29069	Negative binomial	Log	8
1988	18	85398	Negative binomial	Log	Not specified
1989	11	23003	Normal	Log	Not specified
1990	12	40201	Normal	Gaussian	8
1991	15	81162	Normal	Log	Not specified
1992	15	23602	Normal	Gaussian	Not specified
1993	18	125996	Negative binomial	Log	Not specified
1994	16	34783	Negative binomial	Log	5
1995	17	84903	Negative binomial	Log	Not specified
1996	15	61067	Negative binomial	Log	Not specified
1997	18	56935	Negative binomial	Log	Not specified
1998	19	158037	Negative binomial	Log	Not specified
1999	19	38113	Negative binomial	Log	Not specified
2000	20	132045	Negative binomial	Log	Not specified
2001	20	148960	Normal	Gaussian	Not specified
2002	17	113567	Normal	Gaussian	Not specified
2003	20	93280	Negative binomial	Log	Not specified
2004	20	127499	Negative binomial	Log	Not specified
2005	20	163446	Negative binomial	Log	Not specified
2006	21	84476	Normal	Gaussian	Not specified
2007	13	168658	Normal	Gaussian	8
2008	20	109523	Negative binomial	Log	Not specified
2009	20	122017	Normal	Gaussian	Not specified
2010	19	186640	Normal	Gaussian	Not specified
2011	20	82208	Normal	Gaussian	Not specified
2012	19	174469	Negative binomial	Log	Not specified
2013	20	122886	Negative binomial	Log	Not specified
2014	19	94916	Normal	Gaussian	Not specified
2015	19	77697	Negative binomial	Log	Not specified
2016	20	156532	Negative binomial	Log	Not specified
2017	20	57312	Negative binomial	Log	Not specified
2018	20	64374	Normal	Log	Not specified
2019	20	122017	Negative binomial	Log	Not specified
2020	21	68866	Normal	Gaussian	Not specified
2021	20	44273	Normal	Gaussian	Not specified

Editorial responsibility: Matthew Godfrey,
Beaufort, North Carolina, USA
Reviewed by: T. Eguchi, J. A. Mortimer and
1 anonymous referee

Submitted: August 24, 2022
Accepted: March 1, 2023
Proofs received from author(s): May 20, 2023