

Olive Ridley Mass Nesting Ecology and Egg Harvest at Ostional Beach, Costa Rica

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ABSTRACT. – The olive ridley sea turtle (*Lepidochelys olivacea*), a species listed by the International Union for Conservation of Nature as vulnerable, is characterized by its mass-nesting behavior, also known as arribada. For decades, this phenomenon has facilitated the utilization of this species by coastal communities, much of it illegally. At Ostional beach, Costa Rica, a community-based egg-harvest program operates legally to generate important income for the community while promoting the protection of the ridley nesting assemblage. However, to date, no analysis exists that indicates the long-term viability of the egg harvest program as a sound management tool. To address this void, we generated baseline abundance data of the major arribada events that occurred in the period 2006–2010, as well as egg harvest data, along with preliminary hatching success. Arribadas ranged between 3564 and 476,550 egg-laying females, which indicated a large variability in the magnitude of the mass nesting events. Estimated mean egg harvest was 4746.4 and ranged from 1527 to 8138 total clutches. In relation to the estimated number of clutches laid, the estimated mean of clutches harvested was 21.2%, ranging from 1.5% to 102.4%. Estimated monthly mean hatching rates ranged from 0.0% to 32.6%. It is not clear whether arribadas underwent a significant change in abundance during the study period, although the number of years covered is too short to establish a long-term trend. However, when compared with historical data, the population appears to have declined. Based on our data, we present various management recommendations aimed at increasing hatching rates.

KEY WORDS. – *Lepidochelys olivacea*; arribada abundance; hatching rate

The olive ridley (*Lepidochelys olivacea*) is thought to be the most abundant sea turtle species. This is due to its pantropical distribution and to its impressively large mass synchronous nesting aggregations, known as arribadas, a nesting phenomenon in which tens of thousands to hundreds of thousands of turtles may participate over the course of a few nights (Fig. 1). Although impressive, this mass nesting behavior has facilitated the harvest, and sometimes the decimation, of olive ridley assemblages by humans. Indeed, at least 2 large arribada rookeries in Mexico vanished due to overexploitation, with 4 of the largest Mexican nesting assemblages reported as collapsed by 1982 (Cliffon et al. 1982). A recent status review for the olive ridley confirms these collapses (Plotkin 2007). Nesting olive ridley population declines have been more severe in the Mesoamerican beaches over the past 50 yrs, in part, because of the legal and illegal

take of eggs (Cornelius et al. 2007). The threat of the egg take for human consumption continues today.

Ostional beach in northwest Costa Rica is an arribada rookery that supports a large mass-nesting assemblage along with a legal community-based egg-harvest program (Fig. 2) (Campbell 1998; Hope 2002; Campbell et al. 2007). This rookery was first discovered by the scientific community in 1970 (Richard and Hughes 1972). However, the community of Ostional settled in the area decades before this discovery, and it is thought to have collected eggs for local consumption now for over half a century (Morera 2010). In spite of the egg take, it was not until 1987 when the fully legalized harvest of ridley eggs began (Campbell 1998). The rationale that supported the Ostional egg harvest was based on analysis of data that showed that a significant number of clutches is destroyed



Figure 1. Day time arribada nesting at Ostional beach. This arribada was estimated at 62,757 (CI_{95%}, 72,408–53,106). Photo taken by P.J. Baltodano the morning of 14 November 2006.

during arribadas by nesting turtles, that hatching rate at this beach is very low, perhaps too low to sustain the adult population, and that legalizing the harvest may help to limit the previously uncontrolled illegal take of eggs (Alvarado-Ulloa 1990; Cornelius et al. 1991). Two important conditions to sustain the Ostional legal egg

harvest were that the program had to demonstrate its biological feasibility and that the community would organize to collect the eggs while protecting the turtles. In compliance with these requirements the Ostional community formed the Association for the Integral Development of Ostional (ADIO for its acronym in

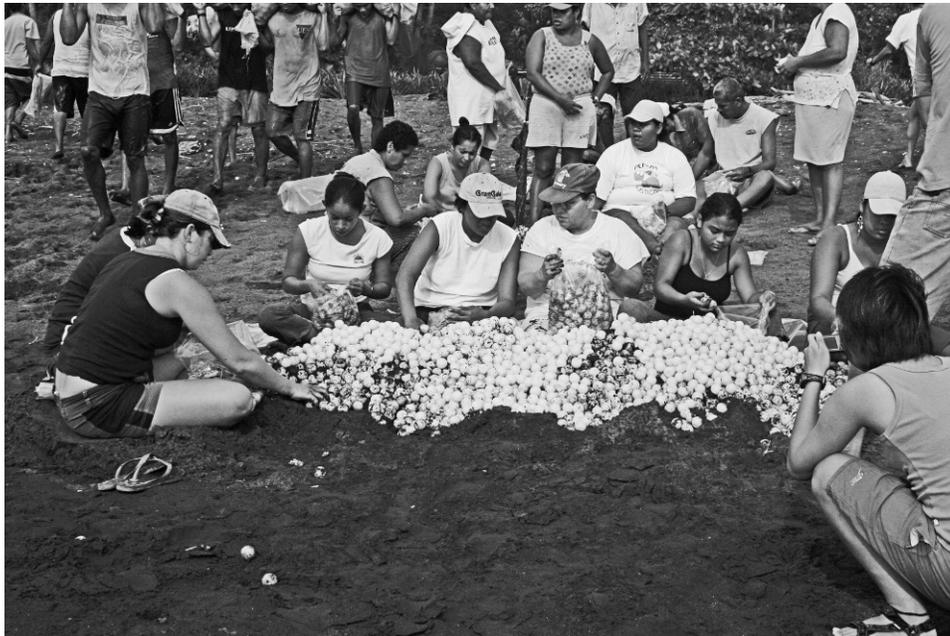


Figure 2. Selection and packaging of olive ridley eggs harvested during an arribada. Eggs are sold and distributed in the Costa Rican market. Photo by R.A. Valverde.

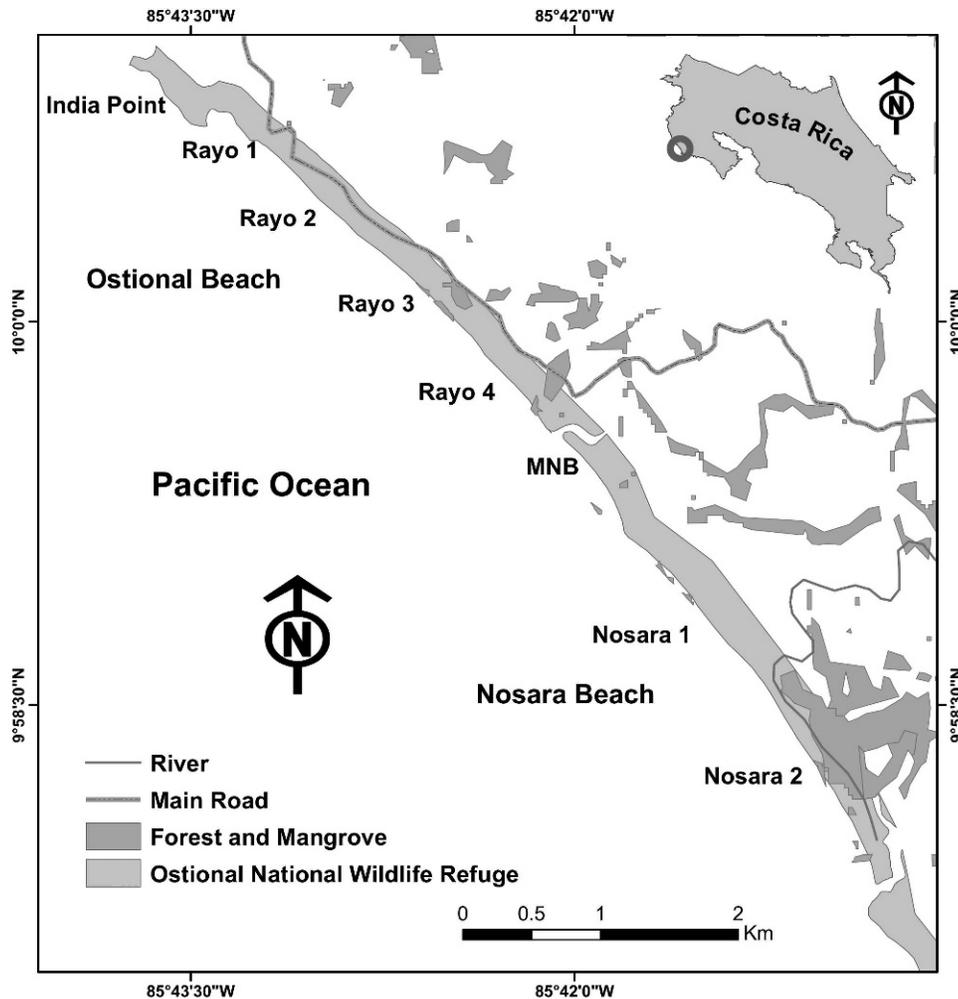


Figure 3. Map of the Ostional area showing the Ostional National Wildlife Refuge (the beach width is approximately 200 m from the average high tide line). The map includes the various beach sections (Rayos, main nesting beach [MNB], and Nosaras) in which the beach is divided to facilitate field work.

Spanish). Today the egg harvest functions much as it was suggested by the scientific community: the associates are allowed to harvest eggs for the first 2.5 d of each arribada (the first 2 d for commercialization and the last half a day for local consumption), while keeping the beach clean and reducing the impact of feral predators (Pritchard 1984; Ordóñez et al. 1994). The harvest is sanctioned by the government, and the proceeds are administered by ADIO, with the profits shared between the associates and the community (Campbell 1998; Campbell et al. 2007). Although, from the socioeconomic standpoint, the egg harvest has made important contributions to community development, very little biological data from the program have been scrutinized by the scientific community in the form of scientific publications, and much of these publications remain in the gray literature. The lack of empirical data collected by using sound and robust methodologies has created much confusion in the scientific community as well as in the government and the public opinion. Although this significant gap has not prevented adaptive changes in the way the project

operates, peer-reviewed basic information to ascertain the health of the Ostional ridley population is urgently needed. Thus, this article reports on 5 yrs of data collection on the adult nesting population, along with hatching success and rate of egg take.

METHODS

Study Area. — The Ostional National Wildlife Refuge (ONWR) is located on the northwest coast of Costa Rica (lat 9.993913°N, long -85.700403°W). The ONWR includes approximately 7 km of beach on its northern section, with a variable width (Fig. 3). The beach was marked with posts every 50 m, from northwest to southeast, into subsections: Rayo 1 (approximately 850 m, posts 1–17), Rayo 2 (approximately 550 m, posts 18–29), Rayo 3 (approximately 500 m, posts 30–40), Rayo 4 (approximately 900; posts 41–59), main nesting beach (MNB; approximately 900 m, posts 60–78), Nosara 1 (approximately 2300 m, posts 79–125), and Nosara 2 (approximately 700 m, posts 126–140). Arribadas tended

to concentrate on the MNB; however, large events sometimes occupied adjacent beach sections, as has occurred in the past (Ballesterio et al. 2000). An estuary of approximately 16,850 m² was located behind the MNB; this estuary commonly broke through the beach into the ocean seasonally due to the heavy rains, thus destroying many clutches. The village of Ostional, populated by approximately 450 people, is located adjacent to the north end of the MNB. In 1983 the Ostional Wildlife Refuge was founded by law 6919 to protect the arribada assemblage nesting at this beach. Since 1987, this beach has supported a legal harvest of olive ridley eggs.

Arribada Census. — Before every arribada, we set up transects perpendicular to the length of the beach at every 50-m post at a rate of 21 transects per km in the area where the bulk of the turtles were nesting. The length of each transect was fixed for the duration of each arribada and was determined by the width of the beach, which extended from the last high tide line before the onset of the arribada to the vegetation line. We established transects with a fixed width of 2 m by burying 1-m-long stakes in the sand with a piece of garden hose attached to the upper end and by following parallel imaginary lines. The garden hoses had reflective tape and were clearly visible to the observer at night and allowed turtles to freely crawl about the beach with minimal disturbance to the stakes. Once transects were established, they were not modified in any way for the duration of each arribada. Transect censuses, i.e., we counted every single turtle in the transects that displayed unambiguous egg-laying activity (UELA) as defined by Gates et al (1996), started when an estimated 100 turtles were present on the beach (to avoid censusing the beach during high solitary nesting activity) and continued until fewer than an estimated 100 turtles were visible on the beach, as arbitrarily defined by an experienced observer. Transects were not censused during the daytime to keep in line with historical methodology. Daytime nesting occurred only during a day or two of some of the largest arribadas. The end of the arribadas was characterized by the emergence of a significant proportion of injured or otherwise unhealthy turtles that were unable to nest or had great difficulty doing so. We conducted systematic censuses every 2 hrs from the high tide line to the vegetation line, starting at one end of the MNB and ending at the opposite end. We conducted censuses by walking the transects at a steady pace, stopping briefly only to verify egg-laying activity. We estimated that 21 transects were censused in approximately 45 min during peak nesting hours. Because only UELA turtles were counted, 1 turtle was equivalent to 1 clutch.

We analyzed data collected during transect censuses over the duration of each arribada by using the Arribada Portal software, a Web-based application with algorithms specifically written for this purpose based on published strip transect methodology (Gates et al. 1996; Valverde

and Gates 1999). This application allowed us to compute an estimate of the effective number of arribada females that participated in each arribada as well as the variance of the estimate for unequal transect lengths, with its respective approximate 95% confidence intervals (CI_{95%}), standard error, and coefficient of variation (CV) (Gates et al. 1996; Valverde and Gates 1999). The effective number of nesting turtles is defined as the number of turtles that actually laid eggs.

To calculate arribada estimates, it was first necessary to calculate the effective nesting area, defined as the portion of beach where the bulk of the nesting population laid its eggs. This was done by using the approximation method according to Simpson's rule, with transect lengths defining the width of the area. The length was defined by the section of beach between the first and the last transects by using the formula:

$$As = \frac{1}{3}h[(y_0 + y_n) + 4(y_1 + y_3 + \dots + y_{n-1}) + 2(y_2 + y_4 + \dots + y_{n-2})]. \quad [1]$$

Where: *As* = area by approximation according to Simpson's rule (m²), *y*₀, *y*₁, *y*₂, ..., *y*_{*n*} = lengths of individual, equally spaced parallel transects from first (*y*₀) to last (*y*_{*n*}) (m), *h* = distance between transects (50 m). Equation 1 was applicable when the total number of transects was even. We implemented a modification to deal with uneven transect numbers by eliminating the first transect and by applying the formula to all remaining transects. We then calculated the missing area for the eliminated 50-m section by obtaining an average length of the first and second transects and then multiplying by 50 m; the resulting area was then added to the area approximated by Simpson's rule as explained above. In addition, we measured egg-laying time (time lapse between first and last egg) and the number of eggs per clutch in a subset of arribada turtles during multiple arribadas, under diverse conditions (e.g., time, density) during the term of the project. Mean egg-laying time was used to compute abundance estimates for all arribadas sampled, thus reducing variability among estimates.

Hatching Rates. — During the 2007 arribadas we marked nests randomly selected across the entire nesting area by using a wire mesh cage of 30 × 30 × 50 cm, by tying a piece of PVC pipe with a unique identifier and date of oviposition to the top of the cage. Cage nest protection was necessary to ensure that a minimum number of clutches would survive to term, undisturbed by subsequent nesting turtles, predators, or egg harvest. We refer to these as term nests (Cornelius et al. 1991). Starting on day 40 of the incubation period, we inspected nests 3 times daily (midnight, morning, noon) for signs of hatchling emergence. All clutches were exhumed 2 d after the last hatchling emergence or 55 d from oviposition. Exhumation data included number of empty shells, number of live and dead hatchlings in the nest, number

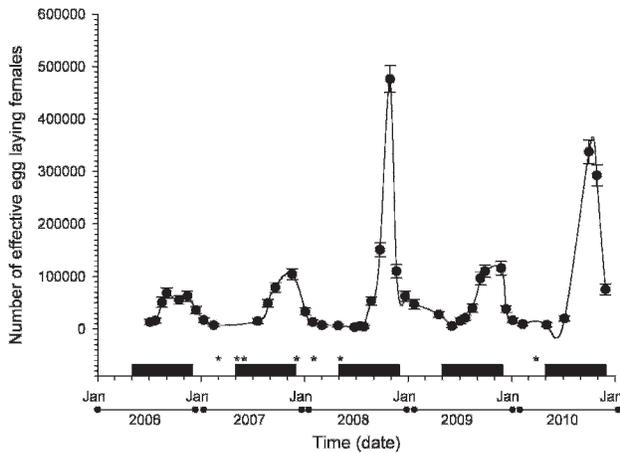


Figure 4. Estimated arribada abundance and approximate 95% confidence intervals at Ostional beach for the years 2006–2010 by using the strip transect in time method. The time in the abscissa refers to the date when each arribada started. Asterisks indicate arribadas that occurred that were not sampled. Heavy horizontal bars indicate rainy season months.

of emerged hatchlings, and eggs with and without apparent embryo development. In addition, we made general observations on destroyed clutches to elucidate the possible cause of destruction. We calculated hatching rate for each surviving clutch as the following: (number of empty egg shells)/(total number of eggs) \times 100.

We conducted an analysis of arribada abundance estimates by comparing the approximate $CI_{95\%}$ for each estimate: if the CIs of 2 estimates did not overlap, then the estimates were deemed significantly different. Mean hatching rate data were analyzed by 1-way analysis of variance, followed by Bonferroni adjusted multiple means comparison post hoc test, all at $\alpha = 0.05$.

RESULTS

Arribada Estimates. — Between July of 2006 and December of 2010, a total of 49 arribadas occurred at the Ostional beach; of these, we empirically sampled 42 arribadas using the strip transect in time method to estimate abundance of egg-laying female olive ridleys (Fig. 4). We did not sample arribadas in March, May, June, and December 2007; February and May 2008; and April 2010, due to a lack of personnel (indicated by an asterisk in the figure). Egg laying time of UELA turtles was 13.15 min (range, 4.42–35.42 min; $n = 887$). We used this time to compute abundance estimates for all arribadas sampled, thus reducing variability among estimates. By taking into account the start date of all arribadas, we determined that the mean interesting interval for our study period was 37.9 d (range, 13.0–155.0 d; median, 30.0; mode, 35.0). The largest mass nesting event was the October 2008 arribada with an estimated 476,550 ($CI_{95\%} = 451,151\text{--}501,948$; $\%CV = 2.7$) egg laying turtles and the smallest was the June 2008 arribada with an estimated 3,564

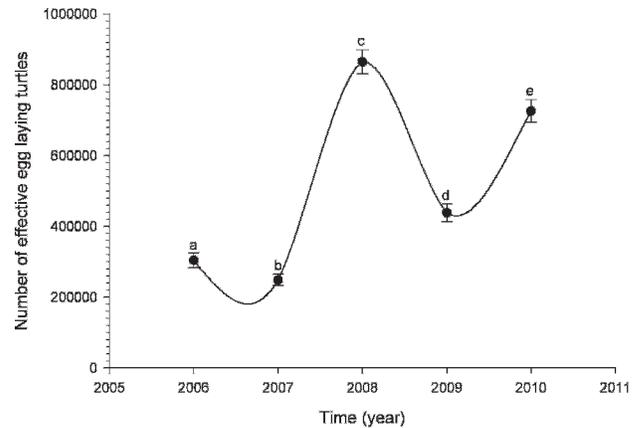


Figure 5. Estimated effective yearly arribada nesting population abundance and approximate 95% confidence interval estimates for the 2006–2010 period at Ostional beach by using strip transect methodology. Only arribada data from July through December were included for each year. Different lower case letters indicate statistically significant differences among estimates. Annual effective nesting population size was obtained by dividing the estimated arribada abundance season totals by estimated olive ridley nesting frequency of 2.21 (van Buskirk and Crowder 1994).

($CI_{95\%} = 1904\text{--}5223$; $\%CV = 23.3$). There were significant differences (nonoverlapping $CI_{95\%}$) between arribada estimates during the term of the study.

The effective nesting population abundance, defined as the estimated number of turtles that actually laid eggs, is shown in Fig. 5. We estimated the number of effective egg laying turtles by dividing the total annual estimated nesting events by the nesting frequency reported for olive ridleys of 2.21 clutches/female \times season (van Buskirk and Crowder 1994). Different letters indicate that estimates are significantly different as their $CI_{95\%}$ do not overlap. An important caveat is that a large December 2007 arribada was not empirically sampled and thus the estimate could not be included in the season total. In addition, the 2007 September arribada was large, and turtles nested in Rayo 1 through Nosara 2 (posts 3–140), with maximal nesting between markers 33–52; however, due to the high water level in the Ostional estuary, we were unable to census transects 61–140. As such, the number of turtles for 2007 was larger than actually shown. In summary, large interannual variation, with no clear decreasing or increasing trends in the number of egg laying females within the study period, is shown in Fig. 5.

Hatching Rate. — During the months of July, August, and September of 2007, and January of 2008, we marked an average of 27 nests per month. In 2007, the October arribada did not occur, and we did not mark nests from the November and December arribadas due to logistic problems. However, we were able to observe the mass hatching event of the November arribada, which occurred in early January. We sampled unmarked November nests ($n = 25$) that produced hatchlings. All nests came from Rayo 1 (sections 3–12) and Nosara beach (sections 98–108). Although biased because clutches that

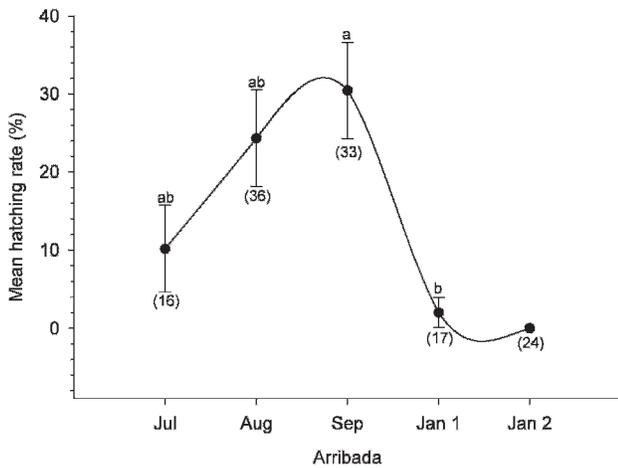


Figure 6. Longitudinal estimation of mean hatching rate and associated standard error at Ostional beach during the peak months of the 2007 nesting season. The second January arribada does not include an error estimate because no clutches produced any hatchlings. Means with different letters indicate statistically significant differences ($F_{3,87} = 4.65$; $p = 0.005$).

did not produce hatchlings were not included, these estimates showed that some clutches were capable of producing a large number of hatchlings outside the most used nesting area. The November arribada, the largest in 2007, occupied sections 3–118, with some nesting on the northern section of Nosara beach. The approximate incubation period for these clutches was 49.5 d (range, 45–52 d). Mean hatching rate was 79.3% (range, 21%–99%). No damage by beetle larvae was observed.

Overall, we report an 18.4% hatching rate for term nests at Ostional (range, 0.0%–99.1%; $n = 126$, and 2.96 SE) for the arribadas of July, August, and September of 2007, and of 1 and 2 January 2008, all 5 combined (Fig. 6). However, we observed that the hatching rate was variable across the months, with rainy season clutches being more productive. Thus, during wet months mean hatching rate was $24.3\% \pm 3.7$ SD ($n = 85$). We randomly marked a total of 16 nests on the MNB (section 64–73) during the July arribada, where the main focus of the arribada occurred. Of these, 8 clutches were destroyed (1 poached and 7 impacted by fly larvae) and 6 clutches produced hatchlings, with a mean incubation period of 49.5 d (range, 49–50 d). These yielded a hatching rate of 10.2% (range, 0.0%–82.7%). In August, we randomly marked 36 nests from Rayo 1 through MNB (sections 16–75). This arribada concentrated in sections 38–78. Of these, 16 clutches yielded hatchlings, with a mean incubation period of 50.5 d (range, 48–52 d). These clutches exhibited a hatching rate of 24.3% (range, 0.0%–99.1%). Eleven of these clutches (35.6%) exhibited beetle damage. In September, we randomly marked a total of 33 nests from Rayo 2 through Rayo 4 (sections 21–42). Of these, only 18 clutches (54.6%) produced hatchlings, with a mean incubation period of 53.7 d (range, 51–57 d). This arribada concentrated between sections 31–52, away from the MNB. Hatching rate was 30.5% (range, 0.0%–97.8%).

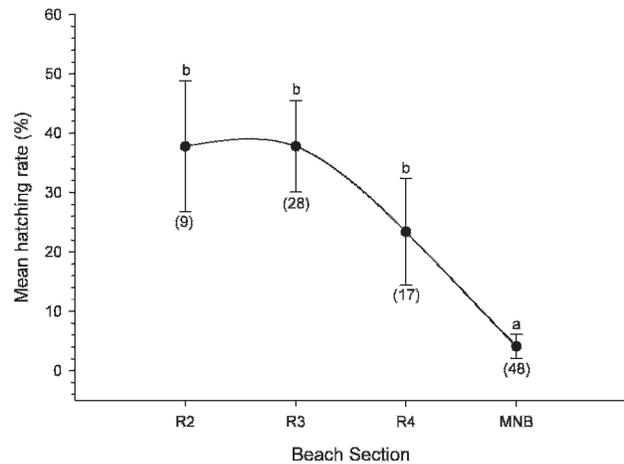


Figure 7. Mean hatching rates and respective standard error in different zones at Ostional beach. Means with different letters indicate statistically significant differences ($F_{3,109} = 15.63$; $p < 0.001$). Nests from the second January arribada were eliminated from this analysis because all of them failed to produce hatchlings. R2, Rayo 2; R3, Rayo 3; R4, Rayo 4; MNB, main nesting beach.

Beetle larvae predated 8 clutches (27.6%). In the first January arribada, we randomly marked 17 nests on the MNB (sections 65–69). This arribada concentrated between sections 63 and 77. Of these, only 2 clutches located close to the estuary produced hatchlings, with an incubation period of 31 d and mean hatching rate of 2.0% (range, 0.0%–33.0%). In the second January arribada, we randomly marked 24 nests on the MNB (sections 60–71). This arribada concentrated between sections 60–73. No hatchlings were produced from this arribada. Only 2 clutches contained beetle larvae in the first January arribada, and none in the second arribada. Statistical analysis of mean monthly hatching rates revealed that clutches from the first January arribada exhibited the lowest values ($F_{3,98} = 3.89$; $p = 0.011$) (Fig. 6). The hatching rate of the second January arribada was 0.0% and was excluded from this analysis because it showed no variability (i.e., all 24 marked nests failed to produce hatchlings, likely due to lethal incubation temperatures, Valverde et al. 2010).

The same data were rearranged by section of beach and analyzed (Fig. 7). Analysis of the data showed that the hatching rate at MNB was significantly lower than at any of the other sections studied ($F_{3,98} = 9.18$; $p < 0.001$). However, it is important to keep in mind that this analysis does not take into account the effect of nest microclimate across the season.

Egg Harvest. — We obtained egg harvest data from reports of the ADIO biologist to the corresponding government offices for the years 2006–2010. Egg harvest data originally reported as the number of eggs were converted to the number of clutches by dividing the reported total eggs harvested every arribada by the estimated mean of 98.9 eggs/clutch (range, 36–163; $n = 536$). We plotted the data as estimated number of

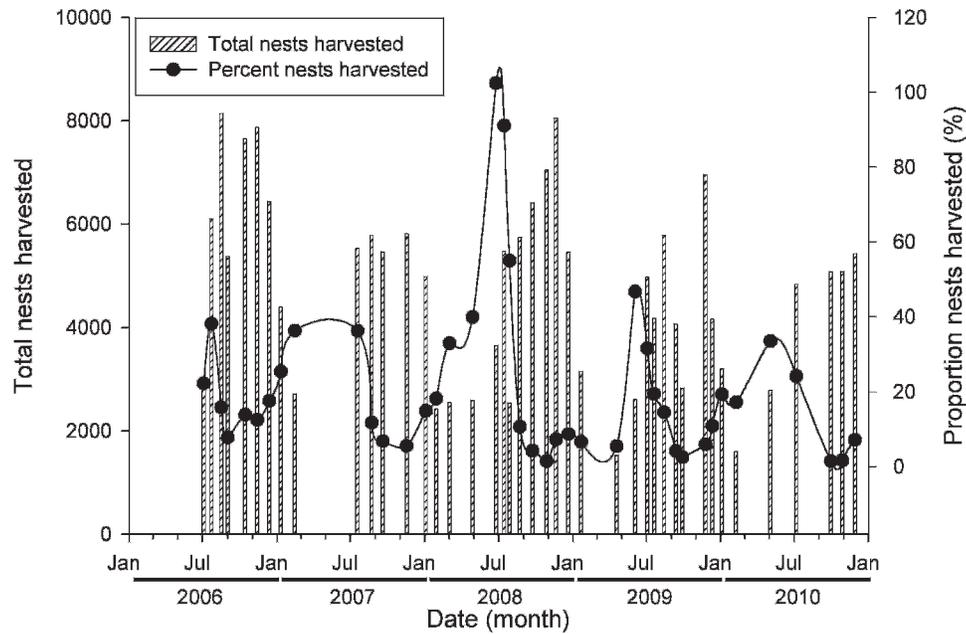


Figure 8. Total number of clutches harvested and their proportion relative to corresponding total estimated number of clutches at Ostional beach for the arribadas for which we obtained abundance estimates by empirical sampling during 2006–2010.

clutches harvested for each arribada empirically sampled by the strip transect in time technique to obtain an estimate of total clutches harvested. These data were used to calculate the proportion of clutches harvested during each arribada relative to the estimated number of clutches laid during the corresponding arribada (Fig. 8). The estimated mean total number of clutches harvested per arribada was 4746.4 (range, 1527–8138; $n = 42$). The estimated mean percentage clutches harvested per arribada was 21.2% (range, 1.5%–102.4%; $n = 42$). The highest estimated percentage harvest of 102.4% resulted from the mathematical conversion of eggs to nests and the error in the estimated number of clutches laid. In practical terms, this value suggests nearly complete egg harvest.

DISCUSSION

The Strip Transect in Time Method. — Olive ridley arribadas are complex and massive nesting phenomena that involve tens of thousands to hundreds of thousands of females that nest synchronously over a few nights (Valverde et al. 1998). It is perhaps for this reason that we know relatively little about this phenomenon, because especially designed techniques must be developed and applied to extract meaningful information from such massive events. Indeed, counting every single nesting female that participates in each arribada event is impractical at best due to the large number of females and the heterogeneous behavior they exhibit during each event in which some females may be simultaneously crawling, digging, camouflaging, or laying eggs. For this reason, we resorted to empirical sampling of each event to estimate the number of egg-laying females by using the

strip transect in time, or “transect” method (Gates et al. 1996; Valverde and Gates 1999). This method allowed us to estimate the number of egg-laying olive ridley females that participated in the arribadas. The method considers only female turtles exhibiting UELA activity. As such, our abundance estimates can be interpreted as either the number of effective egg-laying females or as the number of clutches laid. The possibility of recounting the same individual was eliminated by including only UELA turtles. This was a significant improvement over previous methodologies (e.g., Márquez-M. and Van Dissell 1982; Valverde et al. 1998), which allowed the transect method to yield robust, unbiased, and reliable estimates. Bias was also avoided by keeping transect widths to a manageable dimension (2 m), given that bias increases with transect width (Burnham et al. 1985). Overall, our method complied with all relevant assumptions of strip transect methodology (Eberhardt 1978; Eguchi et al. 2007), i.e., all UELA turtles in transects were counted, no turtle was counted more than once, UELA turtles were not affected by observers during censuses because females exhibited little reaction to external stimuli while laying eggs, the sighting of a turtle was independent of the sighting of another one, and turtles were randomly and independently distributed over the census area.

Transect method estimates can be directly compared between arribada beaches. For instance, in the months of August through November for the year 2007, there were only 2 major arribadas at Nancite beach, with an estimated total of $17,576 \pm 4934$ (estimate \pm CI_{95%}) effective nesting females that year (Fonseca et al. 2009). For that same year and period, 3 major arribadas at Ostional were estimated at a total of $233,565 \pm 15,869$ effective nesting

females, which indicated that the Ostional assemblage that year was approximately 13-fold larger than that of Nancite, which is consistent with reports that the Nancite assemblage has undergone a significant decline over the past 2 decades (Fonseca et al. 2009).

Assessment of Ostional Arribada Assemblage. — Adequate assessment of a population is a highly complex task that involves the collection of data from multiple sources by using different approaches over a biologically meaningful time frame (Seminoff and Shanker 2008). In the case of Eastern Pacific olive ridleys, this task is complicated by the scarcity of peer-reviewed information from the rookeries in the region. In spite of the fact that the Ostional arribada assemblage was discovered in 1970 by the scientific community (Richard and Hughes 1972) and that the Ostional nesting assemblage has supported a legal and extensive community-based egg harvest program since 1987, only a few scientific publications regarding this assemblage have been generated. This is particularly delicate because the law that authorizes the egg harvest stipulates that this activity may take place only if the harvest does not cause damage to the population. Peer-reviewed data supporting the egg harvest date from the early 1980s (Cornelius et al. 1991), before the legal egg harvest began. The lack of current reliable empirical data regarding the robustness of this assemblage has the potential to weaken support for the egg harvest program within the public and the scientific communities. Moreover, the Inter-American Convention for the Protection of Sea Turtles, of which Costa Rica is signatory, states that any exceptions to the prohibition of commercialization of sea turtle eggs must take into account the status of the turtle population. Under the exception rules, the Member State is to establish a management program that includes a limit in the rate of intentional take. Setting a take limit, however, is difficult given the lack of information. There are unpublished reports on arribada estimates (e.g., Chaves-Cordero 2002; Chaves-Cordero et al. 2006); however, none of these have had the benefit of the peer-review process. Examination of some of these reports reveals significant methodological biases. Most importantly, the arribada estimates in those reports do not refer to the number of egg-laying females that participate in each event and, as such, cannot be compared with any historical estimates. Thus, our data represent a significant effort to fill in the void in reliable data necessary to assess the Ostional arribada assemblage.

Our study demonstrates the feasibility of generating reliable and robust estimates of turtle abundance during small and large arribadas at this complex beach. Analysis of our data showed that the Ostional nesting assemblage is one of the largest in the world, second only to La Escobilla, Mexico (R.A. Valverde, unpubl. data, 2010). In addition, contrary to what has been suggested (Cornelius et al. 2007; Eguchi et al. 2007), analysis of our data showed that the Ostional nesting assemblage exhibited large intra- and interannual fluctuations, and that no particular trend could be discerned. We believe that it is

important to continue application of our technique for the equivalent time of age to maturity, which may be approximately 13 yrs for the olive ridley (Zug et al. 2006), or longer before we draw conclusions regarding the stability of this population. However, a different perspective arises when comparing our estimates with historical data. Data collected between 1988 and 1997 by using the quadrat method (see Valverde et al. 1998, for a description) exhibit some of the same features of our data set, particularly the high arribada-to-arribada variability (Ballesterio et al. 2000). The researchers of the non-peer-reviewed summary indicated that their data likely represent underestimates of the population given that the fixed quadrats used to estimate the number of egg-laying females missed the bulk of population whenever turtles concentrated in areas where quadrats were absent. In spite of being underestimates, between 1988 and 1997, the mean annual estimated nesting population was 588,501, which fluctuated between 232,318 and 1,147,969 egg-laying turtles (Ballesterio et al. 2000), much higher than our estimates. With this being the case, we would conclude that the Ostional assemblage has actually decreased in abundance in the past 2 decades. This is not surprising, given the many years of low hatching rates at this beach (see below).

The variation in size of the effective nesting population at Ostional may be related to the occurrence of El Niño events in the eastern Pacific Ocean. The sharp decline in the population of olive ridleys nesting at Nancite in 1983 was associated with a strong El Niño event (Valverde et al. 1998; Fonseca et al. 2009). It has been suggested that the reproductive frequency of leatherback turtles (*Dermochelys coriacea*) at Playa Grande in Costa Rica (north of Ostional) was affected by the El Niño and La Niña conditions in their foraging areas (Saba et al. 2007; Reina et al. 2009). It is possible that the variation in numbers of turtles in the Ostional arribadas is also affected by changes in productivity in their foraging areas, because females will need time to amass sufficient nutrients to support their metabolic investment in migratory and reproductive activities.

Egg Harvest and Hatching Rate. — Legal and illegal egg harvest occurs at a few arribada beaches in the eastern Pacific region (Hope 2002), although the legal Ostional harvest is by far the largest and most organized. The primary justification for the harvest is the large proportion of eggs destroyed by subsequent nesting turtles during arribadas, which can be as high as 50% of the clutches laid (Cornelius et al. 1991). A benefit of the sale of eggs is that it provides the Ostional community with a significant source of income, which adds significant conservation value to this nesting population in the eyes of Ostional residents (Campbell 1998; Campbell et al. 2007). Another reason to support the harvest is the potential of flooding the markets with cheap legal eggs to discourage the more expensive poached eggs from other beaches, a concept that has yet to prove effective (Arauz-Almendor et al.

2001; Cornelius et al. 2007). The use of the egg harvest as a management tool to reduce egg clutch density and increase hatching rates has been a less articulated reason to exploit arribada ridley eggs at Ostional beach. Empirical support for such a strategy is based on a study that showed that hatching rates of arribada clutches are inversely proportional to clutch density (Honarvar et al. 2008). Unfortunately, it is not clear from this study exactly how clutch density may regulate embryo development. Results of a more recent study suggested that bacterial communities associated with high density clutches may be somehow responsible for ridley embryo mortality at arribada beaches (Honarvar et al. 2011). However, the study did not look at fungal communities and failed to establish cause and effect. A mechanistic study that examined the nest microenvironment of arribada nests found that eggs incubated in clean sand exhibited higher hatching rates, which suggests that the microbial load of the substrate, as influenced by decomposing organic matter from previously broken eggs, may be more relevant than clutch density (Clusella-Trullas and Paladino 2007). The latter study is consistent with previous observations, which indicate that beach sections that are eroded away and redeposited during annual rains or high tides (e.g., sections fronting estuaries) tend to produce more hatchlings, both at Nancite and Ostional beaches (Cornelius et al. 1991). Thus, simply reducing clutch density may not be an effective tool to increase hatching rates at these beaches, other than by reducing clutch destruction rates. This is supported by a study that showed that Ostional beach areas with egg harvest did not exhibit increased hatchling production relative to areas without egg extraction (Arauz and Mo 1994). Alternatively, it has been hypothesized (Cornelius et al. 1991; Valverde et al. 1998) that the microorganism community is mainly responsible for the elevated embryo mortality observed at Costa Rican arribada beaches. High clutch densities are thought to promote clutch destruction and higher microbial load (Cornelius et al. 1991; Valverde et al. 1998). Thus, increasing egg harvest may be a reasonable endeavor, at least on an experimental basis. But how many clutches could be safely harvested? It appears that at current harvest levels Ostional beach remains above carrying capacity given the persisting low hatching rates, when assuming that these are driven by excessively high clutch densities. In fact, it seems that hatching rates have remained below suboptimal levels for decades. Indeed, 2 studies showed that hatching rates of term nests were 11.3%, 15.3%, and 6.0% in the month of August of the years 1984, 1988, and 1989, respectively (Alvarado-Ulloa 1990; Cornelius et al. 1991). These low hatching rates, along with the high clutch destruction rates during arribadas, may threaten the long-term survival of the Ostional assemblage, assuming low recruitment of hatchlings to the population (Cornelius et al. 2007). Thus, determining the carrying capacity of this beach along with recruitment rates should be of paramount importance to implement better informed management policies.

In general, although eggs are reproductively less valuable than subadult and adult turtles given the high mortality rates associated with early life stages, eggs must be protected to promote the long-term survival of populations, especially if populations are not stable (Heppell 1997). Legally, the 1999 decree 28203 that authorized the Ostional egg harvest only by ADIO associates justifies this activity because it does not “alter” the population. However, as discussed above, caution must be exercised with egg harvest activities given that this population may be exhibiting signs of decline. Should egg harvest be too large to prevent sufficient recruitment of hatchlings to the adult population, it is conceivable that arribadas would undergo a decline, as may have been the case for Nancite beach (Valverde et al. 1998; Fonseca et al. 2009).

Analysis of harvest data obtained from ADIO unpublished reports indicates that the maximum number of clutches collected in an arribada during the study period approximated 8000 clutches. This estimated maximum resulted from market demand combined with the limited manpower of ADIO to harvest eggs. Analysis of our data indicated that the mean harvest rate was 21.2% during the study period, similar to previous estimates (Ballesteros et al. 2000), and that most values fluctuated between 1.5% and 47.0% of the clutches laid during arribadas, although we documented 2 instances, May and June of 2008, when nearly all clutches laid were estimated to have been harvested. Although this was a rare occurrence, it is important to prevent overharvesting of eggs, especially at times when hatching rates are expected to be higher. It has been shown that lower hatching rates are associated with higher clutch density and higher incubation temperatures (Honarvar et al. 2008; Valverde et al. 2010). Both these conditions are presumed to be lessened in June and July when rainfall increases and incubation temperatures decrease below dry season lethal incubation temperatures and when the arribadas still exhibit low abundance. Although analysis of our data showed that hatching rates in July were not significantly different from those recorded later in the rainy season, we recommend that the egg harvest be restricted during the months when rainfall is high and clutch density is low. Likewise, until a more refined study is conducted across the year, which includes measures of hatchling recruitment and not just hatching success of protected clutches, we suggest that the egg harvest may be increased in the dry months as well as in large arribadas, when clutch density or incubation temperatures are higher, in agreement with prior recommendations (Cornelius et al. 1991; Valverde et al. 2010). Finally, because the beach sections away from the MNB (Rayos 1, 2, and 3) appear to be more productive, we recommend that the egg harvest be prohibited in these sections as an important conservation tool to give these clutches the best chance to contribute hatchlings to the population.

In conclusion, our recommendations geared to increase hatching rates necessitate the consideration of

one important caveat. If high clutch densities are indeed responsible for the low hatching rates, increasing hatching rates through an increased egg harvest may eventually, over a decadal scale, lead to an increase in the nesting population. This may again exacerbate the negative effect of increased clutch density and drive down hatching rates, as currently documented. Should this be the case, it may be better to continue harvesting eggs at current rates. Clearly, the lack of data regarding hatchling recruitment is a major impediment to understanding the dynamics of the Ostional mass nesting population.

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