## Decline of the Olive Ridley Sea Turtle (Lepidochelys olivacea) Nesting Assemblage at Nancite Beach, Santa Rosa National Park, Costa Rica

ROLDÁN A. VALVERDE<sup>1,4</sup>, STEPHEN E. CORNELIUS<sup>2</sup>, AND CLAUDETTE L. MO<sup>3</sup>

<sup>1</sup>Department of Biology, Texas A&M University, College Station, Texas 77843 USA; <sup>2</sup>Sonoran Institute, 10221 East Glenn St., Tucson, Arizona 85749 USA; <sup>3</sup>Programa Regional de Manejo de Vida Silvestre, Universidad Nacional, Apdo. 1350-3000, Heredia, Costa Rica; <sup>4</sup>Present Address: Department of Biology, University of Michigan, Ann Arbor, Michigan 48109 USA [Fax: 734-647-0884; E-mail: roldan@biology.lsa.umich.edu]

ABSTRACT. – The olive ridley sea turtle nesting colony at Nancite beach, Costa Rica, was monitored since 1980. Estimates of numbers of nests oviposited throughout the term of the study were obtained by empirical sampling of the mass nesting assemblages (*arribadas*) occurring during the peak nesting months of August through November for 15 years. The method to obtain these estimates is described and discussed. The number of nests laid during each *arribada* averaged 37,960 and varied in size from 148,000 nests in October 1980 to 350 nests in August 1993. Data showed a steady decline in the number of nests laid and in frequency of occurrence of *arribada* events at Nancite beach. There was a sharp decline during 1983 and consecutive poor nesting periods during 1987–96. Whereas nesting during any one year may be affected by environmental factors such as El Niño-Southern Oscillation events, we suggest that low hatching rates recorded at this beach may play a significant role in determining the long-term decline of the nesting effort of the Nancite assemblage.

# KEY WORDS. – Reptilia; Testudines; Cheloniidae; Lepidochelys olivacea; sea turtle; arribada; population; nesting; conservation; Costa Rica

The olive ridley sea turtle (Lepidochelys olivacea) is particularly abundant along the Pacific coasts of the American tropics and in the Bay of Bengal in the Indian Ocean (Cornelius, 1986). In the eastern tropical Pacific many beaches are known to support high but non-aggregated nesting by olive ridleys and other sea turtles (Cornelius and Robinson, 1986; Higginson, 1989). Nevertheless, oliveridleys are not restricted to solitary nesting behavior. At two beaches in Costa Rica, Ostional and Nancite, a spectacular phenomenon takes place: thousands of turtles synchronously emerge at regular, nearly monthly, intervals to nest during two to eight consecutive nights (Figs. 1, 2). This event is referred to as an arribada or arribazón, and is exclusive to the genus Lepidochelys (Richard and Hughes, 1972; Márquez and van Dissel, 1982). This phenomenon also occurs at La Escobilla, Mexico (Cliffton et al., 1982), and Gahirmatha and Nadiakhia Muhana, India (Kar, 1982). An example of the magnitude of an arribada is one estimated at 386,036 females at Gahirmatha during March 1987 (Mohanty-Hejmadi, 1987). Unfortunately, the author did not report on the estimation method, making it impossible to compare with other olive ridley rookeries.

The extreme gregariousness displayed by the olive ridley renders it highly vulnerable to human exploitation. At least three former *arribada* beaches in Mexico now support only sporadic nesting, and the collapse is thought to be due to large-scale legal and illegal take of adults (Cliffton et al., 1982). In addition, Ecuadorean fisheries harvested large numbers of olive ridleys from Central American and Mexican nesting colonies for the international turtle product trade (Green and Ortiz-Crespo, 1982).

Since the contribution of Costa Rican olive ridley populations to these fisheries was uncertain, an attempt to fill in the gaps related to the post-nesting movements of these marine reptiles was initiated in 1980 (Cornelius and Robinson, unpubl. report). Since then, more than 50,000 females have been tagged at Nancite beach. The results of this tagging program indicated that olive ridleys are pelagic in their habits and also disperse along the coastal waters from Ecuador to Mexico (Cornelius and Robinson, 1986). These observations were recently confirmed by satellite telemetry studies (Plotkin et al., 1995), and suggest that turtles nesting in Costa Rica were potential targets to the now closed fisheries in these countries (Cornelius and Robinson, 1986). Today, the impact of these fisheries on Costa Rican olive ridleys remains poorly documented.

In spite of the impossibility of making sound inferences on the overall population status, long-term beach surveying aimed at determining the number of seasonal reproductive females is believed to be one of the best methods to study overall trends in a population (Meylan, 1982). In this paper, we use the term "arribada size" to refer to the number of nests laid during an arribada. This is identical to the number of females that effectively nest during one mass emergence since olive ridleys nest only once during each arribada. The objective of this paper is to report on 15 years (1980–84 and 1987–96) of olive ridley nesting activity at Nancite.

### MATERIALS AND METHODS

Field work took place at Nancite during the peak nesting months of August through November from 1980 through 1996, except for 1985–86. The study was conducted by the University of Costa Rica (1980–84) and the Universidad Nacional of Costa Rica (1985–96).



Figure 1. Daytime *arribada* at Nancite heach showing a large number of females crawling on the beach. Daytime emergences are uncommon at Nancite. Photo by Stephen Cornelius, October 1972.

The methodology described here represents an attempt to estimate the number of nests laid during the *arribadas* at Nancite beach. To estimate the size of the nesting assemblage at Nancite beach, the 1 km long beach was divided into ten 100 m sections. Quadrants of  $100 \text{ m}^2 (10 \text{ m} \times 10 \text{ m})$  were established in each section, with the number of quadrants in each section determined by the width of that section. Counts of turtles in these quadrants were made every two hours during each session of an *arribada* (a session is defined here as the consecutive hours in which turtles emerge synchronously to nest within a 24-hr interval, i.e., a nychthemeral cycle). A session typically began at nightfall and ended at sunrise, although in some instances turtles emerged during daylight hours. In this study, an *arribada* was defined as a total of 100 or more females nesting during one session.

Several aspects of the nesting behavior were quantified in an attempt to accurately estimate the number of nesting females that participated in an *arribada*. In order to determine the fate of each emergence, 99 turtles were individually painted on the carapace as they emerged from the water. Individual observations established that 52% of these turtles that engaged in pre-nesting activities (e.g., crawling up the beach, searching for nest site, body pit construction), subsequently nested. Also, 98% of the marked animals that initiated construction of the nest chamber nested successfully.

Three separate counts were made within the quadrants: 1) total number of turtles, 2) number of actual nesting turtles, and 3) number of turtles digging the nest chamber. The effective number of nesting turtles on the beach was calculated using the following two formulas.

The number of turtles nesting on the mid- and lowbeach zones was calculated as follows:

$$P_{i} = \frac{\{N_{i} + 0.98D_{i} + 0.52(T_{i} - [N_{i} + D_{i}])\}125A}{100Q} \times \frac{H_{i}}{1.13C_{i}}$$
[1]

where  $P_i$  = total number of nesting turtles (or nests laid) during the *i*<sup>th</sup> session;  $N_i$  = number of turtles actually nesting in all quadrants during the *i*<sup>th</sup> session;  $D_i$  = number of turtles still digging nest cavities in all quadrants during the *i*<sup>th</sup> session;  $T_i$  = total number of turtles counted in all quadrants



Figure 2. Panoramic view of an *arribada* at Nancite beach. Note the large number of broken egg shells on the sand. Photo by Stephen Cornelius, November 1984.

during the *i*<sup>th</sup> session; A = total available nesting area (m<sup>2</sup>) in mid-beach zone during the *i*<sup>th</sup> session as determined by the reach of high tide;  $H_i =$  number of hours in the *i*<sup>th</sup> session;  $C_i$ = number of survey counts in all quadrants during the *i*<sup>th</sup> session; Q = number of quadrants; **1.25** = extrapolation of the estimate for turtles in the mid-beach zone to include those nesting in the low beach zone below the high tide line; **100** = size of quadrants (m<sup>2</sup>); **0.98** = estimate of the percentage of turtles still digging nest cavities that eventually nested; **0.52** = estimate of the percentage of turtles encountered in pre-nesting stages that eventually nested; and **1.13** = average time in hours a turtle spent on the beach during a successful emergence.

The number of turtles nesting on the upper beach zone was adjusted to correct for the interference of vegetation and calculated as follows:

$$P_{i} = \frac{\{N_{i} + 0.98D_{i} + 0.52(T_{i} - [N_{i} + D_{i}])\}0.7B}{100Q} x \frac{H_{i}}{1.13C_{i}}$$
[2]

where  $\mathbf{B} = \text{size}$  of nesting area under woody vegetation (constant = 8500 m<sup>2</sup>); **0.7** = maximum estimated nesting density in the upper beach zone, instead of 1.25 in formula [1]. The remaining variables and constants in the formula are the same as in formula [1]. For a more detailed description of these formulas see Cornelius and Robinson (1982).

Estimates of numbers of nests deposited for each session were obtained by adding the totals from formulas [1] and [2]. The overall *arribada* size estimate results from adding the totals for each of the sessions of a given *arribada*. For the purposes of this study only empirically derived estimates of the size of the *arribadas* registered during the main nesting months of August through November are included.

### RESULTS

Figure 3 shows the size of the *arribadas* in terms of number of nests recorded per *arribada* during the study. A total of 44 *arribadas*, lasting an average of 4.6 sessions (standard error = 0.25), were recorded during the term of the study. The average number of nesting females per *arribada* was 37,960 turtles. The largest *arribada* recorded totaled

148,000 nests in October 1980 and the smallest totaled 350 nests in August 1993. Complete data sets are not available for *arribadas* that occurred during 1985 and 1986, and these were not considered in this study. An *arribada* that lasted four sessions was observed in September 1993, but no sampling was conducted. No *arribadas* were recorded in August of 1988, 1993, 1995, and 1996, in September of 1988, 1989, 1992, 1995, and 1996, in October of 1990, 1995, and 1996, and in November of 1983, 1987, 1989, and 1993. In 1995 there were two *arribadas* in November. Data from other *arribadas* witnessed outside the peak nesting months were not considered in the analysis because these relatively small *arribadas* occurred only sporadically, and because of lack of scientific presence at the beach.

The pattern observed in Fig. 3 is a steady, overall decline in the size of the *arribadas* over time. More importantly, the intra-annual frequency of *arribadas* decreased significantly between 1987 and 1996, with several *arribadas* missing during this period.

#### DISCUSSION

The formulas applied in this study to estimate the number of nests laid during the mass nesting emergences of olive ridleys contain several empirically derived parameters. Since it was not possible to calculate the error associated with the derivation of these parameters, it was difficult to acquire a precise estimate of the overall nesting effort. Nevertheless, consistent application of both the sampling method and the formulas through the years suggest that we have a valid index to study population trends. Similar problems regarding the lack of precision of *arribada* size estimates are found in an alternative method (Márquez et al., 1982; Márquez and van Dissel, 1982). An improved method to estimate the number of nests laid during an *arribada* provides a means to compute the variability of these estimates (Gates et al., 1996). Unfortunately, the latter method cannot be applied to the data included in the present study due to substantial differences in data collection methodology.

Some of the parameters in the formulas applied in the present study may have varied in absolute terms from year to year (and possibly even from arribada to arribada), such as the estimates used to correct for non-effective nesting behavior of participating turtles during the arribadas (e.g., the percentage of turtles encountered in pre-nesting stages that eventually nested). It was not practical to continuously assess these parameters due to logistical limitations, particularly because the task was time consuming and incompatible with other aspects of the project. Accordingly, these parameters were maintained at the levels estimated early in the study. This methodological difficulty might have led to differences in the estimates of absolute numbers of clutches laid over the years. Despite these caveats, a consistent protocol was employed throughout the project period providing an acceptable estimate of the relative size of the different arribadas.

The monitoring of the *arribadas* at Nancite beach started in 1971 (Richard and Hughes, 1972). At that time. *arribadas* were estimated at 115,000 and 70,000 nesting

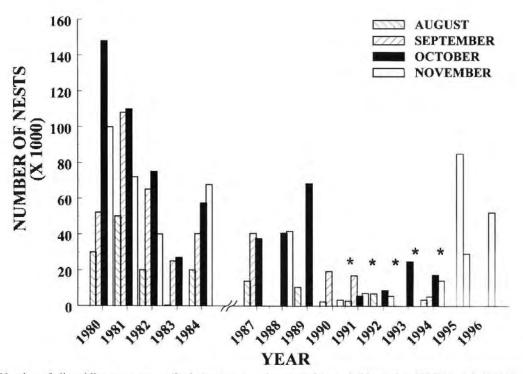


Figure 3. Number of olive ridley nests per *arribada* (one per month, except for two in November 1995) recorded at Nancite beach. Santa Rosa National Park, Costa Rica, during the 1980–96 period. The missing columns indicate the absence of an *arribada* in the corresponding month. Asterisks above yearly columns indicate estimates obtained by field assistants and may represent underestimates of the nesting effort of the assemblage during the 1990–94 period. Nevertheless, estimates are offered here as lower bounds and to show the occurrence of the corresponding *arribadas*.

females in September and November 1971, respectively (Hughes and Richard, 1974), and 122,000 and 20,000 in September and November 1972, respectively (Cornelius and Robinson, unpubl. report). Similar large aggregations persisted through the early 1980s (Cornelius et al., 1991), although no systematic data collection was conducted for the period 1973-79. Since 1987, the Nancite nesting population underwent a marked decline, which was more pronounced toward the end of the study when the intra-annual frequency of arribadas decreased from 3.8 arribadas per study period before 1987, to 2.5 arribadas per study period thereafter. This represents a loss of about 493,480 total nests between 1987 and 1996 with respect to the expected number of nests for this period. If we assume that most females nest twice in a single reproductive cycle, as seems to be the case for the Nancite turtles based on tag recapture (Cornelius and Robinson, unpubl. data) and endocrine data (Plotkin et al., 1995, 1997), then the loss of nesting females would be equivalent to 246,740 between 1987 and 1996.

Cornelius and Robinson (unpubl. report) proposed four hypotheses to explain the transient decline in the size of the *arribadas* that occurred during the 1980–84 period. These were 1) poor hatching and consequent low recruitment to the adult population in past years, 2) natural endogenous variations, 3) overfishing by Mexican and Ecuadorean fisheries, and 4) the impact of the El Niño phenomenon. These conjectures remain useful today since the olive ridleys continue to be exposed to similar conditions.

Many sea turtle populations have been documented to exhibit wide interannual fluctuations in their nesting effort (Carr, 1980; Meylan, 1982; Richardson and Richardson, 1982; Magnuson et al., 1990). Although the reason why all individuals in the adult population do not reproduce every year is not known, it is possible that turtles need some time to replenish their nutrient reserves, which are heavily taxed by reproductive processes and by the long, energy-demanding migrations between breeding and foraging grounds (Bjorndal, 1985). The differential ability of individual turtles in a population to undergo synchronized gonadal recrudescence and to conserve energy during the reproductive journey may determine to a large extent the interannual number of reproductive individuals. Thus, trends in the status of a nesting population are best determined by long-term monitoring studies (Meylan, 1982; Magnuson et al., 1990).

Large fisheries in Ecuador and Mexico are known to have taken many olive ridleys. In mainland Ecuador about 100,000 olive ridleys were harvested during 1979 alone, whereas in Mexico an estimated two million turtles were caught between 1965 and 1969 (Cliffton et al., 1982; Green and Ortiz-Crespo, 1982). Tag-recapture and satellite telemetry studies have determined that Nancite olive ridleys nest cohesively but distribute independently throughout the eastern tropical Pacific (Cornelius and Robinson, 1986; Plotkin et al., 1995). This strongly suggests that many members of the Nancite reproductive assemblage were victims of these fisheries, although the extent cannot presently be determined. Fortunately, Ecuador banned sea turtle fisheries in 1981 (Frazier and Salas, 1982), Mexican turtle fisheries officially closed down in 1990 (Aridjis, 1990), and the Peruvian turtle fishery (Vargas et al., 1994) stopped in 1995 (MDP, 1995).

Limpus and Nicholls (1988) suggested that the El Niño-Southern Oscillation (ENSO) may impact the remigration frequency of the green turtle in northern Australia by limiting food resources. ENSO events are known to disrupt marine food chains (Barber and Chávez, 1983; Barber and Kogelschatz, 1990). ENSO has been registered three times in the last 17 years (the ongoing 1998 event not taken into account). The first one extended from 1982 through mid-1983, the second from mid-1986 through 1987, and the third from mid-1991 through 1994 (Quinn, 1992; McPhaden, 1993; C.A.C, 1995). Thus, it is conceivable that ENSO impacted the interannual nesting of olive ridleys by diminishing food resources during the study period, which may have curtailed or completely abolished gonadal recrudescence in a significant portion of the population.

Two other factors may explain the observed decline in olive ridleys nesting at Nancite. These are 1) beach exchange and 2) incidental mortality in shrimp nets. Between 1980 and 1984 a total of 29 Ostional turtles were observed at Nancite and 35 Nancite turtles were recorded at Ostional (Cornelius and Robinson, unpubl. report). This dynamic movement between beaches is remarkable and may represent an exception to the natal homing hypothesis as applied to green turtles (Bowen et al., 1992). It is possible that beach exchange is part of a complex mechanism that olive ridleys use to colonize or even move to another beach altogether. On the other hand, total incidental sea turtle capture in shrimp nets was estimated at some 60,000 animals along the Pacific coast of Central America for 1993 (Arauz, 1995), the large majority of these animals being olive ridleys. Unfortunately, sound mortality estimates due to the incidental capture of these turtles were not reported. As most of the turtles captured in this fishery are reportedly females (Cornelius, 1982), and assuming a shrimping-associated mortality of 66.6% (Arauz, 1995), a gradual decline (possibly spanning decades) would be expected in nesting at Nancite.

The extent to which all the aforementioned factors have impacted the nesting of the olive ridley assemblage at Nancite is not known. The relative contribution of each factor should be studied in order to devise appropriate protective measures. One important consideration regarding the effects of all these factors is that they should impact all eastern tropical Pacific olive ridley nesting populations in a similar fashion. However, anecdotal observations suggest that numbers of nesting animals at Ostional and La Escobilla beaches may have increased in the last few years (A. Chaves, pers. comm.; Márquez, unpubl. report). If confirmed, these observations would suggest that the decline of the Nancite assemblage is due to an endogenous factor limited to Nancite. Thus, it is plausible that the above factors are of secondary concern and that poor hatching success at Nancite is the primary long term cause of reduced arribada size and frequency.

Low Hatching Rate. — Cornelius et al. (1991) estimated the hatching rate of term nests (i.e., nests that were undisturbed throughout the incubation period) at Nancite as 6.7% over a four-year period. Similar estimates are available for nests at Ostional (Cornelius et al., 1991). These hatching rates are significantly lower when compared to those of other olive ridley populations (Reichart, 1993).

A large proportion of the nests at Nancite (up to 84% in 1981) showed no evidence of embryonic development (Cornelius et al., 1991), suggesting either that there is very high embryonic mortality associated with the early stages of the incubation process or that a large proportion of the eggs are infertile. The latter possibility is supported by the low number of observations of mating in front of Nancite (Hughes and Richard, 1974), although mating could take place at a different location, away from Nancite, and at a time other than the peak nesting months.

High mortality of early stage embryos in arribada beaches may also be due to the increased proliferation of microorganisms associated with the large numbers of clutches deposited during each arribada event (Cornelius et al., 1991) or with physical factors, such as temperature and humidity (Mo et al., 1990, 1992). Microorganism proliferation is thought to result from the increased amount of eggderived organic matter found in these beaches as a direct consequence of nest destruction by other nesting turtles (Fig. 2), as well as by predators, beach erosion, and high tides (Cornelius et al., 1991). Nest disturbance increases as the nesting density increases, either during a single arribada or as the season progresses toward larger arribadas. This is due to the limited size of the nesting area and to the fact that arribada nesting intervals are commonly shorter than the incubation period (Cornelius et al., 1991). If we estimate that 25% of 340,000 nests (of ca. 100 eggs each) were destroyed by turtles nesting during 1981 (Cornelius et al., 1991), and if the average mass of the eggs is 32.6 g (Reichart, 1993), then about 277 metric tons of organic matter were added to the beach that year as a consequence of nest disturbance by other nesting females. This figure increases significantly if we include embryos that die at different stages during incubation and that also contribute to the low hatching rate documented at Nancite (Cornelius et al., 1991).

Given the tremendous amount of decomposing organic matter from the many broken eggs, the level of oxygen available for development of healthy embryos may not be optimal. Indeed, eggs may be deposited at Nancite in a nearly anoxic environment. Turtle eggs require an optimal respiratory environment to develop properly (Ackerman, 1980). Further, experimental data indicates that embryo mortality increases sharply as gas exchange between egg clutch and surrounding environment decreases (Ackerman, 1981), assuming no competition for air among egg clutches. It is tempting to speculate that increased embryo death may result as a consequence of the direct competition for air by adjacent clutches. At Nancite, nest density is quite high as evidenced by the elevated rate of nest destruction by turtles in the subsequent nights of an *arribada* (Cornelius et al., 1991). Thus, it is conceivable that early embryo mortality at Nancite could be due to a large extent to low availability of oxygen brought about by the massive decomposition of organic matter and by the competition for air among nearby egg masses. Research is required to evaluate these hypotheses.

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An aspect of major concern regarding the low hatching rate at Nancite is the maintenance of the breeding population. The low production of hatchlings may cause the Nancite arribada assemblage to collapse in the near future (Cornelius et al., 1991), leading to periods of low density nesting alternating with periods of heavy nesting (after natural recovery of the population) over several sea turtle generations. Alternatively, low hatching rates may not be pervasive at Nancite over long periods. Sporadic exceptionally large hatchling production events have been observed (Cornelius and Robinson, unpubl. report), and it is possible that annual production of hatchlings is highly variable. This would result in large interannual fluctuations on a scale of decades, such as the ones registered in this study. This suggests the possibility that arribada beaches undergo natural, selfregulated cycles, alternating between periods of high and low numbers. Unfortunately, the relatively short historical record of arribada events at Nancite does not offer adequate resolution of this issue. Only through the continued monitoring of this population will we be able to improve our understanding of the biology of the arribada phenomenon at Nancite beach.

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#### LITERATURE CITED

ACKERMAN, R.A. 1981. Growth and gas exchange of embryonic sea turtles (*Chelonia, Caretta*). Copeia 1981:757-765.

ACKERMAN, R.A. 1980. Physiological and ecological aspects of gas exchange by sea turtle eggs. Amer. Zool. 20(3):575-584.

- ARAUZ, R. 1995. A description of the Central American shrimp fisheries with estimates of incidental capture and mortality of sea turtles. In: Keinath, J., and Keinath, D. (Compilers). Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-387, pp. 5-9.
- ARIDJS, H. 1990. México proclama la veda total para la captura de huevos y tortugas marinas. Noticiero de Tortugas Marinas 1:1-3.
- BARBER, R.T., AND CHAVEZ, F.P. 1983. Biological consequences of El Niño. Science 222:1203-1210.
- BARBER, R.T., AND KOGELSCHATZ, J.E. 1990. Nutrients and productivity during the 1982/83 El Niño. In: Glynn, P.W. (Ed.). Global ecological consequences of the 1982-83 El Niño-Southern Oscillation. New York: Elsevier Science Publishing Company Inc., pp. 21-53.
- BJORNDAL, K.A. 1985. Nutritional ecology of sea turtles. Copeia 1985:736-751.
- BOWEN, B.W., MEYLAN, A.B., ROSS, J.P., LIMPUS, C.J., BALAZS, G.H., AND AVISE, J.C. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. Evolution 46:865-881.
- C.A.C. 1995. Climate Diagnostics Bulletin, Near Real-time Analyses Ocean/Atmosphere. Washington, DC: U.S. Department of Commerce, NOAA.
- CARR, A. 1980. Some problems of sea turtle ecology. Amer. Zool. 20:489-498.
- CLIFTION, K., CORNEJO, D.O., AND FELGER, R.S. 1982. Sea turtles of the Pacific coast of Mexico. In: Bjorndal, K. (Ed.). Biology and Conservation of Sea Turtles. Washington, DC: Smithsonian Institution Press, pp. 199-209.
- CORNELIUS, S.E. 1982. Status of sea turtles along the Pacific coast of middle America. In: Bjorndal, K. (Ed.). Biology and Conservation of Sea Turtles. Washington, DC: Smithsonian Institution Press, pp. 211-219.
- CORNELIUS, S.E. 1986. The sea turiles of Santa Rosa National Park. Fundación de Parques Nacionales, Costa Rica. Monograph. San José, 134 pp.
- CORNELUS, S.E., ALVARADO-ULLOA, M., CASTRO, J.C., MATA DEL VALLE, M., AND ROBINSON, D.C. 1991. Management of olive Ridley sea turtles (*Lepidochelys olivacea*) nesting at playas Nancite and Ostional, Costa Rica. In: Robinson, J.R., and Redford, K.H. (Ed.). Neotropical Wildlife Use and Conservation. Chicago: University of Chicago Press, pp. 111-135.
- CORNELIUS, S.E., AND ROBINSON, D.C. 1986. Post-nesting movements of female olive ridley turtles tagged in Costa Rica. Vida Silvestre Neotropical 1:12-23.
- FRAZIER, J., AND SALAS, S. 1982, Ecuador closes commercial turtle fishery. Marine Turtle Newsletter 20:5-6.
- GATES, C.E., VALVERDE, R.A., MO, C.L., CHAVES, A.C., BALLESTERO, J., AND PESKIN, J. 1996. Estimating *arribada* size using a modified instantaneous count procedure. Journal of Agricultural, Biological, and Environmental Statistics 1:275-287.
- GREEN, D., AND ORTIZ-CRESPO, F. 1982. Status of sea turtle populations in the central eastern pacific. In: Bjorndal, K. (Ed.). Biology and Conservation of Sea Turtles. Washington: Smithsonian Institution Press, pp. 221-233.
- HIGGINSON, J. 1989. Sea turtles in Guatemala: threats and conservation efforts. Marine Turtle Newsletter 45:1-5.
- HUGHES, D.A., AND RICHARD, J.D. 1974. The nesting of the Pacific ridley turtle *Lepidochelys olivacea* on Playa Nancite, Costa Rica. Mar. Biol. 24:97-107.
- KAR, C. 1982. Discovery of second mass nesting ground for Pacific ridley sea turtles in Orissa, India. Marine Turtle Newsletter 23:3.
- LIMPUS, C.J., AND NICHOLLS, N. 1988. The Southern Oscillation regulates the annual numbers of green turtles (*Chelonia mydas*) breeding around northern Australia. Aust. J. Wildl. Res. 15:157-161.
- MAGNUSON, J.J., BJORNDAL, K.A., DUPAUL, W.D., GRAHAM, G.L., OWENS,

D.W., PETERSON, C.H., PRITCHARD, P.C.H., RICHARDSON, J.L., SAUL, G.E., AND WEST, C.W. 1990. Decline of the Sea Turtles: Causes and Prevention. National Academy Press, Committee on Sea Turtle Conservation, pp. 252.

- MÁRQUEZ, R., PENAFLORES, S.C., VILLANUEVA, O.A., AND DÍAZ, F. 1982. A model for diagnosis of populations of olive ridleys and green turtles of West Pacific tropical coasts. In: Bjorndal, K. (Ed.). Biology and Conservation of Sea Turtles. Washington, DC: Smithsonian Institution Press, pp. 153-158.
- MÅRQUEZ, R., AND VAN DISSEL, H.G. 1982. A method for evaluating the number of massed nesting olive ridley sea turtles, *Lepidochelys* olivacea, during an arribazón behavior. Netherlands Journal of Zoology 32:419-425.
- MCPHADEN, M.J. 1993. TOGA-TAO and the 1991-93 El Niño-Southern Oscillation Event. Oceanography 6:36-44.
- MDP. 1995. Prohíben la captura dirigida de todas las especies de tortugas marinas existentes en aguas jurisdiccionales peruanas. El Peruano (normas legales), Ministerio de Pesquería, Res. Min. 103-95-PETI: 130366.
- MEYLAN, A. 1982. Sea turtle migration-evidence from tag returns. In: Bjorndal, K. (Ed.). Biology and Conservation of Sea Turtles. Washington, DC: Smithsonian Institution Press, pp. 91-100.
- Mo, C.L., CABALLERO, M., AND SALAS, I. 1992. Microorganism infection of olive ridley eggs. In: Richardson, J.L. and Richardson, T.H. (Compilers). Proceedings of the Twelfth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-361, pp. 81-84.
- Mo, C.L., SALAS, I., AND CABALLERO, M. 1990. Are fungi and bacteria responsible foroliveridley's eggloss? In: Richardson, T.H., Richardson, J.I., and Donnelly, M. (Compilers). Proceedings of the Tenth Annual Workshop on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-278, pp. 249-252.
- MOHANTY-HEIMADI, P. 1987. Unique second arribada at Gahirmatha. Marine Turtle Newsletter 40:7-8.
- PLOTKIN, P.T., BYLES, R.A., ROSTAL, D.C., AND OWENS, D.W. 1995. Independent versus socially facilitated oceanic migrations of the olive ridley. *Lepidochelys olivacea*, Marine Biology 122:137-143.
- PLOTKIN, P.T., ROSTAL, D.C., BYLES, R.A., AND OWENS, D.W. 1997. Reproductive and developmental synchrony in female *Lepidochetys olivacea*, J. Herpetol, 31:17-22.
- QUINN, W.H. 1992. A study of Southern Oscillation-related elimatic activity for A.D. 622-1900 incorporating Nile River flood data. In: Diaz, H.F., and Markgraf, V. (Ed.). El Niño: Historical and paleoclimatic aspects of the Southern Oscillation. Cambridge: Cambridge University Press, pp. 119-149.
- REICHART, H.A. 1993. Synopsis of biological data on the olive ridley sea turtle *Lepidochelys olivacea* (Eschscholtz, 1829) in the Western Atlantic. NOAA Technical Memorandum NMFS-SEFSC-336, pp. 78.
- RICHARD, J.D., AND HUGHES, D.A. 1972. Some observations of sea turtle nesting activity in Costa Rica. Mar. Biol. 16:297-309.
- RICHARDSON, J.L., AND RICHARDSON, T.H. 1982. An experimental population model for the loggerhead sea turtle (*Caretta caretta*). In: Bjorndal, K. (Ed.). Biology and Conservation of Sea Turtles. Washington, DC: Smithsonian Institution Press, pp. 165-176.
- VARGAS, P., TELLO, P., AND ARANDA, C. 1994. Sea turtle conservation in Peru: the present situation and a strategy for immediate action. In: Bjorndal, K.A., Bolten, A.B., Johnson, D.A., and Eliazar, P.J. (Compilers). Proceedings of the Fourteenth Annual Symposium on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFSC-351, pp. 159-162.

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