

## Downward but Stable Trend in the Abundance of Arribada Olive Ridley Sea Turtles (*Lepidochelys olivacea*) at Nancite Beach, Costa Rica (1971–2007)

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**ABSTRACT.** – Although the olive ridley sea turtle (*Lepidochelys olivacea*) is the most abundant sea turtle in the world, the species has exhibited a significant decrease in the size of arribadas at Nancite Beach, Costa Rica, since its discovery in 1970. In the present study, we compiled data on number of nesting females per arribada from previous authors for the period 1971–1997 and collected new data using a total count methodology and a strip transect method for the arribadas during 1999–2007. We used generalized additive models to assess the trend of arribada size for the period 1971–2007. Our data indicate a significant reduction of 42%, 84%, and 90% in the number of nesting females per arribada in the periods 1971–1984, 1971–1992, and 1971–2007, respectively. Although we could not determine the specific reasons for this attrition we speculate that this decline may be driven by embryo-associated mortality due to a poor nest microenvironment in this beach. Our data confirm that the Nancite arribada population has undergone a significant decrease over the past 36 years but that the population currently appears to be at a stable low point. In addition, our data show that hatchling production may be increasing at this beach, which suggests the possibility that this population may recover over a few decades. The significant attrition observed in this study underscores the ephemeral nature of arribada populations in general and the need for the continued monitoring of the Nancite population.

**KEY WORDS.** – Reptilia; Testudines; Cheloniidae; *Lepidochelys olivacea*; Arribada; monitoring; population trend; hatching success; sea turtle; Nancite Beach; Costa Rica

Knowledge of sea turtle population status is essential to devise appropriate conservation measures. However, there is little known about population dynamics of the olive ridley sea turtle (*Lepidochelys olivacea*) that nests massively at a few locations along the Eastern Tropical Pacific rim. Indeed, there is significant lack of published information regarding population parameters such as age to sexual maturity, internesting interval, annual nesting frequency, range of foraging and mating areas, age-associated survival probability, hatching rate and sex ratios, and long-term population trends (Cornelius and Robinson 1985, 1986; Plotkin et al. 1995, 1996, 1997). Much of the gap in the information may be due to logistic constraints associated with the migratory habits of these reptiles and to the difficulty of distinguishing between adult and subadult stages. These logistic constraints explain the preponderance of beach studies. However, studies of the nesting ecology of the different species of sea turtles are essential because they allow the observer to evaluate the health of a population when conducted systematically over long periods of time. Accordingly, the study of the Nancite nesting population has been

conducted by estimating the number of females that nest during arribadas (Hughes and Richard 1974; Cornelius et al. 1991; Clusella-Trullas 1998; Valverde et al. 1998). Arribadas consist of the massive synchronous nesting of hundreds or thousands of turtles over several consecutive days (Cornelius et al. 1991; Fig. 1). This event also occurs at beaches in Mexico (La Escobilla and El Morro Ayuta), Costa Rica (Ostional), and India (Gahirmatha and Rushikulya), with minor arribada beaches also present in Nicaragua (La Flor and Chacocente) and in Panamá (Isla Cañas) (Bernardo and Plotkin 2007).

Nancite Beach was first discovered by the scientific community as an arribada beach in 1970 during an exploratory flight over the Pacific coast of Costa Rica (Richard and Hughes 1972). Hughes and Richard (1974) estimated that at least 70,000 olive ridley females nested at Nancite Beach in the early 1970s, with the largest arribadas including as many as 115,000 individuals. Similar estimates have been reported for the period 1980–1984 at this beach (Valverde et al. 1998). A significant decrease in the size and frequency of the arribadas has also been reported for the period 1987–1996



**Figure 1.** Photograph of an arribada at Nancite Beach taken the morning of 11 November 2007 during the second session of the arribada. Arribadas used to exceed 100,000 egg-laying turtles in the 1970s and 1980s at this beach.

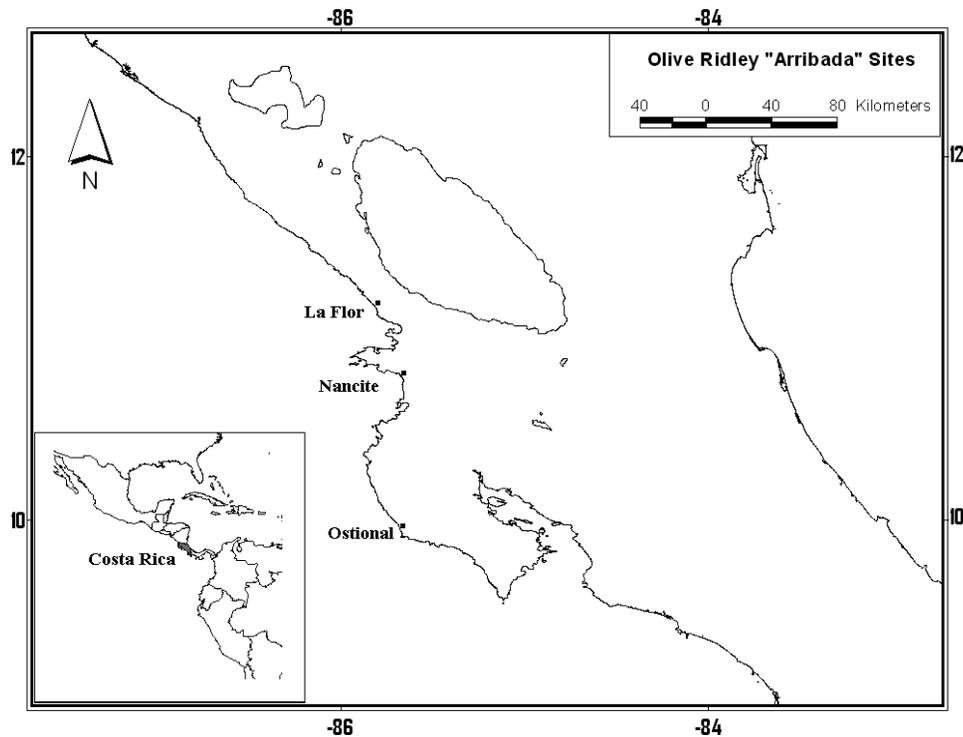
(Valverde et al. 1998). It has been suggested that this decrease may have been due to a low recruitment to the adult population as a consequence of the low hatching rate that Nancite has exhibited for many years (Cornelius et al. 1991). This low hatching rate is hypothesized to be a result of the large amount of organic matter on the beach in the form of unhatched and broken eggs from nests destroyed during arribadas by nesting turtles (Valverde et al. 1998; Clusella-Trullas and Paladino 2007). It has been suggested that organic matter may influence biotic and abiotic factors that impact the development of embryos at the beach by altering the respiratory microenvironment in the nest (Ackerman 1997), and recent evidence supports this (Clusella-Trullas and Paladino 2007; Honarvar et al. 2008). Other variables that may play a role in the decline of the Nancite nesting population include the possible switch of adult females to nearby beaches, such as Ostional (Cornelius and Robinson 1986) or to the large take by sea turtle fisheries that occurred in Mexican (Cliffon et al. 1982) and Ecuadorian (Green and Ortiz-Crespo 1982) waters that operated heavily until the early 1980s and mid-1990s (Frazier and Salas 1982; Aridjis 1990; MDP 1995) within the distribution range of the olive ridleys that nest at Nancite Beach (Cornelius and Robinson 1986; Plotkin et al. 1995). However, large turtle takes would have been expected to impact similarly nearby arribada rookeries, which does not seem to be the case according to a recent report that supposes an increase in olive ridley abundance in the region (Eguchi et al. 2007). In spite of the decline observed in the mid 1990s it has been hypothesized that Nancite Beach arribadas may

undergo population cycles of high and low numbers on a decadal scale as a function of elevated hatching success that may take place when the nesting population is significantly low (Valverde et al. 1998). Accordingly, the main goal of this study is to establish whether the Nancite arribada population has collapsed since the last status report and if it is exhibiting signs of recovery.

The specific objectives of this study were to 1) report on the arribadas occurred at Nancite since 1999, 2) analyze the population trend since 1971 to the present, and 3) compare current hatchling production with historical values to provide a perspective for the potential future outlook of the Nancite population. Our data verifies that the Nancite arribada population has undergone a collapse but that currently the population may be stable.

## METHODS

*Study Site.* — Nancite Beach is fully protected from intrusive human activities within the Guanacaste Conservation Area (ACG), in Costa Rica's Northwest coast (10°48'N and 85°39'W; Fig. 2). The beach length is approximately 1050 m and exhibits a suitable nesting area of approximately 13,000–22,000 m<sup>2</sup>, which varies according to beach erosion, run off, and tidal influence. On the northern and central areas of the beach there are estuaries that may break through the beach during the heaviest rains of the year thus reducing the nesting area. This beach exhibits well-defined dry and wet seasons, where the driest months span January–March and the wettest months span September–November. Heaviest yearly nesting coincides



**Figure 2.** Regional map of the Northwest coast of Costa Rica showing the location of Nancite, Ostional, and La Flor beaches.

with the heaviest rains and lowest temperatures. The beach is mainly occupied by button mangrove trees (*Conocarpus erecta*) and red mangrove (*Rhizophora mangle*) that occupy the northwestern section of the mid and upper beach; whereas, the vegetation behind the mangrove line comprises mainly hibiscus (*Hibiscus tiliacea*), brazilwood (*Haematoxylon brasiletto*), and madrone (*Gliricidia sepium*), with occasional substantial coverage of the mid and high zones by beach morning glory (*Ipomoea pes-caprae*) (Cornelius and Robinson 1985).

**Arribada Estimation.** — In the present study we used the criterion of Valverde et al. (1998) to define an arribada as the presence of 100 or more females on the beach at any given time during a session. A session is defined as the period of consecutive hours in which females nest massively and synchronously within a 24-hour period (Valverde et al. 1998). Data for the years 1971–1972 were obtained from Hughes and Richard (1974), and for the period 1980–1996 from Valverde et al. (1998). For the year 1997 we used data collected by Clusella-Trullas (1998). No data were available for the periods 1973–1979, 1985–1986, and for the year 1998. We estimated arribada size at Nancite since 1999 during the main mass nesting months of August–November. Although arribadas were known to have occurred at Nancite outside the main nesting months, those arribadas were significantly smaller and infrequent and thus not considered. During the period 1999–2005 we estimated the size of the arribadas by direct counts, conducting censuses of egg-laying females and placing small paint marks on their backs to avoid counting the same individual twice. For the years 2006–2007 we

used the strip transect in time method (Gates et al. 1996; Valverde and Gates 1999) to estimate the number of effective nesting females (i.e., the number of females that actually laid eggs) per arribada.

**Index of Abundance.** — We examined the long-term trend in arribada size of nesting olive ridley sea turtles using a Generalized Additive Model (GAM). GAM is a robust and precise tool to model smoothed trends of nonlinear functions over time and consequently assess changes in abundance of wildlife populations (Fewster et al. 2000). We fit 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. The analysis assumes that there are no changes in abundance during the periods 1973–1979 and 1985–1986 when data are missing; we feel that this is a reasonable assumption because of the consistency between early 1970s arribada estimates and those of early 1980s. We modeled the smoothing function using 9 degrees of freedom (df). The criterion for the selection of df was 0.3 times the length of the time series analyzed (27 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 abundance for each year [ $I_{(t)}$ ] was calculated according to Fewster et al. (2000) as

$$I_{(t)} = \frac{\exp[\hat{s}(t)]}{\exp[\hat{s}(1)]} \quad (1)$$

where  $I_{(t)}$  is the index of abundance,  $\exp[\hat{s}(t)]$  is the total

predicted count for year  $t$  and  $\exp[\hat{s}(1)]$  is the total predicted count for year 1.

We estimated the percent change in the number of females per arribada for specific time periods by comparing the indices of abundance calculated for the 1971–1984, 1971–1992, and 1971–2007 time periods in the dataset. Year 1971 was selected as the base year because it is when the first arribada estimate was generated (Hughes and Richard 1974); the years 1984 and 1992 were selected because they correspond with 2 major depressions in the index of abundance; and finally, 2007 was the last year included in our data set. The percent change between year  $t_1$  and year  $t_2$  for the various time periods was calculated as:

$$\% \Delta = \frac{I_{(t_2)} - I_{(t_1)}}{I_{(t_1)}} \times 100 \quad (2)$$

where  $\% \Delta$  is the percent change in the index of abundance,  $I_{(t_2)}$  is the index of abundance at time 2, and  $I_{(t_1)}$  is the index of abundance at time 1. Their respective 95% confidence intervals were obtained by bootstrapping as described above. We implemented the GAM analysis in R 2.6.0 (R Core Team 2008) using the functions provided by Rachel Fewster (<http://www.stat.auckland.ac.nz/~fewster/trends.html>).

*Hatchling Production.* — Hatchling production was estimated for 2007 arribadas by calculating the percent hatchling emergence based on observations from marked nests and compared with an early data set from 1984 (Cornelius et al. 1991). We estimated the proportion of nests destroyed (by predation, nesting turtles, or any other cause) for each arribada by placing a 20-cm plastic ribbon inside the nest chamber (one unique ribbon color for nests from each arribada). In this manner, 202 nests were marked during the October arribada and 50 were marked for the November arribada. The beach was patrolled for plastic ribbons every morning during and after each arribada. Presence of the ribbon from either arribada on the beach surface was indicative of nest destruction. We estimated the proportion of viable nests based on the number of destroyed nests in relation to the total number of nests estimated to have been laid each month according to the strip transect method. In addition, a group of nests were selected at random for each of the October ( $n = 30$ ) and November ( $n = 29$ ) arribadas and protected by a wire mesh cage of  $40 \times 40 \times 10$  cm placed on top of the nests. Cage-protected nests were exhumed 5 days after the first hatchling appeared on the surface to estimate the number of successful nests (nests with at least one hatchling emerged). Percent emergence was calculated according to the following formula:

$$\% E = \frac{N}{H} \times 100 \quad (3)$$

where  $\% E$  is the percent emergence,  $N$  is the number of emerged hatchlings, and  $H$  is the number of eggs in clutch.

Net hatchling production was calculated using the following formula:

$$\% NP = \frac{SN \times EN \times \% E}{100} \quad (4)$$

where  $\% NP$  is the net hatchling production,  $SN$  is the number successful nests,  $EN$  is the mean number of eggs per nest, and  $\% E$  is the percent emergence.

## RESULTS

*Arribada Estimation.* — Data used in our analysis includes previously published data as well as empirically generated data. The oldest data set (1971–1972) was obtained from one of the original publications on the discovery of Nancite as an arribada rookery (Hughes and Richard 1974). The methodology used by the authors consisted in censusing with unspecified frequency a series of 20-m transects that extended from the surf line to the vegetation, assuming correctly that every turtle remained on the beach for approximately 1 hour. At the end of the arribada data were extrapolated to the entire time and area occupied by the turtles on the beach. A second data set consisted of the first evaluation of the trend of the Nancite arribada population (Valverde et al. 1998), spanning the years 1980–1996. The authors used a method in which the beach was systematically sampled during each arribada using quadrats of  $10 \times 10$  m every 2 hours and then extrapolating the counts to the entire time and area occupied by the turtles on the beach. Details of the formula and method used by the authors in the extrapolation of the data are shown in Valverde et al. (1998). A third data set for the year 1998 was obtained from a report by Clusella-Trullas (1998) using the quadrat method. Finally, we used 2 methods to generate our data set for the period 1999–2007. For logistical reasons we used a total count methodology in which virtually every egg-laying turtle was counted, while avoiding counting the same animal twice by placing a small mark on the carapace of the counted individuals. This methodology represented an exceptional challenge, particularly in the larger arribadas where it was difficult to ensure complete count of individuals. Due to the logistics involved we decided to use the strip transect in time method (Valverde and Gates 1999). This method is statistically robust and unbiased and yields highly reliable estimates that include statistical descriptors of the error associated with the estimate (Gates et al. 1996). From our experience, we recommend the strip transect in time method as the method of choice to generate arribada estimates given its flexibility, statistical robustness, and reliability. Although the methods used to collect the data in our analysis exhibit significant differences among them we believe that they were comparable given that they generated an estimate of the same variable, i.e., number of egg-laying females in each arribada. One important aspect to mention is that the methods employed in the published compiled works may

**Table 1.** Mass nesting dates, estimates, and duration for Nancite beach for the period 1999–2007.<sup>a</sup>

Year	Aug	Sessions	Sep	Sessions	Oct	Sessions	Nov	Sessions
1999	2547	3	20,781	6	NA		41,149	5
2000	ND	4	NA		13,006	6	1134	2
2001	3313	4	8675	5	NA		NA	
2002	5071	3	ND		19,719	5	NA	
2003	ND		NA		ND		6150	5
2004	410	2	2402	3	NA		4950	3
2005	2000	3	NA		NA		12,000	4
2006	ND		3100	3	7900	4	256/2680	2/2
2007	300	2	NA		10,622	5	6954	8

<sup>a</sup> See Methods section for definition of a session. NA, no arribada; ND, no data.

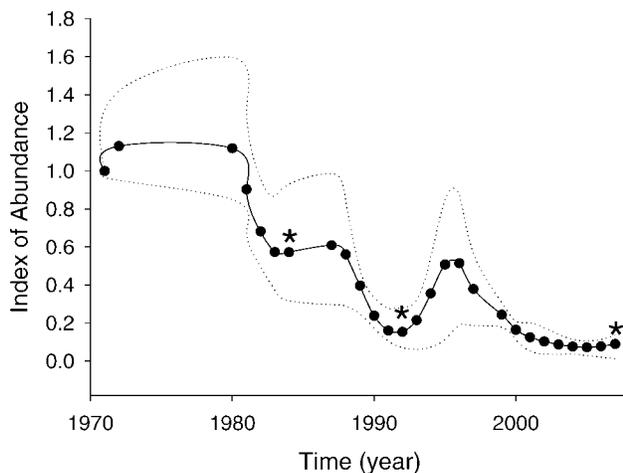
be biased and that these biases may have an effect on our GAM analysis. We have no way to control or measure those biases and assume that any effects on our analysis are negligible. We feel that this is a reasonable assumption given that our empirically derived numbers are clear and show a decreasing trend in abundance.

During the 1999–2007 study period, 22 arribadas were censused (Table 1) with a mean duration of 3.9 sessions per arribada (confidence interval, 3.2–4.6). During the last 10 years of the study the largest arribada was recorded on November of 1999 (41,149 females), followed by the September 1999 (20,781 females) and October 2002 (19,719 females) arribadas. These arribadas each had a duration of 5 sessions (Table 1). The smallest arribadas recorded within this same period were the ones from August 2007 (300 females), November 2006 (256 females), and August 2004 (410 females). All these arribadas had a duration of only 2 sessions (Table 1). November of 2006 was the only time when 2 arribadas (256 and 2680 females) occurred within the same month. No arribadas occurred in October 1999, September 2000, October and November 2001, November 2002, September 2003, October 2004, September and October 2005, and September 2007. Censuses were not conducted (indicated

as “no data” in Table 1) during the August 2000, September 2002, August 2003, and August 2006 arribadas. Limited data were collected only during one session of the October 2003 arribada, with an estimate of about 3000 turtles for that session. Because it was incomplete this data set was not included in the analysis.

*Index of Abundance.* — We used GAM to model the abundance of arribada olive ridleys over the study period based on individual arribada estimates for each month during the peak nesting months in which mass nesting events took place. GAM is a robust, nonparametric modeling tool specifically developed for the analysis of long-term trends of wildlife populations based on estimates derived from empirical counts. For specific technical details on the technique please see Fewster et al. (2000). Figure 3 shows the long-term trend of arribada sizes at Nancite Beach as described by our GAM analysis. Arribadas exhibited a pronounced decline since 1982 and continued until present time with 2 brief rebounds, one in the late 1980s and another one in the mid 1990s. The arribada population seems to have reached a stable low point since the year 2000 and maybe even as early as 1990. GAM analysis indicated that the number of nesting females decreased 42% (95% CI = –68% to –7%) between 1971 and 1984, 84% (95% CI = –92% to –71%) between 1971 and 1992, and 90% (95% CI = –98% to –86%) between 1971 and 2007 (Table 2).

*Hatchling Production.* — We were able to estimate hatchling production only during the peak nesting months of 2007. We compared these estimates with hatchling production estimates from the mid 1980s available in the literature when the Nancite population was thriving to provide a perspective on current hatchling production levels (Cornelius et al. 1991). We estimate that 17,576 nests were laid during the 2007 arribadas, in contrast with



**Figure 3.** Modeled trend for arribada size based on the index of abundance for the Nancite rookery (1971–2007) using a GAM fitted to nesting female estimates with 9 df (solid line) and its 95% bootstrapped confidence limits (dashed lines). Asterisks indicate a significant difference with respect to 1971.

**Table 2.** Estimated percentage change in nesting female abundance per arribada for olive ridley derived from 9 df fitted Generalized Additive Model. Bootstrapped 95% confidence intervals are shown in parentheses.

Percentage population change (95% CI)		
1971–1984	1971–1992	1971–2007
–42 (–68, –7)	–84 (–92, –71)	–90 (–98, –86)

**Table 3.** Comparison of hatchling production estimates from the combined 1984 August and September arribadas and the 2007 October and November arribadas at Nancite Beach.

Arribada parameter	1984 <sup>a</sup>	2007	
	Aug + Sep	Oct	Nov
Total no. of nests	60,300	10,622	6954
% of nests that hatched	27.1	63.3	96.6
No. of nests that hatched	16,341	6723	6717
Mean clutch size	99.5	107	96.09
No. of eggs in successful nests	1,625,959	719,361	645,436
% hatch of successful nests	8.3	17.72	26.75
No. of hatchlings produced	134,955	127,470	172,654
Total no. of hatchlings produced	134,955	300,124	

<sup>a</sup> Data from Cornelius et al. (1991).

the 60,300 nests laid during the August and September arribadas of 1984 (Table 3). An estimated 63.3% and 96.6% nests were successful during the 2007 October and November arribadas, respectively, contrasting with 27.1% for the 1984 arribadas. These rates represent a similar number of successful nests for both years (16,341 nests for 1984, and 12,941 nests for 2007), which is striking given the large difference in nests laid. The estimated hatching rate of 8.3% during 1984 was inferior to that of 17.72% and 26.75% obtained in this study during 2007. Total hatchling production in 2007 was estimated at 290,486, which was superior to that of 134,955 in 1984. This increased production was associated with a 3-fold higher nest density during the 1984 season and a greater number of successful nests during 2007.

## DISCUSSION

Nancite Beach was once considered one of the most important olive ridley rookeries in the Eastern Tropical Pacific due to its large arribadas (Cornelius and Robinson 1982). However, the 90% decrease in the size of the arribadas over the nearly past 4 decades has not only changed its global ranking but is consistent with a collapse of this arribada assemblage. This decrease can clearly be observed in the significant downward trend in the index of abundance for arribada sizes at Nancite (Fig. 2). Indeed, the size of the arribadas over the last 10 years represents the lowest records at Nancite since arribadas were discovered at this beach in 1970. As discussed later, it is unknown whether this trend will continue in the future.

The arribada phenomenon represents a reproductive behavior that may afford an evolutionary advantage to the species of the genus *Lepidochelys*, as explained by the predator satiation hypothesis in which arribada nests are less predated than those of solitary nesting females (Eckrich and Owens 1995). Although data supporting this hypothesis have been questioned (Bernardo and Plotkin 2007), the predator satiation hypothesis seems to apply effectively to Nancite olive ridleys because this explains well the potential mechanism by which arribadas may have originally formed at this beach. An added advantage

of the arribada behavior is that it facilitates mating, as indicated by the increased level of multiple paternity in nests from arribada females (Jensen et al. 2006). This is thought to occur due to the increased availability of females that may gather close to the beach, which will significantly reduce competition among males thus reducing energetic costs of reproduction. Thus, from an evolutionary point of view the increased multiple paternity observed in arribada nests suggests the possibility that the arribada behavior evolved to maximize the chances of fertilization in a seemingly female-biased assemblage. This may be important for the olive ridley because this is a highly migratory species, which can ensure its fertility by congregating in a relatively small area.

In contrast to the hypothesized mechanism that gives rise to the establishment of the arribadas and what advantages this synchronous mass nesting behavior may confer, little is known about the life cycle of such unique phenomenon and whether a particular mechanism may trigger the attrition of a rookery. In the case of Nancite, our empirical data show that this population has undergone a collapse over the last 2 decades, in agreement with its decimation forecasted by previous studies (Cornelius et al. 1991; Valverde et al. 1998). The collapse of arribada populations is not a new event. For instance, at least 3 formerly large arribada assemblages in Mexico vanished as a result of overexploitation of adults and eggs by about the time that the Nancite population was discovered (Cliffton et al. 1982). The 90% reduction in the Nancite arribada population that occurred since the early 1970s may be construed as paradoxical, especially considering that this nesting population has enjoyed full protection within the ACG and has been essentially free from direct impact of anthropogenic activities on the beach since its discovery in 1970. In contrast, other regional arribada beaches that have been subjected to heavy egg extraction by coastal communities and high predation on hatchlings and eggs by domestic animals such as Ostional and La Flor in Costa Rica and Nicaragua, respectively, appear to be stable or increasing in numbers (Eguchi et al. 2007). Among the possible explanations for this difference in nesting trends of arribada beaches in the region factors

such as historical directed and incidental fisheries, El Niño phenomenon, natural endogenous fluctuations in the nesting population, beach exchange, and low hatching success with subsequent low recruitment to the adult population have been suggested (Cornelius and Robinson 1984; Valverde et al. 1998). However, it has been noted that the first 4 factors would be expected to impact all beaches in a similar manner (Valverde et al. 1998) and that in some of those cases would only account for short-term fluctuations in the nesting population. The decrease we report here represents a clear and sustained decline in the nesting population that appears to be site specific. Thus, of the factors mentioned above we believe that low hatchling production is most likely to explain the sustained decline in the Nancite nesting population.

Low hatching rate has been implicated by various studies as an important factor that may impact the stability of the adult nesting population. The first report of low hatchling production at Nancite Beach was published soon after the discovery of the arribadas there when hatching rate was estimated at 0.2% (Hughes and Richard 1974). In the early 1980s hatching rate was reported at 4.2% (Cornelius et al. 1991). More recently, hatching rate has been estimated at Nancite between 8% and 21.6%; although, sample sizes were low and likely not representative of the entire beach (Clusella-Trullas and Paladino 2007; Honarvar et al. 2008). In contrast, these hatching rates at Nancite Beach are significantly lower than those at solitary olive ridley nesting beaches where rates have been estimated at close to 90% (Reichart 1993). Together these results indicate that low hatching rates have pervaded hatchling production at Nancite for decades, the effects of which may only now be showing in the nesting population. Interestingly, our numbers show that hatching rates at Nancite may be improving significantly in recent years as we discuss below.

The reduction in hatchling production at Nancite may be due to density-dependent effects associated with the large numbers of eggs laid during early season arribadas. For instance, Cornelius et al. (1991) reported that the 1984 August and December arribadas produced 134,955 hatchlings from a total of 60,300 nests laid during those 2 months combined. Hatchling production was significantly larger during 2007 when during the October and November arribadas we estimated that 290,486 hatchlings were produced from a total of 17,576 nests laid. This increased production is due to the elevated hatching rates of the 2007 October (17.72%) and November (26.75%) arribadas, in contrast with the 1984 hatching rate of 8.3%, and to the greater number of successful nests during 2007. Thus, our data suggest that hatching rate at Nancite may be on the rise. If this is sustained for several years, it is possible that the Nancite arribada population may recover in a few decades, assuming a concomitant increase in recruitment, in agreement with the speculated cyclical nature of arribada life cycles (Valverde et al. 1998).

It has been suggested that the low hatching rate at Nancite Beach may be due to the organic matter of broken eggs from nests destroyed by nesting turtles and other sources. This organic matter may serve as a substrate for microorganism growth, thus leading to a significant decrease in oxygen availability for embryo development (Cornelius and Robinson 1985; Valverde et al. 1998). Studies have shown that Nancite Beach exhibits a larger microbial community than that of solitary nesting beaches, such as fungi and bacteria, that is thought to be sustained by the availability of organic matter (Mo et al. 1990, 1995). Moreover, these microorganisms may also negatively contribute to impact fertile eggs during the incubation period (Phillott and Parmenter 2001a, 2001b). Recent evidence showing significant early embryo death at Nancite Beach supports this possibility (Clusella-Trullas and Paladino 2007). All these factors may significantly impact overall embryo development, thus limiting hatchling production. Thus, it is expected that sustained low hatching rates for long periods (e.g., decades) may impact recruitment to the adult population and thus lead to the current low nesting, as suggested previously (Cornelius et al. 1991).

Recently studies focusing on the nest microenvironment have been conducted to attempt to elucidate the mechanisms underlying the significant attrition of the Nancite arribada assemblage. In a study looking at the incubation microenvironment of arribada nests at Nancite Beach it was found that nests moved to a hatchery and incubated in clean sand (*ex situ*) exhibited a hatching rate significantly higher than nests incubated *in situ* (Clusella-Trullas and Paladino 2007). During most of the first half of incubation *in situ* nests were found at significantly lower oxygen and higher carbon dioxide partial pressures than *ex situ* nests during the same period. These partial pressure profiles can be explained by the higher metabolic activity of microorganisms found in contaminated sand of *in situ* nests and suggests that lower oxygen and elevated carbon dioxide partial pressures are responsible for the associated lower hatching success of *in situ* nests. This is in agreement with the hypothesis that increased microorganism metabolic activity is an important biotic factor driving the low hatching rates at Nancite Beach by deleteriously regulating the respiratory environment of the embryos (Valverde et al. 1998). It is possible that the low hatching rate at Nancite Beach may be enhanced by density-dependent effects that could alter biotic and abiotic factors of the nest microenvironment such as oxygen and temperature (Ackerman 1997). Accordingly, in another study Honarvar et al. (2008) examined density-dependent effects on hatching rates at Nancite Beach. They found that nests incubated at high nest density (9 nests/m<sup>2</sup>) exhibited a significantly lower hatching rate than nests incubated at low nest density (2 nests/m<sup>2</sup>). Further, they found that during the second half of the incubation period nests from higher density areas also exhibited lower oxygen and higher carbon dioxide amounts in the sand than nests

incubated at lower density. These gas profiles were attributed to increased metabolic activity among adjacent developing embryos during the incubation period (Honarvar et al. 2008). Unfortunately, biotic and abiotic factors such as the ones studied so far have only been examined punctually during a single arribada and not continuously throughout a nesting season. This makes it difficult to determine whether these conditions are representative of the incubation dynamics at Nancite Beach. Indeed, Honarvar et al. (2008) suggest that oxygen and carbon dioxide as well as temperature should be studied throughout an entire nesting season, including periods when nests from different arribadas incubate naturally and simultaneously at the beach, to understand how these factors fluctuate temporally and influence embryo development. Similarly, there is little information regarding biotic and abiotic factors from other arribada beaches. This precludes the comparative analysis among beaches and the verification of the observations that suggest that incubation conditions at Nancite Beach are not optimal for embryo development.

In summary, the arribada size at Nancite Beach during the last 16 years has decreased by 84% to 90% relative to the 1970s. This strong reduction suggests that in the near future arribadas may stop occurring at this beach. However, our trend analysis indicates that this arribada assemblage has reached a low, but stable point. In addition, hatching rates at Nancite Beach seem to be improving recently, which suggests that this arribada population may recover after some time. This is in agreement with the prediction that this assemblage may undergo wide, cyclical fluctuations over large time scales (Valverde et al. 1998). If the prediction is correct, it is expected that over the next few decades hatching rates at Nancite may increase over current levels, followed by a significant rebound in the nesting population. Exactly how long it will take this recovery in hatchling production and arribada sizes to occur or if it will occur at all is unknown. Our findings strongly argue for the continued monitoring of the arribadas at Nancite Beach paying close attention to hatching success at this beach over the next decades. This will provide information that may allow us to evaluate the future evolution of the arribada assemblage at this beach. The importance of these long-term studies can hardly be overstated as they may help us understand the processes that are at play, which may regulate arribada occurrence at other arribada beaches around the globe. If our analysis is correct in that the unsuitable nest microenvironment is responsible for the demise of the Nancite arribada nesting population then how long it will take for other arribada rookeries to follow the same fate remains an open question.

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