Reproductive patterns of the hawksbill turtle *Eretmochelys imbricata* in sandy beaches of the Yucatan Peninsula

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Daily censuses of the hawksbill turtle *Eretmochelys imbricata* were taken during the nesting seasons 1995–2001 in three sandy beaches of the Yucatan Peninsula, Mexico (Celestun, El Cuyo and Isla Holbox), to evaluate aspects of its reproductive biology. A total of 9059 hawksbill turtle clutches was estimated for the study period. Nesting seasons began in mid-April and ended in early September, peaking in May–June. No significant differences were detected in the mean number of clutches per km among beaches. The largest number of clutches was observed in the supralittoral zone (6341: 70%), followed by the dune (2491: 27.5%) and the intertidal (227: 2.5%) zones. Variation in number of clutches showed a main peak in 1999, decreasing in 2000 and 2001. A significant decrease (3 cm) in body size of nesting females was detected between 1995 and 2001. Mean clutch size was 140 eggs/clutch, and a significant positive relationship between curved carapace length and mean clutch size was found at the three beaches. Incubation period, hatching success and emergence success varied between years (lowest values in 1998) and beaches (highest values at Isla Holbox), with no significant differences between the supralittoral and dune zones. Even though there was no evidence of a decreasing trend in nesting activity for the study period, the decrease in 2000–2001 suggests that additional beach monitoring is necessary to identify long-term trends, and to reduce potential losses of nests by human and natural causes in this globally important region for the hawksbill turtle.

INTRODUCTION

The hawksbill turtle, *Eretmochelys imbricata*, has experienced global population declines of at least 80% during the last century, and since 1996 this species was classified by the World Conservation Union (IUCN) as critically endangered (Baillie & Groombridge, 1996; Meylan & Donnelly, 1999). The negative effects of its long history of unregulated commercial exploitation for tortoiseshell (economically valuable material), were exacerbated by additional mortality causes, including incidental capture by fishing, and loss or degradation of coastal habitats (Groombridge & Luxmoore, 1989; Meylan & Donnelly, 1999).

Although most hawksbill populations are declining or depleted, the Yucatan Peninsula (Mexico) remains the largest nesting population in the Caribbean, and one of the five largest in the world, with more than 1000 females nesting annually (Meylan & Donnelly, 1999). The number of nesting hawksbills at Yucatan Peninsula had increased over the period 1977–1996 (Garduño-Andrade et al., 1999), constituting one of the two geopolitical units that reported an increasing nesting trend in the Caribbean region (Meylan, 1999).

Knowledge about spatio-temporal patterns in the number of nests of *E. imbricata* is important to identify nesting trends and to evaluate the conservation status and extinction risk of the species (Meylan & Donnelly, 1999; Hawkes et al., 2005; Broderick et al., 2006). A lack of information for several nesting beaches in the Caribbean Sea and Gulf of Mexico prevents an adequate assessment of population status (Mrosovsky, 2000). This is particularly relevant for the Yucatan Peninsula (Mexico), because it is one of the most important nesting zones in the world for the hawksbill turtle. Unfortunately, nesting data are limited and largely contained in technical reports (Frazier, 1993; Frazier et al., 1993) and, with the exception of two studies (Garduño-Andrade, 1999; Garduño-Andrade et al., 1999), no information has been published on *E. imbricata* in the Yucatan Peninsula, particularly from the mid-1990s onwards. This paper analyses spatial and temporal variability in reproductive characteristics of the hawksbill turtle (*E. imbricata*) in three sandy beaches of the Yucatan Peninsula during the seven-year period 1995–2001.

MATERIALS AND METHODS

Study area

The Celestun Biosphere Reserve is located in the northwest of the Yucatan Peninsula (20°45′N 90°15′W) (INEGI, 1996) and includes a hawksbill nesting beach stretch of 24 km (Figure 1). El Cuyo is located in the northeast of Yucatan State (21°31′N 87°41′W), within the Ría Lagartos Special Biosphere Reserve, and includes a 31-km nesting area (Figure 1). Isla Holbox is at the north-east extreme of the Peninsula, in the State of Quintana Roo (21°30′N 87°24′W) (INEGI, 1996) and has a main nesting beach stretch of 24 km (Figure 1).
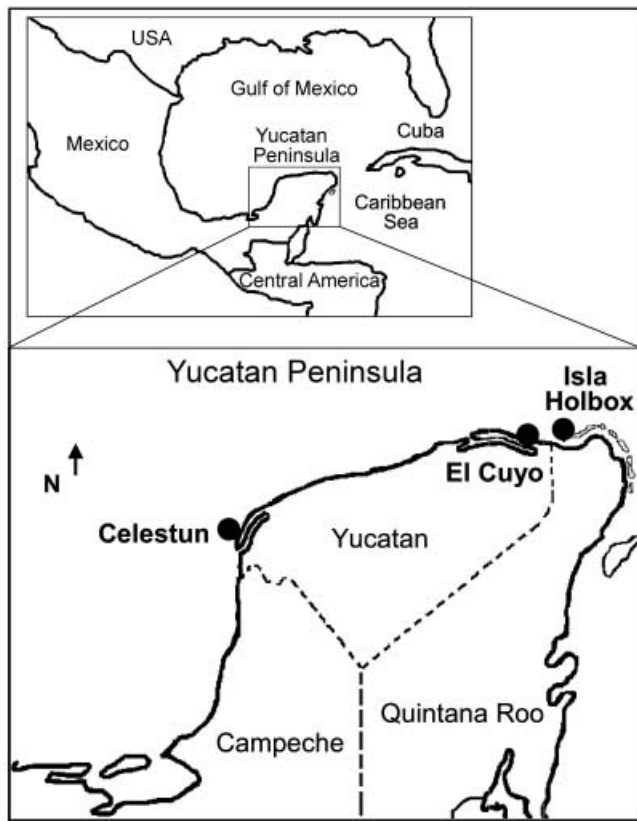
Figure 1. Geographical location of the three studied *Eretmochelys imbricata* nesting areas (Celestun, El Cuyo and Isla Holbox) on the Yucatan Peninsula.

Fieldwork and data analysis

Night-time surveys of the three beaches were carried out once the first turtle or even a crawl track appears in the sand, indicating the beginning of the nesting season. Turtle tracks were followed until the nest or the turtle was located. Once found, the curved carapace length (CCL) of each turtle was measured as the distance between the central anterior edge of the nuchal scute and the posterior edge of one of the supracaudal scutes. To minimize measurement errors, the same team of observers took all measurements of CCL at each beach during the study period.

Clutch size was determined counting eggs at oviposition (Miller, 1999). Across-shore location of the nest was recorded, according to three distinguishable ecological zones of the beach (Defeo & McLachlan, 2005): intertidal, supralittoral and sand dunes. As the study zone is microtidal (astronomic tides close to 0.5 m), the intertidal zone was defined as the zone of water movement over the beach face, after a broken wave (bore) collapses on the sand (swash zone). The supralittoral zone was defined in each sampling occasion as the zone beyond the high tide mark; up the beach; and the sand dune zone was positioned between the top of the beach where vegetation begins and the landward limit of the last nest recorded. The duration of the nesting season in each year 1995–2001 was determined on the basis of daily censuses of turtles nesting in each beach. A nested analysis of variance (ANOVA) was carried out to evaluate differences in number of clutches between beaches (main factor) and zones (nested within beaches). Data were transformed (log $X+1$) to meet the homoscedasticity assumption.
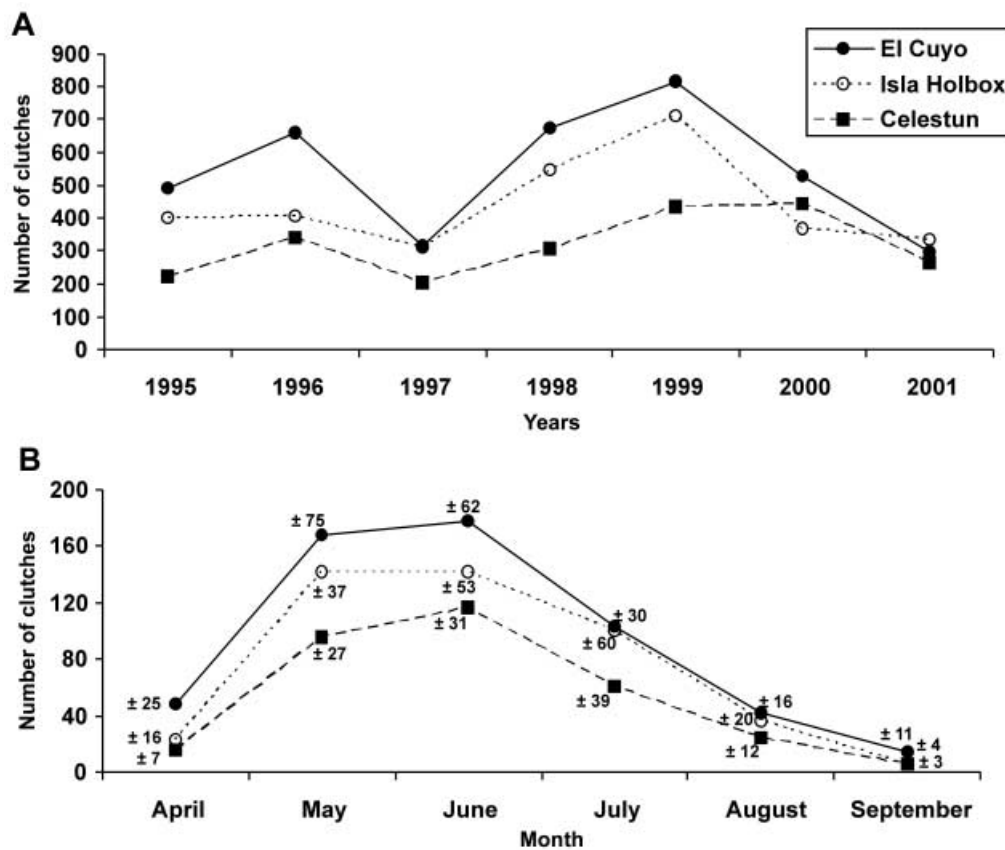

Figure 2. (A) Annual and (B) monthly (mean ±SD of annual values) variation in number of *Eretmochelys imbricata* clutches between 1995 and 2001 at Celestun, El Cuyo and Isla Holbox.
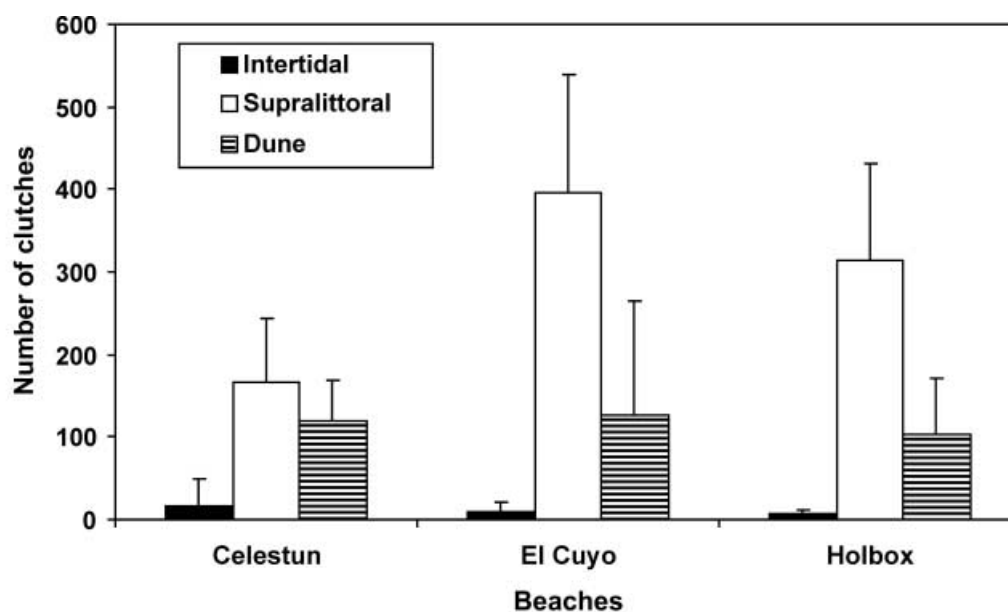
Figure 3. Across-shore mean (±SD) annual spatial distribution of the seven years of *Eretmochelys imbricata* clutches at Celestun, El Cuyo and Isla Holbox.

Incubation period was estimated as the number of days between oviposition and emergence of the first hatchling.

Number of eggs per clutch was estimated after hatchling emergence. The nest was examined to account for the number of eggshells (S), number of live (L) and dead (D) hatchlings inside the nest, number of undeveloped eggs (UD; eggs without apparent embryonic development), unhatched eggs (UH; eggs with obvious embryos, excluding unhatched term). The unhatched term (UHT) consists of apparently full term embryos in egg shell or pipped (with a small amount of external yolk material). The number of depredated eggs (P) was also recorded.

Clutch size (CS: number of eggs laid into the nest), hatching success ($\%Hs$: per cent of hatchlings able to break the egg) and emergence success ($\%ES$; per cent of hatchlings that survived until reaching sand surface) were calculated using the following formulae (Miller, 1999):

$$CS = S + UD + UH + UHT + P$$

$$\%Hs = \left(\frac{S}{CS}\right) 100$$

$$\%ES = \left(\frac{S - (L + D)}{CS}\right) 100$$

To evaluate differences in the number of clutches per km between years and beaches, a two-way ANOVA was done. The same analysis was conducted to determine spatio-temporal variations in the CCL of nesting turtles. The mean clutch size (CS) for each female size-class (grouped by 2 cm CCL) was calculated, and a linear model of the form $CS = a + b*CCL$ was fitted. An analysis of covariance (ANCOVA) was employed to compare the CCL–CS relationships and evaluate differences in the reproductive output between beaches (main factor), using CCL as

covariate and CS as dependent variable. Size-classes with one or two females were not considered in the analysis.

Nested ANOVAs were used to determine spatio-temporal differences in egg incubation time, hatching success and emergence success, using beaches and years as main factors, and zones (supralittoral and dunes) nested in beaches. The intertidal zone was excluded because the number of clutches was negligible and most clutches were relocated to upper beach levels or moved to a protective compound to avoid their flooding. September was also excluded because of the very low number of clutches occurring in this month. The assumption of homoscedasticity was not met and thus the following procedures were carried out: (1) incubation period data were transformed as $X^{1/8}$ and (2) hatching and emergence success data were transformed by the arcsine of the square root of each proportion. The Tukey HSD test for unequal sample sizes was used for multiple comparisons (Zar, 1999). A significance level of 0.05 was used in all statistical analyses.

RESULTS

Variations in the number of clutches followed the same pattern at El Cuyo and Isla Holbox, with a main peak in 1999 and a marked decrease in 2000 and 2001, whereas at Celestun the main peak was observed in 2000 decreasing in 2001 (Figure 2A). Nesting activity showed no significant trends over time (data pooled) for the whole period 1995–2001 (regression: $F_{1,19} = 0.05$, $r^2 = 0.003$, $P = 0.82$) but it showed a significant decreasing trend from 2000 to 2001 (regression: $F_{1,7} = 13.84$, $r^2 = 0.66$, $P < 0.01$). Daily census provided a total of 9059 hawksbill turtle clutches recorded from 1995 to 2001, with a range of 202–817 annual clutches per beach. Celestun had a total of 2210 clutches, El Cuyo had 3779, and Isla Holbox had 3070. Celestun had an annual mean (±SD) of 13 ±6 clutches per km, El Cuyo had 17 ±6 clutches per km and Isla Holbox had

Table 1. *Two-way ANOVA results performed on number of clutches per km and individual size CCL (cm) for* Eretmochelys imbricata, *with beaches (Celestun, El Cuyo and Isla Holbox) and years (1995–2001) as main factors. Significant probability values are highlighted in bold and italics.*

Source of variation	df	MS	F	P
Clutches/km				
Seasons (A)	6	9.483	1.540	0.1732
Beaches (B)	2	9.751	1.583	0.2104
A × B	12	2.686	0.436	0.9449
Error	97	6.157		
Individual size				
Years (A)	6	39.349	4.081	***0.0005***
Beaches (B)	2	8.370	0.868	0.4200
A × B	12	12.835	1.331	0.1944
Error	1159	9.642		

Table 2. *Results of ANCOVA for the CCL–CS relationship among beaches. Test of homogeneity of slopes is also showed.*

Source of variation	df	MS	F	P
Beaches	2	163.488	5.410	*0.011*
Error	26	30.217		

Slope homogeneity: $F_{2,24}=3.5l$; $P>0.09$. CCL, curved carapace length; CS, clutch size

Table 3. *Nested ANOVA results for* Eretmochelys imbricata *in: (a) egg incubation period; (b) hatching success; and (c) emergence success, with beaches (Celestun, El Cuyo and Isla Holbox) and years (1995–2001) as main factors, and zones nested in beaches. Significant probability values are highlighted in bold and italics, and marginally significant values are underlined.*

Source of variation	df	MS	F	P
(a) Egg incubation period				
Years (A)	6	0.0031	5.2440	***0.0028***
Beaches (B)	2	0.0069	14.6014	***0.0284***
Zones (C) (nested in B)	3	0.0005	1.8419	0.1376
A × B	12	0.0025	4.1768	***0.0033***
A × C	18	0.0006	2.3035	***0.0014***
(b) Hatching success				
Years (A)	6	0.0073	5.0612	***0.0033***
Beaches (B)	2	0.1406	22.8208	***0.0153***
Zones (C) (nested in B)	3	0.0006	0.5567	0.6436
A × B	12	0.0080	5.5649	***0.0006***
A × C	18	0.0014	1.3116	0.1690
(c) Emergence success				
Years (A)	6	0.1706	8.4926	***0.0001***
Beaches (B)	2	0.3836	8.8645	<u>0.0550</u>
Zones (C) (nested in B)	3	0.0432	2.1570	<u>0.0909</u>
A × B	12	0.1294	6.4407	***0.0002***
A × C	18	0.0200	1.0015	0.4540

18 ±6 clutches per km. No significant differences were found in clutch density between years and beaches (ANOVA: Table 1). The nesting season began in mid-April and ended at the beginning of September in the seven years analysed, with a peak in May–June (65% of total: Figure 2B).
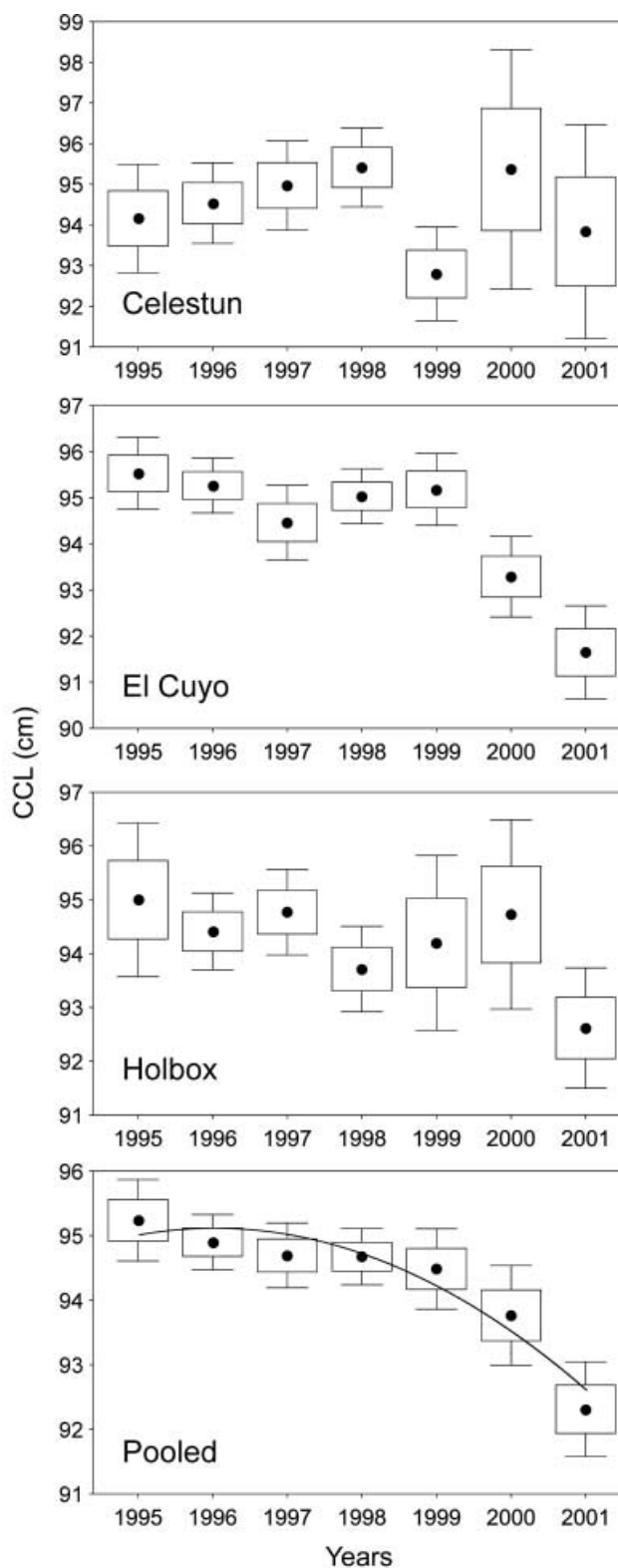
Figure 4. *Eretmochelys imbricata*. CCL (cm) analysis discriminated by beach (Celestun, El Cuyo and Isla Holbox) between 1995 and 2001. Boxes correspond to 1 SE and bars to 1.96 SE. For the pooled analysis, a significant parabolic function of the form $y=a+b\,x-cx^2$ was fitted ($R^2=0.93$, $P<0.05$).

The number of clutches during the seven seasons significantly differed between zones ($F_{6,45}=40.75$; $P<0.001$), with each zone differing from the other ones (Tukey HSD test: $P<0.001$). The supralittoral zone had the highest number of clutches (634l: 70%), followed by the sand
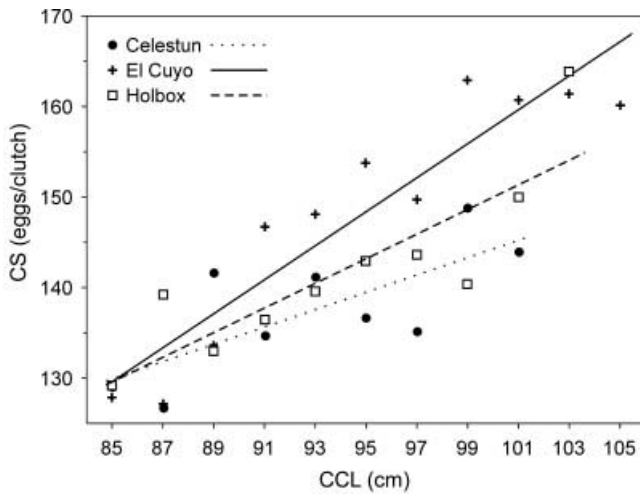
Figure 5. Relationship between curved carapace length (CCL) and clutch size (CS) for *Eretmochelys imbricata* at Celestun (●), El Cuyo (+) and Isla Holbox (□).

dunes (2491: 27.5%) and the intertidal zone (227: 2.5%) (Figure 3).

Individual size (mean CCL ±SD) of hawksbill turtles was 94.4 ±4.1 cm (N=260) at Celestun, 94.7 ±4.1 cm (N=740) at El Cuyo and 94.1 ±4.1 cm (N=392) at Isla Holbox. The CCL frequency distributions at Celestun and El Cuyo had a mode in the range 95–99 cm, while the mode at Isla Holbox was 90–94 cm. The two-way ANOVA showed significant differences in CCL between years (Table 1). The analysis discriminated by beach showed that the decrease of turtle size over time was

particularly marked at El Cuyo, though the same trend occurred at the other two beaches (Figure 4). Pooled analysis showed a 3-cm decrease in mean CCL (±SD) between 1995 (95.24 ±4.16 cm) and 2001 (92.31 ±4.13 cm) following a negative parabolic function (Figure 4). The Tukey test showed that turtle size in 2001 was significantly smaller than in the period 1995–1998, but did not differ from 1999–2000, highlighting the consistent decrease in turtle size in the last three years of analysis.

Mean clutch size was 140 ±9 eggs/clutch (range 60–247, N=1474) at Celestun, 145 ±5 eggs/clutch (range 62–241, N=2894) at El Cuyo and 142 ±7 eggs/clutch (range 60–257, N=2176) at Isla Holbox. The linear CCL–CS model was significant ($P<0.05$) for the three beaches (Celestun, $r^2=0.55$; El Cuyo, $r^2=0.69$; and Isla Holbox, $r^2=0.73$), clearly indicating increasing clutch size with body size. Also, significant differences in the CCL–CS relationship were found between beaches (ANCOVA, $P<0.05$; Table 2): hawksbill at El Cuyo had higher clutch size for a same length than in Celestun and Isla Holbox, which did not differ between them (Tukey test: $P>0.05$; Figure 5).

The mean egg incubation period (±SD) for *Eretmochelys imbricata* was 62 ±4 days (range 51–83, N=896) at Celestun, 63 ±4 days (range 50–80, N=1691) at El Cuyo and 65 ±5 days (range 50–80, N=1249) at Isla Holbox. Nested ANOVA indicated significant differences between years and beaches, but no differences between the supralittoral and dune zones (Table 3). The year 1998 had a significantly shorter incubation period than the other years, and turtles at Isla Holbox had a longer incubation period than at El Cuyo, which in turn had a longer incubation period than at Celestun (Tukey test; Figure 6). Egg hatching success was 89 ±2% (N=1218) at Celestun, 87 ±3% (N=2276) at El Cuyo and 91 ±1% (N=1805) at
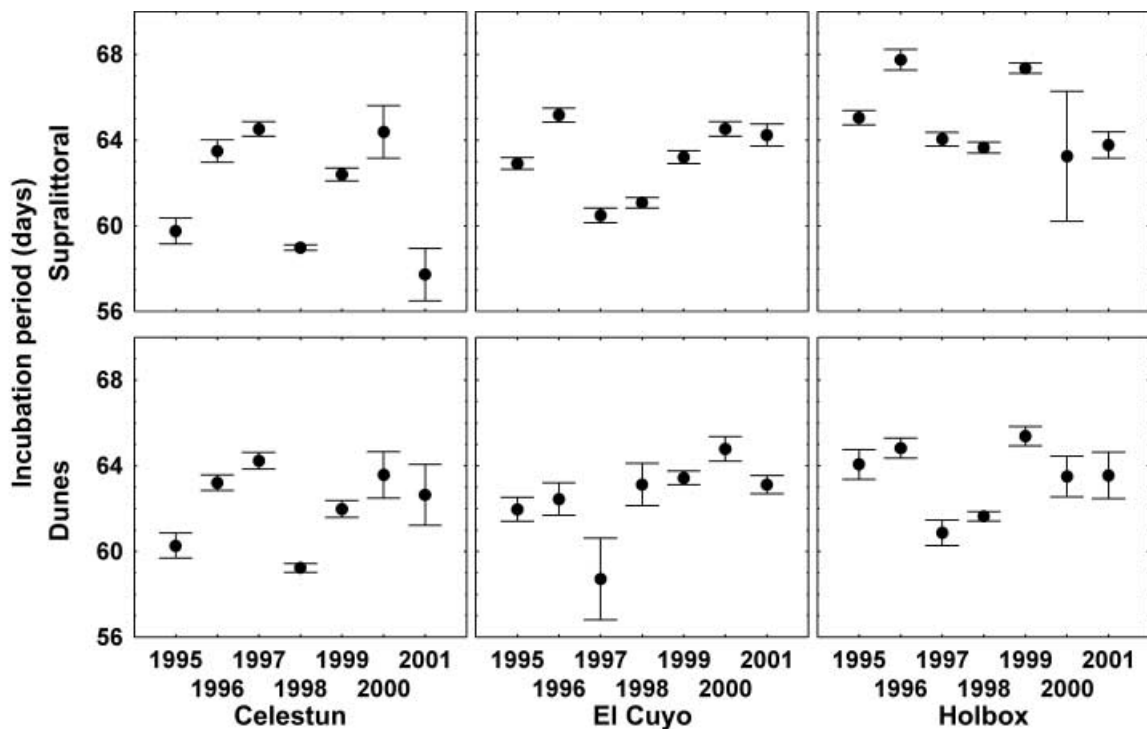

Figure 6. *Eretmochelys imbricata*. Mean (±SE) egg incubation period discriminated by zone (supralittoral and sand dunes), beach (Celestun, El Cuyo and Isla Holbox) and nesting season (1995–2001).
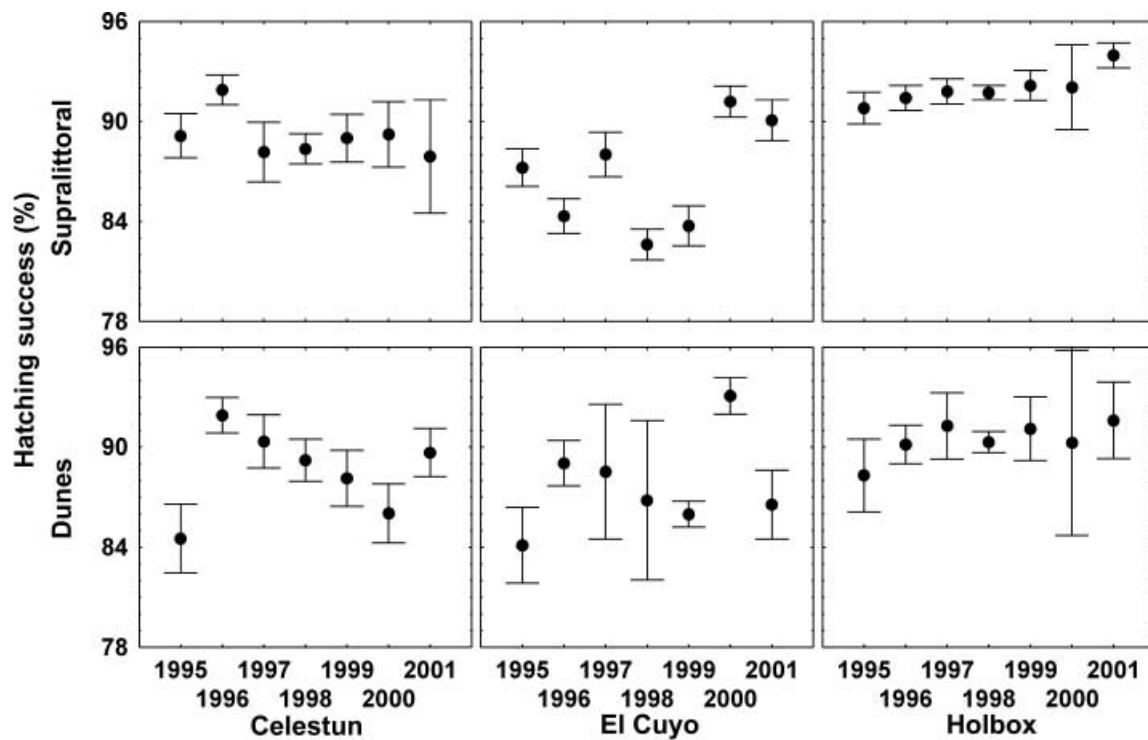
Figure 7. *Eretmochelys imbricata*. Mean (±SE) egg hatching success, discriminated by zone (supralittoral and sand dunes), beach (Celestun, El Cuyo and Isla Holbox) and nesting season (1995–2001).
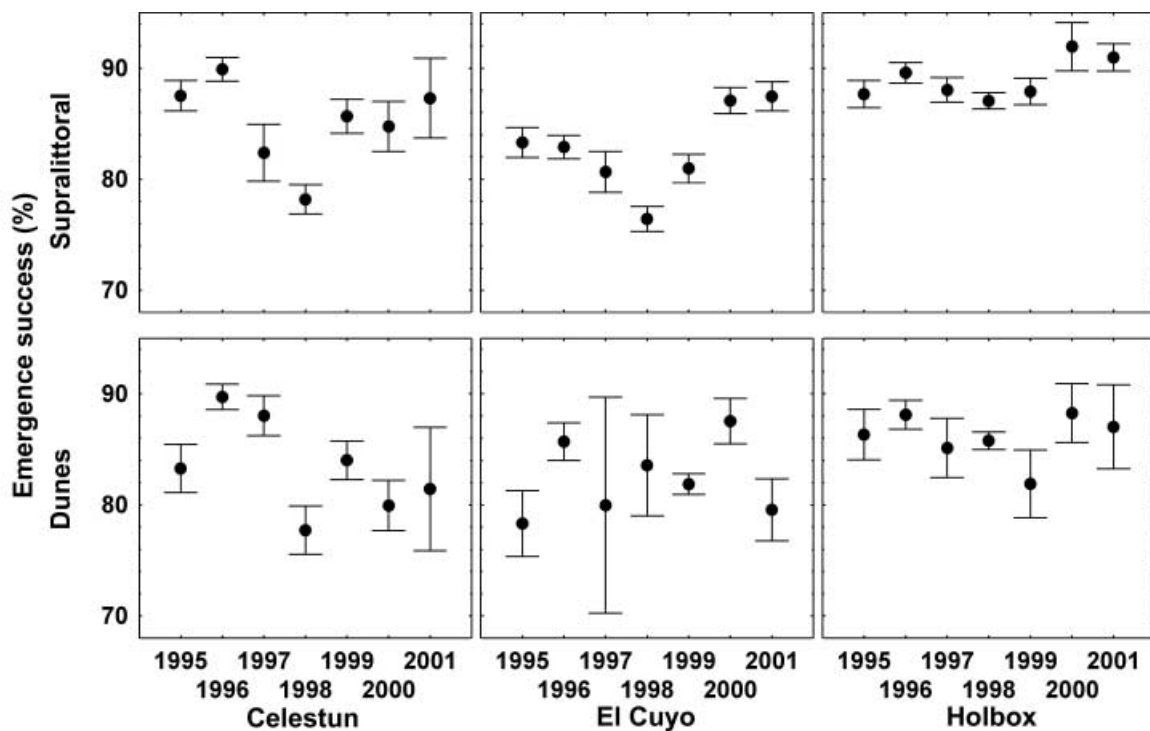

Figure 8. *Eretmochelys imbricata*. Mean (±SE) variation in emergence success discriminated by zone (supralittoral and sand dunes), beach (Celestun, El Cuyo and Isla Holbox) and nesting season (1995–2001).

Isla Holbox. The nested ANOVA also showed significant differences in hatching success between years and beaches (Table 3). A significantly lower hatching success was observed in 1998 and a higher hatching success at Isla Holbox than at Celestun and El Cuyo, which did not differ between each other (Tukey test; Figure 7). Emergence success was 85±4% (N=1218) at Celestun, 82±3% (N=2268) at El Cuyo and 88±1% (N=1805) at Isla Holbox. There were significant differences between years, and marginally significant ones between beaches ($P=0.055$) and zones (Table 3). As with hatching success, emergence success was lowest in 1998 and highest at Isla Holbox, followed by El Cuyo and Celestun (Figure 8).

DISCUSSION

The nesting season of the hawksbill turtle *Eretmochelys imbricata* at Yucatan Peninsula lasted from April to September in all three beaches and the the seven years analysed (1995–2001). This figure, as well as the intra-annual peak of nesting activity (May–June), is similar to other figures reported for this region (Nájera, 1990; Garduño-Andrade, 1999).

The nesting season (April–September) coincided with the warmest months of the year and with high rainfall (Herrera-Silveira & Ramírez-Ramírez, 1996), in agreement with that found by Mortimer & Carr (1987) for green turtles. It has been indicated that temperature appears to be the ultimate factor dictating the seasonality of nesting (Godley et al., 2001). In fact, negligible or no nesting activity has been observed in months with sand temperatures close to the lower limit of the thermal tolerance of embryos (Godley et al., 2002a). Similarly, in our study, the period of no nesting (October–March) coincides with the months of lowest temperatures; however, we have no data to determine the causative processes behind this pattern.

We found no evidence of a decreasing or increasing trend in nesting activity of hawksbills for the whole period 1995–2001. However, a significant decline in the number of clutches was observed in the last two years (2000 and 2001), especially at Isla Holbox and El Cuyo. Inter-annual variability in nesting is common in marine turtles, although this variation differs among species (Broderick et al., 2001). The nesting population of *E. imbricata* in the Seychelles, one of the largest in the world and in a good conservation status (Meylan & Donnelly, 1999), has also shown important inter-annual variability (Broderick et al., 2001). In addition, the coefficient of variation (CV) of number of clutches laid annually in the Seychelles (0.34; Broderick et al., 2001) is similar to those calculated for Celestun (0.30), El Cuyo (0.35), and Isla Holbox (0.32), indicating that inter-annual variability in nesting of *E. imbricata* at the Yucatan Peninsula was within the range reported for this species.

The decreasing trend in number of clutches during the last two years (Figure 2) could be partially explained by fluctuations in remigration of females, which mainly occurs between 2 and 3 years (Garduño-Andrade, 1999; Mortimer & Bresson, 1999). Another explanatory factor could be the recruitment of neophytes (suggested by the decrease in mean body size of females: Figure 4), which lay fewer clutches per year than remigrants (Hawkes et al., 2005). A variety of human impacts (e.g. incidental catch of adults by fishing, illegal hunting of nesting females, deterioration of nesting beaches, and poaching) could also affect the number of nests laid on each season. However, lack of data about human intervention levels makes it difficult to ascertain if the decreasing trend in number of clutches is due to natural or anthropogenic effects.

Hawksbill turtles largely preferred the supralittoral zone for nesting (70% of the clutches). Similar results have been reported by Garduño-Andrade (1999) for this species at the Yucatan Peninsula, and by Hays et al. (1995a) for other sea turtles around the world. The preference for the supralittoral zone might be related to its elevation above the mean sea level (Horrocks & Scott, 1990), and because it provides optimal temperature and humidity conditions for nesting success (López-Castro et al., 2004). The dune zone (27.5% of the clutches) has vegetation that could hide the nest from predators and decreases sediment temperature (Bjorndal & Bolten, 1992). However, the presence of roots impedes digging, redirecting the nesting efforts of females to the open beach (Hays & Speakman, 1993). In addition, nesting in vegetation may result in increased nest invasion by roots, affecting survival of embryos (Whitmore & Dutton, 1985). Similar to our results, Garduño-Andrade (1999) found that the proportion of nests of *E. imbricata* laid in sand dunes was 34.1%. Our results confirm that the inter-tidal zone is rarely used for nesting (2.5% of the clutches), because of nest flooding and higher susceptibility to destruction from wave action (Mrosovsky, 1983).

The across-shore distribution of nests at the three beaches from the Yucatan Peninsula differed from the pattern observed in the Seychelles and some Caribbean Islands (Barbados, Antigua), where hawksbills have a preference for nesting amongst low vegetation beyond the open beach (Diamond, 1976; Horrocks & Scott, 1991; Mrosovsky et al., 1992). However, it has also been found that nesting of hawksbills occurs in the forest borders or still in the forest itself at the island of Guadeloupe, Caribbean Sea (Kamel & Mrosovsky, 2005, 2006).

Mean clutch size estimates coincided with those estimated by Frazier (1993) (140 eggs/clutch and a range 46–244) and by Nájera (1990: 149 to 153 eggs/clutch) for the Yucatan. Mean clutch size was lower than reported by Bjorndal et al. (1985) for Tortuguero, Costa Rica (158 eggs/clutch) and by Aiken et al. (2001) for the Cayman Islands (154 eggs/clutch), but higher than estimates provided by Horrocks & Scott (1990) for Barbados (127 eggs/clutch) and by Moncada et al. (1999) for the Cuban Archipelago (132 to 137 eggs/clutch). The largest clutch size for *E. imbricata* worldwide has been recorded in Cousine Island, the Seychelles (264 eggs/clutch), with a mean value of 177 eggs/clutch (Hitchins et al., 2004). Variations between sites and years may be explained by differences in food availability and quality, population structure of nesting turtles and time of the year when nesting occurs (Broderick et al., 2003; Hitchins et al., 2004).

The linear relationship between turtle female body size and clutch size was significant for the three beaches. A direct carapace length–clutch size relationship has been reported for different species of marine turtles (Frazer & Richardson, 1986; Broderick et al., 2003), including *E. imbricata* (van Buskirk & Crowder, 1994; Hitchins et al., 2004). These results might be explained by differential egg carrying capacity (Hays & Speakman, 1991), suggesting that the decrease in individual size, observed mainly during the last three years (Figure 2) could affect the reproductive potential of nesting turtles. However, this can result either from a decline in remigration of experienced females or recruitment of neophytes. Both hypotheses should be tested in the near future. It would also be convenient to evaluate the accuracy of CCL measurements in order to examine if future changes of mean sizes are without the range of any measurement error (Mrosovsky, 1983).

Nesting females at El Cuyo showed significantly higher clutch size at body length than those nesting at Isla Holbox and Celestun (Figure 5), suggesting differential reproductive potential of the nesting populations. Shine (1992) stated that although body size may set the upper limit to the number of eggs/clutch, this limit may not be reached if conditions are suboptimal. However, these aspects have not been evaluated in hawksbill nesting populations in the Yucatan Peninsula.

Mean incubation period for the hawksbill was close to 63 days, though there were significant variations between beaches and years. This value is within the range reported for *E. imbricata* around the world (53.5 to 65.6 days, van Buskirk & Crowder, 1994). Egg incubation period for sea turtles decreases with increasing temperature (Marcovaldi et al., 1999; Broderick et al., 2000; Godley et al., 2002b), but it can also be affected by sand moisture (McGehee, 1990), nest position, and number of eggs per clutch (Fowler, 1979). However, sand temperature is the most important factor influencing the incubation period (Godfrey & Mrosovsky, 1997, 2001), which is explained by the linearity between temperature and embryonic development (McGehee, 1979). Nesting beaches at Isla Holbox and El Cuyo have white sands because of their proximity to the Caribbean Sea (Figure 1), whereas Celestun has darker sands. Such differences in beach colour determine variations in sand albedo, thus producing differential thermal conditions among nesting beaches (Hays et al., 1995b, 2001). This situation may explain the significantly shorter mean incubation period recorded for Celestun, which has darker sands than in the other two beaches.

Hatching success in Celestun (85%), El Cuyo (82%), and Isla Holbox (88%) were higher than those reported for the Cuban Archipelago (66 to 75%; Moncada et al., 1999), but quite similar to those recorded in Barbados (72 to 89%; Horrocks & Scott, 1990). However, emergence success registered in our study (Celestun 89%, El Cuyo 87%, Isla Holbox 91%) were higher than those reported for hawksbills nesting in Barbados (Horrocks & Scott, 1990). Isla Holbox had a longer incubation period, together with a significantly higher hatching and emergence success than El Cuyo and Celestun, suggesting that longer incubation periods can generate higher hatching and emergence success. This tendency is in agreement with results recorded for *E. imbricata* around the world (van Buskirk & Crowder, 1994). Incubation period, as well as hatching and emergence success, did not differ significantly between supralittoral and dune zones in all the three beaches, suggesting that both beach levels provided adequate environmental conditions (temperature, humidity and gas diffusion) for nesting success. Fowler (1979) also found that nest position (open beach vs beach border vegetation) did not affect emergence success in the green turtle, but eggs in nests on the open beach had shorter incubation periods than those in nests located near or in the beach border vegetation.

Conservation implications

Our results indicate that the number of nests of *E. imbricata* registered annually at Celestun, El Cuyo and Isla Holbox were higher than the number of nests found at these sites at the beginning of the marine turtle protection programme (during the 1970s), but remains in the range reported for the first half of the 1990s (Garduño-Andrade et al., 1999). However, additional beach monitoring is necessary in order to identify long-term trends in nesting populations, and to reduce potential losses of nests resulting from human and natural causes.

Given that *Eretmochelys imbricata* is strongly influenced by a natal homing mechanism (return to nest in the region of origin), it would be expected that, if a nesting beach is destroyed or a local population is eradicated, recolonization will not occur (Bass, 1999). This is very relevant for the Yucatan Peninsula, because it is one of the most important zones for species nesting. In this context, beach protection is essential for the conservation of the hawksbill turtle in the long term. The increased tourism development in the eastern part of the Yucatan Peninsula (e.g. El Cuyo and Isla Holbox) could also put at risk the conservation efforts, if nesting beaches experience detrimental effects, such as erosion, accretion or pollution. Thus, the Mexican Government should perform coastal development strategies compatible with the objectives for marine turtle conservation.

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