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Reassessment of the olive ridley sea turtle *Lepidochelys olivacea* nesting population at Nancite Beach, Costa Rica

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Abstract

Nancite is a fully protected beach within the Guanacaste Conservation Area, Costa Rica where olive ridley (*Lepidochelys olivacea*) sea turtles nest in synchronous mass-nesting events known as arribadas. Arribadas decreased in magnitude at this beach by approximately 90% during the period 1971–2007 due to unknown causes. The total count estimate of females nesting in a year also decreased over these decades. In the present study, from August 2009 to February 2021, the trend of arribada nesting female abundance and estimated annual production of hatchlings were assessed and compared with previous trend analyses. A total of 62 mass-nesting events were quantified in the period 2009–2021, with an estimated annual average of 64,694 nesting females. Trend analysis indicated that during our recent study period, the number of females per arribada event increased by an estimated 14% (8%, 20% $CI_{95\%}$). During this period, a mean hatching rate of 33.4% was estimated, corresponding to an overall estimated production average of 2,165,597 per season, which represented an increase of 82.7% compared with a previous estimate for the period 1980–1984, when the arribadas were larger. We suggest that the growth in hatchling production over the past four decades is at least in part responsible for the slight increase in the estimated size of arribadas since 2009/2010. However, because maximal hatching success did not increase above 60%, the beach may be close to reaching carrying capacity, and it seems that high hatchling production may soon level off or begin to decrease. Thus, it is not clear whether current hatchling production will lead to the recovery of the Nancite population to the historical levels documented in the 1970s and early 1980s.

KEYWORDS
arribada, hatching rate, *Lepiodochelys olivacea*, nesting population trend, olive ridley

1 | INTRODUCTION

The regulation of the size and dynamics of a population results largely from the interaction of density-dependent factors, in which populations tend to grow and then decline when the number of individuals exceeds the carrying capacity of the environment (Hixon et al., 2002; Ray & Hastings, 1996; Sibly et al., 2005). In the case of sea turtle populations, the nest microenvironment plays an important role in hatchling production, and successful hatchling production is clearly required to support the adult population (Cornelius et al., 1991). When adult females nest in high densities, large numbers of clutches can work in detriment of the nest microenvironment, resulting in a decrease in hatching rates (Honarvar et al., 2008). This is particularly true in the case of mass-nesting events or arribadas, which represent an alternate nesting strategy to solitary nesting behavior of olive ridley (*Lepidochelys olivacea*) sea turtles. Arribada is the synchronized mass nesting of hundreds or thousands of ridley turtles during one or several consecutive nights (Bernardo & Plotkin, 2007). This phenomenon occurs only at a few beaches around the world but most of them are located on the shores of the Eastern Tropical Pacific (ETP; Pritchard, 2007; Valverde et al., 2012), endowing this ocean basin with the largest number of sea turtles on the planet.

Nancite Beach, a well-known arribada beach, was discovered by the scientific community in 1970, during flights searching for sea turtle nesting beaches on both Caribbean and Pacific coasts of Costa Rica (Richard & Hughes, 1972). Using a quadrat approach where nesting females were counted in an area of known dimensions, arribadas composed of 70,000 to 115,000 females were estimated at this beach in 1971 (Hughes & Richard, 1974), and in 1980 the October arribada was estimated at approximately 150,000 nesting females (Valverde et al., 1998). Nancite stands out from the other arribada beaches in the region due to the absence of egg poaching, as a consequence of its remoteness, and because since 1971 it has been protected within the Santa Rosa National Park (Cornelius et al., 1991; Cornelius & Robinson, 1985). Despite being free from significant human egg exploitation, the size, frequency, and duration of the arribadas at Nancite exhibited significant decreases starting in 1983 (Valverde et al., 1998), dropping by as much as 90% from the 1971 estimates by 2007 (Fonseca et al., 2009). A prevalent hypothesis to explain this significant drop in the adult population is the poor nest microenvironment observed at this beach that led to low hatchling production (Cornelius et al., 1991), where the clutch density was high as a result of large arribadas containing as many as 148,000 egg-laying females in the ~1 km beach (Valverde et al., 1998). Mean clutch density has been estimated at Ostional beach at 4 clutches per m^2 as a result of the large arribadas (Bézy et al., 2016), and it exemplifies the high clutch densities that can be attained at arribada beaches.

Viability of sea turtle embryos in the nest microenvironment is regulated by factors such as the incubation temperature of the eggs (Ackerman, 1997; Valverde et al., 2010), precipitation (Houghton et al., 2007; Matsuzawa et al., 2002; Ragotzkie, 1959), tides (Caut et al., 2010; Foley et al., 2006), and the presence of predators (Cornelius et al., 1991; Eckrich & Owens, 1995). These factors regulate embryo development, sex ratios, and hatchling production, regardless of the number of turtles that nest on a beach. However, there are also density-dependent factors that influence clutch performance (Clusella-Trullas & Paladino, 2007; Honarvar et al., 2008). The effect of density-dependent factors such as clutch density, clutch destruction by other nesting turtles, oxygen availability, and microbial load on olive ridley (*Lepidochelys olivacea*) embryo development are considered to be the main causes of the drastic decrease in the size of the arribadas at Nancite Beach that occurred beginning in the mid-1980s (Bézy et al., 2014, 2015; Clusella-Trullas & Paladino, 2007; Fonseca et al., 2009; Honarvar et al., 2008; Valverde et al., 1998). It is presumed that this reduction was caused by the low recruitment rate to the nesting population during the 1970s when the large arribadas occurred, because the clutch carrying capacity of the beach was exceeded (Fonseca et al., 2009; Valverde et al., 1998). Honarvar et al. (2008) tested this hypothesis at Nancite and determined that the density of clutches increased the incubation temperature and reduced the availability of oxygen, which resulted in hatching rates as low as 29.5% in high-density plots compared with 71.6% of low-density plots. Additionally, eggs destroyed by other nesting turtles decomposed and further contributed to significant microbial load, leading to contamination of the sand and to an anoxic environment (Bézy et al., 2014, 2015; Clusella-Trullas & Paladino, 2007; Honarvar et al., 2011; Mo et al., 1990, 1995). Sustained very low hatching rates for decades presumably impacted the Nancite arribada nesting population.

Because the nesting population has declined over almost four decades at Nancite, we hypothesized that the combined effect of lower nest abundance and destruction contributing to a reduced microbial load is currently allowing increased embryo survival, as demonstrated by the increased hatchling production during the 2007 season (Fonseca et al., 2009). To verify the current condition, this study evaluated hatching success, estimated the size of arribadas and their trends during the last 12 nesting seasons, and compared the results with historical data.

2 | MATERIALS AND METHODS

2.1 | Study site

Nancite Beach is located on the Pacific Northwest coast of Costa Rica (10.804978, −85.699843), in the Santa Rosa National Park, Guanacaste Conservation Area (Figure 1). The beach is devoid of human populations given its National Park status. The beach is 1050 m long and is flanked North and South by two ~50 m tall rocky outcrops. The northernmost 300 m of high and mid beach are covered by white mangrove (*Conocarpus erecta*). In the center of the beach there is an estuary, which is normally disconnected from the ocean and represents the widest section of the beach, at times reaching over 45 m between high tide and the vegetation line. This is the section of beach where the bulk of nesting takes place. From this estuary to the south, beach width oscillates between 5 and 20 m, depending on the tides. The vegetation in this section of the beach includes Beach Hibiscus (*Hibiscus tiliaceus*) and Brazil Wood (*Haematoxylon brasiletto*). The understory includes seashore saltgrass (*Distichlis spicata*) and Beach Morning Glory (*Ipomoea pes-caprae*).

2.2 | Arribada estimation

Field work was conducted every year from 2009 to 2020 for the duration of each arribada season, which spanned from August of 1 year to February of the next. The number of egg-laying females (NEFL) was estimated using the strip transect in time methodology (Gates et al., 1996; Valverde & Gates, 1999). Before each arribada, we placed transects perpendicular to the length of the beach at each 50 m post, for a total of 18 transects. We censused transects every 2 h during

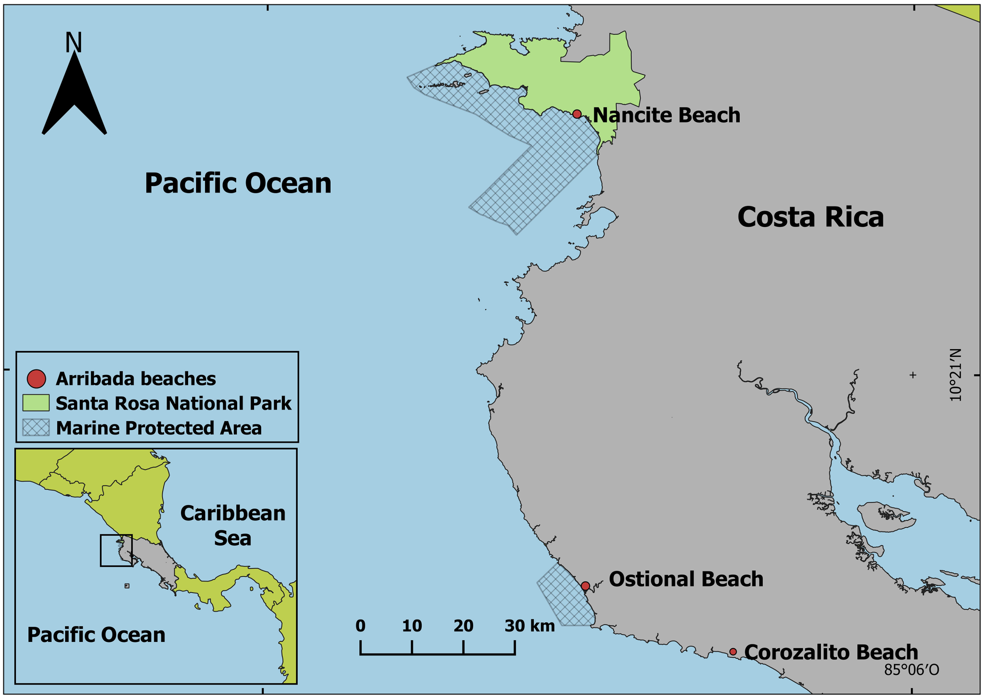

FIGURE 1 Geographic location of Nancite Beach on northwest Costa Rican Pacific coast. Included are also the other two arribada beaches of Ostional and Corozalito.

TABLE 1 Month and year of arribadas recorded at Nancite Beach, Costa Rica during study period. Number of egg-laying females was estimated using the transect method for largest arribadas, and directly counted for the smallest arribadas (bold numbers).

	Month							
Season	July	August	September	October	November	December	January	February
2009–2010	NA	**130**	3810	8271	5696	3164	NA	1906
2010–2011	NA	NA	33,931	NA	29,261	**4000**	**1200**	NA
2011–2012	NA	5691	**2500**	9260	35,652	6715	**1300**	NA
2012–2013	NA	**180**	3819	10,000	16,736	NA	NA	NA
2013–2014	NA	NA	8234	15,617	7674	3877	NA	2143
2014–2015	NA	10,859	28,609	16,383	NA	8385	3009	NA
2015–2016	**300**	3555/17,213	9703	15,836	26,306	5218/2179	1089	NA
2016–2017	NA	**300**	NA	NA	32,525	NA	12,777/13,784	**350**
2017–2018	**200**	2527	28,829	NA	53,932	31,370	NA	NA
2018–2019	NA	**1500**	28,829	26,776	13,190	**500**	7411	NA
2019–2020	NA	**2000**	19,513	26,301	27,439	12,476	NA	NA
2020–2021	NA	NA	NA	NA	57,907	16,377	**3844**	NA

Note: Two estimates separated by dash line represent two different arribadas in the month.

Abbreviation: NA, no arribada.

the peak nesting activity (>100 nesting females) of each arribada by walking from the high-tide marker to the sector marker and counting the number of nesting females with eggs in the nest chamber within the 2-m width of the transects. We analysed transect results with the use of the Arribada Portal web application (Valverde, 2013) to estimate the NELF in each arribada (Valverde et al., 2012). For the purpose of this study, we defined the arribada size as the NELF that participated in each mass-nesting event. When the abundance of nesting females was less than about 4000, estimates of number of breeders were determined by direct counts (Table 1).

2.3 | Arribada trends

We evaluated the trend in the size of the arribadas for the period between the 1980/1981 and 2020/2021 nesting seasons, using a

Generalized Additive Model (GAM) (Fewster et al., 2000). We fitted the GAM to the estimated data from each arribada using a Poisson distribution and a log link function to model the trend as a smooth, nonlinear function of time. We modeled the fit function of the model using 13 degrees of freedom (df), a value that represents 1/3 of the duration of the analysed time series (40 years) as suggested by Fewster et al. (2000). Ninety-five percent confidence intervals for the trend curve were calculated by percentile bootstrapping using 399 replicates (Fewster et al., 2000). The index of relative abundance for each year [$I_{(t)}$] was calculated according to Fewster et al. (2000) as: $I_{(t)}=\exp[\hat{s}(t)]/\exp[\hat{s}(1)]$, where $\exp[\hat{s}(t)]$ is the total predicted count for year t and $\exp[\hat{s}(1)]$ is the total predicted count for year 1 (1980/1981). This produced a time series arbitrarily initiating with an index of abundance value of 1.0. We evaluated changes in the abundance index of arribadas [$\%\Delta$] over time for four decades (1980/1981–1989/1990; 1980/1981–1999/2000; 1980/1981–2009/2010; and 1980/1981–2020/2021), using the following formula: $\%\Delta=(I(_{t2})-I(_{t1}))/I(_{t1})*100$, where $I(_{t2})$ is the index of abundance at time 2, and $I(_{t1})$ is the index of abundance at time 1. Data for the years 1980/1981–2007/2008 were obtained from Valverde et al. (1998), which were based on quadrat counts, and Fonseca et al. (2009), which used strip-transect methodology. No data were available for the seasons 1985/1986, 1986/1987, 1998/1999, and 2008/2009.

2.4 | Disturbed clutches

During each arribada, we randomly marked between 50 and 250 clutches in different parts of the beach. To mark each clutch, we used a 60 cm long monofilament thread. A plastic bottle was tied to one end of the thread, and a 1.5 × 6.0 cm PVC anchor tube was tied to the other end. During oviposition, the PVC tube was introduced into the nest chamber. We wrote the clutch code and oviposition date on flagging tape, and the tape was placed inside the plastic bottle. We kept the plastic bottle on the surface of the sand to facilitate clutch search during the incubation period. If a PVC tube was detected on the sand surface, we regarded it as a disturbed clutch. We classified each disturbed clutch in one of three categories: excavated by other turtles, eroded (effect of tidal overwash), and depredated by raccoons or ghost crabs (the latter determined during excavation). These numbers allowed us to estimate the number of destroyed clutches (DC) during each arribada. We compared these results with the studies conducted by Cornelius et al. (1991) and Fonseca et al. (2009).

2.5 | Hatching rate and hatchling production

We excavated the marked clutches to determine hatching rate 2 days after the last observed hatchling emergence, or 55 days after oviposition. During excavation, we counted the number of shells, estimating hatched eggs whenever more than 50% of the broken shell was found. Unhatched eggs were divided into four developmental categories according to the size of the embryo in relation to the content of the egg: I = 0–25%, II: 26–50%, III: 51–75%, and 76–100% (Santidrián-Tomillo et al., 2009). We estimated hatching rate using the formula $HR=S/(S+U)*100$, where S was number of hatched eggshells and U is number of unhatched eggs. This method of estimating hatching rates may include an error (Ceriani et al., 2021). However, this is the only means by which to compare with hatching rates reported by others. We estimated hatchling production for all arribadas by calculating the hatching rate based on observations from marked clutches and compared with an early dataset from the period 1981/1982 to 1984/1985 (from Cornelius et al., 1991), and the data for the season 2007/2008 (Fonseca et al., 2009). This comparison was calculated as follows: HP = (NELF–DC)*NE*HR, where HP is the production of hatchlings, NELF is the number of egg-laying females (see above), DC is the number of clutches that were destroyed by turtles, etc. (see above) and did not complete incubation process, NE is the mean number of eggs per clutch, and HR is the hatching rate.

2.6 | Data processing and analyses

We used R Software v. 3.6.3 to conduct statistical analyses of changes in the relative abundance of turtles nesting in arribadas (R Core Team, 2020). We implemented the GAM analysis using the functions provided by Rachel Fewster (https://www.stat.auckland.ac.nz/~fewster/trends.html). All means are reported with their respective confidence interval (CI) of 95%.

3 | RESULTS

3.1 | Arribada estimates

Between August 2009 and February 2021, we recorded a total of 62 olive ridley arribadas, of which we estimated 47 by the strip transect in time method. The remaining 15 arribadas were too small to apply this method (Table 1), since their numbers never rose above 100 turtles across the night, and thus were quantified by direct counting of nesting females on the beach. The largest arribada occurred in the month of November and the smallest during the month of August (Table 1). Usually, a single arribada occurred in any month, except in the August and December of 2015/2016 season, and January of the 2016/2017 season when there were two in each (Table 1). A total of 21 months during the study period exhibited no arribada (Table 1). The mean number of arribadas per season was 5.17 (SD = 1.21, min = 3, max = 8), with fluctuations throughout the study period. The lowest and highest accumulated NELF estimates per season occurred in 2009/2010 with 22,977 turtles ($CI_{95\%}$: 11,728–34,226) and 2017–2018 with 116,858 ($CI_{95\%}$: 136,482–97,234), respectively (Figure 2). Transect estimates showed that the average accumulated NELF per season was 65,839 ($CI_{95\%}$: 50,764–80,927).

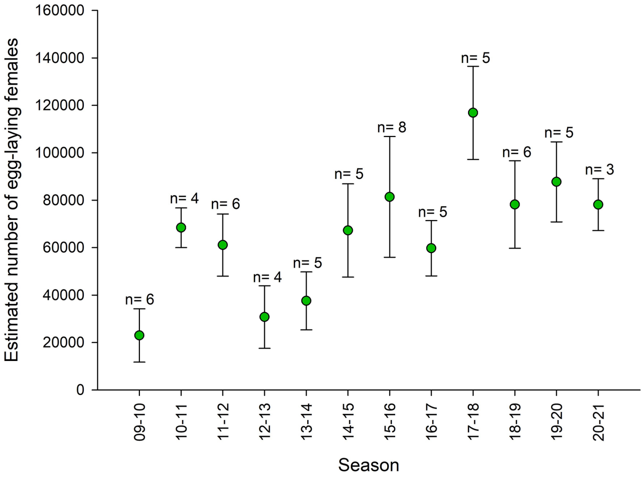

FIGURE 2 Estimated seasonal arribada nesting population abundance estimates and approximate $CI_{95\%}$ for the 2009/2010–2020/2021 period at Nancite Beach using strip-transect methodology (*n* = number of arribadas per season). Estimates with non-overlapping confidence intervals are significantly different.

3.2 | Arribada trends

An analysis of the yearly trend in clutches determined by the GAM showed that from 2009/2010 to present the Nancite arribada population has experienced a significant increase in about 14% (Figure 3a; Table 2). Population trend analysis confirmed that the abundance of nesters in olive ridley arribadas has been drastically reduced since 1980, with the proportional change in abundance relative to 1980 stabilizing at around 2001/2002 (Figure 3b; Table 2). The model showed two peaks of relative abundance: one in the mid-1990s and the second one in the 2018/2019 season. Since approximately the 2000/2001 season the relative population size has been stable with small fluctuations that tended to increase since 2010. The percent change in the abundance index showed that by the 2020/2021 there was a significant reduction of 79% ($CI_{95\%}$: 71–85%) in the size of the arribadas at Nancite Beach, relative to the 1980 estimate, indicating that the population is currently well below the historical estimate.

3.3 | Disturbed clutches

During the 2009/2010–2020/2021 study period we marked a total of 4039 clutches. These data were compared with data from the 1980/1984 season (Figure 4). In the period 2009/2010–2020/2021, on average 17.2% of the nests were disturbed during incubation. The source of disturbance can be broken down as follows: 6.6% excavated by other turtles, 7.8% eroded, and 2.74% predated by raccoons or ghost crabs. In the last 12 years of the study period, the number of disturbed clutches was significantly lower than those recorded in the early 1980s, when this was nearly 40% of the marked nests (Figure 4). Additionally, the percentage of clutches excavated by other turtles was significantly higher in the 1980s than those reported in this study, consistent with a lower nesting population.

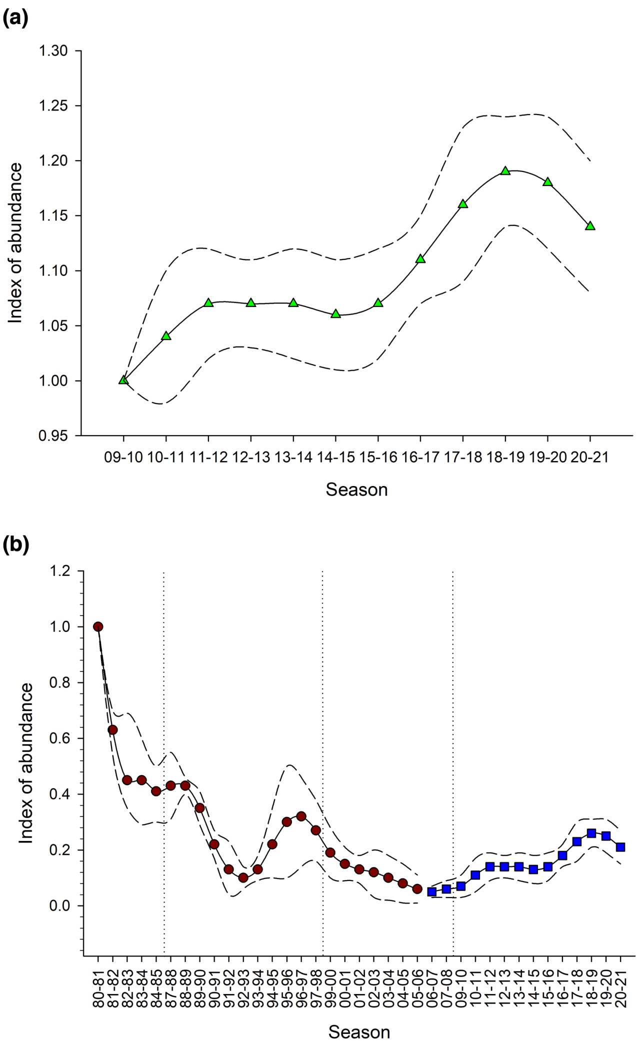

FIGURE 3 Modeled trend for arribada size based on the index of abundance for the Nancite rookery for the (a) 2009/2010 to 2020/2021 period, and (b) annual abundance relative to the 1980/2001 estimate, each year through 2020/2021, using a GAM fitted to nesting female estimates and its bootstrapped $CI_{95\%}$ (dashed lines). Red dots represent egg-laying estimates obtained either by direct counts or by the quadrat method (see Fonseca et al., 2009 for details). Blue squares correspond to egg-laying estimates obtained by the transect method (Gates et al., 1996). Vertical dotted lines represent breaks in the time line.

3.4 | Hatching rate and hatchling production

Overall, mean hatching rate was 33.4% (*n* = 4039, SD = 11.7) for the last 12 years of the study. This was seemingly higher than the 4.2% (range 0.8%–10%) estimated for the period 1980–1984 (Cornelius et al., 1991). Raw data for the early 1980s were not available to calculate $CI_{95\%}$ (Figure 5a). Mean annual hatching rate ranged between 18.8% (in 2009/2010, *n* = 143) and 59.6% (in 2010/2011, *n* = 333) (Figure 5a). Over the duration of the study, an estimated total of 27,343,758 hatchlings ($CI_{95\%}$: 21,423,470–33,119,224) was produced. The estimated annual production of hatchlings varied during the study period, with the highest number estimated in 2017/2018

(4,334,779 hatchlings) and the lowest in 2009/2010 (373,204 hatchlings) (Figure 5b).

4 | DISCUSSION

The monitoring of the arribadas at Nancite Beach, which began in 1971, represents to date one the most extensive datasets for a mass-nesting beach in the world (Fonseca et al., 2009; Valverde et al., 1998). The strip transect in time method (Gates et al., 1996; Valverde & Gates, 1999) used in this study has been widely considered the most reliable for the estimation of arribada turtle abundance by the IUCN Marine Turtle Specialists Group (Valverde & Gates, 1999) and has been systematically implemented on arribada beaches in Mexico (Vega Bravo, 2016), India (Shanker et al., 2004) and Costa Rica (Fonseca et al., 2009; Valverde et al., 2012). Additionally, this method allows a direct comparison between beaches to estimate the number of arribada nesting females when applied consistently.

Our results confirmed that the Nancite olive ridley arribada population continues to exhibit lower abundance values than those recorded in the 1970s and early 1980s. A caveat of this conclusion is that arribada estimates before 1996 were generated by the quadrat method (Cornelius et al., 1991). The transect method used in the present study began to be used in 1996 (Gates et al., 1996). Although both methods estimate the NELF, we have no way of knowing how both methods compare. As such, we assumed in this study that arribada estimates prior to 1996 were equivalent to those generated afterward. In support of this assumption, it is clear that the numbers of turtles reported by others were significantly larger in the 1970s and early 1980s when arribada estimates were in the hundreds of thousands (Cornelius et al., 1991; Hughes & Richard, 1974; Richard & Hughes, 1972). Our analysis also showed that since 2009/2010, the size of the arribadas at Nancite has increased significantly by 14%. These results agree with the hypothesis that the Nancite arribada population is regulated mainly by endogenous factors, where hatching rates are inversely proportional to the size of the nesting population (Valverde et al., 1998). According to this hypothesis, the Nancite arribada population abundance is cyclical over a decadal scale, with steep increases in the abundance of nesting females, concomitant with low hatchling production. This dynamic is presumed to lead to a lower recruitment rate of individuals to the adult population, and the subsequent drop in abundance of the nesting population, similar to the collapse observed in the early 1980s (Valverde et al., 1998). If the lack of recruitment is what caused the crash, then the downward trend of the population is expected to be reversed when the low abundance of adult females yields a higher production of hatchlings (Fonseca et al., 2009; Valverde et al., 1998), as seems to be occurring at present time. However, it is not possible to predict the actual time this cyclicity will take because we do not have sufficient information about mortality rates of juvenile and subadult stages of olive ridleys in the ETP and the rate of recruitment of these stages into the adult population (Seminoff & Shanker, 2008). As such, this lack of information precludes us from making inferences on the future long-term trend of the Nancite nesting population.

TABLE 2 Estimated percent change in nesting female abundance per arribada, showing that only in the current study period has there been a significant increase in the population.

Period	Percentage population change ($CI_{95\%}$)
1980–1981/1989–1990	−65% (−59%, −71%)
1980–1981/1999–2000	−81% (−72%, −90%)
1980–1981/2009–2010	−93% (−89%, 97%)
1980–1981/2020–2021	−79% (−71%, −75%)
2009–2010/2020–2021	14% (8%, 20%)

Note: Estimates were derived from 12 df fitted Generalized Additive Model; bootstrapped 95% confidence intervals are shown in parentheses.

Since the 2009/2010 season, the arribada Nancite population has exhibited significant growth with respect to the abundance reported for the 2007/2008 season (Fonseca et al., 2009). If we assume that the median age to sexual maturity in olive ridleys is 13 (Zug et al., 2006), then the mechanism involved in this increase in

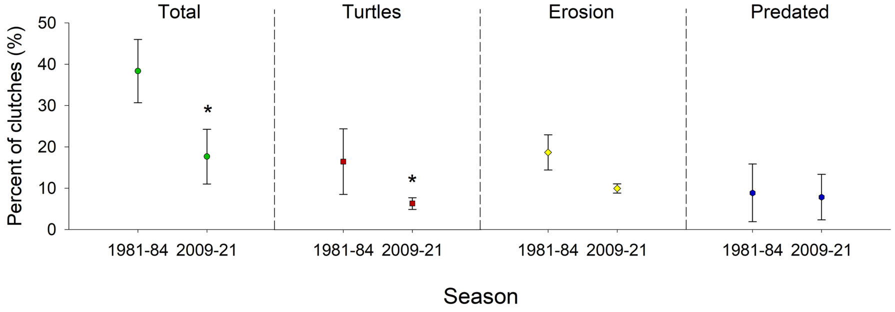

FIGURE 4 Mean percentage of olive ridley (*Lepidochelys olivacea*) clutches disturbed per year during 1981/1984 (*n* = 4) compared with 2009/2021 (*n* = 13) nesting seasons at Nancite Beach by the different factors explained in text: Total = overall value for each study period; turtles = destroyed by nesters excavating previous nests; erosion = eroded by high tides and other climatic conditions; predated = natural predation. Means with non-overlapping confidence intervals were significantly different (asterisks).

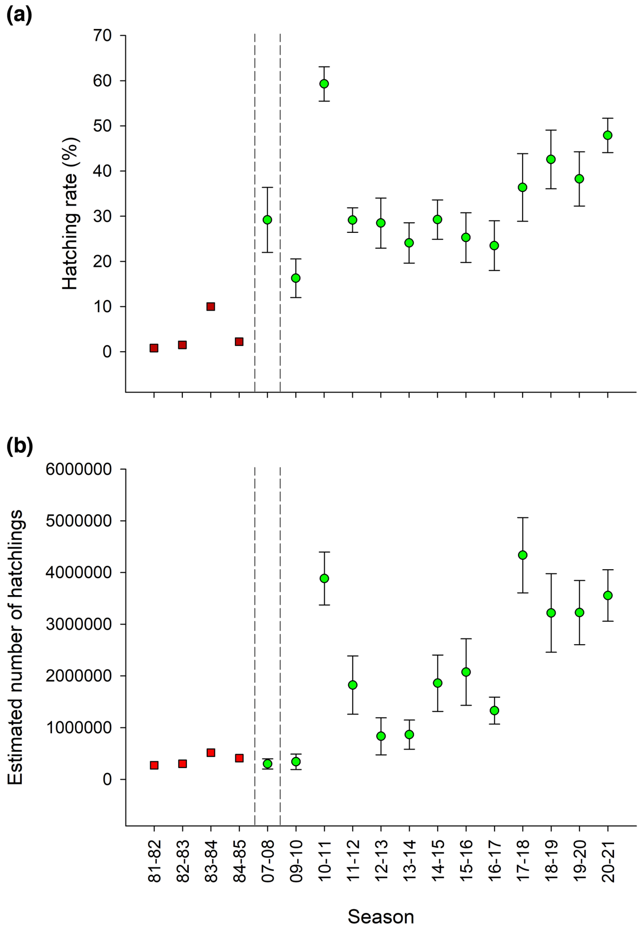

FIGURE 5 Mean hatching rate (a) and associated $CI_{95\%}$ and estimated number of olive ridley hatchlings (b) per season of olive ridleys at Nancite Beach over the 2007/2008–2020/2021 period (green circles). Red squares represent values obtained from Cornelius et al. (1991) for the 1981–1985 period. Vertical dashed lines represent breaks in the time line. Means with non-overlapping confidence intervals are significantly different.

the nesting population is likely based on higher hatchling production during the last four decades, stemming from a lower density of clutches and, therefore, a lower microbial load (Bézy et al., 2014, 2015; Honarvar et al., 2008). Our data show that clutch disturbance by nesting turtles was lower since the 2009/2010 season relative to the levels documented in the early 1980s, in agreement with lower clutch density resulting from a lower number of nesting females. During the period covered by our study, two natural events at Nancite contributed evidence to support the microbial load-based hypothesis. These events were exceedingly high tides observed in June of 2011 that flooded the entire beach, and tropical storm Nate (we registered more than 1000 mm of rainfall in 3 days during this storm, which is unusually elevated for the region) in October of 2017, both of which caused significant erosion of the beach's surface, removing most of it, along with old egg clutches and contaminated sand from previously destroyed clutches. Hatching rates of arribadas that followed these events were 78.7 and 58.2%, respectively (this study). Studies have demonstrated that mechanical removal of surface sand and flooding with seawater have significant hatching-promoting influence on arribada beaches (Bézy et al., 2014, 2015). Indeed, we estimated a production of 2,870,872 hatchlings during the latter arribada alone, which was higher than the 1,452,000 hatchlings reported for the years 1981–1984 combined (Cornelius et al., 1991). These events showed that at least occasionally, Nancite is capable of producing significant pulses of hatchlings. Whether these pulses result in an increased recruitment of females to the arribada nesting population remains to be demonstrated.

One significant caveat is that hatching rates at Nancite fluctuated mostly between 20 and 50% during our study period, which were lower than the nearly 80% hatching rate reported for olive ridleys on solitary nesting ETP beaches (Binhammer et al., 2019; Dornfeld et al., 2015). Although this 20–50% is higher than the 4.2% (range 0.8–10%) reported for Nancite in the early 1980s (Cornelius et al., 1991), it is difficult to imagine a recovery of the nesting population to match the abundance of the 1970s and early 1980s, based on the hatchling production levels we report here. This is because as the number of nesting animals increases, we expect to see continued deterioration of the nest microenvironment, leading to further decreases in hatching rates over time (Bézy et al., 2014, 2015; Fonseca et al., 2009; Valverde et al., 2012). Thus, it may be that the nesting population will remain for many years at levels similar to what we report here. In summary, we do not know exactly how moderate hatching rates are linked to a possible recovery of the Nancite arribada population as there are still many unknowns related to this population, particularly with regard to juvenile survival and recruitment to the adult population. Most importantly, because the Nancite arribada population has been depressed since 1983, it is reasonable to assume that hatching rates have been similarly elevated as in the present study since that year. And yet, the nesting population has not shown a dramatic increase that would place its arribadas at a similar standing as those documented in the 1970s and early 1980s. This suggests that other as of yet unknown factors are playing a significant role in the regulation of the size of the arribadas at this rookery and that we simply do not know enough about the biology and ecology of the phenomenon to draw accurate conclusions and make sound predictions. Thus, only the sustained, long-term monitoring of this important rookery may yield the necessary insight to provide an improved understanding of the mechanics of the arribada phenomenon at this beach.

Given the current dynamics of the arribada phenomenon as documented since 1971, which includes high and low nesting abundance associated with moderately low and high hatching rates, respectively, we speculate that the Nancite arribada population originally established itself quickly and relatively recently, bypassing the need for sustained high hatching rates. To this point, no one has ever documented the natural evolution of an arribada rookery. Interestingly, Corozalito, a small arribada beach recently discovered just south of Ostional beach (Rojas-Cañizales et al., 2022; Viejobueno et al., 2011), is relatively rapidly becoming established as a sizeable arribada rookery. A key aspect revealed by research conducted at that rookery is that arribada populations in Costa Rica are not closed systems and that there exists significant movement of nesting females up and down the coast (Rojas-Cañizales et al., 2022). Thus, it may be that females born at Nancite in the previous five decades are now nesting at Corozalito and Ostional, and elsewhere in the region. Long-term monitoring of these three arribada rookeries could provide valuable insight into the evolution of the arribada phenomenon in this region of the ETP.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions. We thank four anonymous reviewers for their willingness to read and provide editorial suggestions that improved the original manuscript.

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