

Population ecology of the green/black turtle (*Chelonia mydas*) in Bahía Magdalena, Mexico

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Abstract The mangrove channels of Bahía Magdalena, Mexico, are important developmental areas for juvenile green, or black turtles (*Chelonia mydas*), but incidental bycatch and illegal hunting threaten population persistence. We studied size distribution, condition index (CI), growth rates, and mortality of black turtles in Estero Banderitas, the largest mangrove channel in Bahía Magdalena, to supply information for the development of effective conservation strategies. A total of 213 black turtles (including 88 recaptures) were caught in entanglement nets between July 2000 and July 2003. Average yearly catch per unit of effort (CPUE, 1 unit: 100 m of net fishing for 12 h) dropped during the study from 2.19 to 0.76. About 97% of all turtles were considered juveniles, average size was 54.6 ± 9.5 cm. Turtles were significantly smaller at the

head of Estero Banderitas than in the central part of the Estero and in the open bay, indicating size-based habitat segregation. Average growth rate was 1.62 cm/year and declined with increasing size. Growth was seasonal and three times higher in summer (0.28 cm/month) than in winter (0.09 cm/month), body CI was also significantly higher during the summer months. A seasonalized von Bertalanffy growth function (VBGF) was used to model growth for the size range studied (43–73 cm SCL), with the parameters: $L_{\infty} = 101$ cm SCL; $K = 0.04 \text{ year}^{-1}$; $t_0 = 0$; $C = 0.4$ and $t_s = 0.75$. Growth data indicate that black turtles may spend up to 20 years in Bahía Magdalena before they reach maturity at about 77 cm SCL. The total mortality estimate (Z) from the length converted catch curve was 0.16, corresponding to a yearly survival probability of 0.85.

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Introduction

The green turtle (*Chelonia mydas*) is listed as globally endangered on the IUCN Global Red List (IUCN 2004). In the eastern Pacific it is commonly called black turtle, due to morphological and color variations and will be referred to as such in this study (Nichols 2003). The black turtle has been protected in Mexico, since 1990, when a total ban on sea turtle fisheries and use of sea turtle products was declared (Aridjis 1990; Diario Oficial de la Federación 1990). The black turtle is found in the Mexican Pacific during all life history stages and the coastal waters of the eastern Pacific and Gulf of California provide important feeding and developmental habitat (Cliffton et al. 1982; Seminoff et al. 2002a, b; Nichols 2003). One of the most important nesting beaches is located in Michoacán, Mexico, other nesting

populations occur on the Galapagos Islands (Ecuador), and the Revillagigedos and Tres Marias Islands (Mexico) (Cliffton et al. 1982; Awbrey et al. 1984; Márquez 1990).

The decline of the black turtle was mainly caused by commercial fisheries from the 1950s to the 1970s when Mexico contributed about 50% to the world's catch of sea turtles, mainly olive ridley (*Lepidochelys olivacea*) and black turtles (Márquez and Doi 1973; Márquez et al. 1982; Márquez 1990). At the same time, intense egg harvest severely impaired recruitment and accelerated the decline (Cliffton et al. 1982; Nichols 2003). As a consequence, the nesting population on the Mexican index beaches Colola and Maruata in Michoacán decreased by over 95% from the late 1960s to the late 1990s (Cliffton et al. 1982; Alvarado et al. 2001; Seminoff 2004). In recent years, nesting has been increasing, and current levels are approaching those of the early 1980s (Alvarado-Diaz, pers comm.).

Several bays and lagoon systems along the coast of the Baja California Peninsula provide important habitat for black turtles (Pacific: Laguna Guerrero Negro, Laguna Ojo de Liebre, Laguna San Ignacio, Bahía Magdalena; Gulf of California: Bahía de Los Angeles, Bahía Concepción, Bahía de La Paz) (Nichols 2003; Seminoff et al. 2003; Koch et al. 2006). Black turtles recruit to these neritic foraging habitats in Bahía Magdalena at a carapace size of 35–40 cm (Brooks 2005), similar to values reported for Hawaiian (Balazs 1980) and Australian (Limpus et al. 1994) green turtles. They spend over ten and possibly up to 20 years (Seminoff et al. 2002a; Nichols 2003; Seminoff 2004) in these developmental habitats where they feed mostly on sea grass and algae (Felger and Moser 1973; Seminoff et al. 2002b).

Bahía Magdalena, the largest of the coastal lagoons in northwest Mexico, is also the most important fishing ground on the Baja California peninsula for many small-scale fisheries that target a large variety of fin- and shellfish (Carta Nacional Pesquera 2004). Bottom set gill nets are commonly used for stingrays, halibut and other demersal fish species, and black turtles are a frequent, and usually welcome, bycatch. The black turtle is also targeted directly, as sea turtle meat is still considered a delicacy in the region, and poaching rates are high (Gardner and Nichols 2001; Koch et al. 2006; Peckham and Nichols 2002; Nichols 2003). Mortality estimates for poaching and incidental bycatch are at least 200 black turtles per year for the Bahía Magdalena region (>90% consumption) (Koch et al. 2006), and a consumption mortality of at least 7,800 black turtles per year has been estimated for the Baja California Peninsula (Nichols 2003).

Estero Banderitas is the largest mangrove channel in Bahía Magdalena (Brooks 2005) and harbors a large population of mostly juvenile black turtles that primarily feed on algae and sea grasses (Lopez-Mendilaharsu 2002).

Black turtles show pronounced tidal movements within the confines of Estero Banderitas, and demonstrate high site fidelity (Brooks 2005). Illegal fisheries pose a significant threat to turtles in the Estero and proposals are being prepared by local nongovernmental organizations and the state and federal government to declare Estero Banderitas a marine protected area.

The main objective of this study was to investigate the population ecology of black turtles in Estero Banderitas using year-round sampling to supply necessary information for the development of effective conservation strategies. Specifically, we determined: (1) population size structure and size differences among different sites; (2) seasonal variations in body condition index (CI); (3) seasonal and yearly growth; and (4) mortality rates of black turtles in Estero Banderitas.

Methods

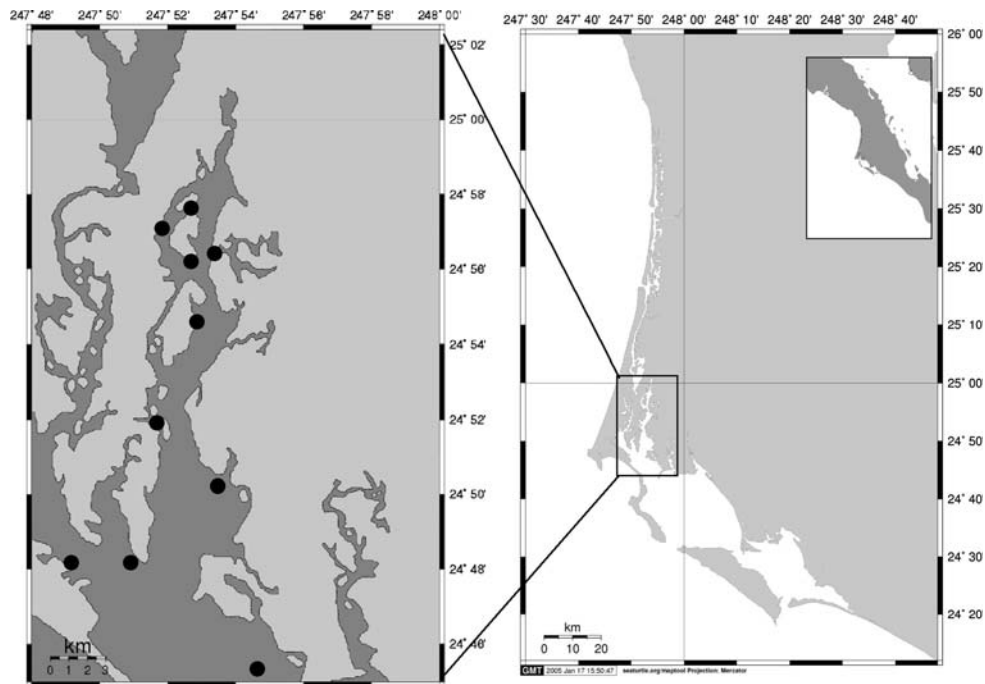
Study area

Bahía Magdalena-Almejas on the Pacific coast of Baja California Sur (Fig. 1) encloses an area of more than 1,000 km² and is one of the largest coastal lagoons in Mexico (Funes-Rodriguez et al. 2001). Average depth in the bay is less than 15 m and large intertidal and shallow water areas are present (Alvarez-Borrego et al. 1975). Sea grass and red algae are abundant and extensive mangrove stands are located in the northern part of the bay. Estero Banderitas, the largest mangrove channel in Bahía Magdalena, covers an area of approximately 42 km², substrate consists of sand and mud with patches of algae and sea grass beds (Lopez-Mendilaharsu 2002; Brooks 2005). Depth in the Estero ranges between 1 and 9 m and is less than 3 m on average, tidal amplitude exceeds 2 m at spring tides and tidal currents are strong. Salinity and water temperature at the mouth of Estero Banderitas range from 36.9 to 38.7 practical salinity units (PSU) and 18–31°C, respectively (Alvarez-Borrego et al. 1975).

Sea turtle capture and measurements

Between July 2000 and July 2003 turtles were captured with specifically designed entanglement nets. Two nets were used, one made of monofilament (100 m long), the other of black multifilament (140 m long). Both nets were 8 m high and had a mesh size of 50 cm stretched. Nets were set at different locations within Estero Banderitas and in the northern part of Magdalena bay (Fig. 1). Sampling time was generally 10–24 h and nets were checked every hour for entangled turtles. Turtles were kept in the boat or

Fig. 1 Map of Bahía Magdalena and Estero Banderitas. The *black dots* show several of the sampling sites where turtles were netted



in a shaded area and released when the measurements were completed (holding time never exceeded 10 h).

Straight carapace length (SCL, from notch to tip of distal marginal scute) and straight carapace width (SCW) were measured with metal forester's calipers to the nearest 0.1 cm. Turtles were weighed to the nearest kilogram using a spring scale and a piece of tuna purse seine netting. From 12 short-term recaptures (less than 7 days) error estimates for the SCL and weight measurements were obtained: average SCL deviation was 0.08 cm and average weight deviation was 0.64 kg. Few turtles showed abnormally high or low measurements, as the occasional measurement error could not be avoided due to fatigue after up to 24 h of constant monitoring. To detect inconsistent measurements, data sheets were checked for errors and Grubbs' test (Grubbs 1969) was used to eliminate outliers. After completing the measurements, turtles were tagged with metal Inconel tags (Type 681, National Band and Tag Company, Newport, KY, USA) proximal and adjacent to the first large scale on each rear flipper (Balazs 1999).

Seasonal comparisons

As the sampling was conducted year-round, the present study offered the unique opportunity to make seasonal comparisons. Thus, data for catch per unit of effort (CPUE), body CI and growth were grouped into summer (May–October) and winter (November–April) seasons. Between May and October turtles were more active in the area, which was verified through personal observations, information

from local fishermen and from the fact that CPUE was on average 60% higher during summer months when compared to winter (see results). The limits of summer and winter season coincided closely with a water temperature of 22°C (Fig. 2). Possibly, turtles become sluggish at lower water temperatures, reduce activity and feeding levels (Moon et al. 1997) and may even hibernate (Felger et al. 1976).

CPUE

One effort unit was defined as deploying 100 m of net fishing for 12 h, CPUE was calculated by dividing the total number of sea turtles caught on each sampling occasion divided by the number of effort units. Yearly and seasonal CPUE values were compared using a Kruskal–Wallis test,

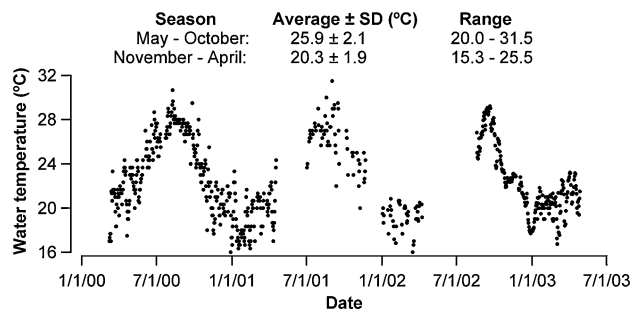


Fig. 2 Average daily temperature at Estero San Buto (approx. 15 km south of Estero Banderitas) from March 2000–April 2003, taken at a depth of 2–3 m. Average temperatures, standard deviation and range are given for both summer (May–October) and winter (November–April) season

as data were strongly skewed due to large amounts of zeroes (no capture) prohibiting the use of ANOVA. Effort data were reported only for about 80% of the sampling occasions and the reported total effort for each year in Table 1 is, therefore, an underestimate. However, average CPUE estimates for each year are reliable, because the reported cases were representative for each sampling period.

Population structure

For the analysis of population structure, only first captures were used ($n = 212$) to avoid bias introduced by multiple recaptures. A size frequency histogram was constructed to determine the most abundant size classes in the study area. The percentage of juveniles and adults was estimated using mean nesting size of black turtles in Michoacán (77.3 cm: Alvarado-Díaz and Figueroa 1990; Márquez 1990; IUCN 2004) as an estimate for size at maturity in females, which was found to be close to average nesting size in sea turtles (Limpus and Walter 1980; Limpus 1990, 1992; Limpus and Limpus 2003). Size-based habitat segregation was determined by comparing size distributions for three different areas: upper Banderitas, Conchalito, and open bay. Data were tested for significant differences using a one-way ANOVA and Tukey's post-hoc comparison with log transformed data to homogenize variances (Sokahl and Rohlf 1995; Zar 1999).

Condition index

For the CI analysis, first captures and recaptures at large for more than 11 months were used ($n = 236$), to avoid introducing a bias from (multiple) recaptures during the same year. We calculated CI with the SCL and weight (W) measurements from each turtle, using the following formula (Bjørndal et al. 2000):

$$CI = (W/SCL^3) * 10,000 \quad (1)$$

We used a two-way ANOVA comparing year and seasons, using a significance limit of $P = 0.05$. As sampling started

in July 2000, we delimited sampling years from July 2000 to June 2001, July 2001 to June 2002 and July 2002 to July 2003. The slope of the regression of SCL versus CI was not significantly different from zero, and consequently turtles of all size classes were used for the analysis.

Growth

Each recaptured turtle was identified by its tags, and measured and weighed as described above. Seasonal differences in growth were evaluated by grouping growth rates into summer (May–October) and winter (November–April) season, as described above. Only individuals that were caught and recaptured, or had spent at least 80% of their time at large within a given season, were used ($n = 20$). For example: a turtle caught on the 15th of April and recaptured on the 31st of August qualifies as a “summer” turtle, it spent 138 days at large, of which 16 days (15th–30th of April) were spent in the winter season (11.6% of total time at large). An independent t test was used to detect seasonal differences (Zar 1999).

Yearly growth rate was calculated from recaptures at large for >11 months ($n = 18$), and plotted against SCL, to detect how growth rate changes with size. A third-order polynomial regression was used to fit the data points.

The seasonalized von Bertalanffy growth function (VBGF) (von Bertalanffy 1934; Ricker 1975) was used to model the growth of black turtles for the size range covered by the 57 size increment data points from recaptures at large for >2 months:

$$SCL_t = SCL_\infty * [1 - \exp^{(-K(t-t_0) - (C*K/2\pi * \sin 2\pi*(t-t_s))} \quad (2)$$

where SCL_t , straight carapace length at time (t); SCL_∞ , asymptotic SCL; K , von Bertalanffy growth constant; t_0 , time at length zero; C , amplitude of seasonal oscillation; t_s , “summer point” (time of the year when growth is fastest). To estimate growth parameters, a non-linear iterative fitting algorithm was used (generalized reduced gradient, GRG 2) (Fylstra 1998), provided in a spreadsheet developed by Brey (2001). To illustrate how the individual

of effort defined as 100 m of net soaking for 12 h) and CPUE as average \pm 95% confidence intervals

Table 1 Summary of catch statistics from July 2000–July 2003 in Estero Banderitas, including number of turtles caught per year, number of recaptures (including multiple captures), total effort (1 unit

Sampling period month/year	No. of turtles		% recaptures	Total effort units	CPUE mean \pm 95% CI
	First captures	Recaptures			
July 2000–June 2001	50	5	9.1	36.9	2.19 \pm 1.19
July 2001–June 2002	82	36	30.5	64.7	1.72 \pm 0.68
July 2002–July 2003	80	39	32.8	71.5	0.76 \pm 0.28
Total	212	80		173.1	

growth data fit the calculated growth curve, age at first capture was estimated for each recaptured turtle using the inverse of the VBGF, so that the data point at first capture fits on the growth curve.

Mortality

Total mortality rate (Z) of black turtles was estimated with the length converted catch curve (Ricker 1975; Sparre et al. 1989), that uses the size frequency distribution of the population (only first captures, $n = 213$), and the parameters of the seasonal VBGF (K , L_∞ , C , and WP , see above). Data were fitted to a negative exponential model:

$$N_{t_2} = N_{t_1} \cdot \exp^{-Z(t_2 - t_1)} \quad (3)$$

where N_{t_1} and N_{t_2} are the number of individuals at times t_1 and t_2 , respectively, and Z is the total mortality rate. For the regression only the right, descending arm of the catch curve is used as the left arm represents the smallest individuals that are not sampled quantitatively. Z is equal to the negative slope of the resulting regression line and was later converted into a yearly survival probability for comparison with other studies. Catch curve analysis was done using the computer package FiSAT (Gayanilo et al. 1996).

Results

CPUE

From July 2000 to July 2003, a total of 212 black turtles were caught on 292 capture occasions (i.e., 80 recaptures), employing a minimum of 173.1 effort units (100 m of net soaking for 12 h) (Table 1). Average CPUE declined steadily for the duration of the study, however, the Kruskal–Wallis comparison showed no significant differences between years ($P = 0.133$). While average CPUE was over 60% higher in summer (1.5 turtles; 95% CI 0.89–2.11) than in winter (0.9 turtles; 95% CI 0.57–1.23), no significant differences were found (Kruskal–Wallis, $P = 0.216$), partly due to large amount of zeros and large variation in CPUE between samplings.

Population structure

The size distribution of black turtles was strongly skewed towards smaller turtles, with 45–55 cm being the dominant size classes (Fig. 3). About 97% of all turtles caught were below 77.3 cm SCL and therefore considered juveniles. Average size was 54.6 ± 9.5 cm SCL. Size distributions

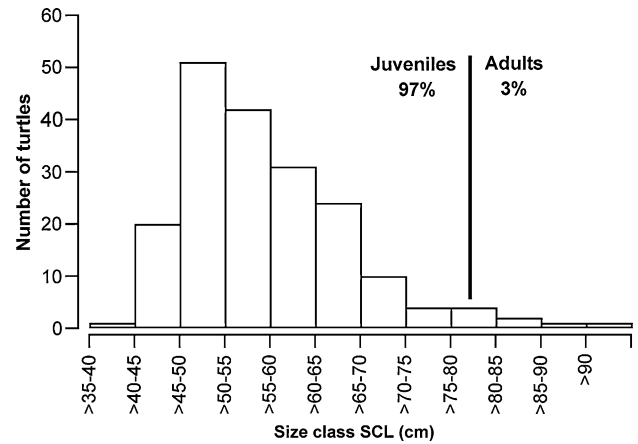


Fig. 3 Size distribution of black turtles (*C. mydas*) caught in Estero Banderitas and northern Bahía Magdalena during the study period. Only first captures were used, the percentage of juvenile and adult sized turtles is given in the graph

differed significantly among all three areas (Fig. 4) ($P < 0.001$ Tukey's HSD, pair wise comparisons, Table 2a). Turtles were smallest in upper Banderitas and became progressively larger towards the less protected open bay.

Condition index

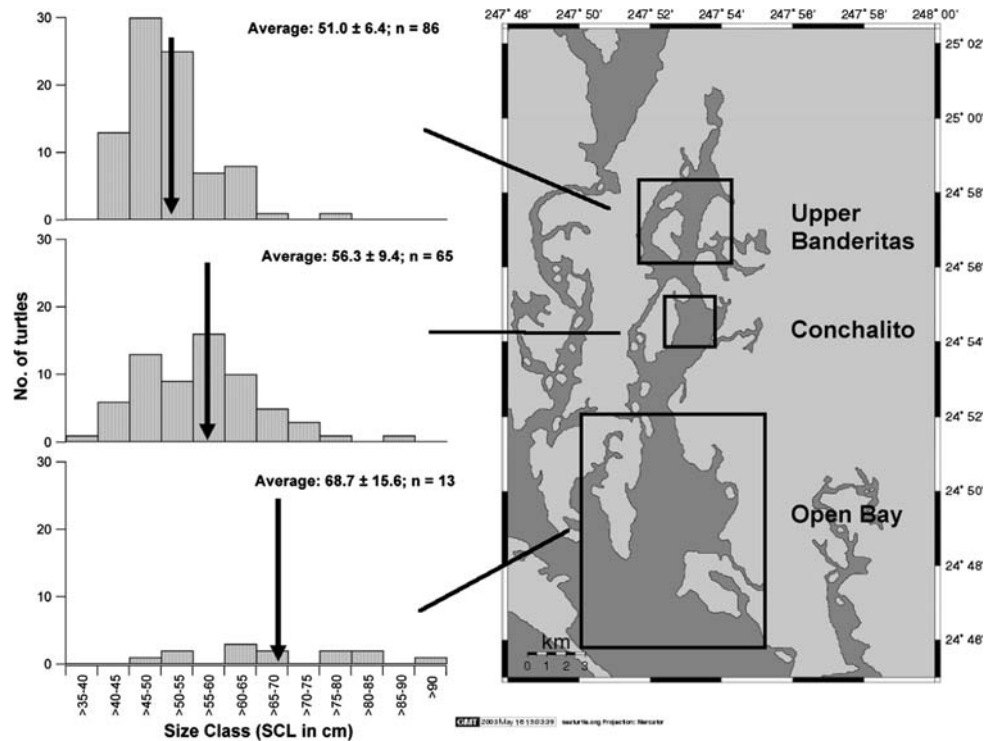
The CI of black turtles varied between 1.03 and 1.74 (outlier excluded) with an overall mean and standard deviation of 1.35 ± 0.127 . Turtles caught in summer had a significantly higher CI ($P < 0.001$, Table 2b) with 1.37 ± 0.129 than those caught in winter with 1.30 ± 0.111 (Fig. 5). This represents a weight difference of slightly more than 5% between winter and summer for a given turtle. CI was not significantly different between sampling years and we found no interaction between season and year (Table 2b).

Growth

Recapture rates of black turtles increased from 9.1 to 32.8% throughout the study period (Table 1). Recapture intervals varied from 1 to 973 days. Twenty turtles were recaptured between two and four times during the study period. Individual turtles were recaptured in different seasons and years. Growth was strongly seasonal (Table 3), with growth rates being over three times greater in summer (May–October) than in winter (November–April) (independent t test, $P = 0.02$).

Growth rate of turtles at large for >11 months was $1.62 \text{ cm year}^{-1}$ (size range 46–67 cm) and decreased with increasing SCL (Fig. 6). A third-order polynomial was

Fig. 4 Size distribution of black turtles (*C. mydas*) in three different areas in Estero Banderitas. The arrows denote the average size in each area, the ANOVA results are shown in Table 2



fitted to the data and is shown in Fig. 6. Growth rates of similar sized turtles varied considerably which is reflected in the low r^2 value (0.199) and large residuals.

The individual growth increments fit the calculated VBGF well over the size range studied (Fig. 7). Seasonality was reflected by the sine wave fluctuations in the curve and compares well to the seasonal growth rate comparison presented above. According to the model estimate, black turtles would need approximately 16 years to grow from 43 to 73 cm SCL. This corresponded to a

yearly growth rate of 1.8 cm, only 12% higher than the value calculated directly from long term recaptures.

Mortality

To calculate total mortality rate, the rightmost point in the graph was excluded from the regression. This point represents the largest animal caught during the study, a female black turtle with an SCL of 103 cm weighing over 150 kg. Age calculation becomes unreliable in very large individuals, and their inclusion would bias the mortality estimate (Ricker 1975; Sparre et al. 1994). Total mortality rate (Z) derived from the length-converted catch curve, was 0.16 year^{-1} , with a 95% confidence interval of $0.13\text{--}0.19 \text{ year}^{-1}$ (Fig. 8). This corresponds to a yearly survival rate of 0.85 (95% CI: 0.83–0.88). Assuming a 15 (or 20) year residence of black turtles in the area and a constant survival probability of 0.85 year^{-1} , only 9 (or 4) out of 100 turtles would survive.

Table 2 ANOVA tables

Effect	SS	DF	MS	<i>F</i>	<i>P</i>
(a)					
Sites	1.018	2	0.509	23.19	<0.0001
Error	3.534	161	0.02195		
(b)					
Year	0.046	2	0.023	1.559	0.213
Season	0.242	1	0.242	16.280	<0.001
Year × season	0.012	2	0.006	0.398	0.672
Error	3.420	230	0.015		

(a) 1-way ANOVA comparing average size of black turtles at three different sites in Estero Banderitas. Data were transformed to their natural logarithms to homogenize variance. Size differed significantly ($P < 0.0001$) between all sites (Tukey's post-hoc comparison). See also Fig. 3. (b) 2-way ANOVA comparing CI of black turtles between summer and winter seasons (May–October; November–April) and among years (each sampling year starts in July). Results of Tukey's post-hoc comparison are shown in Fig. 3

Discussion

CPUE

Catch per unit of effort (CPUE) in our study was higher than values from Bahía de Los Angeles in the Gulf of California [converted from Seminoff et al. (2003)].

Fig. 5 Boxplots for CI of turtles caught in different years (July 2000–June 2001; July 2001–June 2002 and July 2002–July 2003), and seasons (winter: November–April; summer: May–October). Letters in the graphs denote homogeneous groups as defined by ANOVA and Tukeys post-hoc comparison (Table 2)

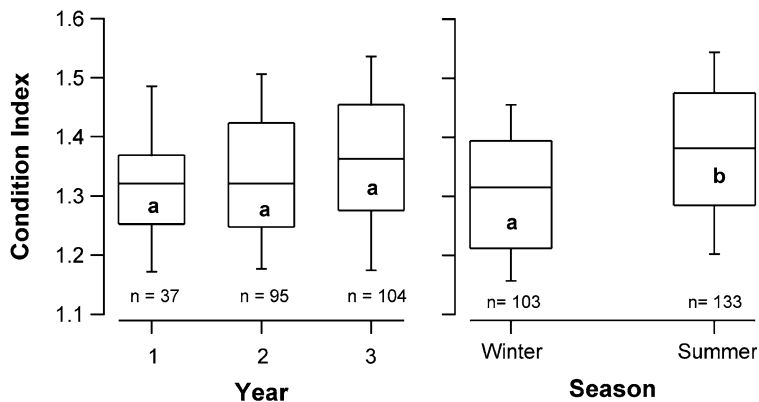


Table 3 Monthly growth rates of black turtles caught in Estero Banderitas. Seasonal growth rates were taken from turtles that were caught and recaptured from May to October (Summer) and November to April (Winter), including turtles that had spent over 80% of their time at large in either season

Growing season	Growth rate (cm SCL month ⁻¹)		Size range (SCL, in cm)	n
	Mean ± 95% CI	Range		
Summer	0.275 ± 0.135	0.02–0.71	45.8–64.3	10
Winter	0.087 ± 0.058	–0.05–0.27	43.5–62.4	10
≥1 year	0.135 ± 0.029	0.08–0.25	45.9–67.4	14

Growth rates of turtles at large for more than 11 months, are shown in the last row

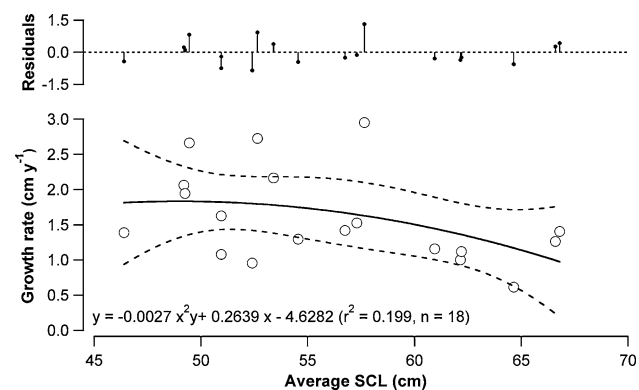


Fig. 6 Yearly growth rates of black turtles between 47 and 67 cm SCL. A third-order polynomial was fitted to show the trend in the data, the dotted lines are 95% confidence bands, regression statistics are shown in the graph

However, CPUE at other monitoring sites on the Pacific side of the peninsula, where the “Grupo Tortuguero” is working (Delgado and Nichols 2005), are much higher: Punta Abrejos CPUE, 15; Laguna San Ignacio CPUE, 5; Laguna Ojo de Liebre CPUE, 4 (Koch et al. in preparation). It is also of concern that CPUE has diminished by

almost 50% over the duration of the study, a pattern that was also observed in Bahía de los Angeles from 1999 onwards (Seminoff et al. 2003). While resource availability may contribute to the different population densities among locations, artisanal fishing effort in Bahía Magdalena is much higher than at the other sampling sites. This probably results in higher sea turtle mortality, which is corroborated by the large number of butchered carcasses found in Bahía Magdalena (Nichols 2003; Koch et al. 2006) and reports of an increase in poaching of black turtles by local fishermen (Solis-Hernández, pers comm.). While the short duration of the study does not permit to identify a clear trend, CPUE needs to be monitored over a longer time period, which is currently done by the Grupo Tortuguero and the School for Field Studies.

Population structure

Our results clearly demonstrate that mangrove channels such as Estero Banderitas provide habitat for juvenile black turtles in the early neritic stage (45–55 cm SCL). The smallest turtles were around 40 cm SCL, consistent with the size where pelagic juveniles switch to a neritic lifestyle in the area (Nichols 2003). Data on black turtle carcasses in Bahía Magdalena also showed that >90% of dead turtles were under 77.3 cm, corroborating the dominance of juveniles in the area (Koch et al. 2006). The average size of black turtles in Bahía Magdalena (54.6 cm) seems to be typical for the Pacific coast of the Baja California Peninsula, where values vary from 52.7 to 59.7 cm at other monitoring sites (Mariscal unpublished data).

The population structure in the study area is very different from that reported in the Gulf of California (Bahía de los Ángeles), where average SCL is 74.3 cm (Seminoff et al. 2003) and large juveniles and adult turtles dominate. This size difference between Gulf and Pacific coast turtles is also corroborated by the ongoing monitoring of the Grupo Tortuguero (Melania López, pers. comm. 2007) and

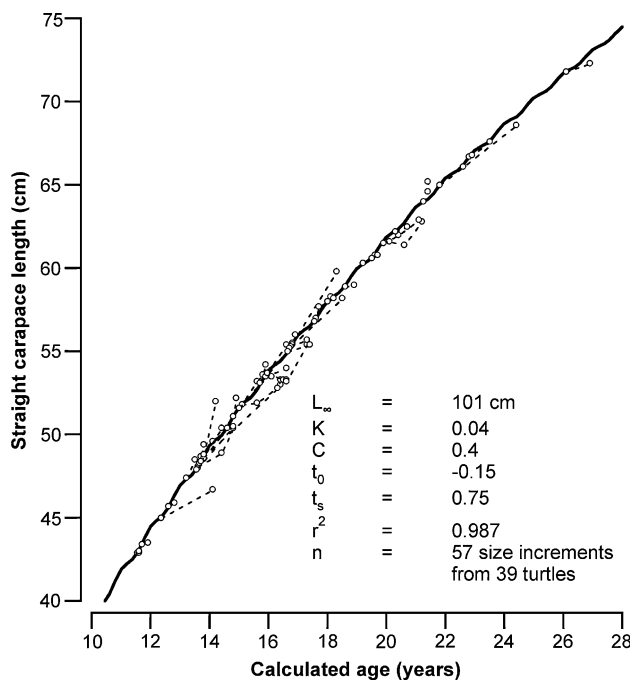


Fig. 7 Seasonal VBGF for black turtle recaptures from Estero Banderitas, Bahía Magdalena. The parameters for the growth curve are shown in the graph, the white dots connected with dotted lines represent individual turtles that were recaptured at least once. The age at first capture for each turtle was estimated using the VBGF, size increments from each turtle show the growth variation of individuals around the calculated curve

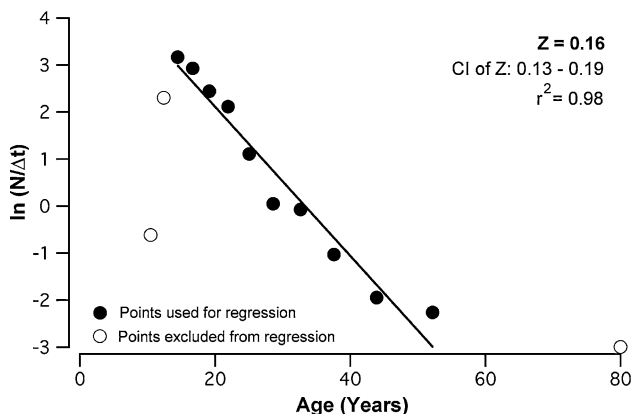


Fig. 8 Length converted catch curve for the black turtle (*C. mydas*), total mortality (Z) and 95% CI for Z are shown in the graph. Only the descending right arm of the curve was used for the regression (black dots), the ascending arm represents size classes that are not yet fully represented in the sampling (Ricker 1975). The last point on the right was excluded because the oldest animals are too close to L_{∞} rendering age calculation unreliable (for further explanation, see Methods)

is probably the result of an ontogenetic habitat shift. The capture sites in the Pacific are in relatively protected and shallow coastal lagoons with sandy bottoms and mangrove coverage, while the sites in the Gulf are mostly rocky and are generally deeper (Seminoff et al. 2003).

A size-based habitat segregation of black turtles occurs also on a small scale within Bahía Magdalena. Turtles captured at the head of Estero Banderitas were significantly smaller than turtles caught in less protected, deeper areas of Bahía Magdalena. This was also reported by López-Mendilaharsu (2002), who found larger black turtles on the open Pacific coast when compared to the mangrove channels of Bahía Magdalena. The reasons for this difference remain unknown, but it is likely that smaller turtles seek shelter in the shallow, protected areas where they are less exposed to large predators such as sharks. Additionally, feeding preferences may play a role, as larger turtles in Magdalena Bay were found to feed mostly on sea grass, whereas smaller turtles ate predominantly algae (López-Mendilaharsu (2002). Ontogenetic habitat shifts may help sea turtles to maximize growth rates (Werner and Gilliam 1984; Bolten 2003) and may also play a role in small-scale habitat segregation of different sized turtles. However, this question remains to be more thoroughly addressed in future studies that include diurnal and seasonal movements of different sized turtles in relation to food abundance and distribution.

Condition index

When compared to other studies, black turtles caught in Estero Banderitas had intermediate CI values. Our average CI (1.35) was higher than the values reported by Bjorndal et al. (2000) for Caribbean green turtles, except for the years 1979–1980, when the population density at their study site was lowest. In the Gulf of California however, CI values of black turtles were slightly higher by about 5% (Seminoff et al. 2003). Sea turtle density and thus resource availability at a given site have direct effects on body CI (Bjorndal et al. 2000; Seminoff et al. 2003). The decreasing CPUE coupled with a positive trend in CI in our study indicates that this relationship also holds true for the black turtle, although much less pronounced than in the Caribbean (Bjorndal et al. 2000). The trend (although not statistically significant) towards higher CI of black turtles in Estero Banderitas may be suggestive of a decrease in abundance, as has been described by Seminoff et al. (2003) for Bahía de los Ángeles in the Gulf of California.

Two factors are probably responsible for the seasonal differences in CI in our study: food abundance and water temperature. Abundance and productivity of sea grass and algae, the main food items of the black turtle (Felger and Moser 1973; Bjorndal 1997; Seminoff 2002b), are much higher during the summer months in the Estero (González Ramos and Santos Baca 2005). Higher food availability and consequently more efficient foraging thus probably lead to “fatter” turtles. Food quality may also differ

between seasons but there are no data available about seasonal differences in nutritional value and digestibility of the main food items of black turtles. Water temperature influences metabolic and activity levels of sea turtles (Moon et al. 1997) and black turtles are known to hibernate during winter in the northern Gulf of California (Felger et al. 1976), reducing their activity to conserve energy. While this does not seem to happen in Bahía Magdalena, black turtles were less active during the colder months (Brooks 2005) and probably foraged less. This, combined with lower food abundance, probably resulted in lower food intake and reduced body condition. While the low water temperatures in winter (18–22°C) lowers the metabolic rate of the turtles, it apparently does not prevent net energy loss, resulting in “skinnier” turtles during the colder months.

Growth

Our average growth rate (1.62 cm year⁻¹) is higher than values reported from the Galapagos Islands (Green 1993) and Bahía de Los Ángeles (Seminoff et al. 2002a), and similar to growth rates of immature green turtles in Australia (Limpus and Chaloupka 1997). In the Caribbean, much faster growth rates of up to 8 cm year⁻¹ were measured in juvenile green turtles (Bjorndal et al. 2000), indicating ocean basin differences in growth performance. Possible reasons for these differences include warmer temperatures in the Caribbean, density dependent resource limitation (Bjorndal et al. 2000), genetic differences among populations and differences in food quality and abundance (Boulon and Frazer 1990; Collazo et al. 1992; Bjorndal et al. 2000; Seminoff et al. 2002a, b). Growth rates of black turtles in other coastal lagoons further north on the Pacific side of Baja California were 30–100% higher than our value (data from monitoring sites of the Grupo Tortuguero, Mariscal, pers comm.) although water temperatures there are generally lower. Similar variations in growth rate were also observed by Bjorndal et al. (2000) in the Caribbean and were attributed to differences in resource availability.

Size-specific growth rates at other Pacific feeding areas are non-monotonic and increase to a maximum for large juveniles and then decrease as animals approach maturity (Balazs 1982; Green 1993; Limpus and Chaloupka 1997; Seminoff et al. 2002a). Size specific growth rates in this study did not exhibit this pattern. However, due to the small sample size ($n = 18$), high individual growth variability and the absence of adult sized turtles, it is difficult to conclude whether the size specific growth of black turtles in Bahía Magdalena really differs from that of other populations in the Pacific.

While short-term recaptures have the intrinsic problem of a higher relative measurement error (Bjorndal and Bolten 1988; Chaloupka and Musick 1997), they do have the advantage that seasonal patterns in sea turtle growth can be determined. This aspect has received very little attention as yet, partly because many studies were only conducted during the summer months. As the average measuring error was 0.08 cm SCL, it was decided to use recaptures at large for more than 2 months (turtles would have grown on average 0.32 cm by then). Thus we were able to provide the first data on seasonal growth rate differences for *C. mydas* in the Pacific. The only other information on seasonal growth in green turtles was reported by Coyne (1994), who also found reduced winter growth in the Gulf of Mexico.

The highly reduced growth during the colder months is probably due to: (1) low food availability during the colder months, as abundance of algae and sea grass in Estero Banderitas is lower in winter (Riosmena, pers comm.); and (2) reduced metabolism and activity in winter (Felger et al. 1976; Moon et al. 1997; Koch, pers. obs.) caused by the low water temperatures ($\leq 22^\circ\text{C}$). Lesser winter growth is also corroborated by the lower body CI, indicating that nutritional status of turtles caught during the winter months was not as good as during summer. Surprisingly, it seems that turtles do not hibernate as reported from the Gulf of California (Felger et al. 1976), as turtles were caught during the whole year.

Although the use of the VBGF to model sea turtle growth has been criticized (Chaloupka and Musick 1997; Bjorndal et al. 2000; Heppell et al. 2003b), the actual differences among a variety of growth models were rather small (Bjorndal et al. 2000). We addressed the main criticism by using the VBGF to model the growth *only* over the size range studied. The fit of the resulting model is excellent ($r^2 = 0.987$) and gives a good illustration of black turtle growth between 45 and 73 cm SCL. Another advantage of the VBGF is that instantaneous mortality (and survival probability) can be determined using standard stock assessment methods (Sparre et al. 1989; Gayanilo et al. 1996).

The data on growth and recruitment size allowed for estimating the duration of life history stages of black turtles in Estero Banderitas. The estimated age at maturity (at mean nesting size, 77.3 cm SCL) for east Pacific green turtles is 33.3 years (Seminoff 2004). If post-pelagic juveniles arrive at Estero Banderitas at about 38–40 cm SCL (smallest turtles caught during the study) it would take a turtle about 24 years at this developmental area to grow to 77.3 cm SCL at a rate of 1.62 cm year⁻¹ (from long-term recaptures). This also indicates that green turtles may spend about 9–11 years as pelagic juveniles before recruiting to neritic feeding grounds.

Mortality

Our survival probability (0.85 year^{-1}) compares well to the value of 0.77 year^{-1} determined by Brooks (2005), using a Jolly–Seber model for the turtle population in Estero Banderitas. These values are at the upper end of the range reported for juvenile sea turtles ($0.30\text{--}0.89 \text{ year}^{-1}$) (Frazer 1987; Caillouet et al. 1995; Heppell et al. 2003b; Campbell and Laqueux, 2005; Bjorndal et al. 2005). However, most values do not agree with the prolonged life span and late maturity of sea turtles (Limpus and Chaloupka 1997; Bjorndal et al. 2000). According to Chaloupka and Limpus (2002), a yearly survival of about 0.80 translates into an average life span of <5 years, clearly not in accordance with a life expectation of 50 years or more. Consequently, we would expect very low natural mortality for juvenile black turtles on their neritic feeding grounds, mainly because: (1) only few large predators exist inside coastal lagoons, (2) fibropapilloma is almost non-existent in the Baja-population (Nichols 2003) and only very few turtles with diseases were found during the study, and (3) given the severely reduced population size (89–94%, Alvarado-Diaz et al. 2001; Seminoff 2004), food should not be a limiting factor in the sense that it may lead to higher mortalities.

Nevertheless, a juvenile black turtle that enters Bahía Magdalena at 40 cm SCL and stays until it approaches maturity approx. twenty years later would have only a probability of 4% to survive up to that point, assuming a constant survival probability of 0.85 year^{-1} . Koch et al. (2006) reported that over 90% of black turtle carcasses found in and around Bahía Magdalena had been consumed and it appears that coastal lagoons, once “safe havens” for sea turtles, have become a dangerous place due to high fishing effort, widespread use of gill nets, and the fact that sea turtle meat is still considered a delicacy in northwest Mexico. Several authors (Crouse et al. 1987; Crowder et al. 1994; Crouse, 1999; Heppell et al. 2003a, b) have emphasized that population persistence and recovery in sea turtles is particularly sensitive to small changes in mortality of large juveniles, and the protection of these life stages on the feeding grounds should become a conservation priority.

Conclusions

This study provides important information on the ecology of black turtles and seasonal variations in growth, condition and catchability from a region where in-water studies are scarce. The results highlight the need for better management of the artisanal fishery and the implementation of a concise conservation effort to reduce threat. The mangrove channels of Bahía Magdalena and other

coastal lagoons provide critical habitat for the neritic life stage of the black turtle and require protection to diminish incidental bycatch and poaching of black turtles in the region. Estero Banderitas is an important developmental area, comparable to other well-studied sites in density, survivorship and growth rates and the establishment of a marine protected area could serve as a model for a network of community-based sea turtle sanctuaries and help the black turtle population to recover. It is imperative to continue monitoring the abundance trends in the region to be able to evaluate the outcome of the ongoing conservation efforts.

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