CHELONIAN CONSERVATION AND BIOLOGY

International Journal of Turtle and Tortoise Research

Sea Turtles of Bocas del Toro Province and the Comarca Ngöbe-Buglé, Republic of Panamá

Anne B. Meylan 1,3 , Peter A. Meylan 2,3 , and Cristina Ordoñez Espinosa 4

¹Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 100 8th Avenue S.E., St. Petersburg, Florida 33701 USA [Anne.Meylan@MyFWC.com];

²Natural Sciences Collegium, Eckerd College, 4200 54th Avenue S., St. Petersburg, Florida 33711 USA [meylanpa@eckerd.edu];

³Smithsonian Tropical Research Institute, Balboa, República de Panamá;

⁴Sea Turtle Conservancy, Correo General, Bocas del Toro, Provincia de Bocas del Toro, República de Panamá [cristinao@conserveturtles.org]

Sea Turtles of Bocas del Toro Province and the Comarca Ngöbe-Buglé, Republic of Panamá

Anne B. Meylan^{1,3}, Peter A. Meylan^{2,3}, and Cristina Ordoñez Espinosa⁴

ABSTRACT. - The Bocas del Toro region of Panamá (Bocas del Toro Province and the Comarca Ngöbe-Buglé) has been known as an important area for sea turtles since at least the 17th century. Four species occur in the region: the hawksbill (Eretmochelys imbricata), green turtle (Chelonia mydas), loggerhead (Caretta caretta), and leatherback (Dermochelys coriacea). Multiple life stages of these species are supported by the diverse marine habitats and beaches in the region. We summarize the evidence for stages present and their known distributions in the Bocas region. Annual nest numbers, location, and monitoring status are given for 17 nesting beaches. These beaches support regionally significant numbers of leatherback and hawksbill nests, small numbers of green turtle nests and, rarely, loggerhead nests. We review the history of sea turtle use in the Bocas region and describe "velación," a government-organized system that facilitated the extraction of hawksbills from nesting beaches throughout the Bocas region during the 20th century to supply the market for tortoiseshell. Current threats to sea turtles in the Bocas area include an illegal directed take of turtles at sea and of eggs and turtles on nesting beaches, bycatch in lobster and shark fisheries, and habitat degradation. Coastal development and increasing tourism have gradually become concerns for sea turtle conservation as the economic focus of the region has changed. The history of conservation efforts on behalf of sea turtles in Bocas is also summarized. This contribution was originally written to provide data on sea turtles for a coastal management plan for the region.

KEY WORDS. – sea turtles; *Eretmochelys imbricata*; *Dermochelys coriacea*; *Chelonia mydas*; *Caretta caretta*; Bocas del Toro; Comarca Ngöbe-Buglé; Panamá; threats; life stages; migrations

History of Sea Turtle Use. — Sea turtles have figured prominently in the history of the Bocas del Toro (Bocas) region of Panamá, an area that includes Bocas del Toro Province and the autonomous indigenous area to the east, the Comarca Ngöbe-Buglé. The area extends along the Caribbean coast from the border with Costa Rica (Río Sixaola), eastward to the town (and river) of Calovébora (Fig. 1A). Four species of sea turtles occur in this area: the loggerhead (Caretta caretta), green turtle (Chelonia mydas), hawksbill (Eretmochelys imbricata), and leatherback (Dermochelys coriacea) (Fig. 2).

At the end of the 17th century, hawksbill turtles were hunted in this region by Miskito Indians from Nicaragua who traveled in large dugouts and rendezvoused in places such as Isla Escudo de Veraguas (Fig. 1A) (Parsons 1972). Roberts (1827) reported on extensive trade in tortoiseshell in the Bocas area in 1815. The town of Old Bank on Isla Bastimentos (Fig. 1A) was reportedly founded by turtle fishermen from San Andrés, Columbia, and the Corn Islands, Nicaragua (Roberts 1827; Parsons 1972). Old Bank became the government seat of the province, a role later ceded to the nearby town of Bocas del Toro. Stephens (1987) listed turtles and tortoiseshell among the principal items of trade (with coconuts, cacao, sarsaparilla, and vanilla) in Bocas in the years leading up

to the 1880s, when commercial banana culture reconfigured the economy.

The hunting of hawksbill turtles on nesting beaches in the Bocas area was sufficiently lucrative to support a government-organized system, called velación, from 1904 to 1968 and unofficially for years thereafter (Loftin et al. 1970; Tovar 1973; Heckadon-Moreno 2011). The term is derived from the verb *velar*, meaning to stay awake, i.e., intercepting nesting turtles on the beach required that the workers (veladores) "stayed awake" all night. The rights to take hawksbills nesting on specific beaches or sections of beaches were auctioned annually by the municipality of Bastimentos to lessees who in turn hired veladores to capture nesting hawksbills. In the 1960s, veladores were paid \$1.50 per hawksbill. Leasing of approximately 48 km of beach each year brought revenues to the municipality of as much as \$1600 and constituted almost the entire tax base of the town (Tovar 1973). Loftin et al. (1970) reported that almost everyone in Bastimentos was involved in turtle commerce, either as a turtle buyer, a lessee or sublessee of beaches, or a velador. Beaches included in the velación system extended throughout much of the region.

Although Playa Chiriquí was apparently the main beach where the *velación* system was in use during most

¹Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 100 8th Avenue S.E., St. Petersburg, Florida 33701 USA [Anne.Meylan@MyFWC.com];

²Natural Sciences Collegium, Eckerd College, 4200 54th Avenue S., St. Petersburg, Florida 33711 USA [meylanpa@eckerd.edu];

³Smithsonian Tropical Research Institute, Balboa, República de Panamá;

⁴Sea Turtle Conservancy, Correo General, Bocas del Toro, Provincia de Bocas del Toro, República de Panamá [cristinao@conserveturtles.org]

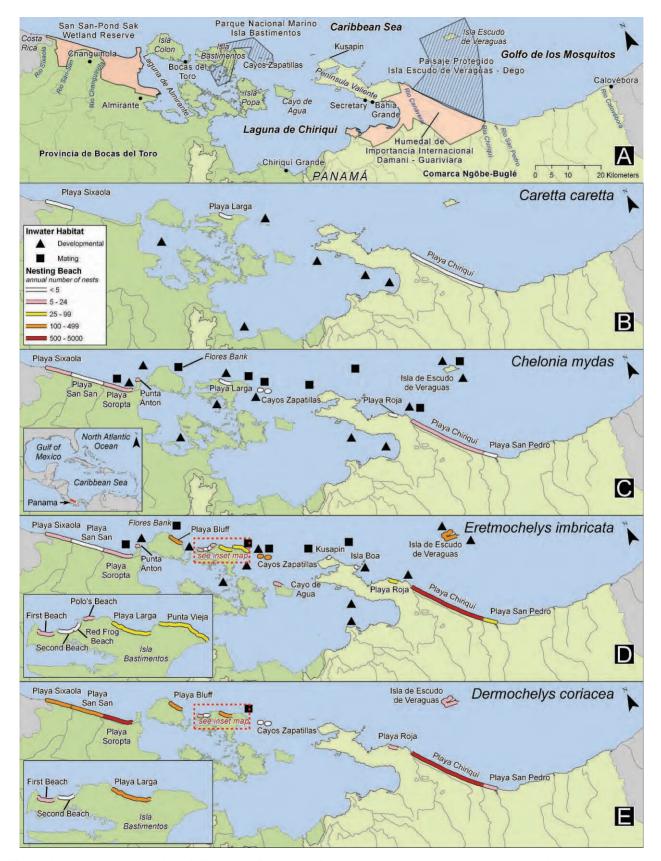


Figure 1. Geographic distribution of life stages of 4 species of sea turtles that occur in Bocas del Toro Province and the Comarca Ngöbe-Buglé, Republic of Panamá. A. Geographic context, including place names, landmarks, and protected areas. B–E. Known locations of benthic developmental habitat, mating sites, and nesting beaches for the indicated species. Range for annual nest totals is given for each nesting beach (see Map B for legend). See Table 1 for additional nesting beach data.

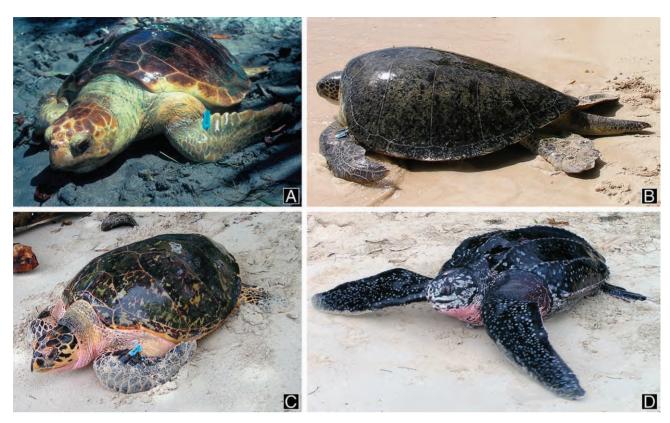


Figure 2. The 4 species of sea turtle that occur in Bocas del Toro Province and the Comarca Ngöbe-Buglé, Panamá. A. *Caretta caretta*, the loggerhead, juvenile from Calabash Bank, Chiriquí Lagoon. B. *Chelonia mydas*, the green turtle, adult male from the Zapatilla Cays. C. *Eretmochelys imbricata*, the hawksbill, adult female from the Zapatilla Cays. D. *Dermochelys coriacea*, the leatherback, subadult from the Zapatilla Cays. All were captured in nets. Photos by Anne and Peter Meylan.

of the 20th century, there was clearly wide-scale extraction of nesting female hawksbills. In interviews, fishermen who had participated in the *velación* system reported that the 3 largest beaches on Isla Bastimentos (First Beach, Second Beach, Playa Larga), the Zapatilla Cays (Cayos Zapatilla), and some of the beaches that extend east from Playa Chiriquí to Santa Catalina had also been leased. Carr (1956) examined an official velación lease for the beaches between Bocas town and the Costa Rican border, and was told that 12-15 men had been employed full-time there during the season, which suggests that hawksbill nesting must have been much more common on those beaches than is observed today and that the velación system may have covered all of the major hawksbill nesting beaches shown in Fig. 1D. Most hawksbills captured on the beach as well as green turtles and hawksbills captured in nets were shipped by launch to markets in Colón, Panamá (Gordon 1982) (Fig. 3).

Tortoiseshell removed from hawksbills killed in the Bocas area supplied international markets. Export data analyzed by Milliken and Tokunaga (1987) and Mortimer and Donnelly (2008) revealed the long-term nature of this trade as well as its magnitude. From 1950 to 1992, Panamá exported 203,774 kg of tortoiseshell, the equivalent of 152,070 individual hawksbills, which makes it the world's largest contributor to the Japanese tortoiseshell market during that period (Mortimer and

Donnelly 2008). Other areas of Panamá, including the Kuna Yala islands, probably contributed some of the shells exported from the country, but Bocas is believed to have been one of the principal sources. When authors A.B.M. and P.A.M. conducted interviews and field surveys in Bocas in the early 1980s, tortoiseshell sold for as much as \$110/kg at the first transaction (fisherman to buyer). By this time, the numbers of hawksbills nesting on area beaches had declined dramatically (e.g., 98% at Playa Chiriquí) from levels reported by *veladores* for the 1950s (Meylan and Donnelly 1999).

The velación system targeted the hawksbill turtle on the nesting beach and principally involved tortoiseshell, although meat and eggs were also taken. Other methods of capture, including nets and harpoons, were also in use for many years in the Bocas area and targeted the green turtle, both for export and local consumption. Green turtles and hawksbills were butchered daily at the public market as recently as the early 1980s (Fig. 4A, B). Netting with large-mesh tangle nets, now prohibited, resulted in the capture of large numbers of adult green turtles as late as the mid 1980s (Fig. 4C). Green turtles also were captured in a harpoon fishery that targeted mating turtles (Fig. 4D). The harpoon fishery in Bocas waters exists almost certainly because of the presence of mating areas and migratory corridors, where mated pairs of green turtles and hawksbills are particularly vulnerable to capture.



Figure 3. Hawksbills (*Eretmochelys imbricata*) and green turtles (*Chelonia mydas*) aboard a coastal launch bound for Colón, Panamá, 1968. Photo by B. Gordon from Gordon (1982) (with permission).

The prominence of sea turtles in the local culture is still evident at the annual Feria del Mar, or Fair of the Sea, which draws people from throughout the region and was formerly an occasion for eating green turtle. In recent years, the event has included informative displays about sea turtles and their conservation. Public awareness of sea turtle biology and conservation in Bocas has recently been influenced by a boom in ecotourism, and opportunities for tourists to view sea turtles are actively being developed. The presence of conservation-minded visitors has also had the effect of discouraging exploitation of turtles, including the sale of meat, eggs, and tortoiseshell jewelry. Nevertheless, harpooning and netting of turtles, taking of eggs, and even capture of females on the nesting beaches, although illegal, still occur.

History of Sea Turtle Research and Conservation. — The late Archie Carr visited Bocas del Toro in the early 1950s and was the first biologist to record the importance of the area for hawksbill nesting (Carr 1956). His observation of hawksbills arriving in wooden canoes, or cayucos, at the public market and his interviews with local fishermen convinced him that Playa Chiriquí was a regionally significant nesting beach for hawksbills. The importance of the Bocas area for the hawksbill was corroborated by historical accounts (Roberts 1827; Parsons 1972; Heckadon-Moreno 2011) and by a government-sponsored analysis of the sea turtle fauna and fisheries of Panama (Tovar 1973).

Extensive surveys of the Bocas sea turtle fauna were carried out by the authors A.B.M. and P.A.M., and A.

Ruiz from 1979 to 1986 as part of a Caribbean-wide survey of sea turtle populations led by Archie Carr (Carr et al. 1982). Officials from several Panamanian government agencies (e.g., Dirección General de Recursos Marinos; Instituto Nacional de Recursos Naturales Renovables) helped to gather information on Panamá's sea turtle fauna for the Western Atlantic Sea Turtle Symposia held in Costa Rica in 1983 (Bacon et al. 1984) and in Puerto Rico in 1987 (Ogren et al. 1989).

An in-water research program on sea turtles in Bocas has been carried out by authors A.B.M. and P.A.M. at Secretary, on the Valiente Peninsula (1989–1993, 1997), and at the Zapatilla Cays, in Parque Nacional Marino Isla Bastimentos (PNMIB) (1990 to present) (see also Meylan et al. 2011). This research program includes a mark–recapture study by using traditional tangle nets to target 4 species of sea turtles and investigate their population structure, reproductive biology, migratory behavior, and genetic identity.

Nesting beaches in the Bocas area have been extensively monitored since the 1990s under the auspices of a variety of organizations, including Autoridad Nacional de Ambiente (ANAM), Asociación Natural Bocas Carey (ANABOCA), Asociación ANAI, Asociación Conservacionista Caribaró, Asociación Nacional para la Conservación de la Naturaleza, Asociación para la Conservación de los Recursos Naturales Ngöbe-Buglé (ACORENANB), the Association of Friends and Neighbors of the Coast and Nature, Asociación para la Protección de los Recursos Naturales Ngöbe-Buglé (APRORENANB), Endangered

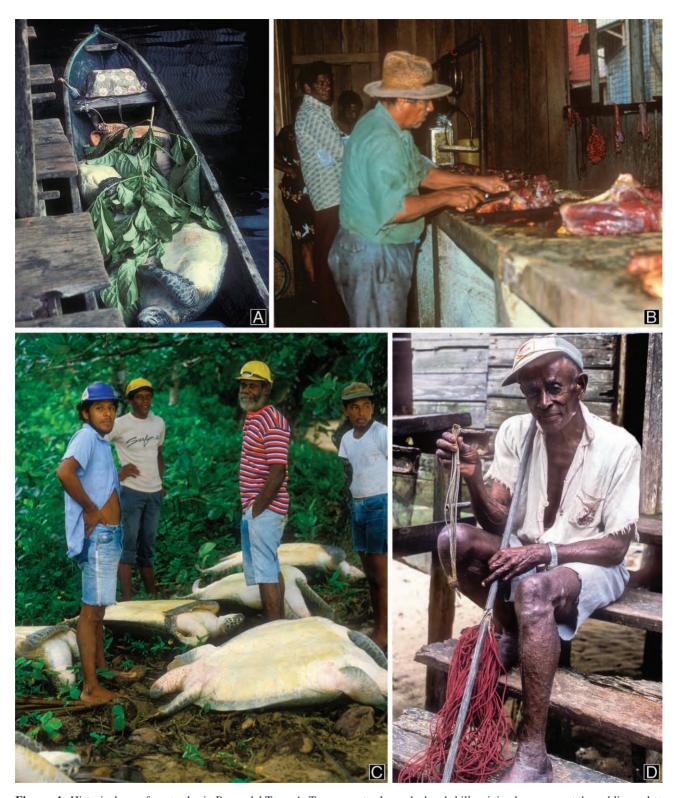


Figure 4. Historical use of sea turtles in Bocas del Toro. A. Two green turtles and a hawksbill arriving by *cayuco* at the public market in Bocas del Toro, 1980. B. Sea turtle meat being prepared for sale in the market in Bocas del Toro, Panamá, 1982. C. Green turtles captured in nets at Punta Vieja, Isla Bastimentos, Panamá, 1986. D. Harpoon fisherman at Bocas del Drago, Isla Colón, Panamá, 1989. Photos by Anne Meylan.

Wildlife Trust (EWT), Institute for Tropical Ecology and Conservation (ITEC), Programa Ambiental Regional para Centroamérica, Fundación PROMAR, the Sea Turtle Conservancy (STC) (formerly the Caribbean Conservation Corporation), and the Wildlife Conservation Society (WCS).

Since 2003, a major collaborative effort has been under way to promote the recovery of hawksbill nesting

populations in Bocas. Regular surveys of nesting activity are made throughout the hawksbill nesting season following standard protocols (see "Methods") at 11 different beaches (Table 1). This recovery effort is being carried out by ANABOCA, APRORENANB, STC, and WCS with logistical support from ANAM and the Smithsonian Tropical Research Institute (STRI).

The Region. — The Bocas region lies in the extreme southwest corner of the Caribbean Sea (Fig. 1C). It is bounded by Costa Rica to the northwest and the Panamanian province of Veraguas to the east (Fig. 1A). The dominant oceanographic feature of the region is Laguna de Chiriquí, which, in combination with Laguna de Almirante, forms the largest estuary along the Caribbean coast of Central America (almost 1400 km²) (D'Croz et al. 2005). Within the estuary is a complex archipelago that consists of 6 major islands, dozens of smaller islands, and many more mangrove keys. A relatively narrow continental shelf along most of Panamá and Costa Rica makes the extensive shallows of the lagoons an important area for benthic-feeding sea turtles. To the north, a wide shelf forms the Miskito Banks off the Caribbean coast of Nicaragua and Honduras. This is an area of unequaled importance for sea turtle foraging in the Atlantic system (Carr et al. 1978; Bass et al. 1998; Lagueux 1998). A smaller but still important foraging area exists to the east of Panamá in the region of the Guajira Peninsula (Carr et al. 1982). Important sea turtle nesting beaches that are relevant to this article include Tortuguero, Costa Rica, the principal nesting beach for green turtles in the western hemisphere, and the beaches along the coast of Costa Rica and eastern Caribbean Panamá, which appear to share a metapopulation of leatherbacks (Troëng et al. 2004; Ordoñez et al. 2007). The major currents of regional relevance include the Caribbean Current, which trends from southeast to northwest and exits the Caribbean into the Gulf of Mexico as the Loop Current, and the Panamá-Colombia Gyre, a counterclockwise circulation in the southwesternmost part of the Caribbean (Andrade et al. 2003).

Marine and coastal ecosystems in the Bocas region provide a variety of habitats (Fig. 5) that are used by up to 4 different stages of the life cycle by the 4 species present (Fig. 6). This article, originally drafted to summarize information about the sea turtle fauna of the Bocas region for a coastal management plan, includes data collected from 1979 up to 2011 (in some cases) on the geographic distribution and seasonality of the life stages of the 4 species found in the Bocas region, discusses linkages between these aggregations and those in the wider Caribbean Sea, and describes current threats in Panama.

METHODS

Collection of the data set that forms the basis of this article began in 1979 with standardized interviews and aerial and ground surveys throughout what was then the

Province of Bocas del Toro (later divided into Bocas del Toro Province and the Comarca Ngöbe-Buglé). The standard interview format given in Carr et al. (1982) was used to gather information from turtle fishermen, turtle butchers, boat captains, coastal residents, and government representatives (municipal, provincial, and national) throughout the area. Aerial surveys of nesting beaches were conducted periodically beginning in 1980; methods and survey dates are given in Meylan et al. (1985), Troëng et al. (2004), and Ordoñez et al. (2007).

Traditional turtle-netting methods were used to sample sea turtles beginning in 1987, first at Secretary, in the eastern end of Chiriquí Lagoon, and later near the Zapatilla Cays in Parque Nacional Marino Isla Bastimentos (PNMIB) (Fig. 1A). Details of the sampling methods and schedule through 2005 are given in Meylan et al. (2011). Subsequent net sampling reported on here was done at the Zapatilla Cays during May and June 2006–2009. Turtle decoys (see Heckadon-Moreno 2011:149) were used on all "swinging nets" (Meylan et al. 2011:7) since 2003.

All turtles captured in nets were tagged on the trailing edge of both fore flippers by using monel, inconel, or titanium metal tags or with one metal and one plastic (Dalton) tag. A series of measurements of the shell and the tail was taken, and turtles were weighed on a spring scale to the nearest kilogram. The standard size criterion used throughout this report is straight notch-to-notch carapace length (SCL) (SCL_{min} of Bolten 1999) and is reported as the mean ± 1 standard deviation (SD). Sex, maturity status, and reproductive condition of a subset of green turtles, loggerheads, and hawksbills were determined by laparoscopic examination of the gonads (Owens 1999; Meylan et al. 2011). For turtles that were not laparoscoped, maturity status was determined in some cases by using relative tail length or other data such as presence on the nesting beach or by examining the gonads of turtles killed in the artisanal fishery. In large, immature males, maturity status was corroborated by testicular biopsy and histology when possible. Life stage terminology follows Meylan et al. (2011).

Nest surveys were conducted by individuals hired from local communities, Panamanian and international students, and the authors. All beach monitors were trained by the authors or by experienced field coordinators. Surveys were conducted early in the morning. Species were identified, and nesting success (nesting vs. nonnesting emergence) were determined by visual examination of the tracks and nest (the presence of eggs was verified for all nests on beaches with monitoring status 2 and 3 in Table 1) following the Index Nesting Beach Survey Protocol of the Florida Fish and Wildlife Conservation Commission (http://myfwc.com/wildlifehabitats/ managed/sea-turtles/conservation-guidelines/). On beaches surveyed regularly but not daily (status 2 in Table 1), all crawls were counted and evaluated during the census (regardless of age); they represented a minimum number

Table 1. Documented sea turtle nesting beaches in Bocas del Toro Province and the Comarca Ngöbe-Buglé, Panamá, listed from west to east. For linear beaches, the limits and length of the beach are given. For islands with encircling or multiple beaches, the coordinates of the westernmost point of the island and the total beach length are given. Punta Antón and Punta Vieja include a series of small beaches between the western and eastern limits in the table. Monitoring status: 1 denotes beaches with irregular or short-term monitoring, 2 denotes beaches with regular but not daily monitoring, and 3 denotes beaches with daily monitoring during the nesting season; if 2 numbers are given (e.g., 3/2), the first pertains to the leatherback season and the second to the hawksbill season. EWT = Endangered Wildlife Trust; AAMVECONA = Asociación de Amigos y Vecinos de la Costa y la Naturaleza; STC = Sea Turtle Conservancy; ANABOCA = Asociación Natural Bocas Carey; WCS = Wildlife Conservation Society; Var. = variable.

Beach name	Data collected by:	Beach length (km)	Yrs of data collection	Caretta caretta	Chelonia I mydas	Caretta Chelonia Eretmochelys Dermochelys caretta mydas imbricata coriacea	Dermochelys coriacea	Western limit latitude (°N)	Western Western limit limit latitude (°N) longitude (°W)	$\begin{array}{c} Eastern \\ Iimit \\ latitude \ (^{\circ}N) \end{array}$	Eastern limit longitude (°W)	Monitoring status ^a
Playa Sixaola Playa San San	EWT EWT,	6.8	2006–2011 2007–2010	< 5	5–24 < 5	5–24 < 5	100–499 100–499	9.572 9.531	-82.563 -82.515	9.531 9.479	$-82.515 \\ -82.455$	3/1 2/1
Playa Soropta (Playa	AAMVECONA EWT	12^{a}	2002–2011		5-24	5–24	200–999	9.477	-82.453	9.416	-82.375	3/1
Changuinola) Punta Antón	STC	Var	2008-2010		5–24	5-24		9.434	-82.352	9.432	-82.343	1
(Funta Solopta) Playa Bluff	STC,	4.8	2010–2011			100–499	100–499	9.419	-82.256	9.390	-82.236	8
(Flaya Flores) First Beach	MCS WCS	1.3	2011			5–24	5–24	9.355	-82.201	9.348	-82.192	1/2
Second Beach	WCS	1.1	2011			\ \$	< ?	9.347	-82.185	9.344	-82.175	1/2
Red Frog Beach	WCS	9.0	2011			\ \$		9.343	-82.174	9.345	-82.168	1/2
Polo's Beach Playa Larga	WCS EWT, WCS	0.7	2010–2011 2006–2011	\ \2	۸ م	5–24 25–99	100–499	9.348 9.335	-82.163 -82.143	9.346 9.316	-82.157 -82.122	1/2
(Long Bay) Punta Vieja	WCS	Var	2009–2011			25–99		9.319	-82.109	9.291	-82.081	2
Cayos Zapatillas Cayo de Agua	WCS WCS	4.2	2003–2011 2005–2008		\ \c	100–499 5–24	\ \S	9.266 9.181	$-82.060 \\ -82.050$	9.170	-82.038	2 1
Playa Roja	STC	2.5	2009–2011		< 5	25–99	5–24	9.058	-81.761	9.043	-81.745	1/2
(Fiaya Colorado) Playa Chiriquí	STC,	24	2004–2011	\ \$	5–24	500–999	1000–4999	9.013	-81.712	8.850	-81.573	3
Isla Escudo de	STC	~ 5.6	$\sim 5.6 2009-2011$			100–499	5–24	680.6	-81.545			1/2
Playa San Pedro	STC	2.5	2.5 2008–2009		<5	25–99	5–24	060.6	-81.573	8.826	-81.544	1

^a Only 8 km were monitored daily, 12 km were surveyed twice weekly.



Figure 5. Habitats used by sea turtles in Bocas del Toro Province and the Comarca Ngöbe-Buglé, Republic of Panamá. A. Small Zapatilla Cay (westernmost) in Parque Nacional Marino Isla Bastimentos (PNMIB); coral reefs and seagrass beds used by foraging and resting turtles, and nesting beach used mostly by hawksbill turtles (*Eretmochelys imbricata*) are visible. B. Mangrove cays within PNMIB. C. Beach used by hawksbills on the north side of Small Zapatilla Cay. D. Playa Soropta, an important leatherback nesting beach. Photos by Anne and Peter Meylan.

of crawls. Night-time patrols were conducted on nesting beaches with monitoring status 3 (Table 1) to study the reproductive biology of nesting females. Turtles encountered on the nesting beach were tagged on both fore flippers with monel or inconel tags (inside margin of hind flippers in leatherbacks) and their midline curved carapace length was measured (CCL_{min} of Bolton 1999).

RESULTS AND DISCUSSION

The Bocas region provides habitat for multiple life stages of loggerheads, green turtles, hawksbills, and leatherbacks; Kemp's ridley (*Lepidochelys kempii*) and the olive ridley (*Lepidochelys olivacea*) have not been documented. The stages represented vary among the 4 species, as shown in Fig. 6. Evidence for the existence of each stage in the Bocas region is provided below. The geographic distribution of 3 stages (nesting, benthic developmental habitat, mating) for the 4 species present is summarized in Fig. 1. Life stages are certain to be more

widely distributed than indicated; sites were only included if firsthand evidence or reliable reports existed. Data on inwater distributions are from netting samples, sightings, tag returns, and reports from cooperating artisanal fishers. Information on the location of nesting beaches and on the annual number of nests for each species is provided in Table 1 and Fig. 1. The frequency and duration of monitoring of these beaches varied as indicated by the monitoring status in Table 1; the accuracy of the estimates varied accordingly. Interview data and aerial surveys (Meylan et al. 1985; Troëng et al. 2004) indicated that beaches that extend east from Rio San Pedro (Fig. 1A) support some turtle nesting activity, but no ground surveys have been conducted in this area. Nesting could not be verified for any beaches within Chiriquí Lagoon.

Loggerhead (Caretta caretta)

Loggerhead turtles are the least common species found in the Bocas area. Nesting occurs very rarely; only

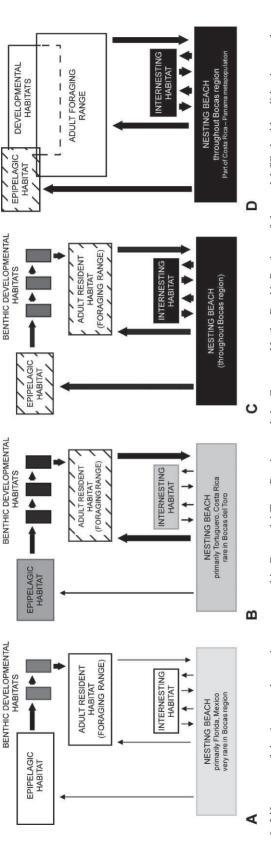


Figure 6. Life stages of the 4 sea turtle species represented in Bocas del Toro Province and the Comarca Ngöbe-Buglé. Portions of the model filled with solid colors, and movements ation and arows, indicate stages for which direct evidence is available; the intensity of solid shading reflects the prevalence of each stage in the region; crosshatching indicates stages that are likely to be present but for which there is not conclusive evidence. A. Caretta caretta. B. Chelonia mydas. C. Eretmochelys imbricata. D. Dermochelys coriacea.

immatures at the benthic developmental stage are typically represented (Figs. 1B, 6A).

Nesting. — Only 6 reliable nesting records exist for loggerheads for 2000–2011: Playa Chiriquí (2), Playa Bluff (1), and Playa Sixaola (3) (Table 1; Fig. 1B). Three of the nests were observed in May, 2 in July, and 1 in September. The rare occurrence of a loggerhead nest at Playa Larga (Carr et al. 1982) is supported by multiple unsuccessful nesting emergences by an individual female loggerhead on this beach between 9 June and 5 July 2011. In the early vears of the project, authors A.B.M. and P.A.M. investigated reports that loggerheads nested on the south shore of Chiriquí Lagoon at Río Daira and Río Guariviara, but no suitable beaches or supporting evidence was found. The nearest known loggerhead nesting beaches are in the Colombian islands (San Andrés Archipelago) off Nicaragua and along the Colombian mainland (Amorocho et al. 1999). The number of nests that occur in these areas appears to be very small. The nearest significant nesting beaches for loggerheads are in Quintana Roo, México (Ehrhart et al. 2003). No records exist of loggerheads in epipelagic habitat in the Bocas area, and occurrences of this stage could be expected to be relatively rare, given the paucity of nesting by this species in the region.

Benthic Developmental Habitat. — Chiriquí Lagoon serves as important benthic developmental habitat for this species. Between 1987 and 1997, authors A.B.M. and P.A.M. netted 82 loggerheads in the southeastern end of the lagoon near Secretary and Bahía Grande (Fig. 1A, B). Excluding a single individual known to be mature, they varied in size from 45.2 to 76.5 cm SCL_{min} (mean 59.8 \pm 6.9 SD, n=81) (Meylan et al. 2011). The single adult was a male (97.3 cm SCL) that had recently lost a front flipper, so his presence in Chiriquí Lagoon may not have been typical.

Ten subadult loggerheads (mean SCL 73.4 ± 7.1 cm SD) were caught in project nets at the Zapatilla Cays from 1990 through 2009 (Fig. 1A, B). Loggerheads have been sighted in other areas of Chiriquí Lagoon and in Almirante Lagoon, but no sightings have been documented outside those lagoons. Thirty-five recaptures of 26 tagged immature loggerheads on the shallow banks near Secretary provided evidence of at least short-term (< 1 yr) residency. Five loggerheads tagged at Secretary were subsequently recaptured in Nicaragua, and one was taken in Cuba (Meylan et al. 2011).

On the basis of genetic analyses, Engstrom et al. (2002) suggested that immature loggerheads captured at Secretary belonged principally to the Florida population (Peninsular Florida Recovery Unit, NMFS and USFWS, 2008) with a smaller contribution from México. The presence of loggerheads that nest in the United States and México, in tropical benthic developmental habitats, had not previously been documented.

Green Turtle (Chelonia mydas)

Green turtles of at least 4 different life stages occur in the Bocas region (Figs. 1C, 6B). They nest rarely but regularly and are also present in the epipelagic and benthic developmental stages, and during reproductive migrations.

Nesting. — Green turtle nests have been observed on Bocas beaches from May to November but in relatively small numbers (Table 1; Fig. 1C). Although monitoring regimes at many beaches (Playa Chiriquí, Isla Escudo de Veraguas, Playa Roja, the Zapatilla Cays, Playa Larga, and Playa Bluff) are effective in detecting green turtle nesting throughout the season, the beaches extending westward from Playa Soropta to the Costa Rican border are monitored principally for the leatherback, and surveys terminate in early to mid July. Thus, any green turtle nesting on these beaches in later months is not currently recorded.

Epipelagic Stage. — Posthatchling green turtles were observed in a Sargassum weed line 40 km off Panamá at lat 9°49.4′N, long 82°17.4′W, approximately 115 km east-northeast of the town of Bocas del Toro (Carr and Meylan 1980). The counterclockwise Panamá-Colombia Gyre is likely to be an important transport mechanism for green turtle hatchlings produced at Tortuguero and could be expected to transport those hatchlings and hatchlings produced on Bocas beaches through waters off the Bocas coast.

Benthic Developmental Stage. — Immature green turtles in the benthic developmental stage are known to occur at many sites (Fig. 1C). Data collected as part of the net–capture programs near Secretary and at the Zapatilla Cays, indicate that these sites support aggregations of immature green turtles throughout the year (Meylan et al. 2011). On the seagrass beds and reefs at Secretary, 135 green turtles were captured in nets between 1987 and 1997, which ranged from 46.7 to 88.0 cm SCL (mean 63.0 ± 9.1 SD; n = 132) at first observation. Fifty-six were examined laparoscopically, and none were found to be mature.

At the Zapatilla Cays, 128 immature green turtles were captured between 1990 and 2005, ranging in SCL at first observation from 29.5 to 92.5 cm (mean 68.6 ± 8.9 cm SD) (Meylan et al. 2011). At Zapatilla, immatures were captured in the same nets as adults during May, June, and July, but in a single January sample, adults were rare (1 of 18 captures), which suggests that, during nonreproductive seasons, this area may principally serve as benthic developmental habitat. Other sites at which immature green turtles have been taken in nets by turtle fishers include the seagrass beds off Playa Soropta, the area of mangrove cays south of Isla Bastimentos (Fig. 5B), Patterson Cay Outer Bank west of Patterson Cay, and Portete near the mouth of Río Cañaveral (Fig. 1A, C). Immature green turtles are regularly sighted around Isla Escudo de Veraguas and at Kusapín.

The well-known adult foraging range off Nicaragua appears to be the primary destination for large immature green turtles that depart from benthic developmental habitats in the Bocas area (Meylan et al. 2011). Nearly all

(94.4%) of 36 international recaptures of green turtles tagged as immatures in Bocas waters through 2005 were made in Nicaragua (Meylan et al. 2011:Fig. 16); 2 others were reported from Colombia, 1 from Cartagena, and 1 from the Guajira Peninsula. A green turtle tagged as an immature (76.8 cm SCL) at the Zapatilla Cays was found nesting at Tortuguero 12 yrs later.

Reproductive Migrations and Mating. — One of the most significant functions that the Bocas area serves for the green turtle is as a migratory corridor and mating station for reproductive turtles that belong to the Tortuguero population. Most adults (82.4%) netted at the Zapatilla Cays from May through July, 1990–2005 (n=131) showed evidence of reproductive activity. They were often caught as mated pairs; many females had copulation scars or fresh bite marks, and males had bite marks or a softened plastron associated with mating (Wibbels et al. 1991; Blanvillain et al. 2008; Meylan et al. 2011). Males were often captured in nets with turtle decoys attached (Fig. 7B), which suggests that they were actively seeking mates.

Between 1990 and 2005, data were collected on 29 mated pairs of green turtles in Bocas waters. Many were captured in research nets set within the boundaries of PNMIB, but others were harpooned by local fishermen offshore from the Zapatilla Cays, off Punta Vieja, and on Flores Bank (Fig. 1C). None were captured inside Chiriquí Lagoon. Mating green turtles have been observed along the Bocas coast from Playa Soropta to Isla Escudo de Veraguas. Mating occurs from at least late May through the end of July (knowledge of the end of the season limited by sampling dates). The seaward extent of the mating area is not known, but, when the weather is calm, harpooners have been observed to travel at least 10 km out to sea in search of mating pairs.

Several types of evidence suggest that Bocas serves as a migratory corridor for reproductive adult green turtles. One is the frequent occurrence of mated pairs during the reproductive season. Because there is little nesting by green turtles on Bocas beaches (Table 1; Fig. 1C), these turtles are likely transiting the area. Since 1990, 12 adult females (based on size and laparoscopy) captured in PNMIB have subsequently been observed on the nesting beach at Tortuguero; 8 were mating at the time of capture in Panama. All adult females examined laparoscopically (n = 22) from late May to mid July had enlarged (> 25 mm) follicles, and 6 also had shelled eggs.

Adult female green turtles tagged on the nesting beach at Tortuguero are regularly recaptured in Bocas waters. Carr et al. (1982) provided details for 54 Tortuguero-tagged green turtles captured along Panama's Caribbean coast, 43 of which were recovered in the Bocas region. We have documented 26 additional recaptures of Tortuguero-tagged females in the Bocas area. When an exact date of recapture was available, it was nearly always June to early

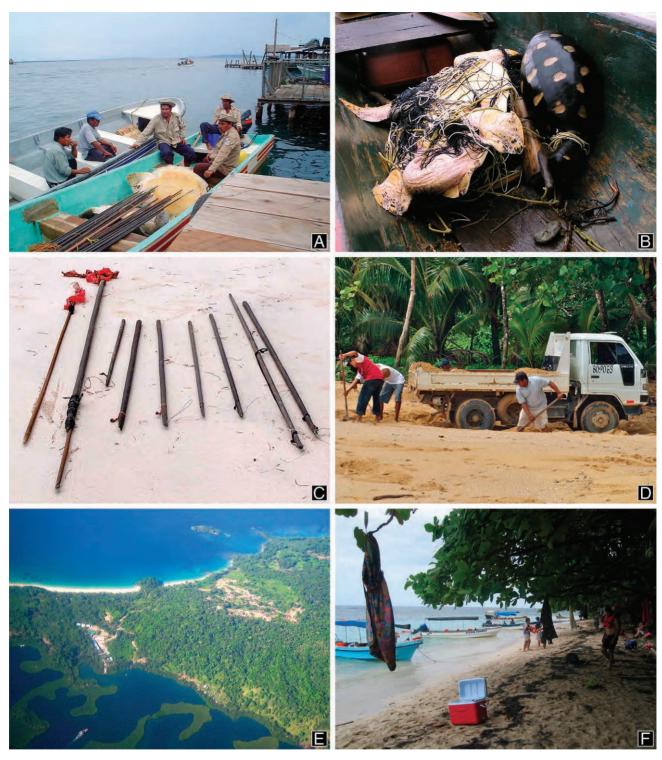


Figure 7. Threats to sea turtles in Bocas del Toro Province and the Comarca Ngöbe-Buglé, Republic of Panamá. A. Harpoons and turtles confiscated by the Panamanian wildlife authority, Autoridad Nacional del Ambiente (ANAM), during a single day in July 2005; 2 adult female green turtles and 18 harpoons are shown. B. An adult male hawksbill (*Eretmochelys imbricata*) captured in a net equipped with a balsa decoy. C. Spears and snares confiscated from lobster divers fishing illegally within Parque Nacional Marino Isla Bastimentos in late May 2005. D. Sand removal from Playa Bluff; this sand was bound for use in construction in Bocas del Toro town. E. Large-scale residential development on the north side of Isla Bastimentos near 2 important nesting beaches, Second Beach and Red Frog Beach. F. Daytime visitors to Parque Nacional Marino Isla Bastimentos, showing density of daytime beach use in a hawksbill (*Eretmochelys imbricata*) nesting area. Photos by V. Valdes Cadogan (A), Peter Meylan (B, E), Stephan Meylan (C), Daniel Suman (D), Ramon Fernández Francés (F).

August, the first few months of the nesting season at Tortuguero.

Nicaragua appears to be the primary foraging range of adult green turtles captured in Bocas waters. As of December 2010, 16 adults (both sexes) captured in nets in PNMIB have been reported from the waters of Nicaragua. The only other international recapture of an adult green turtle tagged in PNMIB waters was an adult male captured in Colombia. The only tag returns of green turtles tagged while nesting in the Bocas area, 3 females from Chiriquí Beach, were also from Nicaragua. Netting results, laparoscopy and tag return data have so far provided little evidence that the adult foraging range for green turtles exists in the Bocas area.

Hawksbill (Eretmochelys imbricata)

The Bocas area provides nesting, internesting, mating, and benthic developmental habitats for hawksbills, and serves as a corridor for reproductive migrations (Figs. 1D, 6C). The area may also provide adult foraging range, but data from this study are inconclusive on this point. Extensive coral reefs and other hard-bottom communities provide adequate habitat, but sampling for turtles has been limited almost entirely to May through July (the reproductive season).

Nesting. — The Bocas region is one of the most important hawksbill nesting areas in the Caribbean region, with more than 1500 nests per year in recent years (Table 1). Only nesting areas in México, Barbados, and Puerto Rico (Mona Island) have reported higher annual nest counts (Mortimer and Donnelly 2008). Hawksbills nest throughout the Bocas region, but the largest numbers of nests are recorded at Playa Chiriquí, the Zapatilla Cays, Isla Escudo de Veraguas, and Bluff Beach (Table 1; Fig. 1D). Since the 1990s, conservation efforts have focused on these 4 beaches, where during 2011, 868, 515, 244, and 153 hawksbill nests were recorded, respectively.

Although hawksbill conservation efforts have focused on these 4 beaches, hawksbills nest throughout the Bocas region. They are known to nest on a wide variety of beach types, including wide, high-energy beaches such as Playa Chiriquí and Playa Soropta (Fig. 5D); narrow beaches, such as the ocean-facing beach on the Small Zapatilla Cay, where there is little dry beach at high tide and turtles ascend a bank and enter the woods to nest (Fig. 5C); small cove-head beaches, including some on Isla Escudo de Veraguas; and intermittent sandy patches along rocky coastlines (Punta Vieja area). Several beaches used by hawksbills are not typically used by the other species (Table 1). We are not aware of any nesting by sea turtles inside Chiriquí Lagoon at present, but Gordon (1982) reported seeing hawksbill hatchlings entering the water at a beach near the mouth of the Cricamola River in the 1970s. Hawksbill nesting activity has been observed in all months, but most activity occurs from May to October with a peak in July and August.

In recent years, 400–500 hawksbill nests have been recorded annually on the 2 Zapatilla Cays (Table 1). With only 4.2 km of nesting beach, these cays currently support the highest nesting density (> 100 nests km⁻¹ yr⁻¹) in the Bocas area. Playa Chiriquí has the highest total number of nests, and, because it is 24 km in length, this beach offers the greatest opportunity for population recovery.

Refinement of the estimates of annual hawksbill nest totals for the region will require more intensive monitoring efforts. Beaches from Playa Soropta westward are only monitored during the leatherback season (until early July). A few beaches in the Bocas area have not yet been surveyed (other than a few aerial surveys) but are physically similar to known hawksbill nesting beaches and are likely candidates for hawksbill nesting: e.g., Lime Point and Mimitimbi (on Isla Colón), Playa Uva (Peninsula Valiente), and beaches extending eastward from Río San Pedro to Calovébora.

The value of the most important hawksbill nesting beaches has been recognized by Panamanian authorities. In 1988, PNMIB was established, in part, to protect sea turtles and thus included the Zapatilla Cays and Playa Larga (Resolucion J.D. 022-88 del 2 Septiembre de 1988). The importance of Playa Chiriquí was recognized by the RAMSAR Convention, by the inclusion of this beach in the "Damani-Guariviara Wetland of International Importance" (Resolution AG-0346-2004 of the Legislative Assembly of Panama, 14 September 2004). Designation of the Isla Escudo de Veraguas-Degó Protected Landscape in 2009 Resolution AG-0095-2009 recognized this area as an important site within the Comarca Ngöbe-Buglé.

Epipelagic Stage. — No data are available on hawksbills in epipelagic habitat in Bocas. However, hatchlings that enter the sea from Bocas nesting beaches could be expected to be transported by the Panamá-Colombia Gyre, where small green turtles have been documented.

Benthic Developmental Stage. — Benthic developmental habitat (Fig. 6C) for hawksbills exists throughout the region. Juvenile hawksbills have been captured in research nets and by lobster divers at numerous locations (Fig. 1D). From 1990 to 2009, 18 immature hawksbills were captured in nets at the Zapatilla Cays (mean 55.7 ± 9.0 cm SD SCL). No international tag returns of immature hawksbills have been received. This lack of returns and the small number of captures at Zapatilla Cays over the years may be due to significant take by local lobster divers.

Reproductive Migrations and Mating. — Reproductive hawksbills of both sexes, including mated pairs, are frequently caught in our research nets set near the Zapatilla Cays. Mating hawksbills are also regularly observed off Playa Soropta, on Flores Bank, in the Punta Vieja area, off the ocean side of the Valiente Peninsula, and at Playa Chiriquí (Fig. 1D). Bocas waters serve as a

migratory corridor for adult hawksbills en route to nesting beaches along the Bocas coast. During interviews conducted by authors A.B.M. and P.A.M. in the early 1980s, harpooners, who follow mated pairs to strike them, reported that adult hawksbills could be seen traveling east toward Playa Chiriquí at the same time that adult green turtles were seen traveling to the west, presumably on their way to Tortuguero. Gordon (1982:130) reported similar observations.

Adult female hawksbills were regularly captured in project nets within PNMIB either before they were first observed on the nesting beach that year (migratory corridor) or between nesting events (internesting habitat). Eleven were captured and subsequently nested on area beaches (Zapatilla Cays, 10; Playa Chiriquí, 1). Three others were captured between nesting emergences, one of which was mating at the time of capture. At least one female tagged while nesting at Playa Chiriquí was captured while mating at the Zapatilla Cays in a subsequent year; another was caught by local fishermen in waters just east of PNMIB. Thus, the waters of PNMIB must be considered a migratory corridor, a mating station, and internesting habitat for this species (Fig. 6C).

There have been a small number of international tag returns of nesting hawksbills originally tagged on our study beaches. These include 7 individuals (from 3 different nesting beaches) that were recaptured in Nicaraguan waters, and a single female tagged at Playa Larga that was found dead in Belize. We also have unpublished satellite tracks of female hawksbills from nesting beaches in Bocas that documented travel to Honduras and the Pedro Cays of Jamaica (A. Meylan, P. Meylan, and C. Ordoñez, unpubl. data, 2006). In addition, a hawksbill tagged as a juvenile at Monito Island, Puerto Rico, was observed nesting on Playa Larga 14.9 years later (Ordoñez Espinoza et al. 2010).

Leatherback (Dermochelys coriacea)

Leatherbacks nest on beaches throughout the Bocas region. Other life stages are not well represented (Figs. 1E, 6D).

Nesting. — Nesting by leatherbacks has been documented at numerous beaches along Panama's Caribbean coast (Carr et al. 1982; Meylan et al. 1985; Troëng et al. 2004; Ordoñez et al. 2007). Nesting beaches in the Bocas region are shown in Fig. 1E. The most important nesting beach for leatherbacks in Caribbean Panama is Playa Chiriquí, where several thousand nests are documented annually (Table 1). This is more nests per year than at any other beach in Caribbean Central America (Ordoñez et al. 2007). Five other beaches (Playa Sixaola, Playa San San, Playa Soropta, Playa Bluff, and Playa Larga) also have significant nesting; 4 are within the 100–499 nest/yr range and 1 in the 500–999 nest/yr range (Table 1; Fig. 1E).

The nesting season lasts from mid February to mid July with peak nesting occurring in May (Ordoñez et al.

2007). Leatherbacks have emerged on Playa Chiriquí that had been tagged on nesting beaches in Colombia, Costa Rica, and elsewhere in Caribbean Panamá, including, Playa San San, Playa Sixaola, Playa Soropta, Playa Bluff, and Playa Larga (Ordoñez et al. 2007; C. Ordonez, unpubl. data, 2007–2011). These and other documented movements of tagged animals among nesting beaches in the southwest Caribbean suggest that these leatherbacks belong to the same metapopulation (Troëng et al. 2004; Chacón-Chaverri and Eckert 2007). Based on aerial surveys, Troëng et al. (2004) estimated that Playa Chiriquí accounted for 37%–52% of leatherback nests along the 370-km Caribbean coastline of Costa Rica and Panamá.

Beaches used by leatherbacks in the Bocas area, such as Playa Soropta (Fig. 5D), tend to be wide, high-energy beaches with access unobstructed by reefs. Some narrower beaches within the area that are well used by hawksbills (e.g., Zapatilla Cays) are used very infrequently by leatherbacks.

Reproductive Migrations, Mating, and Internesting Behavior. — A small number of leatherbacks were observed in either the migratory corridor or internesting habitat during netting studies at the Zapatilla Cays. Seven females were captured that were also observed (previously or subsequently) on area beaches (Playa Larga and Playa Chiriquí). Leatherbacks captured between nesting emergences were in the internesting interval and thus the waters of PNMIB must be considered internesting habitat for this species (Fig. 6D). The other turtles may have been migrating to or from their nesting beaches. In all cases, their capture in nets set in relatively shallow waters within PNMIB indicates that reproductive female leatherbacks at least occasionally travel near shore where they are susceptible to fisheries and other nearshore activities. Interviews with turtle fishermen were consistent with our observations; they reported that leatherbacks were regularly captured in nets set in the ocean for green turtles and hawksbills but were rarely kept. Only 2 instances of mating leatherbacks were observed by project staff, both in the vicinity of Punta Vieja on Isla Bastimentos.

Given the large amount of nesting by leatherbacks in the southwestern Caribbean, hatchlings and posthatchlings can be expected to be common in the waters along the Bocas coast from April to September; however, none were observed in this study. A single record exists of a subadult leatherback in the Bocas area. We captured a 110-cm individual (curved carapace length) in a net near the Small Zapatilla Cay in June 2005 (Fig. 2D).

Foraging by leatherbacks has not been observed within the Bocas region. One adult female traveled from presumed adult foraging habitat off Nova Scotia to nest on Playa Chiriquí (Ordoñez et al. 2007). Satellite tracking of postnesting females released at Playa Chiriquí provided information on migratory routes out of the Caribbean and suggested possible foraging areas in the Gulf of México,

the north Atlantic Ocean (including the waters of Nova Scotia), and around the Azores (Evans et al. 2008).

Threats

Although sea turtles in the Bocas region die from natural causes such as disease, predation, and weather-related nest destruction, the most significant impacts come from anthropogenic sources. These include directed in-water fisheries, directed take of nesting turtles and their eggs, fisheries bycatch, predation by dogs, and habitat loss and degradation.

Directed fishing for sea turtles in the Bocas region is now much less common than in the past, but it remains a serious threat. Both harpoons and nets (Fig. 7A, B) are still used clandestinely to capture green turtles and hawksbills, especially in areas away from the town of Bocas del Toro. Our netting studies showed that green turtle mating areas overlap with hawksbill mating areas and internesting habitat (Fig. 1C, D). Although the primary motivation for turtle harpooners and netters is the availability of mated pairs of green turtles, mated pairs of hawksbills, single adults of both species, and subadults of both species are also taken. Striking boats typically carry 2 harpoons (Figs. 4D, 7A), and strikers try to harpoon the female first, in the hope that the male will not release the female and can be struck with the second harpoon. The harpoon fishery is concentrated on banks where mated green turtle pairs are regularly encountered during the mating season (Fig. 1C). Netting for sea turtles was carried out all along the coast in recent decades. As recently as 1986, a single commercial turtle-netting operation at Punta Vieja captured and killed more than 300 adult green turtles and hawksbills in approximately 3 mo. Nets are now used less frequently, but a few are still confiscated almost every year, usually along the oceanfacing side of the Peninsula Valiente.

The most serious current threat to sea turtles in terrestrial environments is the take of adult female hawksbills on the nesting beach. Possibly due to increased nesting levels in recent years, poaching of nesting females has once again become a serious threat even within protected areas. Evidence of poaching of adult female hawksbills is seen every nesting season. During 2011, a nesting female was poached on Playa Larga (in PNMIB) and at least 7 nesting females and 17 clutches of eggs were poached on Isla Bastimentos outside of park boundaries. The presence of PNMIB guards is essential to deter poaching. To the east, at Playa Chiriquí, the poaching of eggs has been reduced in recent years. However, as recently as 2004, an individual was caught trying to sell more than 700 hawksbill eggs taken from this beach (C. Ordoñez unpubl. data, 2004).

Beginning in the late 1980s, leatherback turtles were hunted on the western beaches of Bocas del Toro Province, principally for their eggs but also for their meat (Ordoñez et al. 2007). Competing poachers

sometimes cut the eggs from the oviducts of nesting females encountered on the beach rather than wait for the turtles to deposit their eggs. Carcasses found on the beach were often otherwise whole. C. Ordoñez (unpubl. data, 1999–2002) observed approximately 30 dead females per year on Playa Soropta from 1999 to 2002, and similar numbers at Playa San San and Playa Sixaola. Conservation efforts that started in the late 1990s have reduced the numbers of leatherbacks killed on the patrolled portions of these beaches significantly: to 0 per year at Playa Soropta (since 2002) and Playa Sixaola (since 2007); and to 1 or 2 per year at Playa San San (since 2007). However, poaching continues to be a problem on areas that are not patrolled. For example, on the 4 km of Playa Sixaola that are not monitored, poachers have killed 1-3 nesting leatherbacks per year and have taken more than 70% of nests since 2010. Once the leatherback season is over and monitors are no longer present, poachers patrol these western beaches and kill nesting female green turtles and hawksbills and/or poach their nests.

Captures of turtles by local lobster divers also pose a serious threat. The divers focus on the spiny lobster but also take conch, crabs, octopus, fish, and turtles. Hawksbills are easy targets for divers, who use a variety of spears and slings (Fig. 7C) to remove turtles from hiding places in the reef. They constitute a regular part of their catch. Small green turtles are also encountered, but they are less frequently captured because they tend to swim away, whereas hawksbills hide in the reef and are still accessible. The most destructive aspect of this fishery is the extent of coverage and the frequency with which reefs are visited. Shallow reefs throughout most of the region are visited by lobster divers regularly, with some areas getting almost daily attention. It seems unlikely that small hawksbills can survive on reefs < 30 m deep long enough to reach puberty and migrate to an adult foraging range.

The extent of shark fishing in the region is unknown, but both longlines and large-mesh nets are used, and sea turtles are known to be captured by both (Lutcavage et al. 1997). At least one tag return of an adult male green turtle has been recorded from a local shark-netting operation. The turtle was tagged at the Zapatilla Cays and captured in a shark net at Swan's Key, 34 km to the northwest 16 mo later.

Predation by dogs has been documented to be a significant cause of mortality of leatherback and hawksbill eggs and hatchlings on Playa Chiriquí (Ordoñez et al. 2007). In 2003, 54.3% of 81 monitored leatherback nests were disturbed by dogs; in 2004, that number was reduced to 7.8% of 243 monitored nests. Nearly 28% (96 nests) of the hawksbill nests randomly selected for posthatching evaluations at Playa Chiriquí in 2008 were disturbed by predators, principally dogs, with an average emergence success of only 22.5% (C. Ordoñez, unpubl. data, 2008).

Nearshore habitat degradation in the region appears to have 2 major causes: direct damage to reefs by divers

by using pry bars and chlorine bleach to take octopus, and indirect damage to reefs and sea grass beds caused by runoff from development and agriculture. Clearing of vegetation from the clay soils of the region increases sediment loads in runoff, and sediment plumes are regularly observed where land has been cleared for development and agriculture. Pandolfi et al. (2005) identified Panamá's western Caribbean reefs as some of the most degraded in the Caribbean.

Marine and terrestrial habitats used by sea turtles are also threatened by the trans-isthmian oil pipeline that has its Caribbean terminus in the back of Chiriquí Lagoon (Suman 1987). Reefs and seagrass beds were destroyed in the construction phase of the project, which included the dynamiting of a channel to allow ships to reach the transfer point near Chiriquí Grande. Low-level oil spills have also taken place, some affecting sea turtle nesting beaches, including those in the Zapatilla Cays. The pipeline's level of activity has varied depending on the global oil market. Environmental monitoring in this remote area is minimal. Marine debris such as ghost nets is also a problem in the nearshore environment. On 3 occasions, green turtles were found entangled in ghost nets in or near PNMIB. Ghost nets may be assumed to kill other species of sea turtles as well.

Human disturbance of nesting beaches, including development and the mining of sand for concrete production, is a significant threat, especially on beaches that are accessible from the main population centers of the province. Playa Bluff was until recently the main source of construction sand for projects in the town of Bocas del Toro (Fig. 7D), which reduced the amount of leatherback and hawksbill nesting habitat and altering drainage patterns on the remaining beach. Development along Playa Bluff, First Beach, Second Beach, Red Frog Beach, Polo's Beach, and a series of small beaches near Punta Vieja is reducing the suitability of these areas for nesting (Fig. 7E). Increased human activity, especially at night, increased artificial lighting, and the presence of subsidized predators (cats, dogs, raccoons) are among the negative factors associated with development.

Ecotourism presents some new challenges. The future success of PNMIB as a site of recovery for the hawksbill turtle depends on minimizing negative interactions between visitors and turtles. Visitor density is sometimes very high (Fig. 7F), reaching more than 500 visitors on one cay at one time. Management strategies, including continuing to close the park to all visitors at night, and prohibition of artificial lighting, are essential to maintain quiet, undisturbed, and dark nesting areas.

Threats associated with tourism and development need particular and immediate attention. Most serious among these are proposals for the development of Playa Chiriquí as a Cancún-style resort. This could significantly reduce the probability that nesting densities on this critical beach will reach their full potential and, therefore, would

reduce the role that the Bocas region could play in the recovery of the critically endangered hawksbill. Other large-scale development projects that could impact sea turtles are already underway on Isla Bastimentos and at Punta Anton; smaller construction projects are under way at Playa Bluff. Bocatoreños have historically avoided building on beachfront properties, but this is not the case for new development.

An action plan designed to guide management solutions for threats to sea turtles in Panamá was presented by Ruiz et al. (2007). This document reviews the history of legislation regarding sea turtles, discusses regulatory mechanisms, and details the international agreements to which Panamá is a signatory (see also Bräutigam and Eckert 2006). By actively pursuing the goals of this management plan and continually updating efforts to deal with new threats, Bocas del Toro Province and the Comarca Ngöbe-Buglé can continue their legacy as a center of sea turtle diversity.

ACKNOWLEDGMENTS

Our work in the Bocas region has been possible only because of the assistance of numerous organizations and individuals. The Autoridad Nacional del Ambiente (ANAM) has supported the work since its inception; we thank the ANAM staff: I. Añino, J. Antonio Gonzalez, H. Bonilla, D. Castillo, J. Garcia, and M. Ramos, in particular. The Meylans' work has been supported by the Wildlife Conservation Society since 1988. Additional support has come from the Busch Gardens Sea World Conservation Fund, the Sea Turtle Conservancy, Eckerd College, Florida Fish and Wildlife Conservation Commission (FWC), and Molly and Andy Barnes. C. Ordoñez's work in the Comarca Ngöbe-Buglé is made possible by special agreement with the General and No Kribo Regional Congress of the Comarca Ngöbe-Buglé and has been performed in cooperation with APROR-ENANB (Río Cañaveral) and ACORENANB (Río Chiriquí). It has been supported through the Sea Turtle Conservancy by the National Fish and Wildlife Foundation, US Fish and Wildlife Service (USFWS), US National Marine Fisheries Service, the Marine Turtle Conservation Act, Disney Worldwide Conservation Fund, World Wildlife Fund, Firedoll Foundation, and the Bay and Paul Foundations. Her work in Bocas del Toro Province has also been supported by Institute for Tropical Ecology and Conservation and Endangered Wildlife Trust. Considerable support has been provided to the authors by the Smithsonian Tropical Research Institute (STRI), in particular, by Z. Alain, O. Arosemena, R. Collin, P. Gondola, U. González, G. Jácome, M. Paz, A. Ruiz, and R. Urriola. A. Ruiz has played a critical role in the success of the Bocas sea turtle work by serving as a liaison with Panamanian government offices since 1979. We have been assisted in fieldwork by I. Castillo and his extended family, T. Engstrom, S. Duncan, N. Decastro, R. Fernández Francés, A. Vasquez Wilches, and numerous local beach monitors and international volunteers. E. Possardt (USFWS), D. Godfrey, S. Troëng, E. Harrison, R. Silman (STC), C. Campbell and C. Lagueux (WCS) have been instrumental to this work. From FWC, B. Brost assisted with database management, R. Hardy, L. French, and K. Wendell helped with the figures. We thank B. Crowder, K. Mansfield, T. O'Meara, A. Ruiz, B. Witherington, and 2 anonymous reviewers for comments on the manuscript. We thank B. Gordon, R. Fernández, A. Ruiz, D. Suman, and V. Valdes Cadogan for the use of their photographs. S. Buschbaum of Boxwood Press facilitated the use of B. Gordon's published photo. The work was conducted under a series of scientific permits from ANAM, including most recently SE/A-53-10, SE/A132-10 and SE/A38-12, and STRI IACUC agreements, most recently, 2010-110-2013.

RESUMEN

La región de Bocas del Toro de Panamá (Provincia de Bocas del Toro y la Comarca Ngöbe-Buglé), ha sido conocida como un área importante para las tortugas marinas desde por lo menos el Siglo XVII. Esta región alberga cuatro especies: la tortuga carey (Eretmochelys imbricata), verde (Chelonia mydas), cabezona (Caretta caretta), y baula (Dermochelys coriacea). Múltiples etapas de vida de estas especies están sostenidas por los diversos hábitats marinos y playas en la región. Resumimos la evidencia por etapas presentes y su conocida distribución en la región de Bocas. Números de nidos anuales, localización, y estado de monitoreo están dados por 17 playas de anidación. Estas playas sostienen regionalmente números significativos de nidos de baulas y carey, pequeños números de nidos de tortuga verde, y rara vez, nidos de cabezonas. Al revisar la historia del uso de tortugas marinas en la región de Bocas, describe la "velación", un sistema organizado del gobierno que facilitaba la extracción de tortugas carey de las playas de anidación a través de la región de Bocas durante el Siglo XX, para suplir el mercado de concha de carey. Las actuales amenazas que enfrentan las tortugas marinas en el área de Bocas incluye, cosecha ilegal de tortugas directamente en el mar y de huevos y tortugas en playas de anidación, la captura incidental de langosta y pesquería de tiburón, y degradación del hábitat. El desarrollo costero y el crecimiento del turismo se han convertido en preocupaciones para la conservación de las tortugas marinas, ya que el enfoque económico de la región, ha cambiado. Además, se ha resumido la historia de los esfuerzos de conservación en favor de las tortugas marinas, en Bocas. Esta contribución fue originalmente escrita para proveer información de tortugas marinas para el plan de manejo costero de la región.

LITERATURE CITED

- Aмоrocho, D., Córdoba, B.J.A., and Milkin, H.S. 1999. Current status of nesting sea turtles in northern Colombian Caribbean. Marine Turtle Newsletter 85:6–7.
- Andrade, C.A., Barton, E.D., and Mooers, C.N.K. 2003. Evidence for an eastward flow along the Central and South American Caribbean coast. Journal of Geophysical Research 108:1–16.
- BACON, P., BERRY, F., BJORNDAL, K., HIRTH, H., OGREN, L., AND WEBER, M. 1984. Proceedings of the Western Atlantic Turtle Symposium. Miami, FL: RSMAS Printing, 306 pp.
- Bass, A.L., Lagueux, C.J., and Bowen, B.W. 1998. Origin of green turtles, *Chelonia mydas*, at "sleeping rocks" off the northeast coast of Nicaragua. Copeia 1998:1064–1069.
- BLANVILLAIN, G., PEASE, A.P., SEGARS, A.L., ROSTAL, D., RICHARDS, A.J., AND OWENS, D.W. 2008. Comparing methods for the assessment of reproductive activity in adult male loggerhead sea turtles *Caretta caretta* at Cape Canaveral, Florida. Endangered Species Research 6:75–85.
- Bolten, A.B. 1999. Techniques for measuring sea turtles. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., and Donnelly, M. (Eds.). Research and Management Techniques for the Conservation of Sea Turtles. IUCN/SSC Marine Turtle Specialist Group Publication No. 4, pp. 110–114.
- Bräutigam, A. and Eckert, K.L. 2006. Turning the Tide: Exploitation, Trade and Management of Marine Turtles in the Lesser Antilles, Central America, Colombia and Venezuela. Cambridge, UK: Traffic International, 533 pp.
- CARR, A.F. 1956. The Windward Road. New York: Alfred Knopf, 258 pp.
- CARR, A.F., CARR, M.H., AND MEYLAN, A.B. 1978. The ecology and migrations of sea turtles, 7. The west Caribbean green turtle colony. Bulletin of the American Museum of Natural History 162:1–46.
- CARR, A.F. AND MEYLAN, A. 1980. Evidence of passive migration of green turtle hatchlings in *Sargassum*. Copeia 1980:366– 368.
- CARR, A.F., MEYLAN, A.B., MORTIMER, J.A., BJORNDAL, K.A., AND CARR, T. 1982. Preliminary survey of marine turtle populations and habitats in the western Atlantic. NOAA Tech. Memor. NMFSSEFC-91, 91 pp.
- Chacón-Chaverri, D. and Eckert, K.L. 2007. Leatherback sea turtle nesting at Gandoca Beach in Caribbean Costa Rica: management recommendations from fifteen years of conservation. Chelonian Conservation and Biology 6:101–110.
- D'Croz, L., Del Rosario, J.B., and Gondola, P. 2005. The effect of fresh water runoff on the distribution of dissolved inorganic nutrients and plankton in the Bocas del Toro Archipelago, Caribbean Panama. Caribbean Journal of Science 41:414–429.
- EHRHART, L.M., BAGLEY, D.A., AND REDFOOT, W.E. 2003. Loggerhead turtles in the Atlantic Ocean: geographic distribution, abundance and population status. In: Bolten, A.B. and Witherington, B.E. (Eds.). Loggerhead Sea Turtles. Washington, DC: Smithsonian Institution Press, pp. 157–174.
- ENGSTROM, T.N., MEYLAN, P.A., AND MEYLAN, A.B. 2002. Origin of juvenile loggerhead turtles (*Caretta caretta*) in a tropical developmental habitat in Caribbean Panamá. Animal Conservation 5:125–133.
- Evans, D., Ordoñez, C., Troëng, S., and Drews, C. 2008. Satellite tracking of leatherback turtles from Caribbean Central America reveals unexpected foraging grounds. In: Rees, A.F., Frick, M., Panagopoulou, A., and Williams, K.

- (Comp.). Proceedings of the 27th Annual Symposium on Sea Turtle Biology and Conservation. NOAA Tech. Memor. NMFS-SEFSC-569, pp. 40–41.
- GORDON, B.L. 1982. A Panama Forest and Shore: Natural History and Amerindian Culture in Bocas del Toro. Pacific Grove, CA: Boxwood Press, 178 pp.
- HECKADON-MORENO, S. 2011. A Creole from Bocas del Toro, the Story of Carlos Reid. Panama, Republic of Panama: Editorial Exedra, 275 pp.
- Lagueux, C.J. 1998. Marine turtle fishery of Caribbean Nicaragua: human use patterns and harvest trends. PhD Dissertation, University of Florida, Gainesville.
- LOFTIN, H., FRANQUEZE, A., AND TOVAR AYALA, D. 1970. Informe de visita a la provincia de Bocas del Toro relacionado con la captura de tortugas. Comisión Nacional de Protección de la Fauna Silvestre, Recursos Naturales Renovables, Ministerio de Agricultura y Ganadería, República de Panamá. March 1970, 9 pp.
- Lutcavage, M.E., Plotkin, P., Witherington, B., and Lutz, P.L. 1997. Human impacts on sea turtle survival. In: Lutz, P.L. and Musick, J.A. (Eds.). The Biology of Sea Turtles. Boca Raton, FL: CRC Press, pp. 387–409.
- MEYLAN, A.B. AND DONNELLY, M. 1999. Status justification for listing the hawksbill turtle (*Eretmochelys imbricata*) as critically endangered on the 1996 IUCN Red List of Threatened Animals. Chelonian Conservation and Biology 3:200–224.
- Meylan, A.B., Meylan, P., and Ruiz, A. 1985. Nesting of *Dermochelys coriacea* in Caribbean Panama. Journal of Herpetology 19:293–297.
- MEYLAN, P.A., MEYLAN, A.B., AND GRAY, J.A. 2011. The ecology and migrations of sea turtles, 8: tests of the developmental habitat hypothesis. Bulletin of the American Museum of Natural History 357:1–70.
- MILLIKEN, T. AND TOKUNAGA, H. 1987. The Japanese sea turtle trade 1970–1986. A Special Report Prepared by TRAFFIC (JAPAN). Washington, DC: Center for Environmental Education, 171 pp.
- MORTIMER, J.A. AND DONNELLY, M. 2008. Marine Turtle Specialist Group 2007 IUCN Red List Status Assessment Hawksbill Turtle (*Eretmochelys imbricata*). http://www.iucnredlist.org/apps/redlist/details/8005/0 (19 July 2012).
- NATIONAL MARINE FISHERIES SERVICE AND US FISH AND WILDLIFE SERVICE. 2008. Recovery plan for the northwest Atlantic population of the loggerhead turtle (*Caretta caretta*). Second revision. National Marine Fisheries Service, Silver Spring, MD, 325 pp.
- OGREN, L., BERRY, F., BJORNDAL, K., KUMPF, H., MAST, R., MEDINA, G., REICHART, H., AND WITHAM, R. 1989. Proceedings of the Second Western Atlantic Turtle Symposium. NOAA Tech. Memor. NMFS-SEFC-226, 401 pp.

- Ordoñez, C., Troëng, S., Meylan, A., Meylan, P., and Ruiz, A. 2007. Chiriquí Beach, the most important leatherback nesting beach in Central America. Chelonian Conservation and Biology 6:122–126.
- Ordoñez Espinoza, C., Meylan, A.B., Meylan, P.A., Peterson, I., Diez, C.E., and van Dam, R.P. 2010. Hawksbill tagged as a juvenile in Puerto Rico found nesting in Panama 15 years later. Marine Turtle Newsletter 127:25.
- Owens, D.W. 1999. Reproductive cycles and endocrinology. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., and Donnelly, M. (Eds.). Research and Management Techniques for the Conservation of Sea Turtles. IUCN/SSC Marine Turtle Specialist Group Publication No. 4, pp. 119–123.
- Pandolfi, J.M., Jackson, J.B.C., Baron, N., Bradbury, R.H., Guzman, H.M., Hughes, T.P., Kappel, C.V., Micheli, F., Ogden, J.C., Possingham, H.P., and Sala, E. 2005. Are U.S. coral reefs on the slippery slope to slime? Science 307:1725–1726.
- Parsons, J.J. 1972. The hawksbill turtle and the tortoise shell trade. In: Études de géographie tropicale offertes à Pierre Gourou. Paris: Mouton, pp. 45–60.
- ROBERTS, O.W. 1827. Narrative of Voyages and Excursions on the East Coast and in the Interior of Central America. Reprinted 1965, Gainesville: Univ. of Florida Press.
- Ruiz, A., Díaz, M., and Merel, R. 2007. WIDECAST Plan de acción para la recuperación de las tortugas marinas del Caribe de Panamá. H. J. Guada (Ed.). Informe Técnico del PAC No. 47. UNEP Caribbean Environment Programme, Kingston, 119 pp.
- STEPHENS, C. 1987. Bosquejo histórico del cultivo del banana en la provincia de Bocas del Toro (1880–1980). S. Heckadon-Moreno (Ed.). Revista Panameña de Antropología, Publicaciones Especiales No. 1. Impretex, S.A., Panamá City, Panamá, 50 pp.
- Suman, D. 1987. Socioenvironmental impacts of Panama's transisthmian oil pipeline. Environmental Impact Assessment Review 7:227–246.
- Tovar, D. 1973. Situación de las tortugas marinas en la costa Atlántica de Panamá. La Estrella, 3 January 1973, Panamá City, Panamá.
- Troeng, S., Chacón, D., and Dick, B. 2004. Possible decline in leatherback turtle *Dermochelys coriacea* nesting along Caribbean Central America. Oryx 38:395–403.
- Wibbels, T., Owens, D.W., and Rostal, D. 1991. Soft plastra of adult male sea turtles: an apparent secondary sexual characteristic. Herpetological Review 22:47–49.

Received: 22 July 2011

Revised and Accepted: 20 September 2012

Handling Editor: Jeffrey A. Seminoff