# The Ecology and Migrations of Sea Turtles 8. Tests of the Developmental Habitat Hypothesis

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# THE ECOLOGY AND MIGRATIONS OF SEA TURTLES

# 8. TESTS OF THE DEVELOPMENTAL HABITAT HYPOTHESIS

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# ABSTRACT

The existence of ontogenetic shifts in habitat by marine turtles, and of immature-dominated assemblages in "developmental habitat," were important concepts first proposed by Archie Carr in 1956. Results of long-term, in-water capture programs in Caribbean Panama (17 yr) and Bermuda (37 yr) allow the testing and refinement of these ideas, in particular the developmental habitat hypothesis for *Chelonia mydas*, *Eretmochelys imbricata,* and *Caretta caretta*. A literature survey reviews worldwide studies on these species, and also incorporates *Lepidochelys kempii*. The studies in Panama and Bermuda reported in this paper use netting, mark/recapture, laparoscopy, and satellite telemetry to investigate size distributions, maturity status, residency, site fidelity, and developmental migrations of three species of sea turtles at three study sites. Characteristics of benthic developmental habitat of *C. mydas*, *E. imbricata*, *L. kempii*, and, to a lesser extent, *C. caretta* in the Atlantic Ocean usually include benthic feeding; exclusive or nearly exclusive occupation by immature animals; seasonal or multiyear residency and site fidelity in specific areas; developmental migration from the habitat before maturation; and high genetic diversity. Variation of these traits worldwide, contradictory evidence regarding the concept of developmental habitat, and evolution of this life stage are presented. Laparoscopic data provide information concerning the process of sexual maturation; mean size and size range are presented for three maturity stages of *C. mydas* from Panama and Bermuda, and for size at onset of puberty and maturity for *Eretmochelys* and *Caretta* in the West Atlantic. Nicaragua is the primary site of recovery of immature green turtles tagged in Bermuda, representing a developmental migration of at least 2800 km. To the extent that tag returns and stranding data represent good proxies for mortality, transitions between life stages appear to be periods of decreased survivorship.

# INTRODUCTION

Sea turtles have long and complex life cycles. This has become particularly well appreciated in the past two decades with the addition of satellite telemetry, molecular genetics, laparoscopy, radioimmunoassays, and ultrasonography to the methodologies available to sea turtle researchers. However, much can still be learned from long-term tagging studies, particularly those that target life stages away from the nesting beach and incorporate a range of methodologies. Here we compile the results of three long-term, in-water tagging studies, one in Bermuda and two in Panama, to test the hypothesis that a significant portion of the life cycle of at least four cheloniid sea turtles consists of a benthic developmental stage.

Archie Carr brought many important ideas to the study of sea turtle biology, including the concept of "developmental habitat." This term has frequently been applied to the portion of the life cycle between the epipelagic stage that follows hatching (the lost year or lost years, or oceanic phase of Bolten, 2003) and the occupation of an adult foraging range (fig. 1). The idea of a separate, immature-dominated, benthic life history stage originates from the work of Carr and Caldwell (1956) on green turtles (*Chelonia mydas*) at Cedar Key, Florida. In that study, the authors concluded, "Florida green turtles come in on this current [the Loop Current], perhaps growing to the approximately 10-pound minimum size for Florida specimens on the way, and then exploit the local feeding resources, attain a size and strength that would permit a return to tropical waters by some other route." They noted that the Cedar Key population of *C. mydas* is composed almost entirely of immature animals and described their presumed seasonal occurrence at Cedar Key as a "developmental migration." The concept reappears in Carr et al. (1978) as "developmental habitat." These authors suggested that when sea turtles reappear after the "lost year," they do so in various inshore systems on a regular schedule of arrival and departure. An included figure (Carr et al., 1978: fig. 2; shown here as fig. 1) portrays developmental habitat as geographically separate from both the "lost-year habitat" and the "adult resident habitat." According to this model, neither small pelagic individuals nor adults are found in "developmental habitat." Furthermore, in this model, developmental habitat is portrayed as a series of boxes, implying

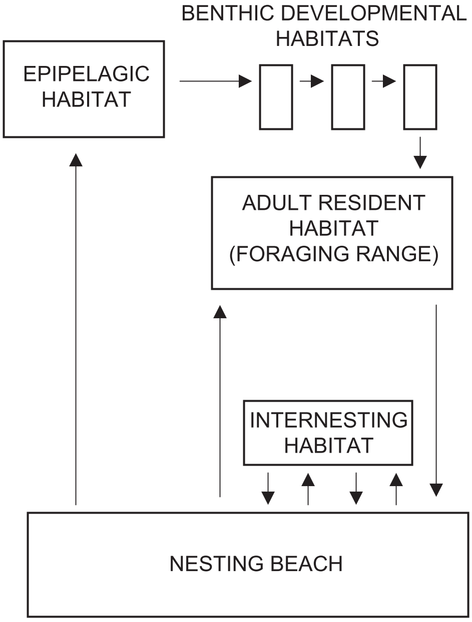

Fig. 1. Life stage model of *Chelonia mydas* redrawn from Carr et al. (1978: fig. 2). Terminology for the two earliest stages has been updated.

that it may occur in a series of locations, not just one.

Carr (1980), citing knowledge of the life cycle of the green turtle, returned to the term "developmental migration." He described it as "at [the end of the lost year], the young shift from pelagic sea-surface life into the benthic littoral habitats in which older immatures are regularly found" (Carr, 1980: 492). He defends the use of the term "migration" in reference to his work at Cedar Key, because young green turtles were caught only between April and November, suggesting immigration and departure. He made the same assumption about green turtles in Bermuda, which had, at that time, been captured only in the summer. He also pointed out that green turtles of different life stages may sometimes be found together and gave the examples of Cedar Key and Florida Bay, where adult and immature greens were found together. He completed his discussion of the topic with the statement, "there thus appears to be some utility in the concept of a developmental habitat."

The terminology for developmental habitat has varied and has evolved, in part, because there are separate names for the life stage itself, the habitat occupied at this stage, the individuals and "populations" or aggregations at this stage, and the migratory movements made by individuals at this stage. Furthermore, certain of these terms are sometimes used interchangeably in the literature. An important improvement in terminology was made by authors who used the term "development" in a more universal sense, by recognizing the "lost year" as a developmental stage. The "lost year" of Carr et al. (1978) has since been referred to as a pelagic stage (Bjorndal et al., 2000a; Bolten et al., 1993, 1995, 1998), oceanic phase (Bolten, 2003; Mansfield et al., 2009), or epipelagic phase (Carr, 1987; Chaloupka and Limpus, 1997; Limpus and Chaloupka, 1997; Schmid, 1998; Diez and van Dam, 2002; Schmid et al., 2003; Seminoff et al., 2003; Casale et al., 2008), referring to use of surface waters. The subsequent stage is referred to as a neritic or benthic developmental stage. Bolten (2003) preferred oceanic and neritic stages; however, posthatchlings are regularly found in both neritic (< 200 m depth) and oceanic (> 200 m depth) zones. In fact, one of the most important studies of this life stage was done in 40 fathoms of water (73 m) (Witherington, 2002). Also, the benthic developmental stage is known to occur at oceanic islands like Bermuda and Hawaii. Thus, the terms epipelagic developmental stage and benthic developmental stage are used here to emphasize the consistency of behavior with respect to the habitat at each stage, rather than the more variable maritime zone with which each is usually associated.

This paper focuses on the benthic developmental stage as described by Carr et al. (1978). Corroboration of the existence of a separate, immature-dominated, benthic developmental stage in the life cycle of cheloniid sea turtles is important for the conservation biology of sea turtles. It would provide further evidence of the existence of a discrete life stage with its own management requirements. Furthermore, the geographic and ecologic separation of immatures from adults of the same population is not the norm for animals with direct development, and its existence in sea turtles would be of general ecological interest (Congdon et al., 1992).

Shifts between habitats are interesting biologically and associated increases in mortality, if any, may be important demographically.

If a separate benthic developmental stage exists, surveys of foraging grounds of sea turtles should result in the identification of areas in which immature, postpelagic turtles are found to the exclusion of the epipelagic size class and adults, and conversely, adults may be found on foraging grounds where immatures are rare or absent. For reasons given below, tests of this hypothesis are compromised in studies in which maturity status is based on size alone. We present here the results of studies conducted on foraging grounds in Panama and Bermuda in which sex and maturity status were determined directly via laparoscopy. The studies focused on the size composition and maturity status of the turtles on these foraging grounds to determine whether they fit the benthic developmental stage model. We provide data on residency and foraging ground site fidelity at this stage and on the eventual departure to adult foraging range. In addition to these field studies, important evidence that contributes to the understanding of benthic developmental habitat is drawn from a survey of the literature. This allows inclusion of *Lepidochelys kempii* in the discussion sections.

## METHODS

STUDY SITES: The fieldwork reported here was conducted at three different sea turtle foraging areas. *Chelonia mydas* was studied on the Bermuda Platform surrounding the oceanic islands of Bermuda; on the western margin of the Caribbean Sea at the Zapatilla Cays, Bocas del Toro Province, Panama; and in a tropical estuary, Chiriqui Lagoon, in the Ngöbe–Buglé Comarca, Panama. Results are also presented for *Caretta caretta* (the loggerhead) from the Secretary and Zapatilla Cays study sites, and for *Eretmochelys imbricata* (the hawksbill) from Bermuda and the Zapatilla Cays study sites.

Bermuda originated as a seamount on the Mid-Atlantic Ridge about 90–110 mya (Aumento and Sullivan, 1974). It is now located at 32°18′N and 64°46′W, 1049 km SE of Cape Hatteras, North Carolina (Smith-Vaniz et al., 1999). It consists of a crescent-shaped chain of low-lying islands with a total land area of 56 $km^2$. The Bermuda Platform includes about 775 $km^2$ of shallow marine ecosystems (fig. 2) including the world's most northerly coral reefs (Smith-Vaniz et al., 1999), as well as extensive sea grass beds and mangroves. The sea grass beds support an aggregation of green turtles that is being studied by the Bermuda Turtle Project, based at the Bermuda Aquarium, Museum, and Zoo. The Bermuda Turtle Project continues work begun in 1968 by H. Clay Frick, Jr., of the Caribbean Conservation Corporation (now the Sea Turtle Conservancy) with support from James Burnett-Herkes of the Bermuda Aquarium (Burnett-Herkes, 1974; Meylan and Meylan, 1998; Meylan et al., 1992, 1994b, 1998; Gray et al., 1998). Green turtles at Bermuda have been sampled nearly every year from 1968 to the present. Since 1992, there has been a deliberate effort to expand the sampling temporally and geographically. An entrapment net has been set at about 40 localities around the Bermuda Platform and samples now exist for most months of the year for at least 10 different sets of grass flats.

The study site in Chiriqui Lagoon, Ngöbe–Buglé Comarca, Panama, is near the village of Secretary on the Valiente Peninsula (9°02.5′N, 81°50.6′W). It includes two sets of banks in the easternmost end of the lagoon (fig. 3). Turtles were netted at one set of banks to the southwest of Secretary, including Tommy Bank, White Bank, and Sopbill Set, and also at a set of banks 6 km ESE of Secretary in the vicinity of Calabash Bank (8°59.0′N, 81°48.5′W). Water depths at all sites ranged from 2–4.7 m. Bottom types included hard bottom, but were primarily sea grass beds on sandy and muddy substrate. Sampling was conducted during May 1987, February and August 1989, May or June 1990–1994, and July 1997.

The Zapatilla Cays, in Bocas del Toro Province, Panama, are two small (each < 1 $km^2$) islands located at the margin of the Caribbean Sea about 20 km ESE of the town of Bocas del Toro. They lie in the mouth of Chiriqui Lagoon between Isla Bastimentos and the Valiente Peninsula (fig. 4), along a chain of fringing reefs. Since 1988, the cays have been part of the Bastimentos Island

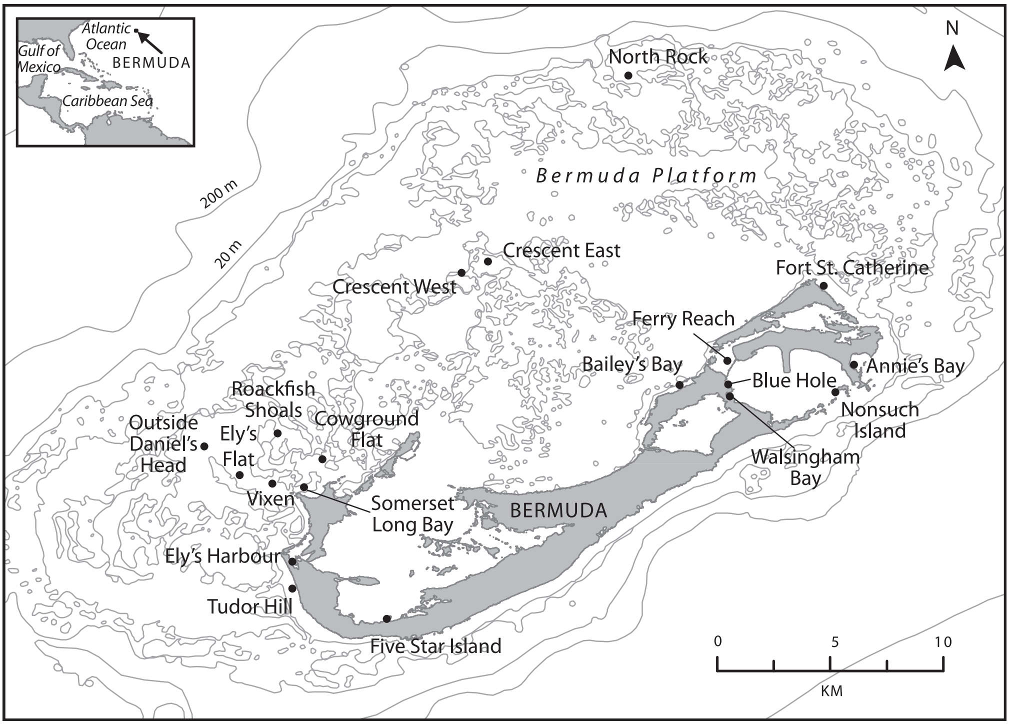

Fig. 2. The islands of Bermuda and the adjacent Bermuda Platform. Labeled sites indicate localities that were regularly sampled with an entrapment net by the Bermuda Turtle Project between 1990 and 2005.

National Marine Park. Nets were set within a 5 km radius of the westernmost of the two islands (9°16.0′N 82°03.4′W). The Zapatilla site was sampled for two to three weeks between late June and late July each year from 1990–1995, 1997, 1998, 2000, and 2002; between mid-May and mid-June 2003–2005; in January 1994; and for two days each September from 2002–2005.

CAPTURE METHODS: The method for capturing turtles varied among sites. In Bermuda, an entrapment net was used that was 613 m long, 6.1 m deep, with a mesh size of 10 cm (bar). It encompassed an area of almost three ha. It had continuous float and lead lines that allowed rapid deployment. It was transported in a 4 m Boston Whaler hull that was towed behind a larger (5.8–7 m) catch boat powered by a 90–135 hp outboard. The net was deployed in a circle to surround turtles on banks ≤ 6 m depth. Snorkelers continuously swam along the net and removed turtles as they became entangled. Turtles were taken to a 16 m research vessel (*R.V. Chelonia* or *R.V. Calamus*) for study.

In addition, turtles were obtained for study in Bermuda from recreational fishermen and divers (who captured mostly hawksbills), by Bermuda Aquarium staff carrying out other sampling activities (hawksbills and green turtles), and through the Bermuda Sea Turtle Stranding and Salvage Network (all species) coordinated by the Bermuda Aquarium. To a limited extent, large-mesh entanglement nets were deployed on sea grass beds that were too deep for the entrapment net. Teams of snorkelers were also used to systematically search shallow reefs for *Eretmochelys*.

Two types of set nets were employed at the Panama sites. A standard set net consisted of a medium- (20 cm bar) to large- (40 cm bar) mesh entanglement net, varying from 60–120 m in length and 2–4 m in depth. Floats were attached to the top line of the net but no lead line was used. Instead, stones of about 500 g each were tied to the bottom mesh of the net at intervals of 7–10 meshes. This

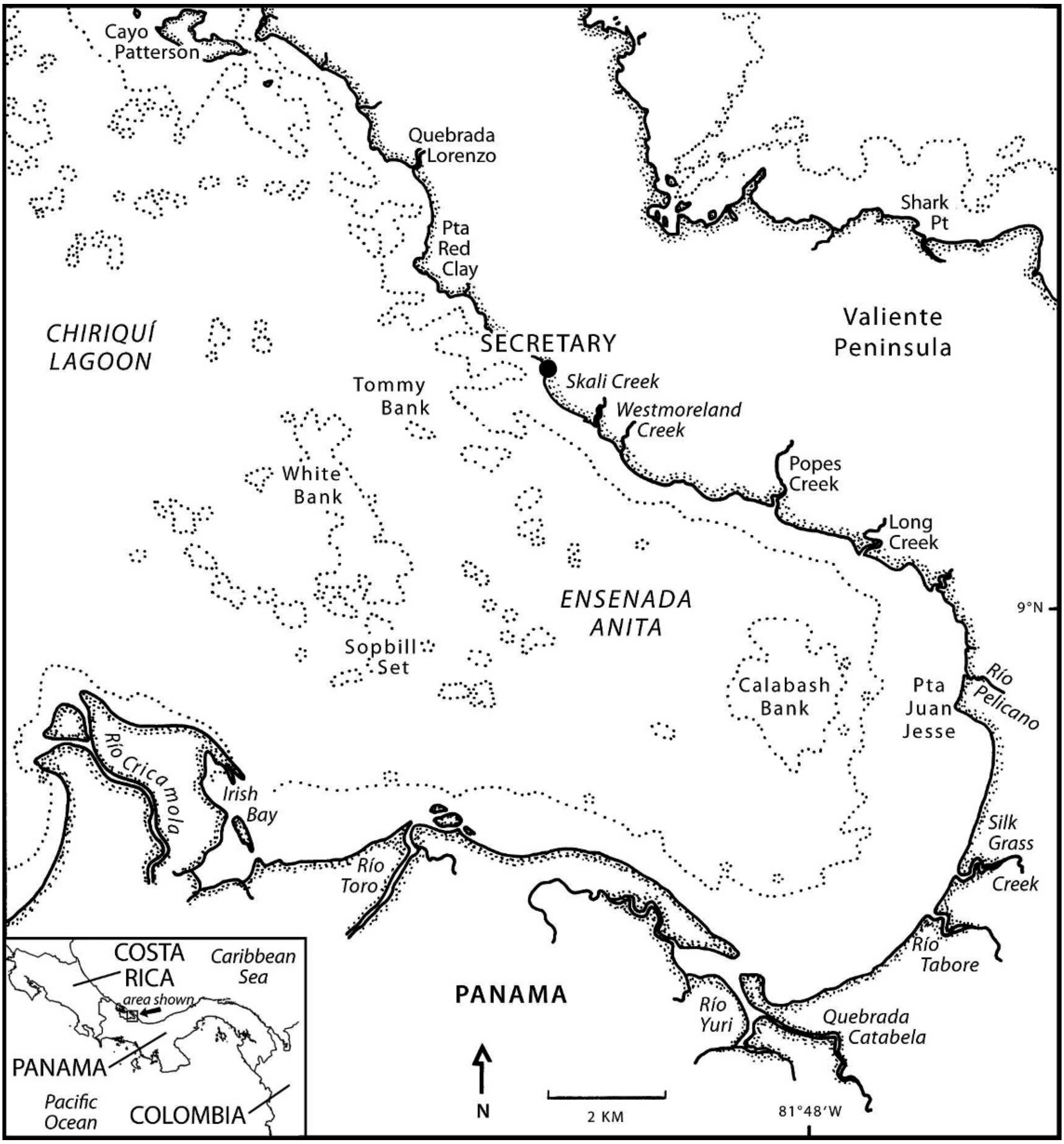

Fig. 3. Study site at Secretary, Chiriqui Lagoon, Ngöbe-Buglé Comarca, Panama. Set nets were deployed on all labeled banks.

system allowed captured turtles to lift the mesh of the net to the surface so that they could breathe. These nets were anchored at each end using a large weight (a large stone) attached to a large balsa wood float. A modification of this method was the "ocean set," which usually involved a deeper net (to 6 m) that was anchored only at one end. These are also called swinging nets because they can turn with changes in current and tide. This type of set was used seaward of the reefs that fringe the Zapatilla Cays (fig. 4). The standard set was used inside (to the south) of the Zapatilla Cays and at all netting sites at Secretary (fig. 3).

TAGGING AND MEASURING: All turtles captured were tagged on the trailing edge of the foreflippers. They were double-tagged

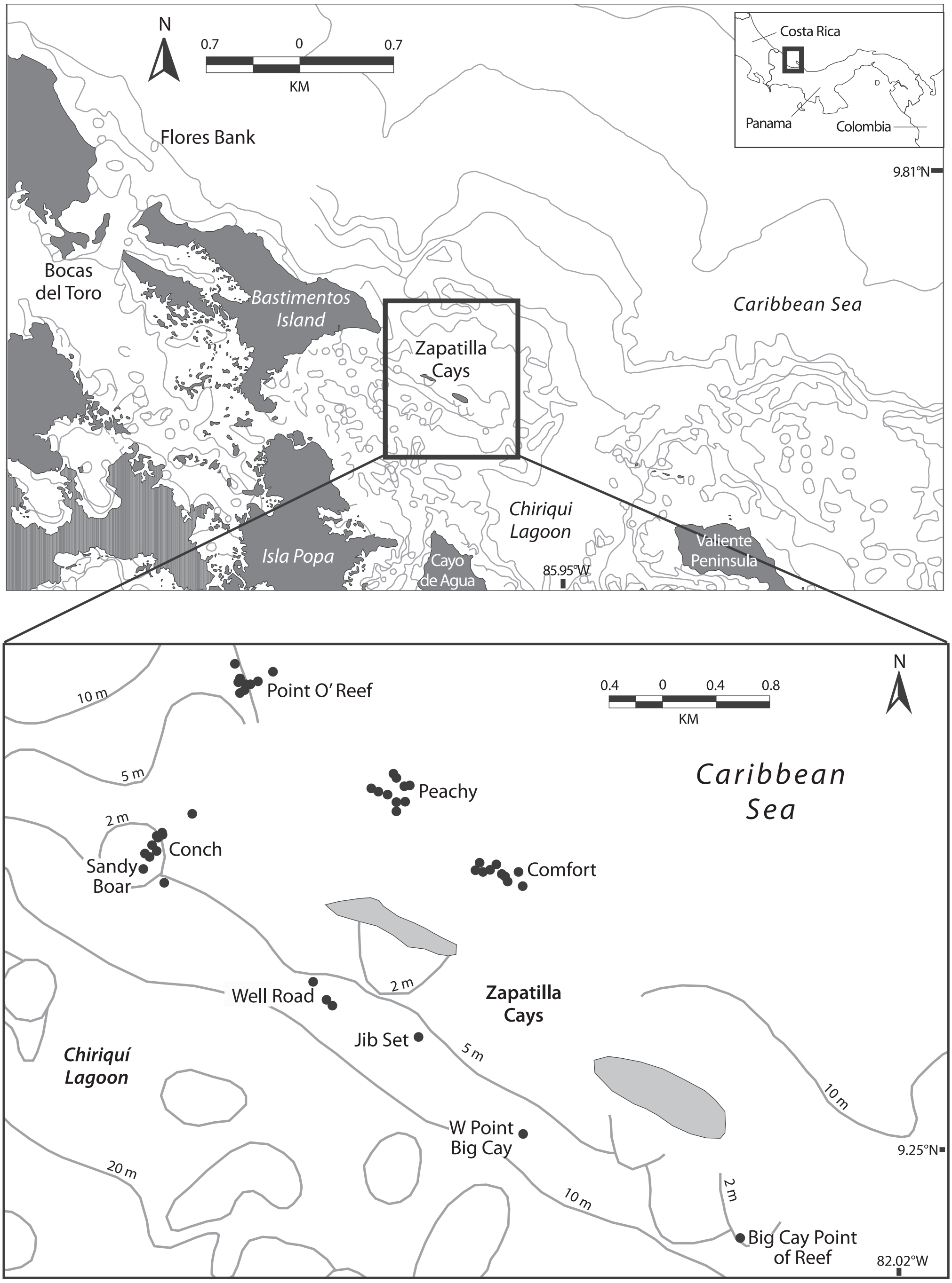

Fig. 4. Study site at Zapatilla Cays, Bocas del Toro Province, Panama. Solid circles indicate sites sampled with nets between 1990 and 2005. Point O' Reef, Peachy, and Comfort are in the Caribbean Sea and were fished with "ocean sets." All remaining sites are within Chiriqui Lagoon and were fished with standard set nets (see Methods).

(beginning in 1992 in Bermuda) with two tags of the same metal (monel, inconel, or titanium) or one metal and one plastic tag (Dalton Rototags). Hole punches and tagging pliers were disinfected between turtles. Beginning in 2001, a PIT tag was inserted into the connective tissue between the radius and ulna of the left foreflipper in all turtles under 30 cm SCL; beginning in 2005, all turtles were PIT-tagged regardless of size.

All turtles were weighed on a spring scale to the nearest kg in Panama, and on an electronic digital scale to the nearest 0.2 kg in Bermuda. A series of measurements of the shell and the tail were taken to the nearest 0.1 cm using tree calipers (all straight-line shell measurements) and a plastic measuring tape (tail measurements and curved carapace length). The standard size criterion used throughout this paper is straight carapace length ($SCL_{min}$ of Bolten, 1999) measured from the nuchal notch to the notch between the posteriormost pair of marginal scales along the midline. Values given as SCL throughout this paper are $SCL_{min}$ unless otherwise stated. Other measurements taken in Bermuda included: straight carapace width (SCW), plastron length (PL), plastron to tail tip (PLTT; TTL of Bolten, 1999), and plastron to cloaca (PL-CLO). In 1996, additional alternative measures of carapace length were taken in Bermuda for 164 turtles and these data were used to generate conversions between various carapace measurements. These included curved carapace length notch to notch ($CCL_{min}$ of Bolten, 1999), straight carapace length notch to tip ($SCL_{n\text{-}t}$ of Bolten, 1999), and straight carapace length tip to tip ($SCL_{max}$ of Bolten, 1999). In Panama, these additional carapace measurements were routinely taken. Measurements are given as mean ± one standard deviation where appropriate. To better understand the use of the Zapatilla Cays study site by *C. mydas,* laparoscopy and size criteria developed from laparoscopy were used to separate adults from immatures for some analyses.

Carapace length data from the literature are given following Bolten (1999) as follows: $SCL_{min}$ (see above), $SCL_{n\text{-}t}$ (see above), $SCL_{max}$ (see above), $CCL_{min}$ (see above), $CCL_{n\text{-}t}$ (measured as $SCL_{n\text{-}t}$ but with a soft tape over the curve), $CCL_{max}$ (measured as $SCL_{max}$ but with a soft tape over the curve). In cases in which the exact carapace length measurement was not specified in a publication, this information was solicited from authors and is given here when available.

An estimate of the average annual growth rate for *C. mydas* in Bermuda was calculated from 71 growth intervals for individuals captured after one year (365 ± 30 days). Growth intervals were for animals that ranged in size from 26.2–65 cm SCL.

LAPAROSCOPY: Sex and maturity status of a large sample of *Chelonia mydas* and smaller samples of *Caretta* and *Eretmochelys* from each of the three study sites were determined by laparoscopic examination of the gonads following the method of Owens (1999). Two adjustable racks were used to secure turtles, a larger one of 2″ × 4″ lumber for turtles > 80 cm SCL, and a smaller one of 2″ × 2″ lumber for turtles < 80 cm SCL. The small sample of laparoscoped *Eretmochelys* from Panama was supplemented with a data set collected by the authors at Mona Island, Puerto Rico (Geis et al., 2003; Diez and van Dam, 2003).

Sex was determined on the basis of appearance, texture, and color of the gonad, following the criteria of Limpus and Reed (1985a). Maturity status was determined grossly for all females and for most males (see criteria below), but in large subadult males (75–90 cm SCL), a small testicular biopsy was examined histologically to detect the presence of sperm whenever possible. Testicular biopsies (about 1 cc in volume) were taken using a second laparoscopy sleeve and biopsy forceps, and fixed in 10% buffered formalin; histological sections were stained with hematoxylin and eosin and periodic acid Schiff.

Following Limpus and Reed (1985a), three maturity stages in males and four in females were recognized. In males, the testes change subtly in color and texture as the animal matures. However, the epididymis goes through obvious changes in gross morphology, and thus is a more useful indicator of the stage of maturity in all three species. In stage 1 males, the epididymis lies flat against the wall of the body cavity. In stage 2 (“pubescent”) males, the epididymis forms a distinct ridge. In stage 3, it is pendulous. Only stage 3 males were considered mature. The use of the term "puberty" to refer to turtles, or "pubescent,"follows previous scientific literature about sea turtles and other turtles, although it is recognized that these terms are typically reserved for mammals (with hair).

In females, the stage of maturity of the gametes is easily seen using laparoscopy (Limpus and Read, 1985a). In stage 1 females, the follicles are uniformly about 1 mm or less in diameter; in stage 2 (pubescent) females, some follicles are enlarged to about 10 mm in diameter. In stage 3, some follicles have reached maturity and are about 25 mm in diameter. Females at Zapatilla Cays, Panama, were occasionally observed to have shelled eggs in the oviducts. This was designated stage 4. Stages 3 and 4 in females were considered mature.

Once the minimum size at sexual maturity for *Chelonia* in Bermuda was established, laparoscopy was no longer carried out and sex was determined by radioimmunoassay of serum androgens, calibrated using turtles that had been laparoscoped (Owens, 1997). During the last four sampling sessions in Panama, laparoscopy was performed only on turtles for which maturity and/or reproductive status was not determinable by other means.

Necropsies performed in Bermuda on dead stranded animals, and gonads salvaged from the artisanal fishery in Panama, provided alternate means to determine the sex and maturity status of turtles of known size. Criteria for maturity status were the same as those given for laparoscopic examination above.

SATELLITE TELEMETRY: Satellite transmitters configured for backpack mounting were attached to the second vertebral scute of the carapace of seven large subadult (65.0–78.6 cm SCL) green turtles captured in the entanglement net in Bermuda from 1996–2008 (see table 7 for transmitter details). Attachment consisted of a Rolyan Silicon Elastomer© base and thin layers of fiberglass cloth and resin, following the method of Balazs et al. (1996). All turtles were released the same day as capture. Four were released at the site of capture; two (PTT 11675, PTT 11676) were released on the ocean side of Coney Island, ~20 km to the east of the capture sites; one (PTT 60810) was released < 1 km away from the capture site on the bay side of Coney Island.

Geographic locations of the turtles were determined via the ARGOS system. Both standard (codes 3, 2, and 1) and auxiliary (codes 0, A, B, and Z) locations were used. The transmitter used in 2008 was GPS-enabled but no GPS locations were received. Data were filtered using the Douglas Argos filter algorithm written for PC SAS (Douglas, 2006). This algorithm applies two independent tests to the Argos data: minimum redundant distance (MRD) and distance angle rate (DAR). The MRD test calculates the distance between near-consecutive Argos locations and excludes those exceeding the user-defined distance threshold (6 km in this study). The assumption of this test is that Argos errors do not occur consecutively at the same location, therefore allowing sequential locations to validate one another. The DAR test excludes locations that are characterized by acute turning angles or travel rates beyond the user-specified thresholds (7 km/hr). A third output of the algorithm is a "hybrid" of the MRD and DAR datasets in which locations passing the MRD filter are supplemented with DAR locations during migratory events. This output is intended to appropriately treat data obtained from migrating animals that exhibit both sedentary and migratory behavior.

The distance between the location where the turtle was captured and the mean center of all filtered Argos locations recorded for that turtle was calculated as a measure of residency and site fidelity. Distance of the mean center of filtered Argos points from any previous net capture locations was also calculated.

Home ranges were calculated using Home Range Tools (Rodgers et al., 2007), written for ArcGIS9.x. Adaptive kernel home ranges were calculated using the least-squares cross-validation bandwidth selection method for each animal from the MRD output of the Douglas Argos filter.

## RESULTS

### BERMUDA – *Chelonia mydas*

SIZE DISTRIBUTION: From 1968 through 2005, the Bermuda Turtle Project made 3336

TABLE 1

**Measurements of immature *Chelonia mydas* from three sites**

Mean ± standard deviation, range, and sample size (*n*) are given. See methods for explanation of abbreviations. Maturity status is based on laparoscopy and size criteria developed from laparoscopy data (see discussion).

| Measurements | Bermuda | Secretary, Panama | Zapatilla Cays, Panama |
|---|---|---|---|
| $SCL_{min}$ (cm) | 47.4 ± 12.5 (22.3–81.0) 2482 | 63.0 ± 9.1 (46.7–88.0) 125 | 69.0 ± 9.1 (29.5–92.5) 118 |
| SCW (cm) | 37.7 ± 9.8 (17.3–69.0) 2475 | 50.0 ± 7.0 (36.7–69.2) 135 | 54.7 ± 7.2 (24.4–76.1) 117 |
| PL(cm) | 38.9 ± 10.3 (18.4–68.0) 2490 | 52.5 ± 7.3 (37.8–73.0) 135 | 57.0 ± 7.3 (25.5–75.3) 117 |
| PL-TT (cm) | 9.3 ± 3.1 (3.5–21.1) 1870 | 12.9 ± 3.1 (7.1–23.0) 134 | 15.3 ± 4.5 (4.5–35.5) 117 |
| PL-CLO (cm) | 6.2 ± 2.3 (1.7–15.1) 1871 | 9.0 ± 2.2 (4.4–16.0) 134 | 10.8 ± 3.4 (3.0–25.5) 117 |
| Weight (kg) | 18.6 ± 14.2 (1.1–86.2) 2496 | 36.7 ± 16.8 (13–100) 135 | 48.1 ± 16.5 (8.3–116.5) 116 |

captures of 2512 individual *C. mydas* using the small-mesh entrapment net at about 40 sites on the Bermuda Platform (fig. 2). These green turtles varied in length (SCL) at first observation from 22.3–81.0 cm (avg. = 47.4 ± 12.5, $n$ = 2482) and in weight from 1.1–86.2 kg (avg. = 18.6 ± 14.2, $n$ = 2496). Morphometric data for these animals at first observation are summarized in table 1. Conversions for three commonly used carapace measurements are presented in table 2 and the size-weight relationship for this sample is given in table 3. The size distribution of Bermuda green turtles in 5 cm size classes (fig. 5A) is not a bell-shaped curve; rather, it is fairly flat from 30–60 cm. The number of individuals in each of the six size classes from 30–60 cm SCL does not differ significantly ($G = 5.996$, $P < 0.05$). Forty-seven hours of additional sampling with large-mesh (25 cm bar) set nets resulted in the capture of four *C. mydas* with an average size of 58.4 cm SCL (39.5, 61.0, 65.9, and 67.3 cm).

In addition to the 2516 individual live *C. mydas* captured as part of the Bermuda Turtle Project, the Sea Turtle Stranding and Salvage Network in Bermuda recovered 152 dead, injured, or sick green turtles between July 1983 and December 2005. Of these, 141 were measurable (range 18.8–97.7 cm SCL, avg. = 36.0 ± 12.8; fig. 5C)

MATURITY: A sample of 131 *C. mydas* from Bermuda (30.5–77.1 cm SCL; fig. 5B) was examined laparoscopically during the early 1990s to check for the presence of mature individuals. The average size of laparoscoped animals (58.5 ± 10.0 cm) was greater than the average for the entire Bermuda sample (47.4 cm). None of the *C. mydas* individuals examined was mature. The maturity status of 54 males and 77 females as determined by laparoscopy is shown in figure 6. Descriptive statistics for maturity status by sex are given in table 4, and the relative increase in the number of individuals in puberty (stage 2) by size class is shown in table 5. Pubescent (stage 2) turtles were significantly larger than individuals that had not reached this stage (stage 1) for both sexes combined ($t = 4.77$, $P < 0.05$).

Seven (0.28%) of 2482 first captures of green turtles in Bermuda (fig. 5A) were larger than the minimum size at sexual maturity (76.7 cm SCL) observed in 178 laparoscopies of *C. mydas* in Caribbean Panama (this study; Meylan and Meylan, unpubl. data).

TABLE 2

**Carapace length conversions for immature *Chelonia mydas***

Conversions to $SCL_{min}$ from three other commonly used carapace measurements are given in the form $SCL_{min} = A(X) + B$ based on 164 *C. mydas* captured in Bermuda during summer 1996. See table 1 for the range of *C. mydas* size at this site.

| Measurement | Conversion to $SCL_{min}$ | $r^2$ | $P$ |
|---|---|---|---|
| Standard straight carapace length ($SCL_{n\text{-}t}$) | $SCL_{min} = 0.9883\ (SCL_{n\text{-}t}) - 0.0460$ | 0.9985 | <0.001 |
| Carr straight carapace length ($SCL_{max}$) | $SCL_{min} = 0.9806\ (SCL_{max}) + 0.0798$ | 0.9991 | <0.001 |
| Curved carapace length ($CCL_{min}$) | $SCL_{min} = 0.9240\ (CCL_{min}) + 1.0205$ | 0.9975 | <0.001 |

TABLE 3

**Length to weight relationships for *Chelonia mydas* and *Caretta caretta***

See tables 1 and 8 for the size ranges at each site. Relationships are given in the form $\text{Log}_e$ weight = A(X) + B.

| Species | Study Site | Length-weight relationship | $r^2$ | $P$ | Sample size |
|---|---|---|---|---|---|
| *Chelonia mydas* | Bermuda | $\text{Log}_e \text{ weight} = (3.12) \log_e \text{SCL}_{\text{min}} - 4.05$ | 0.980 | $< 0.0001$ | 2473 |
| *Chelonia mydas* | Secretary, Panama | $\text{Log}_e \text{ weight} = (2.99) \log_e \text{SCL}_{\text{min}} - 8.85$ | 0.964 | $< 0.001$ | 125 |
| *Chelonia mydas* | Zapatilla, Panama | $\text{Log}_e \text{ weight} = (2.983) \log_e \text{SCL}_{\text{min}} - 8.82$ | 0.963 | $< 0.001$ | 92 |
| *Caretta caretta* | Bocas del Toro, Panama | $\text{Log}_e \text{ weight} = (2.717) \log_e \text{SCL}_{\text{min}} - 7.56$ | 0.965 | $< 0.001$ | 74 |

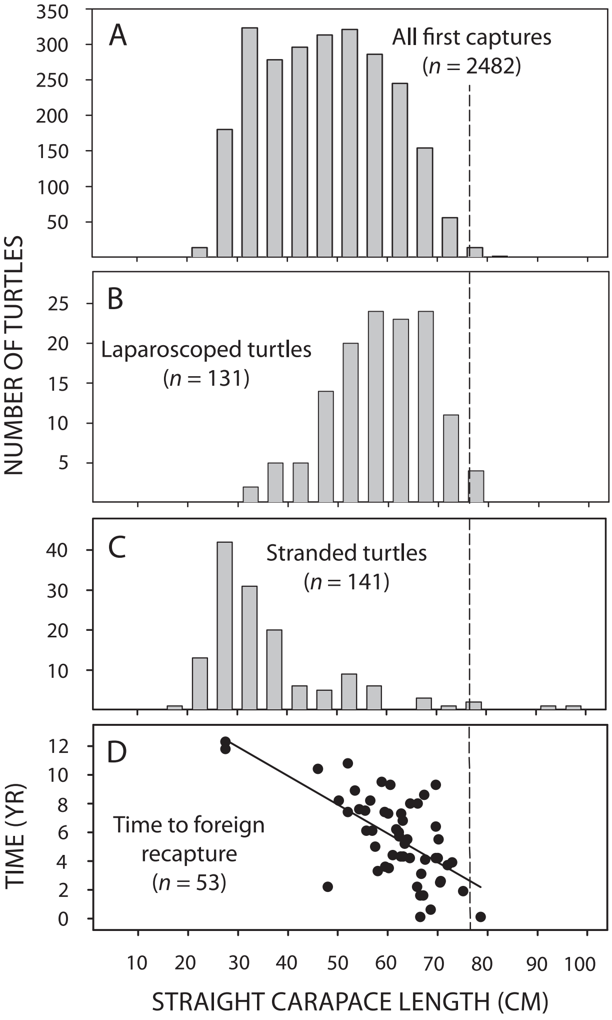

Fig. 5. Size composition of *Chelonia mydas* in Bermuda. **A,** All turtles captured with an entrapment net from 1968–2005 (excludes recaptures). **B,** A subsample of *C. mydas* from Bermuda for which sex and maturity status were determined using laparoscopy; all animals were immature. **C,** Size distribution of 141 *C. mydas* that stranded in Bermuda between 1992 and 2005. **D,** Size ($\text{SCL}_{\text{min}}$) at last capture versus time in years to foreign recapture of 53 *C. mydas* tagged in Bermuda. Minimum adult size, indicated by the dashed line, is based on laparoscopy of 178 *C. mydas* in Bocas del Toro, Panama (this study; Meylan and Meylan, unpubl. data).

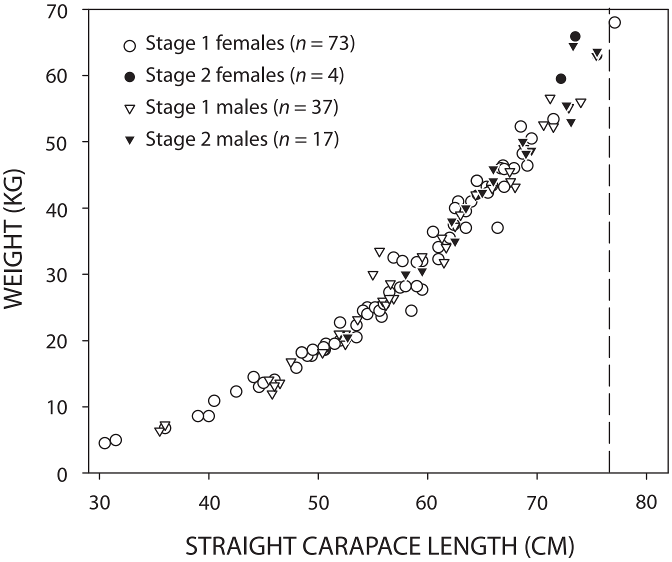

Fig. 6. Carapace length ($SCL_{min}$), weight, and maturity status for 131 *Chelonia mydas* from Bermuda that were examined laparoscopically. Minimum adult size, indicated by the dashed line, is based on laparoscopy of 178 *C. mydas* in Bocas del Toro, Panama (this study; Meylan and Meylan, unpubl. data). For explanation of stages, see Methods.

The four Bermuda green turtles in the 75–80 cm SCL size range that were laparoscoped were immature (fig. 5B).

TEMPORAL AND SPATIAL PATTERNS OF HABITAT USE: Green turtles were sampled with nets in Bermuda during all months of the year. Catch per unit effort (defined as the number of turtles captured per set of the net) varied from 0–41 from 1992–2005; individual sets were not differentiated in the data prior to 1992. The highest average catch rates occurred in April, May, and January; these months also showed the highest variance (fig. 7). Catch rate is plotted against water temperature for 258 sets of the entrapment net from 1992–2005 (fig. 8). During this period, sampling was conducted over a range of water temperatures from 17.6°–31° C.

As of August 2005, 609 (24.2%) of 2512 green turtles tagged in Bermuda since 1968 were recaptured a total of 806 times. Time elapsed between first and last captures is shown in figure 9. One year was the most common interval; the maximum was 14 years.

The greatest number of recaptures of a single turtle with the entrapment net in Bermuda waters was six. Data are available for site of capture, site of release, and site of subsequent recapture for 792 recaptures. The majority of recaptures (88.3%, $n = 699$) occurred at the site of previous capture (table 6). Turtles that were released somewhere other than their previous capture location were subsequently recaptured at their previous capture location only slightly less frequently (81.8%, $n = 181$) than those that were released at the site of capture (90.2%, $n = 611$).

Seven large subadult green turtles were satellite tagged in Bermuda between 1996–2008, with the primary goal of documenting the timing of departure and the route of travel of *C. mydas* leaving the Bermuda Platform. One departure (PTT 11674) was recorded (see Arrival and Departure, below); five other turtles remained on the Bermuda Platform for at least 33–447 days (table 7; fig. 10), providing information on spatial and temporal patterns of habitat use. The seventh satellite transmitter (PTT 11675) transmitted intermittently for eight days, producing only seven transmissions, none of which passed the filter (see methods). Three of the satellite tagged turtles had been captured previously, 1, 6, and 8 years before transmitter application, in all cases at the same set of grass flats.

TABLE 4
**Size of *Chelonia mydas* at three maturity stages**
Mean ± standard deviation, range, and sample size are given for $SCL_{min}$. Maturity for Bermuda based on laparoscopy. Maturity for Panama based on laparoscopy and tail measurements (Meylan et al., 1994). Sample from Tortuguero, Costa Rica, based on measurements of nesting females provided by S. Troëng and the Sea Turtle Conservancy.

| Maturity stage and locality | Mean = 1 SD (range) | Sample size |
|---|---|---|
| Stage 1 males Bermuda | 57.8 ± 9.9 (35.5–74.0) | 37 |
| Stage 1 males Panama | 65.7 ± 7.5 (50.5–83.4) | 35 |
| Stage 1 females Bermuda | 56.3 ± 9.7 (30.5–71.5) | 73 |
| Stage 1 females Panama | 64.6 ± 8.4 (50.3–83.7) | 37 |
| Stage 2 males Bermuda | 66.6 ± 6.5 (52.7–75.5) | 17 |
| Stage 2 males Panama | 72.4 ± 6.9 (59.9–86.2) | 22 |
| Stage 2 females Bermuda | 71.4 ± 4.8 (64.5–75.5) | 4 |
| Stage 2 females Panama | 78.2 ± 7.0 (65.5–92.5) | 16 |
| Mature males Panama | 89.0 ± 4.7 (76.7–103.1) | 56 |
| Mature females Panama | 95.9 ± 4.9 (81.0–105.0) | 51 |
| Nesting females Tortuguero | 99.9 ± 4.7 (84.5–114.3) | 200 |

Table 7 presents data on the distance between the net capture location (XY) for the tracking experiment (and any previous net capture locations) and the mean center of filtered Argos locations; the number of satellite transmissions (raw and filtered); and the size of the core area as defined by the 50% volume contour line. Filtered location data and 50% and 90% volume contours are shown in figure 10. The filtered data for these four turtles and for PTT 74521 (table 7) provided no evidence of departure from the platform.

TABLE 5
**Puberty in Bermuda *Chelonia mydas***
Percentage of *Chelonia mydas* encountered in Bermuda that were undergoing puberty (i.e., Stage 2 maturity) by size class. Maturity status determined by laparoscopic examination.

| Size class SCL (cm) | Sample size | Stage 2 Maturity (%) |
|---|---|---|
| 30.0–34.9 | 2 | 0 |
| 35.0–39.9 | 4 | 0 |
| 40.0–44.9 | 5 | 0 |
| 45.0–49.9 | 14 | 0 |
| 50.0–54.9 | 19 | 5.3 |
| 55.0–59.9 | 25 | 8.0 |
| 60.0–64.9 | 22 | 18.2 |
| 65.0–69.9 | 25 | 24.0 |
| 70.0–74.9 | 11 | 45.5 |
| 75.0–79.9 | 4 | 75.0 |

ARRIVAL AND DEPARTURE: The smallest green turtle captured in the entanglement net in Bermuda between October 1968 and August 2005 was 22.3 cm SCL (fig. 5A). Only 14 (0.56%) entrapment net captures were in the 20–25 cm SCL size class; 180 (7.25%) were in the 25–30 cm SCL class. The smallest green turtle that was recovered by the stranding network in Bermuda from July 1983–December 2005 was 18.8 cm SCL (fig. 5C); it was the only turtle in the 15–20 cm SCL size class. Thirteen (9.4%) were in the 20–25 cm SCL size class; 42 (30.4%) were in the 25–30 cm SCL size class.

Eighty-eight foreign recaptures of *C. mydas* tagged in Bermuda were recorded as of January 2006 (fig. 11). The majority (56) occurred in Nicaragua, the principal foraging grounds of adult green turtles in the western Caribbean (Carr et al., 1978; Bass et al., 1998). Seventeen occurred along the northern coast of Cuba, six off the Venezuelan portion of the Guajira Peninsula, and two in the eastern Caribbean (St. Lucia and Grenada). A single tag recovery was made in the harbor of Charleston, South Carolina. Two green turtles tagged in Bermuda were subsequently captured along the southeast coast of Florida. One stranded dead; a second became entrapped in the cooling water intake canal of the St. Lucie Nuclear Power Plant, St. Lucie County, Florida. The latter was fitted

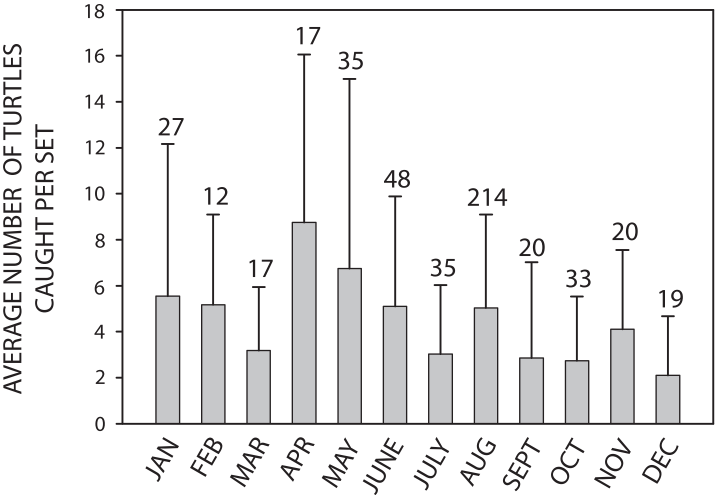

Fig. 7. Average number of *Chelonia mydas* caught per set of the entrapment net at Bermuda by month. Mean and one standard deviation are shown for all sets from January 1992–August 2005. Sample size above each bar is for the number of sets made during each month.

with a satellite transmitter and subsequently tracked to foraging grounds west of the Marquesas Islands, Florida (50 km W of Key West), where it remained for at least eight months (D. Bagley, personal commun.).

The length of time between the last observation of individual green turtles in Bermuda and their subsequent international recapture is shown as a function of carapace length at last observation in Bermuda in figure 5D, with the size distribution of the Bermuda aggregation provided for reference (fig. 5A). Time elapsed varied from 0.6–12.3 yr.

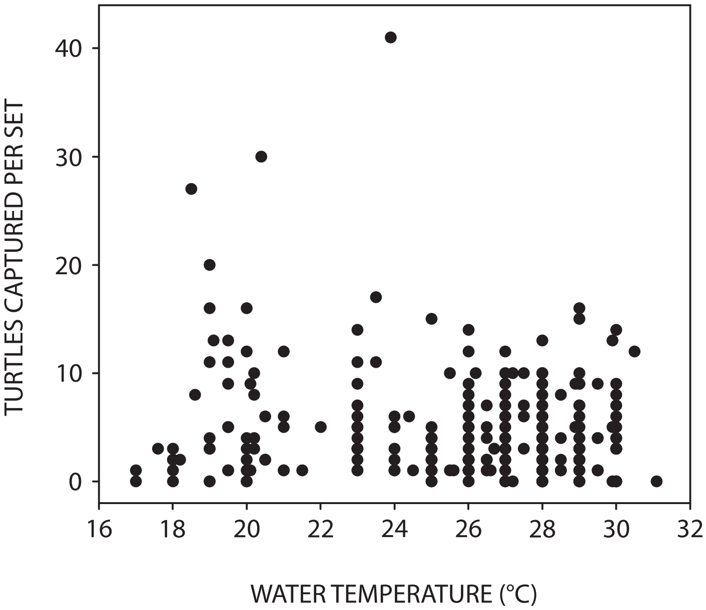

Fig. 8. The number of *Chelonia mydas* caught at Bermuda per set of the entrapment net as a function of water temperature. Data shown are for 258 samples from January 1992–August 2005.

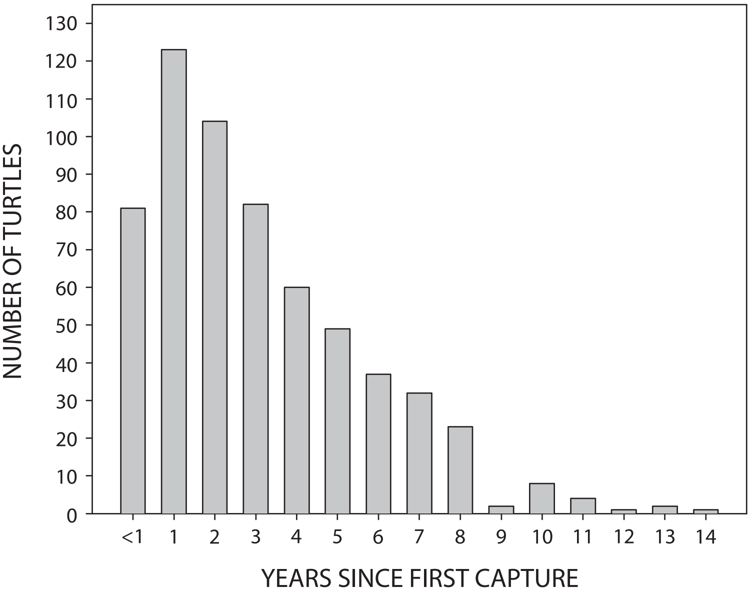

Fig. 9. The time in years from first capture to last recapture for 609 *Chelonia mydas* recaptured in Bermuda waters through August 2005. Time elapsed was calculated as number of months divided by 12, rounded to nearest year.

Only one *C. mydas* tagged from Bermuda has subsequently been observed on a nesting beach. A 59.8 cm SCL green turtle captured in the entrapment net and tagged on 18 November 1992 was observed nesting on a beach in Quintana Roo, Mexico, during the summer of 2006 and in subsequent years (A. Arenas, and J. Zurita, personal commun.).

One of seven subadult green turtles satellite tagged in Bermuda (PTT 11674, table 7) left the platform 18 days after it was satellite tagged (fig. 12). It traveled directly south to the Dominican Republic, and then west to the eastern tip of Cuba, where it was captured and presumably killed. The travel path of this turtle was recreated using the best quality location per day from hybrid (combined MRD and DAR) output.

### BERMUDA – *Eretmochelys imbricata*

A total of 154 hawksbills were documented in Bermuda, 68 as live captures from 1970–2005 and 86 as strandings from 1980–2005. Live hawksbills captured on the Bermuda Platform or on the adjacent Argos Bank

TABLE 6

**Recapture matrix**

The location of recapture (at or away from previous capture site) is considered relative to release location (at or away from previous capture site) for each of 792 *Chelonia mydas* recaptures made in Bermuda for which capture, release and recapture locations were recorded. Data include multiple recaptures of the same turtle. Locations are named netting sites shown in figure 2.

| | | CAPTURE AND RELEASE DATA | |
|---|---|---|---|
| | | Release location = capture location | Release location ≠ capture location |
| RECAPTURE DATA | Recapture location = previous capture location | 551 (90.2%) | 148 (81.8%) |
| | Recapture location ≠ previous capture location | 60 (9.8%) | 33 (18.2%) |
| | Totals | 611 | 181 |

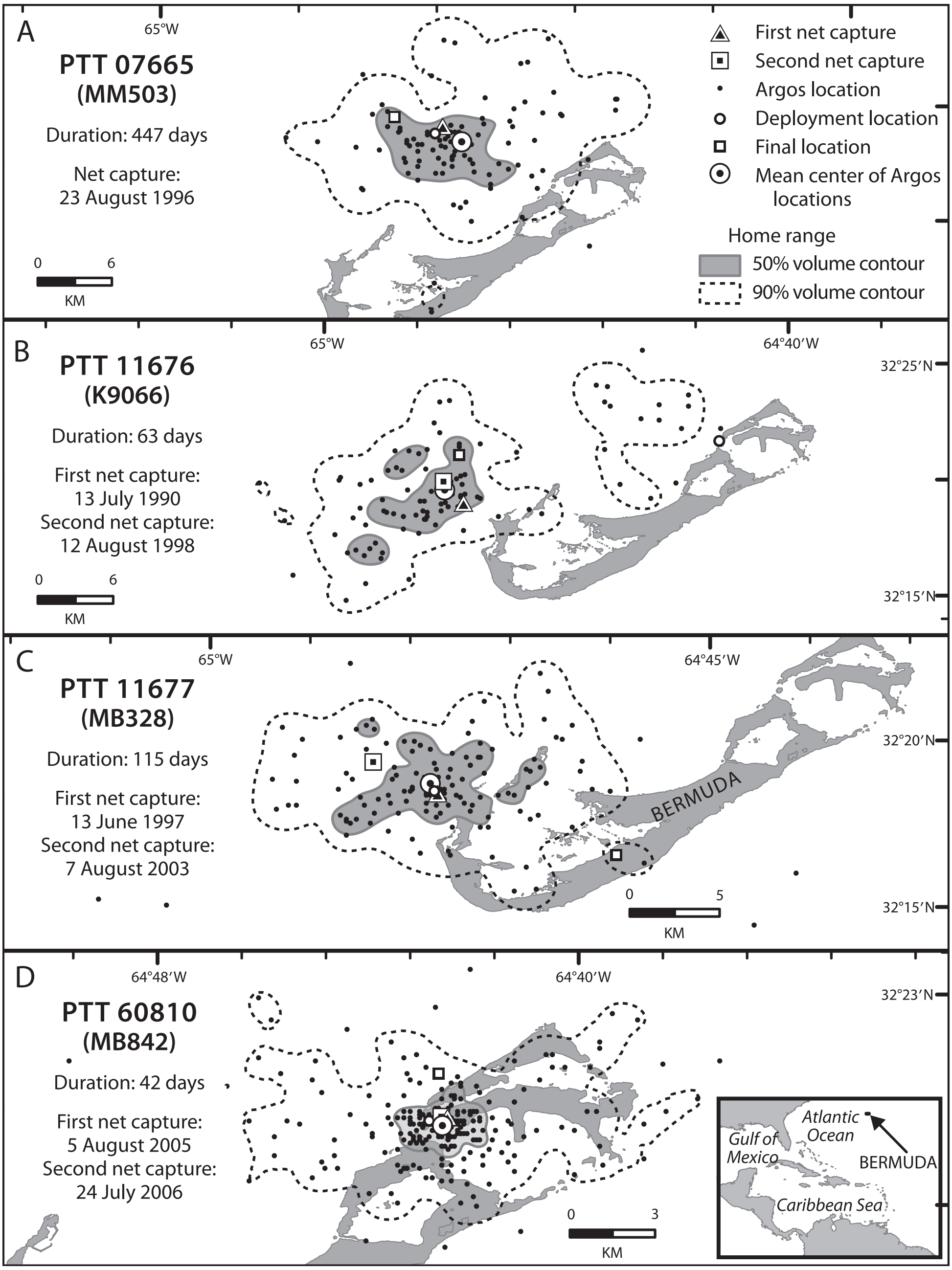

Fig. 10. Satellite transmission histories of four large subadult *Chelonia mydas* from Bermuda. Argos locations displayed are the minimum redundant distance (MRD) output of the Douglas Argos filter algorithm. This output includes points that have a consecutive or near-consecutive neighbor within 6 km. Adaptive kernel density percent volume contours, calculated from the MRD dataset, are also displayed. **A,** Locations ($n$ = 103) and volume contours for PTT 07665 (70.4 cm $\mathrm{SCL}_{\mathrm{min}}$). **B,** Locations ($n$ = 103) and volume contours for PTT 11676 (72.0 cm $\mathrm{SCL}_{\mathrm{min}}$). **C,** Locations ($n$ = 141) and volume contours for PTT 11677 (71.8 cm $\mathrm{SCL}_{\mathrm{min}}$). **D,** Locations ($n$ = 253) and volume contours for PTT 60810 (70.0 cm $\mathrm{SCL}_{\mathrm{min}}$).

## TABLE 7

### Summary of data collected via satellite transmitters

Specifications for and data collected from seven satellite transmitters deployed on subadult green turtles (*Chelonia mydas*) captured on the Bermuda Platform. PTT11674 departed the Bermuda Platform shortly after deployment (fig. 11), and therefore residency metrics are not presented for this record.

| | Net capture history | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PTT | Site | Date | SCL | X | Y | dist. to μ Argos (km) | PTT Model | Duty Cycle (hrs on/ off) | Duration (day) | Trans-missions (*n*) | Passed Filter (*n*) | "Core" (50% volume contour line) area size (ha) |
| 07665 | Crescent East | 23 Aug 96 | 70.4 | −64.801 | 32.397 | 1.9 | Telonics ST-6 | 6/6 | 447 | 194 | 103 | 3829 |
| 11674 | Outside Daniels Head | 5 Aug 98 | 78.6 | −64.919 | 32.323 | . | Telonics ST-6 | 6/6 | 55 | 136 | 44[a] | . |
| 11675 | Outside Daniels Head | 7 Aug 98 | 73.8 | −64.919 | 32.326 | . | Telonics ST-6 | 6/6 | 8 | 7 | . | . |
| 11676 | NW Daniels Head[b] | 13 Jul 90 | 48 | −64.9 | 32.3 | 1.7 | | | | | | |
| | Outside Daniels Head | 12 Aug 98 | 72.0 | −64.9161 | 32.3303 | 0.5 | Telonics ST-6 | 6/6 | 63 | 158 | 103 | 3663 |
| 11677 | Outside Daniels Head | 13 Jun 97 | 56.4 | −64.919 | 32.323 | 3.1 | | | | | | |
| | | 7 Aug 03 | 71.8 | −64.8877 | 32.3081 | 0.3 | Telonics ST-6 | 6/6 | 115 | 244 | 141 | 2640 |
| 60810 | Ferry Reach | 5 Aug 05 | 70.0 | −64.709 | 32.361 | 0.2 | | | | | | |
| | | 24 Jul 06 | 72.4 | −64.7090 | 32.3604 | 0.2 | Telonics ST-20 A-225 | 24/12 | 42 | 288 | 253 | 453 |
| 74521 | Mullet Bay | 12 Aug 08 | 65.0 | −64.692 | 32.375 | 0.1 | Telonics uGPSI-18 | 24/0 | 33 | 167 | 130 | 301 |

[a] Migration of PTT11674 was recreated using the best quality location per day from hybrid (combined MRD and DAR) output.

[b] Release location estimated based on field notes.

Fig. 11. Geographic distribution of 88 foreign tag returns (numbers in circles) through 2005 of *Chelonia mydas* originally tagged in Bermuda. The star indicates the only known nesting by a *C. mydas* tagged in Bermuda. This turtle was tagged in November 1992 and nested near Cancun, Mexico, during the summer of 2006.

ranged in size from 17.6–66.5 cm SCL (fig. 13A). Stranded hawksbills ranged in size from 5.3–75.7 cm SCL (fig. 13B). Between 1993 and 2005, 30 stranded hawksbills were necropsied; none was mature, including a 75.7 cm SCL female. Two local recaptures of hawksbills were recorded in Bermuda through 2005, one after an interval of four months, the other after four years. The four-year recapture occurred on the same reef where the turtle had been tagged; it had grown an average of 1 cm per year (42.8–46.8 cm).

A single international recapture was made of a hawksbill tagged in Bermuda as of January 2006. A 50 cm hawksbill tagged off Daniel's Head, Bermuda, was captured via speargun 11 years later at Sandy Island, Grenada, a minimum distance of 2260 km.

### PANAMA: SECRETARY STUDY SITE – *Chelonia mydas*

SIZE DISTRIBUTION: Between 1987 and 1997, 135 *C. mydas* were captured at the Secretary study site in Chiriqui Lagoon. They varied in length at first observation from 46.7–88.0 cm SCL (avg. = 63.0 ± 9.1, $n$ = 132; fig. 14A) and in weight from 13–100 kg (avg. = 36.7 ± 16.8, $n$ = 135). Morphometric data for these turtles are summarized in table 1; the relationship between SCL and weight is given in table 3.

MATURITY: All but 14 of the 135 green turtles captured at this site were smaller than the minimum size (76.7 cm SCL) at sexual maturity observed in 178 laparoscopies of *C. mydas* in Caribbean Panama (figs. 14A, 15; Meylan and Meylan, unpubl. data). Seven of these 14 were examined laparoscopically and found to be immature, including an 85.7 cm SCL female. All 56 Secretary green turtles that were examined laparoscopically were immature (fig. 15). The largest pubescent male (stage 2) was 77.1 cm; the largest pubescent female in was 85.7 cm SCL (see also table 4).

TEMPORAL AND SPATIAL PATTERNS OF HABITAT USE: Eleven of 134 (8.2%) *C. mydas*

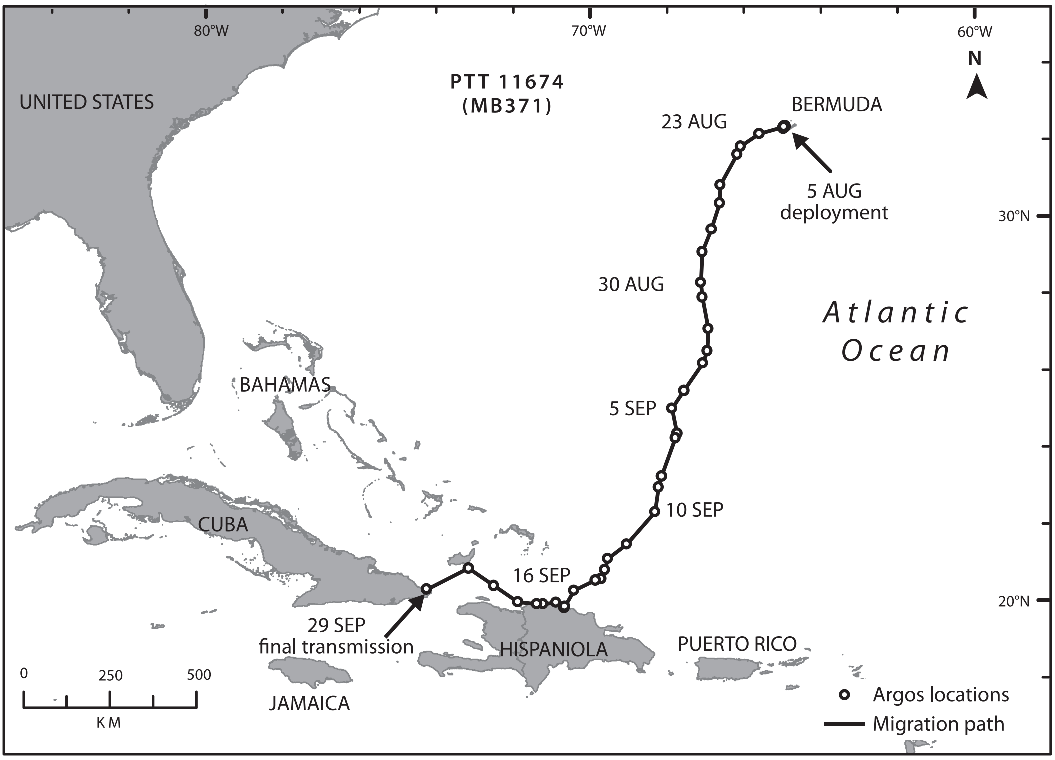

Fig. 12. Satellite transmission history of a large subadult (78.6 cm $SCL_{min}$) *Chelonia mydas* from Bermuda. Argos locations displayed are the highest location class per day, selected from the hybrid output of the Douglas Argos filter algorithm. This output includes points passing the minimum redundant distance filter supplemented with points passing the distance angle rate filter during periods of migration.

tagged and released at the Secretary site were recaptured in project nets. None was captured more than twice. The longest interval to local recapture was one year. Ten of 11 recaptures were on the same bank as the first capture. One turtle changed banks, moving approximately 7 km between Calabash Bank and Sopbill Set (fig. 3). Although sampling was limited at Secretary, green turtles were captured in this study during February, May, June, and August.

ARRIVAL AND DEPARTURE: The smallest green turtle captured in the nets at Secretary was 46.7 cm SCL. Smaller green turtles were not captured or reported in this part of Chiriqui Lagoon. As of October 2006, 11 immature green turtles captured and tagged at Secretary were recaptured in other countries: 10 in Nicaragua and one in Colombia. Figure 16 shows the combined tag-return data for immature green turtles tagged at Secretary and at the Zapatilla Cays (see below). The size of turtles when last observed at Secretary ranged from 49.1–77.1 (avg. = 61.4 ± 8.42 cm SCL) and foreign recaptures occurred from 12–88 months after last observation in Panama (fig. 14C). Data on time elapsed before foreign recapture are presented for both Secretary and Zapatilla Cays green turtles in this figure. Four of these foreign recaptures, including the largest individual (77.1 cm SCL), had been laparoscoped at first capture and were either stage 1 or stage 2 maturity; four others were considered immature on the basis of size, using criteria developed from laparoscopy.

### PANAMA: SECRETARY STUDY SITE – *Caretta caretta*

SIZE DISTRIBUTION: Eighty-two loggerheads were captured in nets within the

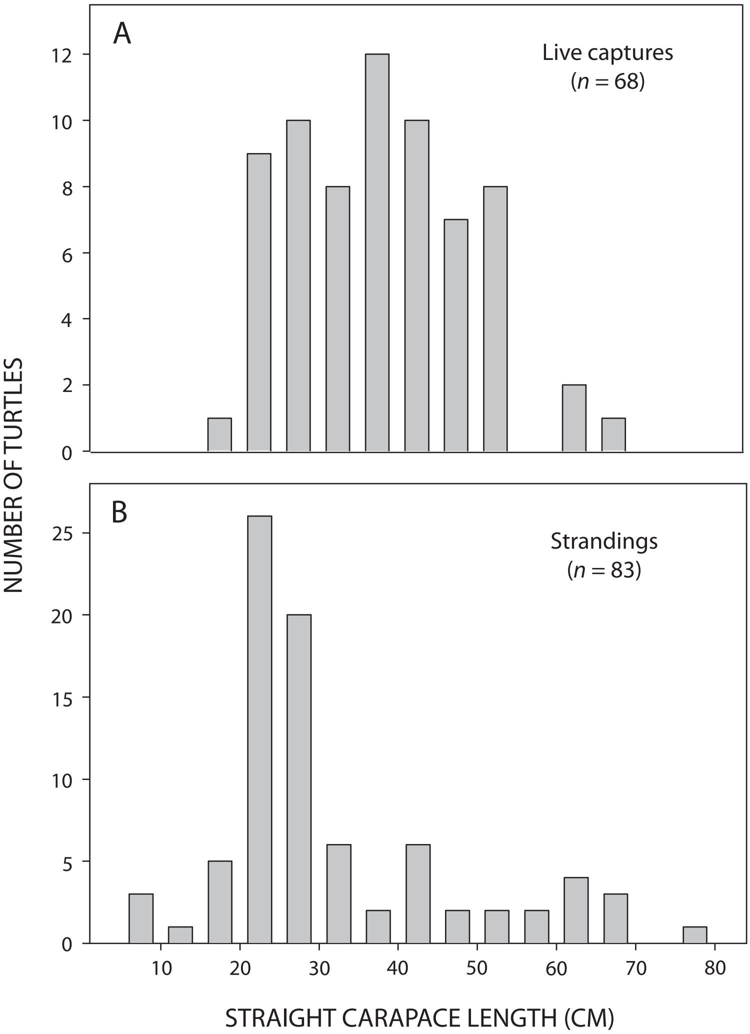

Fig. 13. Size distribution of *Eretmochelys imbricata* from Bermuda. **A,** Individuals captured alive by scuba, snorkeling, or in the entrapment net (1970–2005). **B,** Stranded individuals that were dead, injured, sick, or trapped in marine debris (1980–2005).

Secretary study site between 1987 and 1997. Eighty-one of these varied in SCL from 45.2–76.5 cm (avg. = 59.8 ± 6.92), and 16–67 kg (avg. = 35.3 ± 10.90, $n = 78$; fig. 17). These statistics exclude a 98 cm SCL adult male that was judged to be mature on the basis of laparoscopy; tail length (PLTT) was 52 cm. This is the only certainly mature *Caretta* that was captured at this site. It had recently lost its entire right front flipper, and its appearance within the study site may be an anomaly. Table 8 summarizes other morphometric data for Secretary *Caretta*; table 9 presents conversion formulas for other commonly used carapace measurements. The relationship between size (SCL) and weight is presented in table 3.

MATURITY: The results of laparoscopy of 17 *Caretta* from Secretary and five from the Zapatilla Cays are given in figure 18. With the exception of the 98 cm male (see above), all of the loggerheads laparoscoped at Secretary were immature; three were pubescent. The five loggerheads from the Zapatilla Cays were all immature; they included two large males, 84.0 and 85.3 cm SCL, that were

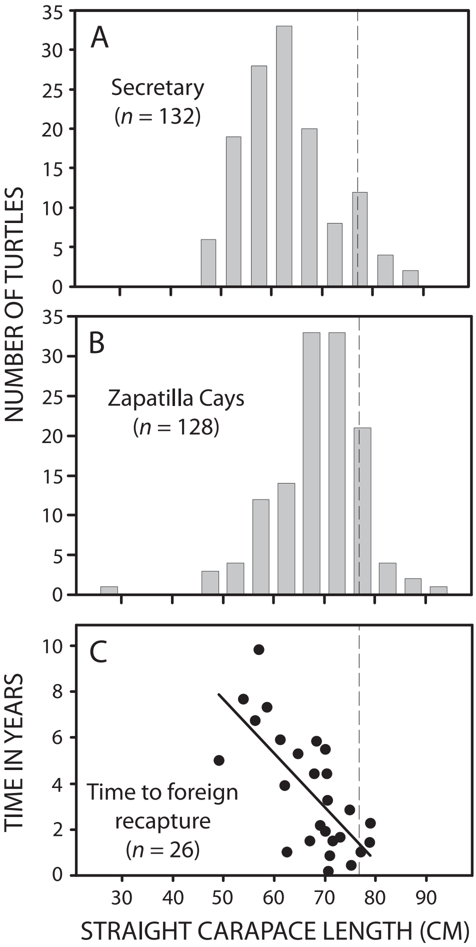

Fig. 14. Size distribution of all *Chelonia mydas* captured **(A)** at Secretary, Chiriqui Lagoon, Panama, 1989–1997, and **(B)** immature *C. mydas* captured at the Zapatilla Cays, Panama, 1990–2005. **C,** Size at last capture versus time in years to foreign recapture of 26 *C. mydas* captured at these site ($y = -2.830x + 233.75$, $r^2 = 0.4996$, $P < 0.001$ Minimum adult size, indicated by the dashed line, is based on laparoscopy of 178 *C. mydas* in Bocas del Toro, Panama, and size criteria developed from laparoscopy data (this study; Meylan and Meylan, unpubl. data).

pubescent. Among the 23 *Caretta* that were laparoscoped, the smallest stage 2 male and female were 65.2 and 66.1 cm SCL, respectively; the largest stage 2 male and female were 85.3 and 72.1 cm SCL, respectively.

TEMPORAL AND SPATIAL PATTERNS OF HABITAT USE: The rate of recapture of *Caretta* at Secretary was higher than for *C. mydas*. Twenty-six (32%) of 82 *Caretta* were recaptured within the study area 35 times. Six were recaptured after one year; none was recaptured after longer time periods. Ten (28.6%) of 35 recaptures involved movements from one bank to another. A 53.5 cm SCL loggerhead tagged on 24 May 1987 was recaptured locally by a fisherman near Bluefields on the Valiente Peninsula (about 20 km away) on 14 June 1991.

ARRIVAL AND DEPARTURE: The smallest loggerhead captured in the nets at Secretary was 45.2 cm SCL (fig. 17). This was one of six in the 45–50 cm SCL size class. As of October 2006, six (7.3%) of 82 *Caretta* tagged at Secretary, Panama, were recaptured outside Panama. Five were taken in nets by fishermen in Nicaragua; one was captured off the southern coast of Cuba (fig. 16). Sizes at last sighting in Panama ranged from 56.3–74 cm SCL (avg. = 65.2 ± 8.42). The shortest time period between last sighting in Panama and recapture in Nicaragua was 13 months for a loggerhead that was 72.6 cm SCL at last observation in Panama.

### PANAMA: SECRETARY STUDY SITE – *Eretmochelys imbricata*

Seven hawksbills were captured at the Secretary site as of 1997, three in nets and four by local divers. Net captures were made at Sopbill and White Bank (fig. 3); the divers captured hawksbills at four sites in the western part of Ensenada Anita (Buck Bank, Chiriqui Bank, Cricamola Bank, and Playa Verde). Sizes ranged 40.8–74.9 cm SCL (avg. = 57.0 ± 14.1). The smallest of these, a 40.8 cm SCL, stage 1 male from Cricamola Bank, was harpooned four months later off Playa Lorenzo, 13 km north of the capture site. Three of these *Eretmochelys* were laparoscoped; the results are reported with those from the Zapatilla Cays below.

### PANAMA: ZAPATILLA CAYS STUDY SITE – *Chelonia mydas*

SIZE DISTRIBUTION: Between 1990 and 2005, 265 individual green turtles were captured at netting sites around the Zapatilla Cays (figs. 4, 19). The sample includes both mature and immature individuals ranging in

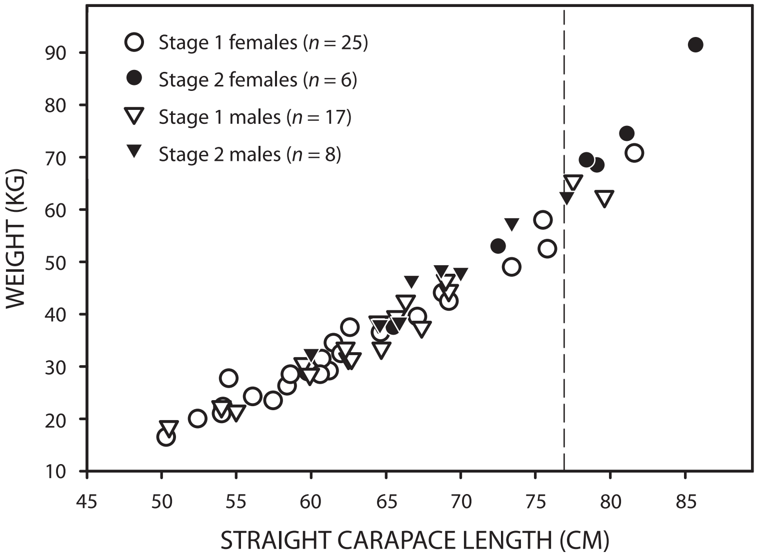

Fig. 15. Carapace length ($SCL_{min}$), weight, and maturity status for 56 *Chelonia mydas* captured at Secretary, Panama, (1989–1997). For explanation of stages of maturity status, see Methods. Minimum adult size, indicated by the dashed line, is based on laparoscopy of 178 *C. mydas* in Bocas del Toro, Panama, and size criteria developed from laparoscopy data (this study; Meylan and Meylan, unpubl. data).

Fig. 16. International recaptures of 36 immature *Chelonia. mydas* and 6 immature *Caretta caretta* (in parentheses) tagged in the Bocas del Toro area of Panama. Turtles tagged at both the Secretary and Zapatilla Cays study sites are shown.

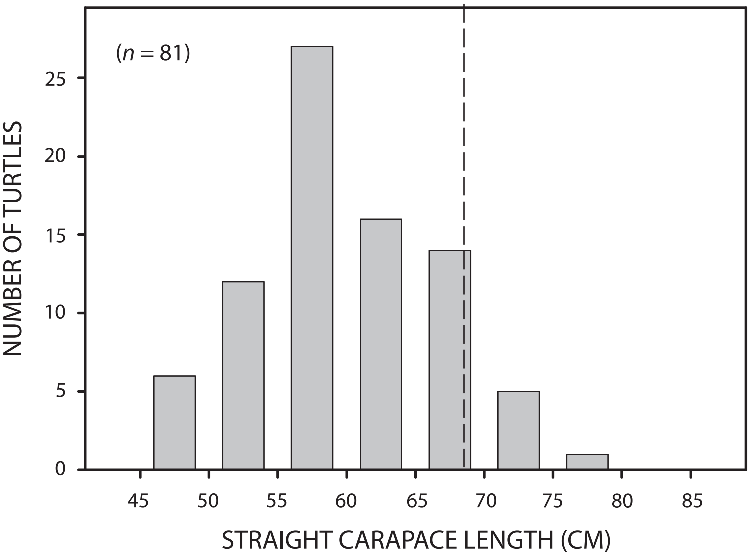

Fig. 17. Size distribution of 81 *Caretta caretta* at first capture near Secretary, Panama (1987–1997). $SCL_{min}$ for seven turtles calculated from standard carapace length ($SCL_{n\text{-}t}$); see table 9.

size from 29.5–105.0 cm SCL at first observation. Nearly all sampling was carried out in May, June, July, and September, during the reproductive season for green turtles that nest at Tortuguero, Costa Rica (Carr et al., 1978, 1982; fig. 19A). To collect data on the size of turtles present at the Zapatilla Cays outside of the reproductive (and migratory) season, a netting session was conducted in January 1994. Seventeen immatures and one adult were captured (fig. 19B). Four of the immatures were recaptures from previous sessions. The single adult was a reproductive female with fresh corpora lutea (seen via laparoscopy).

Based on laparoscopic examination or on size criteria developed in conjunction with laparoscopy, 156 captures of 128 different immature *C. mydas* were made at netting sites at the Zapatilla Cays between 1990–2005 (figs. 4, 14B). At first observation, these immatures varied in length (SCL) from 29.5–92.5 cm (avg. = 68.6 ± 8.9, $n$ = 128) and in weight from 8–116 kg (avg. = 47.5 ± 16.9, $n$ = 120). Table 1 summarizes morphometric data for these animals. The relationship between size (SCL) and weight is presented in table 3. Eighteen turtles (8 males, 10 females) larger than the minimum size at sexual maturity (76.7 cm SCL) were determined to be immature based on direct examination of the gonads via laparoscopy.

MATURITY: Maturity status of 69 immature green turtles laparoscoped at the Zapatilla Cays from 1990–2005 is shown in figure 20. Pubescent (stage 2) females spanned a wide size range, 62.8–92.5 cm SCL (avg. = 77.0 ± 7.8, $n$ = 14). Two large females (82.3 and 83.7 cm SCL) were at stage 1 (“prepubescent”), showing no signs of follicular enlargement. Pubescent males also spanned a wide size range, 59.9–86.2 cm (avg. = 74.9 ± 6.1, $n$ = 19). The female:male ratio

TABLE 8

**Measurements of *Caretta caretta* from Secretary, Panama**

Mean ± standard deviation, range, and sample size are given. See methods for explanation of abbreviations. A single known adult male from Secretary is not included.

| Measurements | Mean + 1 SD (range) | Sample size |
|---|---|---|
| $SCL_{min}$ (cm) | 59.8 ± 6.9 (45.2–76.5) | 73 |
| SCW (cm) | 50.9 ± 5.4 (32.6–61.2) | 78 |
| PL (cm) | 47.1 ± 5.4 (36.7–59.8) | 80 |
| PL-TT (cm) | 11.8 ± 1.9 (7.6–16.0) | 73 |
| PL-CLO (cm) | 9.2 ± 1.5 (5.8–12.5) | 73 |
| Weight (kg) | 35.3 ± 10.9 (16–67) | 78 |

TABLE 9

**Carapace length conversions for subadult *Caretta caretta***

Conversions to $SCL_{min}$ from three other commonly used carapace measurements are given in the form $SCL_{min} = A(X) + B$ based on *Caretta caretta* captured at Secretary, Panama. See table 8 for the size range of *Caretta* at this site.

| Measurement | Conversions to $SCL_{min}$ | $r^2$ | $P$ | Sample size |
|---|---|---|---|---|
| Standard straight carapace length ($SCL_{n\text{-}t}$) | $SCL_{min} = 0.9827\ (SCL_{n\text{-}t}) - 0.201$ | 0.9944 | $<0.001$ | 67 |
| Carr straight carapace length ($SCL_{max}$) | $SCL_{min} = 0.9694\ (SCL_{max}) - 0.155$ | 0.9931 | $<0.001$ | 59 |
| Curved carapace length ($CCL_{min}$) | $SCL_{min} = 0.9188\ (CCL_{min}) + 0.262$ | 0.9856 | $<0.001$ | 73 |

of the 69 laparoscoped immature green turtles was 30:39.

Temporal and spatial patterns of habitat use: Immature *C. mydas* tagged at the Zapatilla Cays were regularly recaptured in nets at this site. Seventeen (13.3%) of 128 tagged immatures were recaptured 20 times within the Zapatilla Cays study area (fig. 4) at intervals greater than one month. Fifteen were recaptured once, one was recaptured twice, and one was recaptured three times. Only three (2.2%) of a sample of 137 *C. mydas* considered mature on the basis of laparoscopy, carapace length, or tail length were recaptured in the study area after a period of one month or longer. These three were adult males recaptured during subsequent reproductive seasons almost exactly one, two, and five years after first capture.

Arrival and departure: The smallest green turtle captured in the nets at Zapatilla Cays was 29.5 cm SCL (fig. 14B). The next smallest was 46.2 cm SCL and was one of three turtles captured in the 45–50 cm SCL size class.

Twenty-five (19.5%) of 128 immature green turtles tagged at the Zapatilla Cays were encountered outside Panama as of

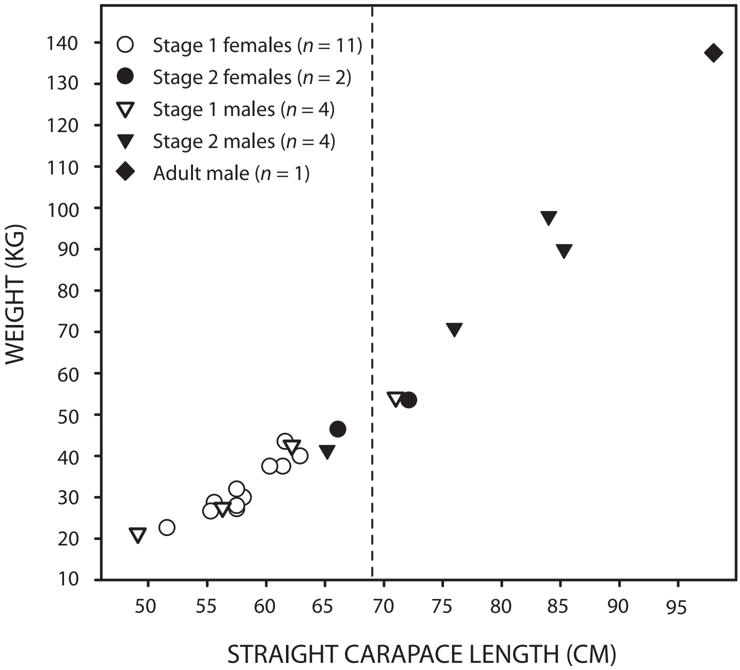

Fig. 18. Carapace length ($SCL_{min}$), weight, and maturity status as determined by laparoscopy for 22 *Caretta caretta* from Bocas del Toro Province and the Comarca Ngöbe-Buglé, Panama. Seventeen were captured at the Secretary study site and five at the Zapatilla Cays study site. For explanation of maturity stages, see methods. Minimum adult size, indicated by dashed line, based on Kaufmann (1975; see Discussion).

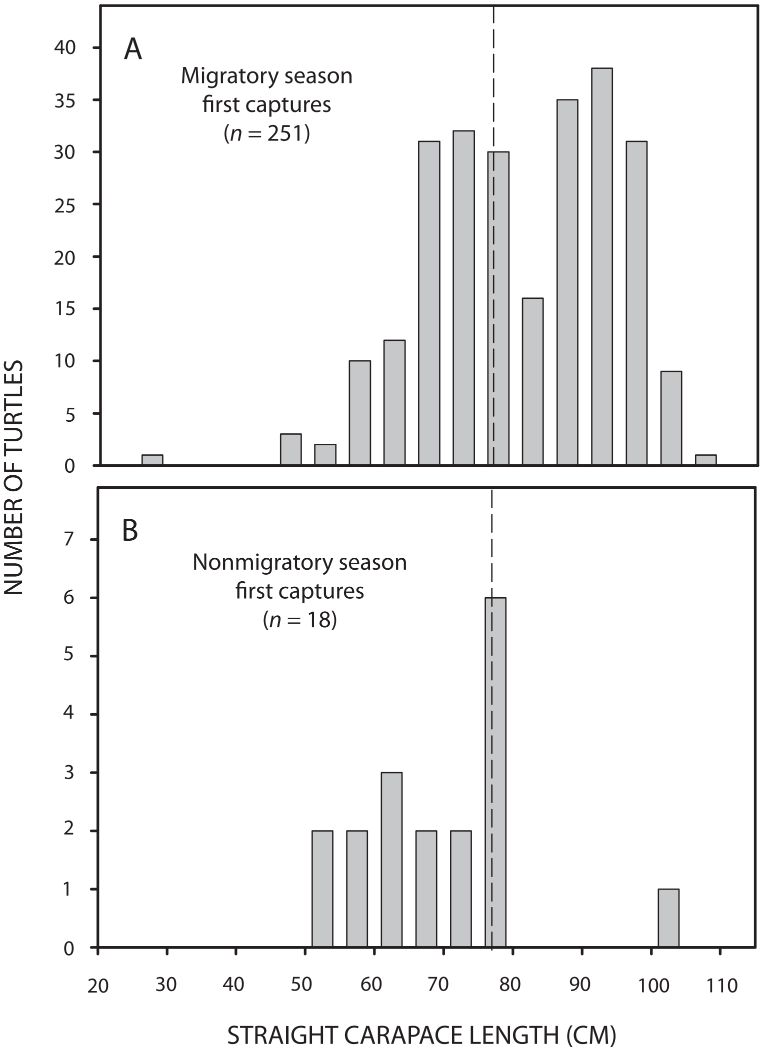

Fig. 19. Size distribution of *Chelonia mydas* at Zapatilla Cays, Bocas del Toro Province, Panama. **A,** Captures made during 13 migratory season samples (May, June, July, and September), 1990–2005. **B,** Captures from one nonmigratory season sample, January, 1994. Minimum adult size, indicated by the dashed line, is based on laparoscopy of 178 *C. mydas* in Bocas del Toro, Panama, and size criteria developed from laparoscopy data (this study; Meylan and Meylan, unpubl. data).

October 2006: 24 in Nicaragua, and one in Costa Rica (fig. 16). Figure 16 combines long-distance tag recoveries of immature green turtles tagged at both the Zapatilla Cays and Secretary study sites. At least 23 of 24 recaptures in Nicaragua were made by fishermen using nets. The single turtle tagged at Zapatilla and found in Costa Rica was found floating dead at Tortuguero. The size at last capture and time to foreign recapture of immature *C. mydas* from Zapatilla Cays is depicted with those from Secretary in figure 14C. The average size at which immature *C. mydas* tagged in the Zapatilla Cays were last seen before they were recaptured outside of Panama, was 68.9 ± 7.0 cm (range 53.9–78.9).

## PANAMA: ZAPATILLA CAYS STUDY SITE – *Caretta caretta* AND *Eretmochelys imbricata*

In addition to the 265 *C. mydas* netted at the Zapatilla Cays through 2005, seven

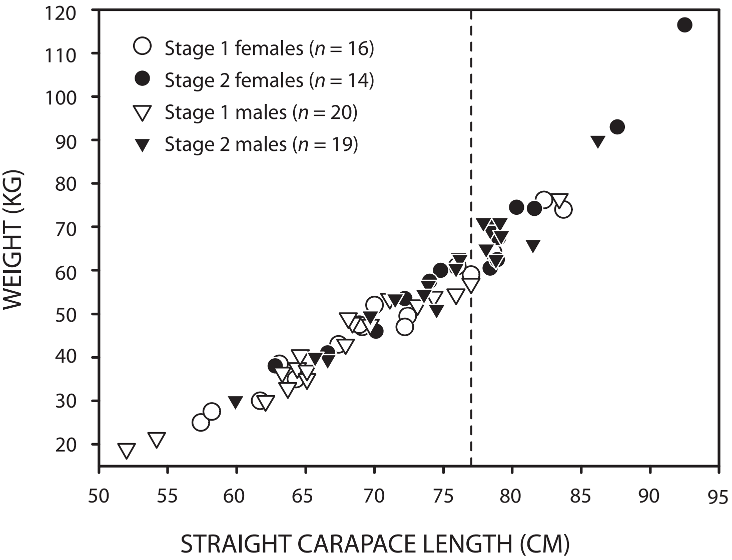

Fig. 20. Carapace length ($SCL_{min}$), weight, and maturity status for 69 immature *Chelonia mydas* from Zapatilla Cays, Bocas del Toro Province, Panama. For explanation of maturity stages, see Methods. Maturity status is based on laparoscopy. Minimum adult size, indicated by the dashed line, is based on laparoscopy of 178 *C. mydas* in Bocas del Toro, Panama, and size criteria developed from laparoscopy data (this study; Meylan and Meylan, unpubl. data).

*Caretta* and 29 *Eretmochelys* were also captured. The *Caretta* ranged in size from 62.2–85.3 cm (avg. = 74.9 ± 8.0). Five were immature based on laparoscopy, and two (71.5 and 74.0 cm SCL) were of unknown maturity status. The 74 cm SCL *Caretta* was recaptured in Nicaragua four years after it was observed in Panama (fig. 16).

Thirty-six net captures of 29 *Eretmochelys* (30.0–85.2 cm SCL, avg. = 70.9 ± 11.32) were made at the Zapatilla Cays through 2005. Maturity status for 29 *Eretmochelys* from Panama (both study sites) are shown along with results from 16 laparoscopies of this species done at Mona Island, Puerto Rico (Geis et al., 2003; Diez and van Dam, 2003), in figure 21. The smallest mature individual from Panama was a 70.5 cm SCL stage 3 male and the largest stage 2 male was 65.8 cm SCL.

## DISCUSSION

## SIZE DISTRIBUTION AND MATURITY

### *Chelonia mydas*

BERMUDA: Green turtles captured on the Bermuda Platform over a 37-year period varied in length from 22.3–81.0 cm SCL. The smallest net capture was 22.3 cm SCL but individuals in the 25–30 cm size range were seen with much greater frequency than those in the 20–25 cm range (fig. 5A). The mesh size of the entrapment net was 10 cm knot to knot (20 cm stretch mesh), suggesting that the minimum size of capture was not constrained by the entrapment net. Set nets were used to specifically address the question of whether larger turtles might be present but missed by the entrapment net. The four turtles caught by set netting were large (avg. = 58.4 cm SCL), but the largest (67.3 cm) was much smaller than the largest turtle captured in the entrapment net. The most frequently represented size classes are in the 30–60 cm size range.

The stranded *C. mydas* from Bermuda with measurable SCL varied from 18.8–97.7 cm (avg. = 36.0 ± 12.8) and all were within the size range of netted individuals except for one 18.8 cm SCL immature and two adult-sized individuals. One of the adult-size turtles (estimated 90 cm SCL) was in a decomposed condition and its maturity status was not assessed. A 90 cm SCL green turtle is

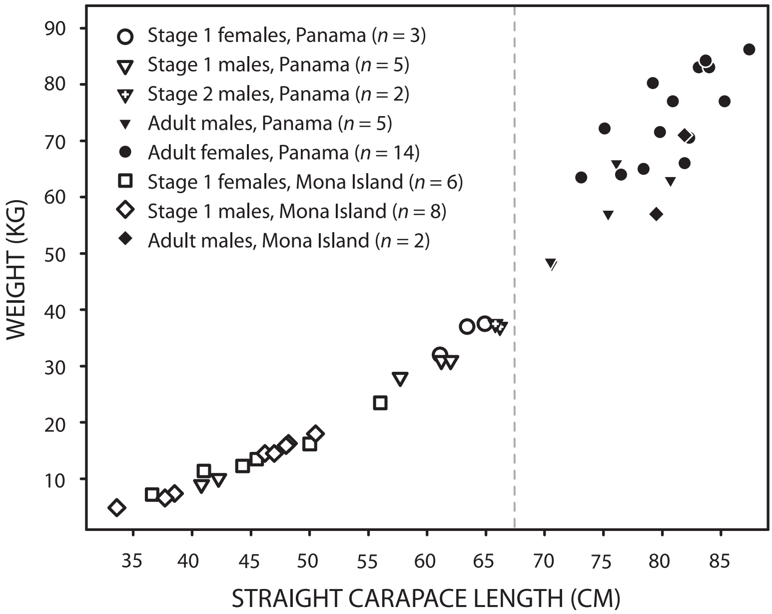

Fig. 21. Carapace length, weight, and maturity status for *Eretmochelys imbricata* from Zapatilla Cays, Bocas del Toro Province, Panama ($n$ = 29), and Mona Island, Puerto Rico ($n$ = 16). Maturity status was determined by laparoscopy or nesting. For explanation of maturity stages, see methods. The minimum size at maturity indicated by the dashed line (67 cm $\text{SCL}_{\text{min}}$), is based on laparoscopies and observations of "soft plastra" in reproductive males (Wibbels et al., 1991a; see Discussion).

likely, but not certainly, mature (table 4; fig. 22). The other, a 97.7 cm SCL, 140 kg female, was found alive outside the reef line in June 1989. Damage to the shell suggested that she had been struck by a boat. This individual produced eggs while in rehabilitation. These are the only records of adult-sized green turtles in Bermuda recorded by the Bermuda Turtle Project.

The near absence of stranded *C. mydas* > 75 cm SCL is consistent with results from the netting work that suggest that *C. mydas* > 75 cm rarely occur in Bermuda waters or in the open ocean near the platform. The stranding network apparently does recover sea turtles that come from waters that are not sampled by the entrapment net. From July 1983 through December 2005, 62 *Caretta* (6.3–74.5 cm SCL, mostly posthatchlings) and three *Dermochelys* (116.8–146.3 cm SCL) were recovered. These species have never been captured in the entrapment net and are likely to come from off the Bermuda Platform. Similarly, the 18.8 cm SCL green turtle recovered by the stranding network is likely to have come from off the Bermuda Platform. Thus, despite sampling widely across the Bermuda Platform (fig. 2) with nets for 37 years, measuring a large sample of stranded individuals (fig. 5C) and conducting limited sampling with large-mesh set nets, only two adult-sized green turtles were recorded.

The smallest size of green turtles at Bermuda corresponds well to sizes at which *C. mydas* first appear at most other foraging grounds in the Western Atlantic (table 10). Among other benthic developmental stage studies in the literature, the site at which the smallest green turtle (20.8 cm SCL) has been captured is a cooling water intake at a power station in Florida (Ernest et al., 1989; Bresette et al., 1998). The continental shelf is relatively narrow at this location and the water intake system for the plant could capture animals from the epipelagic stage. Other sites listed in table 10, including Secretary and Zapatilla, Panama; Cedar Key, Florida; St. Croix, U.S. Virgin Islands; Fernando Noronha, Brazil; and

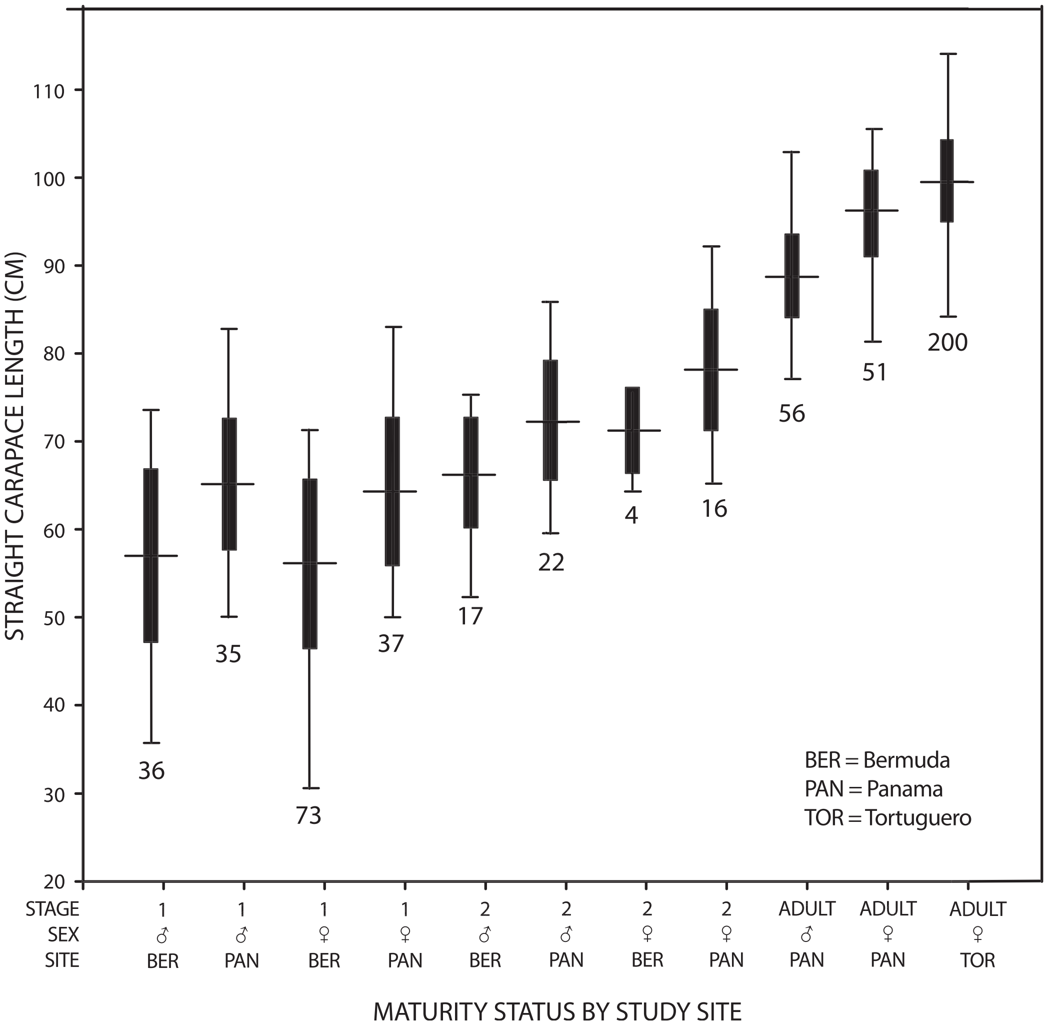

Fig. 22. Mean, range, and one standard deviation for *Chelonia mydas* at three maturity stages (see Methods) at three study sites in Bermuda and Panama and at Tortuguero, Costa Rica. Sample size is shown below each bar. Maturity status is based on laparoscopy except for nesting females from Tortuguero. Statistics for stage 1 individuals in Panama are affected by the absence of small immatures at this site (see Results – *C. mydas*, Panama). Statistics for stage 2 individuals from Bermuda are affected by departure of stage 2 animals from Bermuda waters (see Departure – *C. mydas*, Bermuda). Data for nesting females were provided by Sebastian Troëng and the Sea Turtle Conservancy.

three Pacific sites, have larger minimum sizes. For the two Panama sites presented here, the most likely explanation for the larger minimum size is that immature individuals are recruiting to these sites from other benthic developmental habitats and not from the epipelagic stage. However, in Brazil, and even more likely in the Pacific, immature *C. mydas* may recruit from the epipelagic stage to benthic developmental habitats at a larger size than that seen in Bermuda and other Atlantic sites.

Given Bermuda's mid-Atlantic location, the smallest of the green turtles seen on the Bermuda Platform have to recruit from adjacent epipelagic habitat. These small turtles have a bright white, rather than yellow, plastron and some carry goose barnacles (*Lepas*) that are associated with the pelagic environment. There is evidence

TABLE 10
**Summary of foraging ground data for *Chelonia mydas* from the literature**

| Location | Habitat type | Sample size | Size range (cm) | Mature (%) | Maturity criteria | Residency or site fidelity | Duration of study | Capture method | Reference |
|---|---|---|---|---|---|---|---|---|---|
| **Atlantic Ocean** | | | | | | | | | |
| Bermuda | sea grass beds | 2512 | 22.3–81 $SCL_{min}$ | 0.0 | laparoscopy and size | yes | 32 yr | entrapment net | this paper |
| Panama: Secretary | sea grass beds | 132 | 46.7–88.0 $SCL_{min}$ | 0.0 | laparoscopy and size | yes | 10 yr | set nets | this paper |
| Panama: Zapatilla (immatures) | grass beds and reefs | 92 | 49.3–92.5 $SCL_{min}$ | 46[a] | laparoscopy and size | yes | 10 yr | set nets | this paper |
| Panama: Zapatilla (adults) | grass beds and reefs | 79 | 79.4–105 $SCL_{min}$ | | laparoscopy and size | no | 10 yr | set nets | this paper |
| Florida: Mosquito Lagoon | sea grass beds | 94 | 29.5–75.4 $SCL_{n\text{-}t}$ | 0.0 | size | yes | 2.5 yr | set nets | Mendonca and Ehrhart, 1982 |
| Florida: Indian River Lagoon | sea grass beds | 907 | 24.3–72.4[b] $SCL_{n\text{-}t}$ | 0.1 | size | yes | 14 yr | set nets | Ehrhart et al., 1996 |
| Florida: Indian River reefs | sabellariid worm reefs | 190 | 25.1–67.0 $SCL_{n\text{-}t}$ | 0.0 | size | yes | 6 yr | set nets | Ehrhart et al., 1996 |
| Florida: Indian River Lagoon | sea grass beds | 342 | 24.6–75.4 [b] $SCL_{n\text{-}t}$ | 0.3 | tail size | yes | 5 events | cold stunning | Witherington and Ehrhart, 1989 |
| Florida:Indian River Lagoon | various | 246 | 26.6–77.0 $SCL_{n\text{-}t}$ | 0.0 | | | 6 days | cold stunning | Schroeder and Owens, 1994 |
| Florida:Cape Canaveral | ship channel | 20 | 23.5–68.1 $SCL_{max}$ | 0.0 | size | no | 6 yr | shrimp trawl | Henwood and Ogren, 1987 |
| Florida: NE coast | longshore | 41 | 24.0–55.4 $SCL_{n\text{-}t}$ | 0.0 | Size | no | 6 yr | shrimp trawl | Schmid, 1995 |
| Florida: Broward County | nearshore hard bottom | 187 | 27.4–67.0 CCL | 0.0 | Size | yes | 5 yr | dive / snorkle | Wershoven and Wershoven, 1992 |
| Florida: St. Lucie Co. | nearshore cold water intake | 1673 | 20.8–105.3 $SCL_{min}$ | 1.1 | Size | yes | 22 yr | power plant intake | Ernest et al., 1989; Bresette et al., 1998 |
| Florida:Florida Bay | inshore | 69 | 25.5–66.1 $SCL_{n\text{-}t}$ | | | | 8 yr | nets/rodeo | Schroeder et al., 1998; Schroeder, personal commun. |
| Florida: Cedar Key | sea grass flats | 198 | 34.6–76.3 $SCL_{n\text{-}t}$ | 0.0 | Size | yes | 8 mo | set nets | Carr and Caldwell, 1956 |
| Florida: St. Joseph Bay | | 389 | 26.2–80 $CCL_{n\text{-}t}$ | | | | | cold stunning | Foley et al., 2007 |

TABLE 10
*(Continued)*

| Location | Habitat type | Sample size | Size range (cm) | Mature (%) | Maturity criteria | Residency or site fidelity | Duration of study | Capture method | Reference |
|---|---|---|---|---|---|---|---|---|---|
| North Carolina: Pamlico and Core sounds | inshore | 21 | 24–70 $CCL_{n\text{-}t}$ | | | | 4.5 yr | pound nets, trawls, gill nets | Epperly et al., 1995 |
| Texas: Laguna Madre | jetty and grass flats | 49 | 22.2–81.5 $SCL_{n\text{-}t}$ | | | yes | 2 yr | set nets | Coyne and Landry, 1994 |
| Texas: Mansfield Channel | jetty and grass flats | 43 | 26.6–52.0 $SCL_{n\text{-}t}$ | 0.0 | Size | yes | 3.5 yr | set nets | Shaver, 1994 |
| St. Thomas, St. John: U.S. Virgin Islands | grass flats | 41 | 25.6–62.3 $SCL_{max}$ | 0.0 | Size | yes | 5 yr | entrapment net | Boulon and Frazer, 1990 |
| Inagua: Bahamas | sea grass beds | 964 | 25–70 $SCL_{nt}$ | 0.0 | Size | yes | 17 yr | rodeo | Bjorndal and Bolton, 1988, 1995 |
| St. Croix: U.S. Virgin Isl. | sea grass beds | "large numbers" | 35–60 "carapace length" | | | yes | 1 mo | visual obs./ set nets | Ogden et al., 1983 |
| Culebra: Puerto Rico | sea grass beds | 167 | 24.6–75.3 $SCL_{n\text{-}t}$ | 0.0 | Size | yes | 3 yr | entrapment net | Collazo et al., 1992 |
| Barbados | sea grass and algal habitats | "60" | 31–70 | adults rarely seen | [size] | | 1.5 yr | not given | Luke et al., 2004 |
| Brazil: Fernando de Noronha | bay / harbor | 52 | 32.5–60.0 $CCL_{n\text{-}t}$ | 0.0 | Size | yes | 9 yr | diving | Bellini and Sanches, 1996; Sanches and Bellini, 1999 |
| Brazil: Ubatuba | coastal waters | 2475 | 27.0–96.0 CCL | >1 | Size | yes | 8 yr | mostly floating weirs | Gallo et al., 2006 |
| **Pacific Ocean** | | | | | | | | | |
| Australia: Moreton Bay | sea grass meadow | 784 | 38.8–119 $CCL_{min}$ | 8.5 | Laparoscopy | yes | 2 yr | rodeo | Limpus et al., 1994a |
| Papua New Guinea: Wuvulu Island | fringing reefs | 34 | 36.8–76.2 $SCL_{n\text{-}t}$ | 0.0 | Size | yes | 8 days | diving | Hirth et al., 1992 |
| Hawaii: Palaau | reef flat | 126 | 37.9–79.4 $SCL_{min}$ | n.a. | n.a. | yes | 4 mo | bull-pen netting | Balazs et al., 1987: table 16 |

[a] Benthic developmental habitat overlaps adult migratory route.
[b] Size range excludes adults.

that green turtles use the sargassum mats in the Sargasso Sea during the epipelagic stage that precedes recruitment into a neritic lifestyle (Carr, 1987). Bermuda is located in the northern portion of the Sargasso Sea, so epipelagic *C. mydas* in the Sargasso Sea may need to travel only a short distance to reach suitable benthic foraging grounds.

A contingency test indicates a significant difference in the size distribution of stranded turtles relative to that of live captures on the Bermuda Platform ($\chi^2 = 298.8$, 15 df, $P < 0.05$). One factor contributing to this difference is the relatively large proportion of small turtles present in the stranded sample. Turtles in the 20–30 cm SCL size class made up 39% of the stranded sample compared to 7.8% of the live captures. Assuming that stranding records accurately reflect mortality patterns, it could be inferred that there is disproportionately high mortality associated with green turtles in the size class that is recruiting from epipelagic into benthic developmental habitat.

Laparoscopy of 131 *C. mydas* in Bermuda (54 males, 77 females; figs. 5B, 6) did not reveal any mature individuals. Twenty-one (16.0%) of the laparoscoped turtles showed evidence of puberty, either ridged epididymides in males or differentiation of follicle size in females; but none showed the enlarged testis or pendulous epididymis of adult males or the enlarged follicles and wide oviduct of adult females (Limpus and Reed, 1985a). Thus, it appears that green turtles leave Bermuda before they reach maturity (fig. 5).

The green turtles that occupy the Bermuda Platform appear to be exclusively postpelagic immatures living in an area where adults are absent. Green turtles have received complete protection from harvest in Bermuda since 1973, and there has been ample time for the largest green turtles observed during the early years of this study (first records are from 1968) to mature in Bermuda, if that were the normal pattern. Laparoscopic data from this study indicate that *C. mydas* may begin puberty in Bermuda, but that they go elsewhere to complete the maturation process. The absence of adults, as seen in Bermuda, appears to be a characteristic of a majority of benthic developmental habitats for *C. mydas*, at least in the Atlantic.

PANAMA: SECRETARY AND ZAPATILLA CAYS STUDY SITES: The size distributions of samples at the Secretary and the Zapatilla Cays study sites likely reflect the true range of sizes present at those sites. If larger turtles were present at the Secretary site, they would be captured because the nets used at Secretary are routinely used to catch adult green turtles at the Zapatilla site (see below). Concerning smaller turtles, while it is possible that individuals under about 35 cm could pass through the larger mesh nets (40 cm bar mesh), nets with 20 cm bar mesh have also been used at Secretary. Other investigators using nets with a 20 cm bar mesh size catch green turtles as small as 24.3 cm SCL, and have hundreds of captures in the 30–40 cm SCL range (Ehrhart et al., 1996, 2007). At Secretary, limited testing was also done with a net with a 10 cm bar mesh; no turtles were captured. Nets with this very small mesh size were not routinely used because of bycatch problems.

At both of the Panama study sites, *C. mydas* were observed for the first time in the nets at a larger size than in Bermuda. The smallest were 46.7 cm SCL at Secretary, and 46.2 cm SCL at Zapatilla (excluding one 29.3 cm outlier; fig. 14B), compared to 22.3 cm SCL in Bermuda. Because the nets that were used at both sites in Panama could have caught smaller green turtles, it seems likely that smaller green turtles were not present at either site. Discussions with turtle fishermen indicated that there are sea grass beds elsewhere in Bocas del Toro Province where smaller green turtles do occur. Results presented here from Bermuda and the preponderance of evidence from the literature (table 10) suggest that the most likely explanation for the larger minimum size in the Panama sites is that the smallest green turtles have moved into those sites after spending time in the benthic developmental stage elsewhere.

Of the 132 *C. mydas* observed at Secretary, only 14 were larger than the minimum size at sexual maturity observed for this species in this study. Seven of these 14 were found to be immature via laparoscopy; the maturity status of the remaining 7 (5.3%) was not determined. Thus, Secretary appears to serve primarily, and perhaps exclusively, as benthic developmental habitat for this species.

The size distribution data for *C. mydas* at the Zapatilla Cays (fig. 19) are more complex than those for Bermuda or Secretary. From approximately April to September, large numbers of adult green turtles (maturity based on laparoscopy, size, presence of secondary sexual characteristics, and tag returns from the nesting beach) were observed at this site. Interviews with fishermen, tags on turtles captured at the study site, foreign tag-return data, genetic data, and satellite telemetry all suggest that these adults are migrating to Tortuguero, Costa Rica (Meylan and Meylan, unpubl. data). However, not all of the *C. mydas* at the Zapatilla site are mature. Among the 265 individuals captured, at least 128 were immature.

Green turtles were classified as mature or immature using both laparoscopy and size criteria. *C. mydas* with stage 1 or stage 2 gonads were considered immature, as were individuals that had not been laparoscoped but were less than 76.7 cm SCL. The size criterion was based on the observation that the smallest mature green turtle examined via laparoscopy in Panama was 76.7 cm SCL ($n = 178$) (this study; Meylan and Meylan, unpubl. data). Using these two criteria allowed most turtles to be reliably assigned. However, there were undoubtedly additional immature animals in the sample that were larger than 76.7 cm that were not laparoscoped and may have been incorrectly categorized as adults. However, relatively few individuals fall into this category. Adult turtles were likely to be correctly classified as mature in nearly all, if not all, cases because of the very conservative minimum size at maturity that was used.

The size distribution of immature green turtles at the Zapatilla study site is given in figure 14B. This subset of turtles showed a different pattern of habitat use as well as arrival and departure behaviors than adults (see below). The best explanation for the observations made at the Zapatilla Cays is that this area serves as benthic developmental habitat for large immatures and is shared seasonally with migratory adults (figs. 19A, 23A). If the single, nonmigratory sample from January is representative, the Zapatilla foraging ground is occupied almost exclusively by immatures, except during the reproductive season.

THE LITERATURE: Including the results presented here, we are aware of 22 foraging ground studies of *C. mydas* in the Atlantic system with results that are consistent with the existence of a discrete benthic developmental stage for this species (table 10, fig. 24). These studies were conducted over a wide range of localities and with a variety of capture methods. They included data on thousands of green turtles that were considered immature, usually on the basis of size. The smallest *C. mydas* at these study sites varied from 20.8–46.2 cm SCL and the largest immatures varied in size from 52.0–81.5 cm. Only four of these studies reported observations of mature individuals in their samples and when adults were present, they made up $\leq 1.1\%$ of the sample. In some of these cases, turtles that were actually immature may have been considered mature because they were larger than some minimum size of sexual maturity. In one study in which adults were captured along with immatures (Ernest et al., 1989; Bresette et al., 1998), nesting habitat for *C. mydas* is nearby and internesting habitat could be expected to overlap with benthic developmental habitat (fig. 23B).

Benthic developmental habitat appears to be used seasonally by green turtles along the east coast of the United States, north of Florida (Hillestad et al., 1978; Lazell, 1980; Epperly et al., 1995; Barnard et al., 1989; Morreale et al., 1992; McClellan and Read, 2009). However, green turtles appear at these localities in small numbers and do not represent a significant portion of the individuals that live in the North Atlantic. This differs from the case for *Lepidochelys kempii* and *Caretta caretta* (see below) for which seasonal use of benthic developmental sites along the U.S. east coast appears to be more frequent.

Most foraging grounds for *C. mydas* in the Pacific have both subadults and adults present at the same locality. These examples are presented in a section on contradictory evidence (see below). There are, however, a few Pacific sites at which immatures were reported to predominate, including Palaau, Hawaii (Balazs et al., 1987) and Wuvulu Island, New Guinea (Hirth et al., 1992). At the foraging area at Palaau, Hawaii, Balazs et

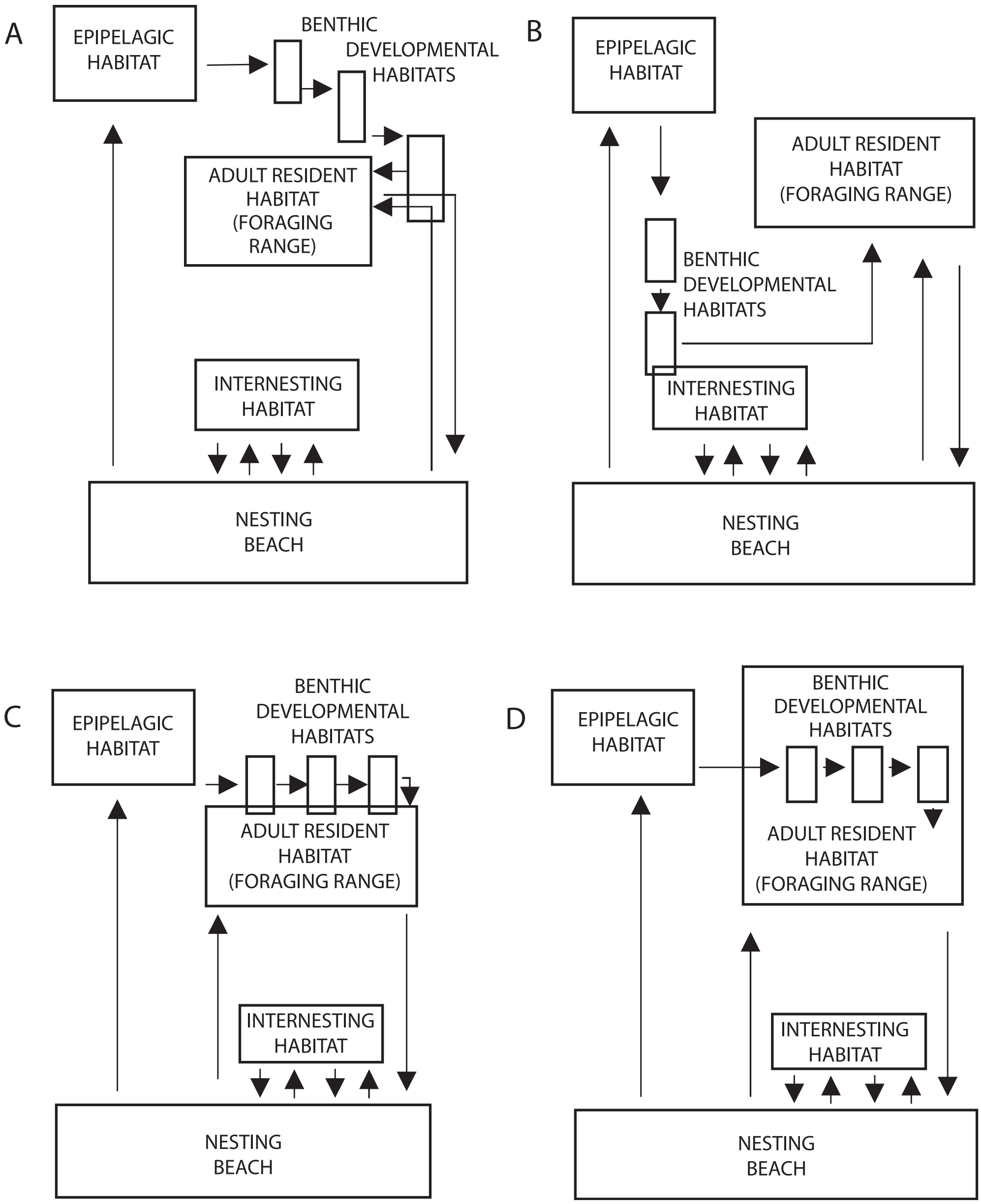

Fig. 23. Life cycle models for cheloniid sea turtles that reflect overlap between benthic developmental habitat and other stages of the life cycle. **A,** Overlap between developmental habitat and the adult migratory pathway as occurs for *Chelonia mydas* at the Zapatilla Cays, Bocas del Toro Province, Panama (this study, Meylan and Meylan, unpubl. data). **B,** Overlap between developmental habitat and internesting habitat that apparently occurs for *Caretta caretta* along the east coast of Florida (Henwood, 1987; Ernest et al., 1989). **C,** Partial overlap between developmental habitat and the adult foraging range as appears to occur for *Eretmochelys imbricata* at Mona Island, Puerto Rico (Van Dam and Diez, 1998b), and around Antigua and Barbuda (Fuller et al., 1992). **D,** Complete overlap between developmental habitat and the adult foraging range that may be common for *Chelonia mydas* in the Pacific (see text on contradictory evidence).

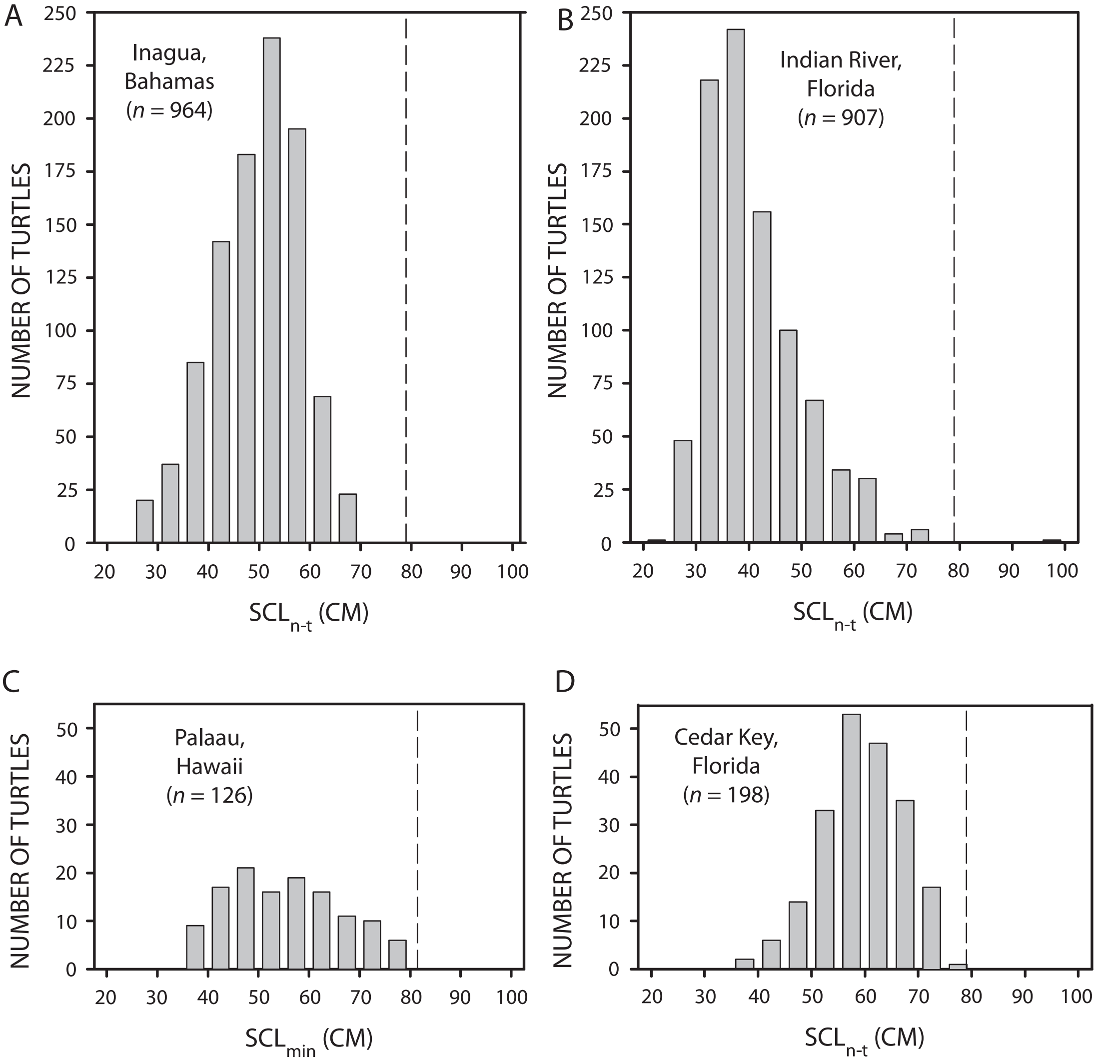

Fig. 24. Size structure on four foraging grounds that presumably represent benthic developmental habitats for *Chelonia mydas*. Minimum adult size, indicated by the dashed line, for *C. mydas* in the Atlantic (A, B, and D) based on 178 laparoscopies of *C. mydas* in Panama (Meylan and Meylan, unpubl. data); that for the Pacific (C) from Balazs (1980). Sources are: A, Bjorndal and Bolten (1995); B, Ehrhart et al., (1996); C, Balazs et al., (1987); D, Carr and Caldwell (1956).

al. (1987) reported 133 individuals between 35 and 80 cm SCL (fig. 24C). However, they added that larger turtles occur at this site at times and/or that larger turtles may have been caught there historically. In his synopsis of the biology of *C. mydas* in the Hawaiian Islands, Balazs (1980) suggested that immatures frequent the same areas as adults. However, he reports that there is a tendency for immatures to use shallower resting sites and that they sometimes use feeding pastures that are too shallow for adults. Thus, any isolation of immatures from adults in Hawaii may occur on a very local scale.

Hirth et al. (1992) observed 173 *C. mydas,* none of which they considered mature, during a brief visit at Wuvulu Island, New Guinea. A subsample of 34 turtles that were captured and measured ranged in size from 36.8–76.2 cm $SCL_{n\text{-}t}$. They also reported that sea turtles at this island have been protected for religious reasons since 1952. This implies that if mature turtles used this site historically, the population has had sufficient time to recover from any previous harvest and adults should have been observed. Thus, this site is an example of benthic developmental habitat for green turtles in the Pacific at which adults appear to be absent.

In summary, ample data support the existence of a benthic developmental stage in the life cycle of *C. mydas* at 22 different foraging grounds in the North and South Atlantic, the Caribbean, and the Pacific. However, there is some contradictory evidence from this species in the Pacific, which is discussed below.

PUBERTY IN *CHELONIA MYDAS* IN THE ATLANTIC: Laparoscopic examination of large numbers of *C. mydas* in Bermuda and Panama provides information concerning the onset of maturation (puberty, following Limpus and Reed, 1985a) and the attainment of maturity in this species in the Atlantic. Figure 22 and table 4 show the mean size and size range by sex for three maturity stages of *C. mydas* from Panama and Bermuda. A sample of 200 nesting females from Tortuguero, Costa Rica, is included for comparison. Departure by green turtles from Bermuda by about 75 cm SCL truncates the size distribution of samples from this site. Nonparametric analysis of variance shows significant differences among the samples; however, Dunn's multiple comparison of means revealed relatively few significant pair-wise differences. Nesting females from Tortuguero and adult females from Panama were significantly larger than all stage 1 samples and stage 2 males from Bermuda; and adult males from Panama were significantly larger than all stage 1 samples.

Laparoscopic data from Panama and Bermuda suggest that puberty in Atlantic green turtles may begin at a smaller size in males than in females (see also figs. 6, 15, 20). The smallest male that showed signs of puberty was a 52.7 cm SCL individual from Bermuda, while the smallest female beginning to mature, also from Bermuda, was more than 10 cm larger, 64.5 cm SCL. Pubescent males (stage 2) from Bermuda (avg. = 66.6 ± 6.4 cm SCL, $n$ = 17) were smaller on average than pubescent females (avg. = 71.4 ± 4.8 cm SCL, $n$ = 4), but not significantly so. The small sample size for the slightly larger pubescent females is likely due to their departure from the study site.

Combining the Secretary and Zapatilla Cays laparoscopy data sets indicates that in Panama, too, male green turtles in the study reached puberty at a smaller average size (avg. = 72.4 cm SCL) than females (avg. = 78.2 cm SCL), but this difference was not statistically significant. Although differences between mean size of stage 2 males and females was not statistically significant (because of large variance), it may be biologically significant. If both sexes grow at equal rates, and males begin sexual maturity at smaller sizes and mature at smaller sizes (minimum 76.7 cm SCL; avg. = 89.0 ± 4.7 cm), then males may, on average, mature a few years before females (minimum 81.0 cm SCL; avg. = 95.9 ± 4.9 cm). Sexual size dimorphism in *C. mydas* has also been reported from Ascension Island (Godley et al., 2002), so this pattern may extend beyond our Panama study.

Puberty was observed at sizes as small as 52.7 cm SCL in male *C. mydas* in Bermuda, but had not begun in an 83.4 cm SCL male from Panama (fig. 20). Puberty was observed in females as small as 64.5 cm (in Bermuda) but had not begun in an 86.2 cm SCL female from Panama. Thus, the onset of puberty, like the attainment of maturity, occurs across a wide range of sizes in this species. This illustrates the problem of using a minimum size criterion for maturity. Although the smallest mature male observed in Panama was 76.7 cm SCL, three (11.1%) of 27 males from Secretary determined by laparoscopy to be immature, and eight (20%) of 40 immature males from the Zapatilla Cays were larger than this minimum size. Similarly, three (11.5%) of 26 immature females from Secretary and three (10.0%) of 30 immature females from the Zapatilla Cays were larger than the smallest mature female (81.0 cm). This overlap in size ranges between immature and mature green turtles could lead to significant errors in the estimation of the number of mature animals at a site if size alone is used as the maturity criterion.

### *Eretmochelys imbricata*

BERMUDA: A combination of 68 live captures and 86 strandings yielded 151 measurable hawksbills at Bermuda that varied in size from 8.7–75.7 cm SCL. The smallest *Eretmochelys* captured alive on the Bermuda Platform were in the 15–20 cm ($n$ = 1) and 20–25 cm ($n$ = 9) size classes (fig. 13A), which is comparable to the minimum size seen in benthic developmental habitats for this species elsewhere (table 11). The stranding sample included some smaller posthatchlings, including five smaller than 15 cm SCL that most likely stranded from the epipelagic habitat adjacent to the Bermuda Platform. A contingency test indicates a significant difference in the size distribution of stranded *Eretmochelys* in Bermuda relative to that expected if they were to strand in proportion to the distribution of live captures on the Bermuda Platform ($\chi^2$ = 43.0, 12 df, $P < .05$). As is the case for stranded green turtles, there is a peak in the size distribution for stranded hawksbills in the smallest size classes (20–25 cm SCL for hawksbills, fig. 13B; 25–30 cm SCL for green turtles, fig. 5C). These data for *Eretmochelys*, like those for *C. mydas* in Bermuda, suggest an increased rate of mortality during the transition between life stages, in this case between the epipelagic and benthic developmental stages. Although increased mortality during life stage transitions are well studied in vertebrates that go through metamorphosis (Searcy and Sponaugle, 2001), this may be a previously undetected phenomenon in turtles. Increased mortality with a shift in habitat has been observed in snakes. Bonnett et al. (1999) noted that snakes in their study were more likely to die when they moved away from their usual home range. In a sense, that is what is occurring when sea turtles move from one life stage to the next.

Although no laparoscopies were performed on hawksbills in Bermuda, necropsies of 30 individuals, including a 75.7 cm SCL stage 2 female, revealed no mature animals. With the exception of this largest individual (fig. 13B), all stranded *Eretmochelys* from Bermuda could have been considered immature on the basis of carapace length alone. Minimum size at sexual maturity for this species in figure 13 was based on laparoscopies, observations of "soft plastra" in reproductive males in Panama (Wibbels et al., 1991a), and emergence on the nesting beach in Panama.

Among hawksbills of known maturity status at Mona Island, Puerto Rico ($n$ = 17) and Panama ($n$ = 30), the smallest mature female and male were 71.8 and 70.5 cm SCL, respectively (fig. 21). However, among the hawkbills captured in Panama were two males (68.9 and 67.1 cm SCL) that were not laparoscoped but had long tails (36.0 cm and 31.8 cm PLTT, respectively) and showed softening of the plastron that is characteristic of reproductive male cheloniid sea turtles. Thus, males may mature at sizes as small as 67 cm $\mathrm{SCL}_{\mathrm{min}}$ in the West Atlantic and this value is used throughout this paper as the best estimate of minimum size at sexual maturity for this species in the West Atlantic. This value is similar to estimates of minimum size at sexual maturity based on histological evidence of spermatogenesis in hawksbills from Cuba (Moncada et al., 1999) and tail length in Puerto Rico (van Dam and Diez, 1998b). See Meylan and Redlow (2006) for additional discussion of size at sexual maturity for both sexes in this species.

Although the sample size of hawksbills of known maturity status in Bermuda is small, the size distribution and maturity status observed there are consistent with the hypothesis that the Platform serves as benthic developmental habitat for this species.

PANAMA: A small sample of hawksbills ($n$ = 7) from Secretary varied from 40.8–74.9 cm SCL (avg. = 57.0 ± 14.1 cm). On the basis of size, the two largest (73.6, 74.9 cm SCL) could possibly have been mature, but this was not verified by laparoscopy. At the Zapatilla Cays, nine of 36 first captures made in nets were immatures based on laparoscopy or size. They varied at first capture from 30.0–66.1 cm (avg. = 56.2 ± 12.7 cm). The smallest mature individual based on laparoscopy was a 70.5 cm SCL stage 3 male. However, two smaller males (68.9 and

67.1 cm SCL) that were not laparoscoped had long tails, suggesting they may have been mature (see above).

THE LITERATURE: There are at least seven sites in the Caribbean Sea at which immature *Eretmochelys* are found and adults are nearly or completely absent (table 11; fig. 25). In the cases in which adults were also present, there were known hawksbill nesting beaches in the immediate vicinity of the study site. The few adults encountered at these sites could result from overlap of developmental and internesting habitat (fig. 23B).

The smallest size at which live hawksbills were captured on the Bermuda Platform (17.6 cm $SCL_{min}$) compares well to the minimum size (20.0 cm $SCL_{n\text{-}t}$) seen at Mona Island, Puerto Rico, and along the southern coast of the Dominican Republic (19.5 cm $SCL_{n\text{-}t}$). These are all smaller than the minimum sizes reported for two study sites in the U.S. Virgin Islands and for four sites in the Pacific (table 11). The maximum size of immature hawksbills observed in Bermuda (75.7 cm SCL) is larger than the largest immature seen in the Dominican Republic (69.7 cm $SCL_{n\text{-}t}$) and Buck Island (70.5 cm $CCL_{n\text{-}t}$).

Recruitment from the epipelagic to benthic stage of the life cycle appears to occur at a larger size in the Pacific than the Atlantic. Limpus (1992), Hirth et al. (1992), and Seminoff et al. (2003) reported minimum sizes of about 32 cm CCL for Pacific sites. However, at Fogg Bay, Western Australia, hawksbills as small as 26.3 cm CCL were reported at an inshore site (Whiting and Guinea, 1998).

One of the Australian study sites (table 11) illustrates the value of laparoscopy for recognizing that a specific foraging area was occupied by turtles at the benthic developmental stage. Limpus (1992) reported on a sample of 152 *Eretmochelys* from the Capricornia section of the southern Great Barrier Reef, Australia (fig. 25D). The maturity status of 109 of these turtles was determined via laparoscopy and only one individual (0.9%) was an adult. This is remarkable because 20 individuals (18.3%) were larger than the minimum size for nesting females in this population (75.0 cm CCL). Most (16) of these larger individuals were examined laparoscopically. Seven were prepubescent, eight were pubescent and one was the single adult identified in the study. Limpus (1992) pointed out that there has probably been no regular harvesting of *Eretmochelys* at this site and that the population is likely to represent a natural, unexploited one.

### *Caretta caretta*

PANAMA: SECRETARY STUDY SITE: Eighty-two *Caretta* were captured at this site. About one-quarter ($n$ = 17) were laparoscoped and a single 98 cm SCL adult male was identified. This turtle had recently lost an entire foreflipper and its occurrence at the site may have been atypical. The size distribution of the remaining 81 *Caretta* is shown in figure 17.

Wibbels et al. (1991b) used 76 cm SCL as a minimum size of sexual maturity of western Atlantic loggerheads on the basis of laparoscopy of 22 immature animals in Florida, laparoscopy of a large number of immature and adult animals in Australia, and the minimum reported size of nesting females in Florida. The average size of nesting female *Caretta* in the Atlantic Ocean is greater than 90 cm (Dodd, 1988). Bjorndal et al. (1983) reported a minimum size of 74.9 cm SCL for nesting females at Melbourne Beach, Florida; Kaufmann (1975) measured nesting females in Colombia as small as 70 cm $SCL_{n\text{-}t}$ (= 68.6 cm $SCL_{min}$; see table 9). This size (68.6 cm) is used as the minimum size at sexual maturity in figures 17 and 18. This is a very conservative estimate, given that loggerheads as large as 85.3 cm SCL were immature at the Zapatilla Cays (fig. 18). However, this low value is used in this paper because it is possible that Colombian loggerheads may occur in developmental habitat in Panama. Buritaca, Colombia, is one of the few known *Caretta* nesting beaches in the southwest Caribbean, although at present it appears to be extremely depleted (Amorocho et al., 1999).

Only 12 *Caretta* captured at Secretary were larger than 68.6 cm. In addition to the outlier mentioned above, the largest was 76.5 cm SCL. One of these 12, a 72.1 cm female, was laparoscoped and was determined to be pubescent (stage 2). Additional laparoscopy of *Caretta* in the 65–85 cm size range is

TABLE 11

**Summary of foraging ground data for *Eretmochelys imbricata* from the literature**

| Location | Habitat type | Sample size | Size range (cm) | Mature (%) | Maturity criteria | Residency or site fidelity | Reference | Duration of study | Method |
|---|---|---|---|---|---|---|---|---|---|
| Bermuda | reef | 68 | 17.6–69.7 $SCL_{min}$ | 0.0 | size, necropsy | yes | this paper | 30 yr | entrapment net, scuba, snorkel |
| PR, Mona Island | reef, walls | 276 | 20–91 $SCL_{n-t}$ | some | nesting, tail | yes | Van Dam and Diez, 1998b | 5 yr | snorkle, scuba |
| Dominican Republic | reef | 300 | 19.5–69.7 $SCL_{n-t}$ | 0.3 | size | yes | Leon and Diez, 1999 | 2 yr | snorkel |
| USVI, St. Thomas |  | 63 | 27.4–60.7[a] $SCL_{max}$ |  | size | yes | Boulon, 1994 | 6 yr | entrapment net |
| USVI, Buck Island | reef | 58 | 27.1–70.5[b] $CCL_{n-t}$ | 1.7 | size | yes | Mayor et al., 1998 | 1 yr | snorkel |
| Brazil: Fernando de Noronha |  | 101 | 30.5–75.5[a] $CCL_{n-t}$ |  | size | yes | Bellini and Sanches, 1996; Sanches and Bellini, 1999 | 11 yr | diving |
| Brazil: Ubatuba | coastal waters | 23 | 32.0–67.0 CCL | 0.0 | size | yes | Gallo et al., 2006 | 8 yr | floating weirs, free diving |
| Australia: southern Great Barrier Reef | reef | 152 | 35.0–87.5 $CCL_{n-t}$ | 0.9 | laparoscopy | yes | Limpus, 1992 | 20 yr | rodeo, beach jump, scuba |
| Australia: Fog Bay | reef | 187 | 26.3–75.5 CCL |  | size | yes | Whiting and Guinea, 1998 | 6 yr | rodeo, beach jump |
| New Guinea: Wuvulu | reef | 32 | 31.8–49.5[a] $CCL_{n-t}$ |  | size |  | Hirth et al., 1992 | 8 days | scuba |

[a] A subsample was measured.

[b] Mature individuals not included in this range.

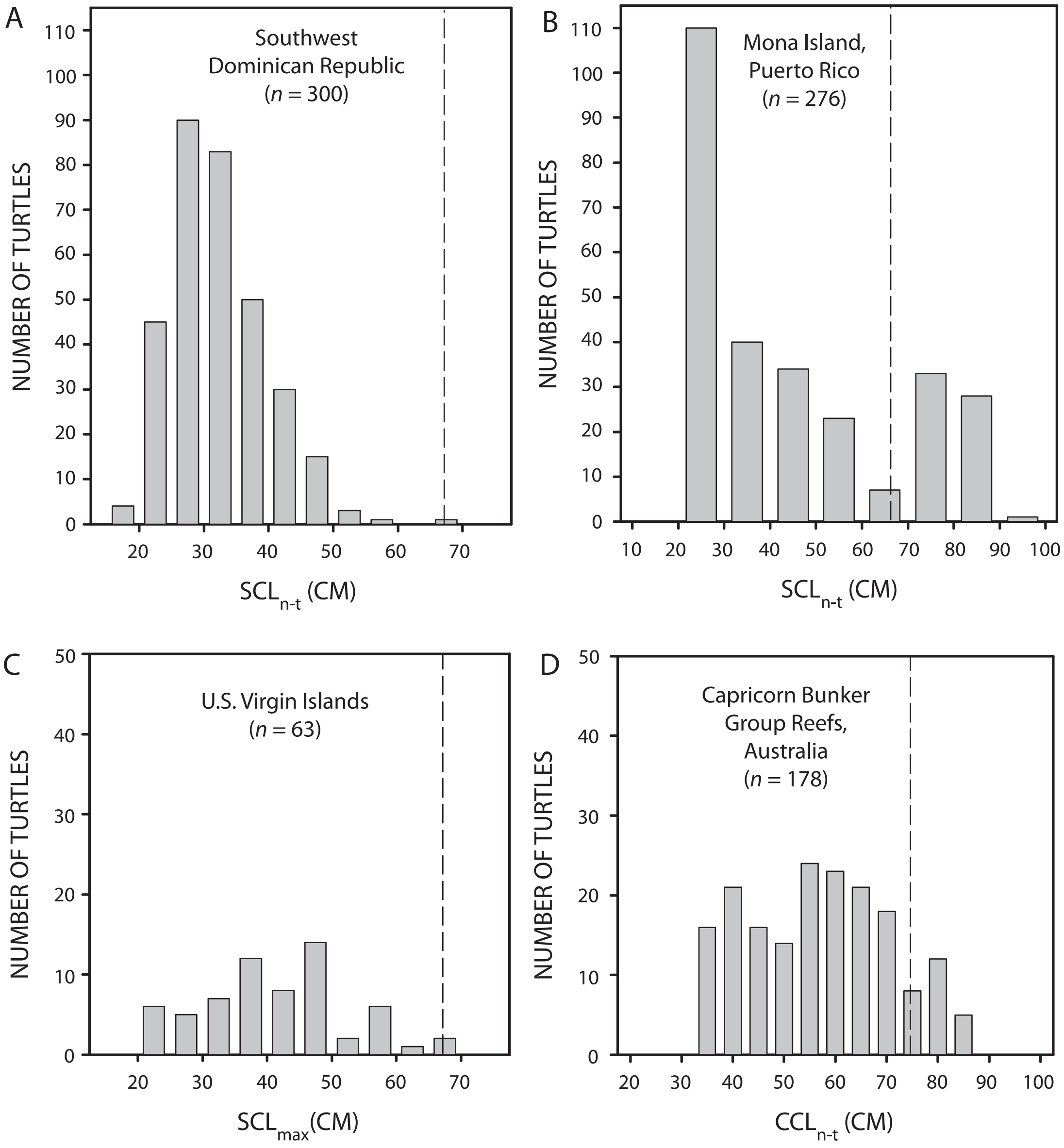

Fig. 25. Size structure for *Eretmochelys imbricata* on four foraging grounds that represent, at least in part, benthic developmental habitat for this species. Minimum adult size, indicated by the dashed line, for A, B, and C is from this study (see discussion), minimum adult size for D is from Limpus (1992). Sources are: A, Leon and Diez (1999); B, Van Dam and Diez (1998b); C, Boulon (1994); D, Limpus (1992). Note that turtle size is given as straight carapace length (SCL) in A–C and as curved carapace length (CCL) in D. Limpus (1992) gives the following relationship for CCL and SCL, SCL = CCL (0.936) + 0.403.

needed for corroboration; however, the eastern end of the Chiriqui Lagoon appears to support immature-dominated, benthic developmental habitat for *Caretta caretta* (see also Engstrom et al., 2002).

A sample of laparoscoped immature loggerheads ($n = 22$) from the two Panama sites suggests that maturation of *Caretta* in Panama begins at about 65 cm SCL in both sexes (fig. 18). Two stage 2 males from the

Zapatilla Cays were about 15 cm larger than the very conservative minimum size at sexual maturity used here.

THE LITERATURE: The large minimum size of loggerheads observed at the Secretary study site (45.2 cm SCL), relative to that seen for *Chelonia* and *Eretmochelys*, reflects the extended pelagic stage in this species (Carr, 1986; Bolten et al., 1993, 1995, 1998; Bolten, 2003). The minimum size for this species at other Atlantic, immature-dominated, inshore, foraging grounds varies from 41.5–47.5 cm SCL except for Chesapeake Bay, which apparently receives occasional (< 1%) epipelagic-stage individuals (table 12). *Caretta* also appears to have regular overlap of adults with immature-dominated, benthic developmental habitats. In all studies listed in table 12 and figure 26, some adults were present, and they made up a variable portion of the sample, from 1.2% at Secretary in Panama to about 20% (based on size) at two sites along the eastern seaboard of the United States (Epperly et al., 1995; Schmid, 1995). However, only the Secretary study used laparoscopy, so the number of matures in the remaining studies is likely an overestimate. In some cases, the presence of adults may result from juxtaposed internesting and immature foraging habitats (fig. 23B), and in others, overlap between the adult foraging grounds and benthic developmental habitat (fig. 23C, D). However, sites like Secretary (fig. 17), Indian River Lagoon (fig. 26A), Mosquito Lagoon, and Charleston Harbor have very few adults and thus support the observations that benthic developmental habitats for *Caretta,* like those for other cheloniid species, can be immature dominated.

There are clear exceptions to the use of benthic developmental habitat by immature *Caretta* in the North Atlantic. Some Atlantic-Mediterranean *Caretta* remain pelagic until they enter adult foraging grounds, as appears to be the case in the Pacific. In the western Mediterranean, off the coast of Spain, large immature loggerheads of all size classes up to adult size are regularly captured in a longline fishery (Gasau and Ninou, 2000: fig. 1). Alternatively, some (or all) individual loggerheads in a population may switch between benthic and epipelagic feeding. This pattern of polymodal foraging is now well established for *Caretta* (Witzell, 2002; Morreale and Standora, 2005; Hawkes et al., 2006; McClellan and Read, 2007; Reich et al., 2010). It appears to occur regularly in a small subset of loggerheads that forage in benthic habitats along the east coast of the United States (Morreale and Standora, 2005; McClellan and Read, 2007; Mansfield et al., 2009). This subset migrates off shore into the Gulf Stream Current instead of migrating south along the coast as water temperatures drop in the fall. Switching between epipelagic and benthic foraging may be the norm for *Caretta* in the Atlantic. To reflect this Casale et al. (2008) proposed a relaxed life history model for *Caretta*, which may be more prevalent in the Mediterranean than western Atlantic Ocean.

In the Pacific, immature *Caretta* are known to remain pelagic until just before reaching sexual maturity. The work of Limpus et al. (1994b) in Moreton Bay, Queensland, and studies of pelagic *Caretta* in the north Pacific (Polovina et al., 2000), suggest that the benthic developmental stage may be absent in Pacific loggerhead populations. Limpus et al. (1994b) reported that there are very few records of *Caretta* in the 30–70 cm size class from eastern Australia, and they suggested that *Caretta* recruit to the Moreton Bay foraging grounds at about 70 cm CCL, while still immature. They then mature and remain resident at this site, which is considered adult foraging habitat. A similar population structure exists for *Caretta* in the southern Great Barrier Reef (Limpus, 1992). Studies of *Caretta* caught as bycatch in the longline fisheries in the North Pacific include animals up to 83 cm SCL (Polovina et al., 2004).

Florida Bay also offers intriguing evidence bearing on the developmental habitat hypothesis. A preliminary report by Schroeder et al. (1998), suggested the possibility that this area is occupied mainly by *Caretta* that are mature or nearly mature. Although there were a few individuals as small as 50 cm, most were in the 80–100 cm range. The smallest nesting females in Florida are about 75 cm SCL (Dodd, 1988). Thus, Florida Bay may represent an adult foraging ground into which large immatures recruit and then go through the maturation process.

TABLE 12
**Summary of foraging ground data for *Caretta caretta* from the literature**

| Location | Habitat type | Sample size | Size range (cm) | Mature (%) | Maturity criteria | Residency or site fidelity | Reference | Duration of study | Method |
|---|---|---|---|---|---|---|---|---|---|
| Panama: Secretary | grass beds and banks | 82 | 45.5–78[a] $SCL_{min}$ | 1.2 | laparoscopy | yes | this paper | 10 yr | set net |
| Florida: Mosquito Lagoon | grass beds | 111 | 44.0–92.5 $SCL_{n-t}$ | 5.4 | size | yes | Mendonca and Ehrhart, 1982 | 3 yr | set net |
| Florida: Indian River | grass beds | 643 | 41.5–82.5[a] $SCL_{n-t}$ | 4.8 | size/tail | yes | Ehrhart et al., 1996 | 14 yr | set net |
| Florida: Cape Canaveral | channel | 3710 | 46–110 $SCL_{max}$ | 2.4–17.4[b] | size | yes | Henwood, 1987 | 7 yr | trawler |
| Florida: St. Lucie Co. | cooling water intake | 1623 | 20.8–105.3 $SCL_{min}$ | 12.7 | size | yes | Ernest et al., 1989<br>Bressette et al., 1998 | 12.5 yr | nets in powerplant intake |
| Florida: NE coast | long shore | 774 | 38.2–110 $SCL_{n-t}$ | 20.0 | size | no | Schmid, 1995 | 6 yr | shrimp trawl |
| Georgia coast | | 149 | 50–107 "estimated CL" | 12.0 | size | | Hillestad et al., 1978 | 7 yr | strandings |
| Georgia coast | | 607 | <29.5–81.6 $SCL_{n-t}$ | ?[c] | size (82 cm) | | Frazer, 1987 | 1 yr | strandings |
| South Carolina: Charleston Harbor | channel | 53 | 47.5–95.5 $SCL_{n-t}$ | 1.9 | size | yes | Van Dolah and Maier, 1993 | 1.33 yr | trawler |
| North Carolina: Pamlico and Core Sounds | "inshore" | 70 | 42–105 $CCL_{n-t}$ | 18.6 | size | yes | Epperly et al., 1995 | 4.5 yr | fishermen |
| Virginia: Chesapeake Bay | | 312 | 21.6–122 "CCL" | "rare" | necropsy, histology | yes | Lutcavage and Musick, 1985 | 3 yr | live and stranded |

[a] Adults (>83 cm) excluded from this range.
[b] Percent given for months when reproduction is not occurring at adjacent beaches.
[c] Adults excluded from this study.

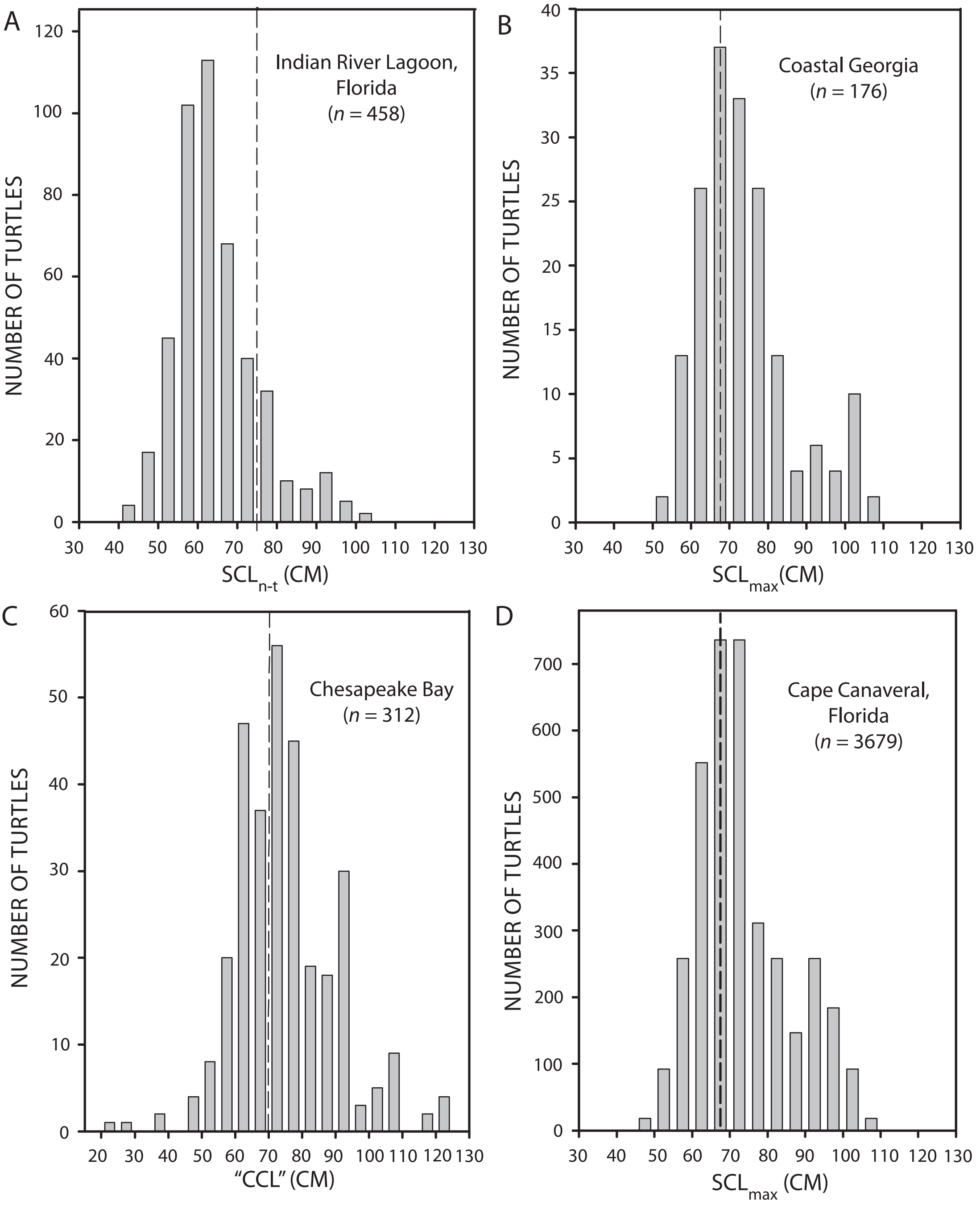

Fig. 26. Size structure for *Caretta caretta* on four foraging grounds that represent, at least in part, benthic developmental habitat. Minimum adult size, indicated by the dashed line, is from Kaufmann (1975). Sources are: A, Ehrhart et al., (1996); B, Ruckdeschel and Zug (1982); C, Musick and Limpus (1996); and D, Henwood (1987).

### *Lepidochelys kempii*

THE LITERATURE: The fieldwork reported here has not resulted in any data on *Lepidochelys kempii*. However, evidence that this species also occupies benthic developmental habitat is abundant in the literature. There are at least 14 studies that provide evidence of an immature-dominated benthic developmental stage in this species (table 13, fig. 27). Eight of these are within the Gulf of Mexico and six are on the Atlantic coast of the United States (see also Schmid and Barichivich, 2006). In three of these studies, small numbers of mature individuals were identified. In two studies, maturity status was evaluated on the basis of size alone (Henwood and Ogren, 1987; Schmid, 1995); in the third (Landry et al., 2005) 20% of the sample was laparoscoped, but it is unclear whether the reported adults were included within that sample. In all 14 studies, *L. kempii* first appeared at benthic developmental foraging areas at about 20 cm SCL and departed by about 66 cm SCL. Minimum size at sexual maturity has been estimated to be 58–60 cm SCL (Schmid and Barichivich, 2006), but few studies report mature individuals.

Evidence of residency, in the form of recaptures, was seen in most of these studies on *L. kempii* (table 13). However, several recent papers emphasized the itinerant nature of immature *L. kempii,* citing movements in and out of benthic foraging grounds, notably along the east coast of the United States (Morreale and Standora, 2005) and the northern Gulf of Mexico (Schmid and Barichivich, 2006). At Cedar Key, Florida, Schmid et al. (2003) showed strong evidence of residency for periods of 2–3 months using sonic tags, but they thought that longer-term tracking would be needed to document seasonal movements.

The behavior of *Lepidochelys kempii* stands in marked contrast to that of *L. olivacea,* which most authors now consider to remain pelagic throughout its life (Musick and Limpus, 1996; Bolten, 2003). Kopitsky et al. (1999) identified a number of immatures in a sample of 145 *L. olivacea* observed at sea during a survey of *Stenella* in the eastern tropical Pacific. Both Zug et al. (2006) and Polovina et al. (2004) obtained mixed samples of immatures and matures from the same general areas for studies of growth and migration, respectively. The few immature *L. olivacea* encountered during the West Atlantic surveys (Carr et al., 1982; Meylan and Meylan, unpubl. data) had been taken at sea by fishermen seeking deepwater fishes, mostly in the major channels between the islands of the Lesser Antilles. Limpus (1975) reported two subadult *L. olivacea* from Cairn's Inlet, Queensland, from shallow coastal waters with a mud bottom bordered by mangroves. However, coastal records for subadults of this species remain rare and we assume that most immature *L. olivacea* remain pelagic, as do the adults.

## TEMPORAL AND SPATIAL PATTERNS OF HABITAT USE

### *Chelonia mydas*

BERMUDA: Carr (1980) interpreted the work of Mowbry and Caldwell (1958) as evidence that *C. mydas* in Bermuda was itinerant. Expansion of the sampling regime at Bermuda since 1992 has shown that immature green turtles are present throughout the year. There was a minimal seasonal pattern with increased catch rates in spring relative to fall (fig. 7). Nonparametric analysis of variance detected significant differences in catch per set of the net by month, but Dunn's pairwise comparison detected only four pairs of months that were significantly different. April was different from September, October, and December, and May was different from December. Turtles were caught during all months and with equal likelihood across the range of temperatures at which sampling took place (17°–30° C; fig. 8). Spearman rank correlation detected no correlation between temperature and capture rate.

Establishing year-round occurrence of green turtles in Bermuda introduces the possibility that individual turtles are continuously resident for extended periods. Residency is suggested by recapture records. Over 24% ($n = 609$) of turtles captured in Bermuda were recaptured one or more times (806 recaptures), up to a maximum of six. As of 2005, 159 *C. mydas* have been recaptured over intervals

TABLE 13
**Summary of foraging ground data for *Lepidochelys kempii* from the literature**

| Location | Habitat type | Sample size | Size range (cm) | Mature (%) | Maturity criteria | Residency or site fidelity | Duration of study | Method | Reference |
|---|---|---|---|---|---|---|---|---|---|
| Texas: Sea Rim State Park |  | 61 | 20.3–55.7 “SCL” | 0.0 |  |  | 3 yr |  | Ogren, 1989 |
| Louisiana to Texas (9 sites) | bays, passes, beachfront | 429 | 19.5–65.8 $\mathrm{SCL}_{\text{n-t}}$ | 2.9 | size | yes, 2.9% recaps | 7 yr | set nets | Landry et al., 2005 |
| Florida: Franklin, Wakulla counties | mud/grass flats | 106 | 20.3–57.9 “SCL” | 0.0 | size | yes | 5 yr | fishermen | Rudloe et al., 1991 |
| Florida: Cedar Key to Crystal River | mud/grass flats | 90 | 40–65 $\mathrm{SCL}_{\text{n-t}}$ | 0.0 | necropsy | yes | 0.67 yr | set nets | Carr and Caldwell, 1956 |
| Florida: Cedar Key | mud/grass flats | 254 | 26.8–56.8 $\mathrm{SCL}_{\text{n-t}}$ | 0.0 | size | yes | 9 yr | set nets | Schmid, 1998 |
| Florida: Ten Thousand Islands | mud/hard bottom | 191 | 21.4–65.2 $\mathrm{SCL}_{\text{min}}$ | 0.5 | size | yes | 2 yr | strike net | Witzell and Schmid, 2004 |
| Florida: Cape Canaveral | ship channel | 113 | 21.5–60.3 $\mathrm{SCL}_{\text{n-t}}$ | 0.9 |  | yes | 5 yr | trawler | Schmid, 1995 |
| Florida: Cape Canaveral | ship channel | 40 | 24.1–66 $\mathrm{SCL}_{\text{max}}$ | 2.5 | size | no | 7 yr | trawler | Henwood and Ogren, 1987 |
| Georgia and South Carolina | offshore | 21 | 20.3–57.2 $\mathrm{SCL}_{\text{max}}$ | 0.0 |  | no | 4 yr | trawler | Henwood and Ogren, 1987 |
| North Carolina |  | 14 | 32–55 $\mathrm{CCL}_{\text{n-t}}$ | 0.0 |  |  |  |  | Epperly et al., 1995 |
| Virginia: Chesapeake Bay |  | 43 | 27–62 “CCL” | 0.0 |  |  | 3 yr | strandings and fishermen | Lutcavage and Musick, 1985 |
| New York: Long Island | Long Island Sound | 97 | 22.5–37.6 $\mathrm{SCL}_{\text{n-t}}$ | 0.0 |  |  | 3.5 yr | strandings | Morreale et al., 1992 |

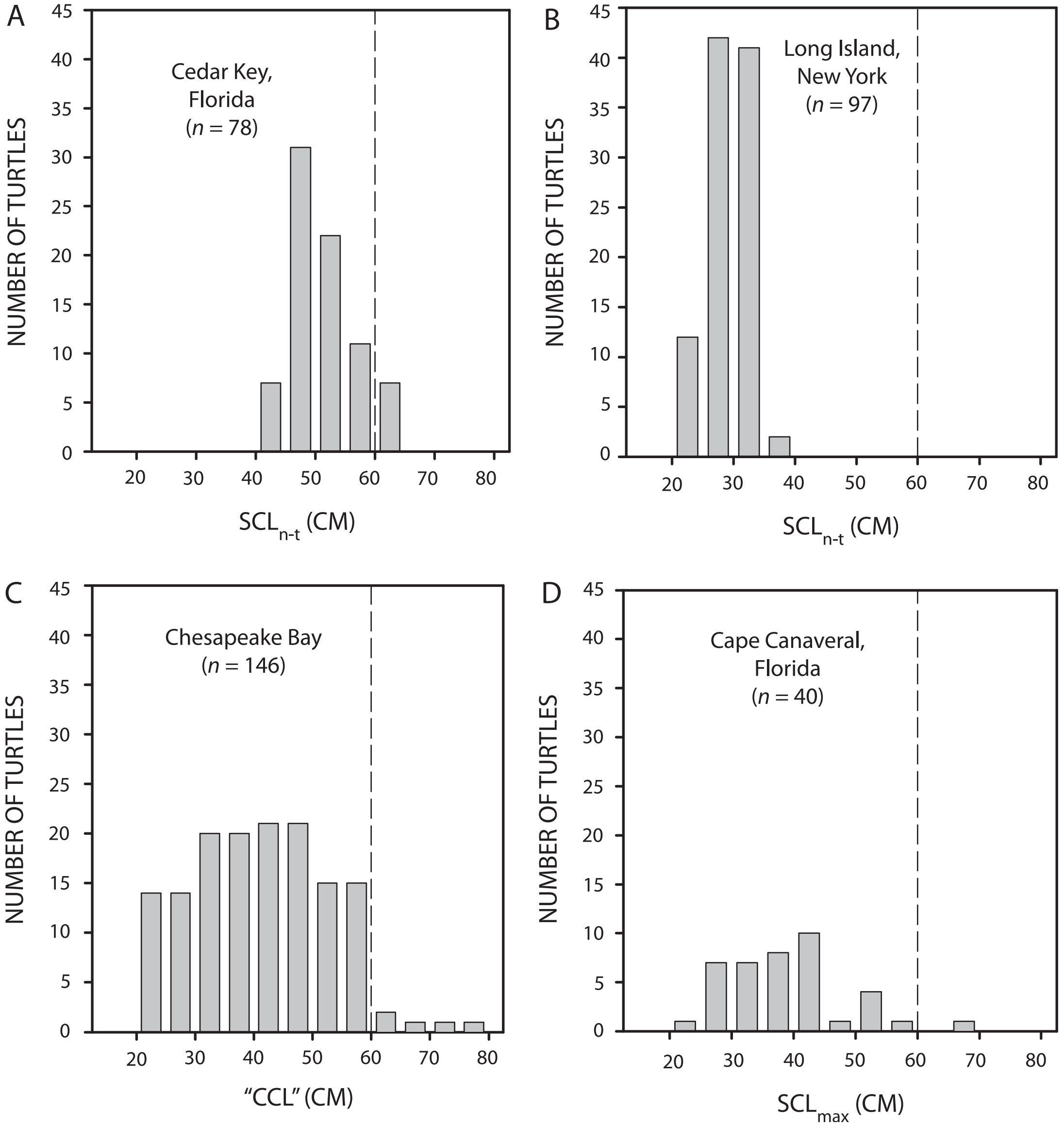

Fig. 27. Size structure on four foraging grounds that presumably represent benthic developmental habitat for *Lepidochelys kempii*. Minimum adult size, indicated by the dashed line, is from Pritchard and Marquez (1973). Sources are: A, Carr and Caldwell (1956); B, Morreale et al. (1992); C, Musick and Limpus (1996); and D, Henwood and Ogren (1987).

of five or more years (fig. 9). Each sampling session yielded evidence of more of these long-term residents. The longest record through 2005 is F3414, first captured on 23 July 1976 at the grass flats at Outside Daniel's Head; this turtle was recaptured over 14 years later, on 14 August 1990, on the same flats.

The great distance from the Bermuda Platform to other possible foraging grounds for green turtles (at least 1000 km to North Carolina) makes transient use of the habitat in Bermuda unlikely. If turtles are resident in Bermuda, however, one might expect a higher recapture rate and longer intervals of observation. A partial explanation for the patterns observed is the vagaries of sampling. A core group of sites (~10) has been sampled frequently since the early years of the project, but the complete suite of sampling locations (> 40) includes sites that are no longer sampled, sites that were sampled only once, and sites that have been added recently. The regular netting sites are purposefully sampled only once or twice per year to minimize disturbance to the turtles. Even at small, discrete sampling sites, such as single grass flats surrounded by deeper water, not all turtles are captured during a sampling event; some sites on the west end of the island encompass as much as 80 ha and may be sampled annually with a single setting of the net. Larger-scale factors that affect the maximum length of time individual turtles are observed in Bermuda include tagging methodology, tag loss, and predation. In the early years of the project only a single tag was applied. Starting in 1985 all turtles were double tagged. Beginning in 2001, PIT tags were added to all turtles under 30 cm SCL and in 2005, to all turtles regardless of size. These measures are expected to increase the recapture rate.

Although direct evidence indicates that individual green turtles may stay in Bermuda waters for as long as 14 years, there is circumstantial evidence that some may reside longer. A preliminary estimate of average annual growth for *C. mydas* in Bermuda, calculated from growth intervals for 71 different individuals (26.2–65 cm avg. SCL during interval) recaptured after one year (365 ± 30 days), was 2.51 ± 1.29 cm/yr. Growth rates in *C. mydas* vary with size, year, sex, and habitat (Bjorndal and Bolten, 1988; Limpus and Chaloupka, 1997; Kubis et al., 2009). They also vary by ocean basin, with turtles from Pacific sites having lower rates of growth than those of the same size in the Caribbean. The preliminary estimate of growth rate in Bermuda is somewhat lower than other Caribbean sites but not exceptionally so. Given the northerly location of the site, and the likelihood of seasonal growth, the estimate of 2.51 cm/yr falls within expectations. Using this rate, it can be predicted that individual *C. mydas* remaining in Bermuda from the smallest (approximately 25 cm SCL) to largest (approximately 75 cm) size class, may be resident as long as 20 yrs. Continued monitoring at Bermuda will allow the direct testing of this prediction.

Recapture data also suggest that site fidelity is well developed in green turtles in Bermuda. Recaptures are typically made within relatively small areas of habitat (i.e., on the same grass flat), and often over long periods of time (see table 14 for examples). Table 6 shows that 88.3% of all recaptures occurred on the same grass flat where the original capture was made. The site of release did not appear to affect the site of subsequent capture, with 90.2% of turtles released where they were captured being subsequently recaptured at that site, compared to 81.8% of turtles released at a different site. Many of the turtles in the latter category were held for one to three days for laparoscopy and were subsequently released at sites 10–20 km from their capture site. They appeared to be able to home effectively (see also Ireland, 1979, 1980).

Satellite tracking results provided some additional data on both residency and site fidelity of green turtles in Bermuda. Five turtles that were captured in the net and tracked for 33–447 days did not appear to leave the Bermuda Platform, i.e., no locations that passed the Douglas Argos filter provided evidence of departure from the Platform. Distances between the capture sites and the mean center of filtered ARGOS locations ranged from 0.1–1.9 km (fig. 10, table 7). For turtles that had been previously captured one, six, and eight years before being satellite tagged, the distances were 0.2, 3.1, and 1.7 km, respectively.

Core areas, defined by 50% volume contours, ranged in size from 301–3829 ha for the five turtles that did not appear to leave the platform. However, the quality of the location data provided by these transmitters (lacking GPS accuracy) is less than ideal for studying home ranges of turtles. The data are used in this paper only to evaluate the hypotheses that turtles are resident and exhibit site fidelity. The data should be considered in combination with the dense recapture records like those shown in table 14. These two lines of evidence suggest that at least some immature green turtles reside in Bermuda waters continuously over

TABLE 14

**Capture / recapture records for four *Chelonia mydas* from Bermuda**

Record for K4222

| Date | Location | Latitude/longitude[a] | SCL (cm) |
|---|---|---|---|
| 20 June 87 | Blue Hole | | 37.5 |
| 20 Aug 91 | Blue Hole | | 44.1 |
| 27 July 92 | Blue Hole | 32°20.972′N 64°42.407′W | 45.7 |
| 9 Aug 92 | Blue Hole | 32°20.914′N 64°42.541′W | 45.5 |
| 6 Aug 98 | Blue Hole | 32°20.975′N 64°42.483′W | 54.6 |

Record for K9099

| Date | Location | Latitude/longitude[a] | SCL (cm) |
|---|---|---|---|
| 19 July 90 | Outside Daniels Head | | 56 |
| 1 July 91 | Outside Daniels Head | | 59 |
| 13 Aug 92 | Outside Daniels Head | 32°19.617′N 64°55.067′W | 61.8 |
| 25 Mar 94 | Outside Daniels Head | 32°19.440′N 64°55.188′W | 65.9 |
| 7 Aug 98 | Outside Daniels Head | 32°19.757′N 64°55.164′W | 74.6 |

Record for BP3580

| Date | Location | Latitude/longitude | SCL (cm) |
|---|---|---|---|
| 11 Mar 92 | Cow Ground Flat | 32°19.140′N 64°52.440′W | 47.2 |
| 31 July 92 | Cow Ground Flat | 32°19.080′N 64°52.440′W | 48.9 |
| 18 Nov 92 | Cow Ground Flat | 32°19.020′N 64°52.200′W | 50.2 |
| 8 June 93 | Cow Ground Flat | 32°19.080′N 64°52.440′W | 50.1 |
| 29 Mar 94 | Cow Ground Flat | 32°19.020′N 64°52.260′W | 53.6 |
| 9 July 94 | Cow Ground Flat | 32°19.020′N 64°52.200′W | 55.3 |
| 10 Aug 94 | Cow Ground Flat | 32°19.080′N 64°52.440′W | 55.7 |

Record for BP 3873

| Date | Location | Latitude/longitude | SCL (cm) |
|---|---|---|---|
| 25 Mar 94 | Outside Daniels Head | 32°19.765′N/64°55.072′W | 49.1 |
| 17 Aug 94 | Outside Daniels Head | 32°19.409′N/64°55.171′W | 51.7 |
| 16 Aug 96 | Outside Daniels Head | 32°19.295′N/64°55.147′W | 58.2 |
| 13 June 97 | Outside Daniels Head | 32°19.361′N/64°55.115′W | 60.1 |
| 3 Aug 99 | Outside Daniels Head | 32°19.391′N/64°55.136′W | 67.2 |

[a] Latitude and longitude were recorded using GPS beginning in 1992.

extended periods of time during which they usually occupy specific sites.

SECRETARY AND THE ZAPATILLA CAYS, PANAMA: Sampling of *C. mydas* at Secretary and the Zapatilla Cays in Panama has been less concentrated than in Bermuda, and there is less evidence of residency and site fidelity. At Secretary, only 11 of 134 green turtles were recaptured at the study site and the longest recapture interval was one year. There was a subsistence fishery in Chiriqui Lagoon at the time of this study and local fishermen were known to set nets within the study site. This would obviously reduce the likelihood of recapturing tagged animals. However, even with this small sample, there is evidence of site fidelity. Ten of the 11 recaptures were made at the same net site as the original capture; in one case, a recaptured immature green turtle had moved 7 km. Seven of the 11 turtles that were recaptured had been released at Secretary after the original capture, rather than at the point of capture, representing a displacement of about 6 km. Their return to the original capture site demonstrates an ability to home to a particular site.

Green turtles smaller than 46.7 cm SCL did not occur on the grass flats at the Secretary study site. That fact, along with the paucity of long-term recaptures, suggests that *C. mydas* may not be resident there for as long as they are in Bermuda. Experienced turtle fisherman in the Secretary area reported that *C. mydas* can be found year-round.

Regular recaptures of immature *C. mydas* at the Zapatilla Cays site suggest that these turtles constitute a distinct resident group separate from the migratory adults. Although sampling efforts primarily targeted adults, immature turtles were routinely captured (fig. 14B) and recaptured (12.1% of 128 tagged immatures). As of 2005, only three of 115 adults captured near the Zapatilla Cays were seen in subsequent seasons. Recaptures of immatures occurred after 0.3, 0.5, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0, 1.0, 1.5, 1.5, 2.0, 2.0, 2.9, 4.0, and 4.5 years, suggesting that they did not correspond to an annual migration cycle. The three recaptures of adults were reproductive males recaptured during subsequent mating seasons almost exactly, 1.0, 2.0, and 5.0 yrs after initial capture.

Further evidence of residency of immature green turtles at the Zapatilla Cays comes from a single netting sample taken outside of the reproductive season during January 1994 (fig. 19B). This sample was composed nearly entirely of immatures. One of 18 *C. mydas* was mature, and the presence of fresh corpora lutea (determined by laparoscopy) in this individual suggested that she may have been intercepted during a reproductive migration. Recapture data, along with the dominance of immatures (17 of 18 captures) during the January sample (see above), suggest that immatures are likely resident at this site year-round. Adults may be present only during the reproductive season. As at Secretary, the smallest green turtles at the Zapatilla Cays are much larger than the smallest green turtles seen in Bermuda, suggesting that the long residency times that are observed in Bermuda probably do not occur at the Zapatilla Cays.

THE LITERATURE: Fidelity to benthic developmental foraging areas by *C. mydas* is strongly supported by numerous studies and multiple lines of evidence. At all of the *C. mydas* study sites reported in table 10, recaptures were made with regularity if appropriate capture methods were used, indicating some degree of residency. The most direct evidence comes from telemetry. Hart and Fujisaki (2010: table 1) summarized telemetry data providing home range estimates for this species at nine sites in benthic developmental habitat. Recaptures for growth studies (e.g., Mendonca, 1981; Bjorndal and Bolten, 1988), population studies (e.g., Ehrhart et al., 1996), and regional studies of *C. mydas* on adjacent foraging grounds also provide evidence for residency and site fidelity. Two long-term studies that sampled adjacent foraging grounds support residency via reports of very few movements between adjacent sites. In Baja California, 1183 presumably immature greens were marked at four sites. Among 154 recaptures, only two had switched sites (Senko et al., 2010). Along the east coast of Florida, 6027 different green turtles were used to study variation in growth rates among four separate sites; only 19 turtles were observed to switch foraging grounds (Kubis et al., 2009).

### *Eretmochelys imbricata*

BERMUDA: Only two recaptures of *Eretmochelys* in Bermuda were made through 2005, one after four months and one after four years. The hawksbill recaptured after four years was found in the same set of reefs where it had originally been tagged. Its very slow rate of growth (1 cm/yr) suggests that hawksbills that arrive in Bermuda at approximately 20 cm SCL (see above) could reside there for periods of more than 30 years if this growth rate is typical and they stay to a size of 55 cm.

THE LITERATURE: Meylan (1999) suggested that high rates of recapture of immature *Eretmochelys* on the foraging grounds where they were tagged indicate long-term residency in developmental habitats. At all sites reported in the literature (table 11), there was some evidence of residency or site fidelity. The most detailed study of immatures on a foraging ground is that of van Dam and Diez (1998a) at Mona Island, Puerto Rico. At this site, *Eretmochelys* that were recaptured an average of 465 ± 331 days after tagging had moved less than half a kilometer

(0.45 ± 0.66 km). More detailed data using sonic tags for three immature hawksbills at Mona Island revealed home ranges between 0.07 and 0.21 km$^2$. These authors concluded that immature hawksbills at this site appear resident for periods of "at least several years". Limpus (1992) and Limpus et al. (2008) came to a similar conclusion about hawksbills on the southern Great Barrier Reef. They suggested that hawksbills there have home ranges that are restricted to a single reef and that individuals occupy small areas for extended periods that may regularly reach 10 years in length. Leon and Diez (1999) reported an average distance between capture and recapture sites for 36 hawksbills on the south coast of the Dominican Republic of 0.36 ± 0.32 km, less than that observed at Mona Island. Recapture rates of hawksbills at other foraging grounds dominated by immatures are consistent with the hypothesis that this species remains resident in a relatively small area over extended periods of time, at least on the order of 5–10 years.

### *Caretta caretta*

SECRETARY, PANAMA: Data on residency of *Caretta* at Secretary, Panama, are limited by short-term, irregular sampling at that site. The majority of *Caretta* were tagged in 1994, but the site was not resampled until 1997. However, nearly one-third of the 81 *Caretta* tagged at the Secretary study site were subsequently recaptured in the study area; none were recaptured after periods of more than one year. Most recaptures were made on the same bank as the original capture, but about 25% were made on adjacent banks up to 8 km from the site of capture. Thus, the degree of site fidelity of *Caretta* at Secretary may be less than for *Chelonia*, or possibly, loggerheads may have a larger activity range or perhaps use polymodal foraging (Reich et al., 2010). One individual was recaptured 20 km away by subsistence fishermen four years after being tagged, providing the best evidence that immature *Caretta* remain in the eastern end of Chiriqui Lagoon (Ensenada Anita) for prolonged periods.

THE LITERATURE: Seven of 10 studies of immature *Caretta* on their foraging grounds (table 12) provided some evidence of residency or site fidelity, usually in the form of recaptures. Mendonca (1981) provided preliminary data on the growth rate of *Caretta* in Mosquito Lagoon, Florida, based of recaptures of 13 of 126 *Caretta* after periods of up to 20 months. In a separate study, Mendonca and Ehrhart (1982) reported residency by *Caretta* in Mosquito Lagoon for periods of up to 15 months. Van Dolah and Maier (1993) reported on eight *Caretta* recaptured in the Charleston Harbor ship channel, five of which were recaptured after nearly one year. Along the eastern seaboard, occupation of benthic inshore sites appears to be seasonal (Lutcavage and Musick, 1985; Keinath et al., 1987; Crouse, 1988; Epperly et al., 1995; Mansfield et al., 2009). However, all of these studies (see also table 12) reported some evidence of residency during single seasons and site fidelity between seasons. Mansfield et al. (2009) provided strong evidence of site fidelity of *Caretta* to foraging areas in a case where the turtles in question could occupy those foraging areas only seasonally.

## ARRIVAL AND DEPARTURE (DEVELOPMENTAL MIGRATIONS)

### *Chelonia mydas*

BERMUDA: After hatching on the nesting beach, hatchling green turtles are thought to spend an extended period, in the range of 3–6 years, in pelagic habitats (Carr et al., 1978; Carr, 1987; Reich et al., 2007). Formerly called the Lost Year stage of the life cycle, this is better termed the epipelagic stage. It remains the least well-known stage for this and all sea turtle species. Green turtle hatchlings are known from *Sargassum* drift lines that exist up current from Bermuda (Carr, 1987; Witherington, personal commun.), and a single green turtle recovered by the stranding network in Bermuda was smaller (18.8 cm SCL) than the smallest size at first capture on Bermuda's benthic foraging grounds (22.3 cm SCL). Thus, there are small green turtles in the pelagic environment around Bermuda that approach the size at which they switch over from a pelagic to a benthic life style.

When considered in light of residency data, the shape of the histogram in figure 5A suggests that *C. mydas* arrive at Bermuda in the 22–30 cm SCL size range, remain there until they reach about 60–65 cm SCL, and then depart. Because it is only the size classes from 30–60 cm that do not differ significantly in representation ($G = 5.996$, $P < 0.05$), it can be hypothesized that departure begins with the 60–65 cm size class. If the shape of the right side of the histogram in figure 5A is due only to departure, then the structure of the histogram suggests that about 14% leave at an average size of 62.5 cm SCL, 32% leave at an average size of about 67.5 cm SCL, 34% leave at an average size of 72.5 cm SCL, 15% leave at an average size of 77.5 cm SCL, and essentially all remaining individuals have left before they reach 80 cm SCL. A weighted average for these figures gives an estimated average size at departure of 70.6 cm SCL. This is about 6 cm smaller than the minimum size at sexual maturity for male *C. mydas*, and 10 cm smaller than the minimum size of sexual maturity for females (based on 178 laparoscopies performed in Panama, this study; Meylan and Meylan unpubl. data). The shortest time intervals (< 1 yr) between the last capture in Bermuda and recapture on a foreign foraging ground (fig. 5D) are also for turtles in the 65–80 cm size range. These could be assumed to be the turtles for which size at departure is most certain.

Puberty is a possible cue for departure. No size class of *C. mydas* from Bermuda (fig. 5A) is made up entirely of pubescent individuals. About 60% of turtles in the largest size class (75–80 cm SCL) were pubescent; turtles in this size class were observed less often than those in smaller size classes. This suggests that pubescent turtles are leaving Bermuda. The onset of puberty and the earliest apparent departures both occur at about 60 cm SCL. Schmid et al. (2003) cited the work of Gregory and Schmid (2001) as providing evidence that the onset of puberty and associated endocrinological changes in *L. kempii* correspond to a habitat shift in maturing individuals of that species.

Tag-return data also provide useful information on departure of *C. mydas* from Bermuda. There is a strong association between the distribution of Bermuda international tag returns and known adult foraging grounds for this species in the Atlantic. The majority of returns (56) have come from Nicaragua, the principal foraging grounds of adult green turtles in the western Caribbean (Carr et al., 1978; Bass et al., 1998). Two tag returns came from the eastern Caribbean (St. Lucia and Grenada) where green turtles that hatch on Aves Island (Venezuela) are known to forage as adults (Carr et al., 1978). Six additional tag returns were made off the Venezuelan portion of the Guajira Peninsula, which is a known foraging area of adult green turtles that nest in Tortuguero, Costa Rica (Carr et al., 1978). One Bermuda green turtle was recaptured in St. Lucie County, Florida, fitted with a satellite transmitter and subsequently tracked to foraging grounds west of the Marquesas Islands (50 km W of Key West) where it remained for at least eight months (D. Bagley, personal commun.). This area west of the Marquesas has recently been shown to serve as adult foraging habitat for *C. mydas* (Bresette et al., 2010).

There is a significant limitation to the use of tag returns to monitor individual turtles through departure from benthic developmental habitat. For any international tag recovery, data exist for a first capture, any recaptures at the tagging study site, and the foreign recapture. The length of time between the last observation at the tagging site and the foreign recapture may be known, but the respective portions of time spent in residence at the tagging site, in migration, and in residence at the foreign recapture site are not. Additional error affecting tag-return data results from the poor accuracy and precision sometimes associated with the reporting by turtle fishermen who return the tags. With these caveats, it is clear that an inverse relationship exists between time to recapture and size at last observation. Individuals that were smaller the last time they were observed in Bermuda took the longest time between that observation and foreign recapture ($y = -0.201, x + 17.955, r^2 = 0.42788, P < 0.001$). Individuals with the shortest time between their last observation in developmental habitat and their foreign recapture provide the best estimates of the size and timing of departure from developmental habitat.

One of seven *C. mydas* equipped with a satellite transmitter, a 78.6 cm SCL female (PTT 11674, table 7), was successfully tracked during departure from Bermuda; the resulting developmental migration was characterized by highly directed travel (fig. 12). The turtle took a SSW heading and maintained a nearly straight course for about three weeks to reach Hispaniola. At least one valid Argos location was obtained on 35 days of the 38-day migration. Minimum distance traveled and average travel speed were calculated using the single best location per day of the "hybrid" filtered dataset. The total migratory distance (great-circle distance between subsequent locations) was 2048 km and the mean speed of travel during migration was 2.3 km/hr ($SD = 0.97$, $n = 35$). Along its route, the turtle crossed the Silver Bank, and while it was off the Dominican Republic, it was exposed to Hurricane Georges, which passed close by. The turtle's intended destination remains unknown, but if it had continued at the rate it was traveling, it could have reached Nicaragua—the site with the greatest number of tag returns of Bermuda turtles—after about 2 months. When the turtle was captured, it was near the Windward Passage between Haiti and Cuba, through which it could have entered the Caribbean Sea.

The absence of sexually mature *C. mydas* in Bermuda waters, the distribution of tag returns from the Caribbean, and the satellite telemetry data collected during this study all indicate that the foraging grounds in Bermuda are not the final habitat occupied by the green turtles that are captured there. That is, Bermuda waters do not serve as adult resident habitat. Given the geographic isolation of the island, *C. mydas* that grow up in Bermuda must make a significant developmental migration to move into the next stage of their life cycle.

SECRETARY AND ZAPATILLA CAYS, PANAMA: The smallest green turtles observed at Secretary and the Zapatilla Cays (46.7 cm and 46.2 cm SCL, respectively) were much larger than the smallest individuals (22.3–34.6 cm) observed at 19 other sites in the greater North Atlantic (table 10) that apparently represent benthic developmental foraging grounds for this species. Data from these studies suggest that the smallest turtles at these two sites in Panama may be recruiting from other benthic developmental foraging grounds rather than from epipelagic environments. Smaller *C. mydas* are known from Bocas del Toro Province and benthic foraging grounds for these smaller size classes are reported by local fishermen to be present at sites that have not been sampled. Lahanas et al. (1998: 350) reported that Inagua, Bahamas, is a site from which immature *C. mydas* depart long before they approach maturation. They also suggested the possibility that a series of foraging areas may be used at this stage. Thus, observations at our two Panama study sites support the Carr et al. (1978) model that portrays benthic developmental foraging grounds as a series of separate sites.

To better estimate the size at which green turtles departed the Secretary and Zapatilla Cays study sites, their size at last sighting in Panama was compared to the time elapsed between that last sighting and the reported foreign recapture date (fig. 14C). As is the case for foreign recaptures of Bermuda green turtles, smaller animals were reported recaptured on foreign foraging grounds after longer intervals than larger turtles, suggesting that smaller turtles may have resided in Panama for longer periods after being tagged. Because there is more certainty about the timing of departure of turtles that were recaptured after shorter intervals, they are more likely representative of the actual size at departure.

Except for one turtle (77.1 cm SCL), the last size recorded for turtles that departed was less than the minimum size at sexual maturity based on laparoscopies (76.7 cm SCL). Many *C. mydas* in the 60–80 cm size range, the size range of departing animals, were observed to be in puberty (fig. 15). Although the average size at which immature *C. mydas* were last seen at the Panama study sites before foreign recapture was 61.4 ± 8.42 cm SCL ($n = 11$) at Secretary, and 68.9 ± 7.0 cm ($n = 22$) at the Zapatilla Cays, the shortest intervals were for 62.5 and 77.1 cm turtles from Secretary and a 72.6 cm turtle at Zapatilla. These values approach the weighted average size at departure from Bermuda (70.6 cm SCL).

THE LITERATURE: Green turtles arrive at benthic foraging grounds in the West Atlantic (not including the two Panama sites) at minimum sizes ranging from 20.8 cm (St. Lucie Power Plant, Florida) to 34.6 cm (Cedar Key, Florida), with an average for 22 sites of 26.0 ± 3.4 cm (table 10). Reich et al. (2007) used stable isotopes to detect this habitat shift in the diet of *C. mydas* smaller than 36 cm in the Bahamas. For three Pacific sites, average size of arrival at benthic foraging grounds is about 10 cm larger (37.8 ± 1.00).

Departure size is more difficult to summarize because at some sites occasional "adults" are reported, but their maturity status was not verified. However, for most sites the largest individuals reported are from about 67–81 cm SCL. Thus, results from Bermuda are typical for the West Atlantic green turtle benthic developmental stage. The Panama results clearly differ and must represent only a latter part of this stage for the green turtles that occur there.

Size at departure for *C. mydas* from Inagua, Bahamas, is approximately 10 cm less than it is for *C. mydas* departing from Bermuda (compare figs. 5A and 24A). This could be due to the relative proximity of adult foraging range for the Inagua turtles.

### *Eretmochelys*

BERMUDA: The histogram showing the size distribution of *Eretmochelys* in figure 13A has the same shape as that for *C. mydas* in figure 5A, with a steep left side, approximately equal columns for size classes 20–55 cm (vs. 30–60 for *C. mydas*), and a drop-off from 60–75 cm. As for *C. mydas*, this shape is best explained by arrival of hawksbills from the epipelagic stage into the benthic developmental stage, residency in Bermuda for much of the immature growth period, and then departure as sexual maturity is approached. The evidence for hawksbills occurring in adjacent epipelagic environments is stronger for this species than for *C. mydas,* with six stranded hawksbills smaller than the smallest hawksbill known from the Platform being documented by the stranding network. The smallest *Eretmochelys* caught on the Bermuda Platform (17.6 cm SCL) is smaller than that reported from other sites that likely serve as benthic developmental habitat for this species, but not remarkably so.

The few necropsies available of large *Eretmochelys* have so far revealed no turtles that were mature. The largest of these was larger that the minimum size of maturity observed to date for this species in the Atlantic. There is a single international tag return of a 50 cm SCL hawksbill tagged in 1989 in Bermuda and recaptured in Grenada in 2000.

Four studies of *Eretmochelys* at foraging sites in the West Atlantic (table 11) show a similar maximum size of immatures; a fifth has nesting sites adjacent to the areas where immatures were being studied.

THE LITERATURE: Studies by Nietschmann (1981), Boulon (1994), van Dam and Diez (1998a), and Meylan (1999) in the Caribbean, and Limpus (1992) in Australia reported relatively few long-distance tag returns of immature hawksbills. In some cases, however, movements of immatures may be extensive. Three *Eretmochelys* tagged as immatures in known benthic developmental habitat in Brazil made trans-Atlantic migrations to West Africa. Marcovaldi and Filippini (1991) reported an immature hawksbill that made a developmental migration of 3680 km, from Atol das Rocas, Brazil, to Dakar, Senegal. The turtle that made this remarkable journey was 74 cm SCL when recaptured, a size at which it would be expected to begin the maturation process on the adult foraging grounds. Two additional hawksbills originally tagged at Fernando de Noronha were recaptured in Corisco Bay on the border between Equatorial Guinea and Gabon (Grossman et al., 2007). Meylan (1999: table 1) summarized the few developmental migrations of hawksbills known from the greater Caribbean.

### *Caretta*

SECRETARY, PANAMA: The smallest loggerheads observed at Secretary (45–50 cm SCL) were similar in size to the smallest individuals reported from other benthic developmental sites (table 12). The appearance of *Caretta* at benthic developmental sites at sizes larger than those reported for *Chelonia*, *Eretmochelys*, and *Lepidochelys kempii* is now generally recognized as a result of an extended epipelagic stage in this species (Bolten, 2003).

Loggerheads that were relatively small (55–60 cm) were not reported as foreign recaptures for longer periods of time than those that were larger at their last capture at the study site. This is consistent with the hypothesis that the intervening years were likely spent at the study site where they would have continued to grow before departing for presumed adult foraging range. At least three of the six foreign recaptures of Secretary loggerheads could be assumed to have been immature at last capture at Secretary, two on the basis of size (both were 57.5 cm SCL) and one based on laparoscopy. The maturity status of the 72.6, 73.3, and 74 cm SCL animals is uncertain, but they are likely to have been immature as well, given their sizes. Thus, it appears that *Caretta* enter benthic developmental habitat in Chiriqui Lagoon at about 45–50 cm SCL. They no longer use this site by the time they reach about 75 cm.

THE LITERATURE: Nearly all studies of loggerheads at foraging sites in the West Atlantic (table 12) report turtles in the 40–50 cm SCL size range as the minimum size observed in their study. Exceptions include a study in Georgia that used strandings (Frazer, 1987) and a long-term study of Chesapeake Bay that included four outliers (Lutcavage and Musick, 1985; fig. 26C).

Although generalizations can be made from the literature about first arrival of *Caretta* into benthic developmental habitats, polymodal foraging by immatures and adults, and frequent occurrence of adults at immature-dominated foraging sites, make recognition of a final developmental migration to adult foraging range very difficult. However, studies of *Caretta* like those conducted by Limpus et al. (1994b) at Moreton Bay, Australia, and Schroeder et al. (1998) in Florida Bay, suggest that certain areas might be characterized as adult foraging range for this species and these sites seem to have few immatures. Thus, at some point in their lives, *Caretta* in the Atlantic (but perhaps not in the Pacific; see above) are likely to switch from more immature-dominated to more adult-dominated foraging areas when feeding near shore. However, this transition in the life cycle of *Caretta* may be more variable than for other species and perhaps should be incorporated into the relaxed life history model for *Caretta* proposed by Casale et al. (2008).

## CONTRADICTORY EVIDENCE

Evidence against the existence of a separate, immature-dominated, benthic developmental stage, distinct from the adult foraging stage, would include the discovery of foraging sites with a well-mixed composition of adults and immatures, or data showing that immature-dominated aggregations are artifacts of modern fishing pressure. The strongest evidence that the immature-dominated benthic developmental stage is not a worldwide pattern for nonpelagic cheloniid sea turtle species comes from *C. mydas* in the Pacific. Mixed aggregations of immature and adult green turtles occur together on the same foraging grounds at a number of sites in the Pacific, including Australia, Baja California, Galapagos, Hawaii, and Peru. In Australia, both adult and immature (as small as 36 cm CCL) *C. mydas* are resident around Heron Island and Wistari Reef in the southern Great Barrier Reef system (Limpus and Walter, 1980; Limpus and Reed, 1985a). Moreton Bay, Queensland, also fits this pattern (Limpus et al., 1994a). In this bay, 10.9% of 393 laparoscoped females were mature, another 2.5% were pubescent; of 206 laparoscoped males, 3.9% were mature and 1.0% pubescent. However, large and small turtles were found to have different distributions among the banks within the bay. The area of Flathead Gutter in Moreton Bay, for example, appeared to have resident immature *C. mydas* that were captured there for periods of up to 3–4 years (Brand-Gardner et al., 1999).

Although *C. mydas* in Australia may not have a separate immature-dominated benthic developmental stage, size composition varies among foraging grounds (Lanyon et al., 1989). Large immatures and adults predominate in certain bays (Moreton Bay, Repulse Bay, Shoalwater Bay; Limpus and Reed, 1985b), while in certain coral reef habitats, small- to medium-sized immatures dominate (Limpus and Reed, 1985a; Parmenter, 1980). On the reef at Heron Island, more than 80% of the turtles (of all species) are immature green turtles 40–90 cm CCL (Limpus, 1980). Some adult *C. mydas* are present, but they are not nearly as prevalent as they are in the lagoons, where 50–80% of the green turtles encountered are adults. Limpus (1980: 9) summarized this early life history stage of *C. mydas* in Australia as follows:

> The young turtles reappear at about the size of a large dinner plate…. [They] take up residence in the shallow water habitats of the continental shelf…these immature turtles may remain in the one feeding ground for extended periods, perhaps years before moving to another major area. At least several such shifts occur in the life of the turtle in this coastal shallow water benthic-feeding stage.

In Baja California at Bahia de Los Angeles, Seminoff et al. (2002) reported a foraging aggregation dominated by *C. mydas* $\geq$ 65 cm $\mathrm{SCL}_{\mathrm{n\text{-}t}}$, the size at which green turtles in this region near maturity. But about 10% of the turtles in this foraging aggregation were less than 65 cm. Other sites on the Baja Peninsula were dominated by smaller size classes (Koch et al., 2006; Senko et al., 2010), but at these sites small numbers of potentially mature (based on size alone) individuals were present. Thus, for *C. mydas* in Baja California, there also appears to be a less complete separation between late benthic developmental sites and adult foraging range than may be present at some Atlantic sites.

In the Galapagos, Green (1993) reported that *C. mydas* ranging in size from 46.2–89.5 cm $\mathrm{SCL}_{\mathrm{n\text{-}t}}$ were marked and recaptured on the same foraging grounds. A minimum size of maturation of 66.7 cm (based on nesting) indicated that roughly two-thirds of the animals recaptured were mature. Additional examples of mixed adult and immature foraging areas are known from Hawaii (Balazs, 1982) and in the eastern Pacific near Pisco, Peru. At the latter site, Brown and Brown (1982) used the term *developmental habitat* for an area from which 89% of a sample of 416 *C. mydas* was immature, based on an assumed size at sexual maturity of 80 cm. Even if some animals over 80 cm were actually immature, their observations of 27 males with elongate tails and the occasional female with shelled eggs, indicate that adult foraging range overlaps that of immatures along this coast.

There is an alternative interpretation for the immature-dominated foraging assemblages reported here. The work of Limpus and colleagues (Limpus and Reed, 1985a; Limpus et al., 1994a; Limpus and Walter, 1980) suggested the possibility that survivorship patterns of sea turtle species could produce some of the observed immature-dominated foraging assemblages. Their work on foraging grounds shared by immatures and adults indicated that large numbers of immatures must be present on shared foraging grounds that produce even a relatively small number of breeding adults. Their observations would explain what appear to be developmental habitats as foraging grounds that were historically shared by adults and immatures, but from which the adults were largely or entirely extirpated. It might be expected at these sites that adults would appear in samples taken over long periods of time, especially if associated nesting beach populations were protected. The Bermuda Turtle Project (begun in 1968) may be the best example of a site where protection has existed long enough that if mature *C. mydas* were going to reappear, they would have done so by now. Other foraging sites with similar circumstances include: the Indian River Lagoon (Ehrhart et al., 1996, 2007), Inagua, Bahamas, (Bjorndal and Bolten, 1996), and Wuvulu Island, New Guinea (Hirth et al., 1992).

The benthic developmental phase is also absent in *Lepidochelys olivacea,* which may be completely pelagic (but see McMahon et al., 2007). The evolution of a pelagic sea turtle could occur through an intermediate step in which the benthic developmental stage is used intermittently to supplement a pelagic foraging mode. *Caretta* models such an intermediate condition. Polymodal foraging (Reich et al., 2010) could represent an intermediate evolutionary step before the complete loss of the benthic developmental stage and loss of benthic foraging in adults.

Thus, the benthic developmental stage is absent in *Lepidochelys olivacea,* alternates with a pelagic foraging mode in some Atlantic *Caretta,* and appears to be absent in Pacific *Caretta*. However, evidence compiled in this paper provides corroboration of a separate benthic developmental stage in *C. mydas*, *Eretmochelys,* and *Lepidochelys kempii.*

## REFINEMENT OF THE DEVELOPMENTAL HABITAT CONCEPT

The goal of this paper has been to test the hypothesis that an "immature-dominated, benthic developmental stage" is a regular part of the life cycle of most species of cheloniid sea turtles. Having assembled the evidence, we believe that the concept is a valid one that can be characterized by the following traits, which are usually exhibited.

BENTHIC FEEDING: Turtles at this stage feed mostly on benthic food items, such as sea grasses, algae, and benthic macroinvertebrates. In the previous, epipelagic stage, they are feeding at the surface or in the water column (Ogren, 1989). Control of buoyancy must be well developed before a turtle can enter the benthic developmental habitat stage. This feature helps to define the lower limit of the stage, but not the upper limit because adults of the species that have this stage are also benthic feeders.

IMMATURES "ONLY": Examination of the hypothesis that certain foraging areas are occupied exclusively or nearly exclusively by postpelagic immatures requires knowledge of the maturity status of the animals. Collection of these data requires laparoscopy in most cases. In too many studies, assessment of maturity is based on size alone. Often the minimum size of sexual maturity for the species is used as an indicator of maturity. This is problematic in species where the size at sexual maturation is highly variable. Furthermore, there is sexual size dimorphism in the green turtle that has gone undocumented until recently (Godley et al., 2002), so using one minimum size for both sexes compounds the error. In studies where laparoscopy has been used, the existence of all-immature populations has been corroborated.

RESIDENCY AND SITE FIDELITY: Immatures of some species previously described as itinerant or transient are now thought to exhibit both residency and site fidelity at some sites. Carr and Caldwell (1956) and Carr (1967) viewed the green turtle population at Cedar Key as itinerant. They considered the site a station on a "developmental migration." Similarly, Mowbry and Caldwell (1958) identified Bermuda as a site where immature green turtles occurred but thought they were transient. Shaver (1994) interpreted the data set from the Mansfield Channel, Texas, to indicate that *C. mydas* there probably remain in the area for a few days to a few months, and do not return to the area after that time. She considered her sample to consist of seasonally resident individuals plus transient animals.

Mendonca (1981) recognized that some degree of residency (up to 2 yr) existed for green turtles in benthic developmental habitats on the east coast of Florida. Mendonca and Ehrhart (1982) described mud covering the margins of shells on 43% of the green turtles they saw in January 1977, and suggested that these turtles may bury themselves during cold weather. But these authors thought that *Caretta* at their study site were more transient than *C. mydas*. Mendonca (1983) tracked *C. mydas* in Mosquito Lagoon and discovered significant differences in movement patterns between winter and summer months. She attributed extensive erratic winter movements to attempts to depart the mostly enclosed Mosquito Lagoon system.

Turtles in the benthic developmental stage appear to be resident, at least in the case of *Chelonia* and *Eretmochelys* in tropical waters in the Western Atlantic. *Caretta, Lepidochelys kempii*, and a small number of *C. mydas* that use seasonally available resources travel up and down the east coast of the United States on a regular schedule (Epperly et al., 1995; Morreale and Standora, 2005; Mansfield et al., 2009; McClellan and Read, 2009). They are probably not itinerant as implied by Carr (1980).

In addition to being resident, *C. mydas* and *E. imbricata* at some sites exhibit site fixity. The green turtles in Bermuda were the subject of homing experiments (Burnett-Herkes, 1974; Ireland, 1979, 1980). The results of those studies and results reported here suggest that individuals of this species can and do return to specific grass flats if removed from them.

Even in areas where immature green turtles occur with adults, they show residency. Sixty-nine of the 71 immatures recaptured by Balazs (1982) were taken in the same "resident area." Additional residency data come from the work of Brand-Gardner et al. (1999) in Moreton Bay where more that one-third of the *C. mydas* involved in a feeding study had been marked at the site 3–4 yrs earlier. Strong philopatry was noted on the part of some individuals during the course of the study, with some individuals being observed in the same 0.05 $km^2$ area up to four times in one week.

MATURATION OCCURS ELSEWHERE: Laparoscopic examinations indicated that maturation was not occurring in the benthic developmental habitats that were studied in Bermuda and Panama. Mendonca and Ehrhart (1982) wrote that immature *Chelonia* and *Caretta* in the Mosquito Lagoon might remain resident there until "they approach maturity." Ehrhart (1983) suggested that the Indian River provided "a good demonstration of developmental habitat" for *Chelonia* and *Caretta,* and that "these turtles move elsewhere to mature." This idea of maturation occurring elsewhere is reiterated by Ehrhart and Witherington (1992) and is supported by the laparoscopy and tag-return data collected in Bermuda and Panama for this study. It is also supported by the work of Limpus (1992) on hawksbills in the southern Great Barrier Reef. However, Ehrhart and colleagues provided data that indicated that at least a small percentage of male loggerheads appear to mature in developmental habitat in the Indian River Lagoon system. Of the 430 *Caretta* handled during the first 14 years of their study, 14 (3.3%) were noted as being "either a maturing male or possibly a maturing male based on relative tail length" (Ehrhart et al., 1996). After 24 years of study, they had seen a total of 704 different loggerheads of which 18 (2.6%) were likely maturing males (Ehrhart et al., 2007).

Boulon and Frazer (1990) also recognized that the maturation process occurs away from their study site in the U.S. Virgin Islands. They studied growth in *C. mydas* at St. Thomas and St. Johns based on the recapture of 41 individuals that were 25.6–62.3 cm SCL at first capture. They noted the absence of larger individuals and suggested that green turtles were completing the maturation process after departing from the habitats in their study area.

Although some authors have suggested that maturity precedes migration to the adult foraging range (van Dam and Diez, 1998a: 22), the studies reported here that incorporate laparoscopy suggest that maturation typically occurs away from benthic developmental habitat. The onset of puberty occurs at about the same size as departure from developmental habitat in Bermuda and in other studies, suggesting the possibility that the maturation process itself might prompt a developmental migration to the adult foraging range.

When immature *C. mydas* depart from study sites in Bermuda and Panama, they reappear at foraging grounds (mostly in Nicaragua) known to support adults. The best explanation for the observed pattern of departure and tag-return data is that these turtles will complete the maturation process at these sites, where they will reside as adults. That is to say, the maturation process is completed at the adult foraging range, not in benthic developmental habitats. Bresette et al. (2010) provided evidence for this conclusion at their study area west of Key West, Florida. On the eastern Quicksands, large subadults occur with adults (composite size range 65–105 cm SCL) and they are geographically separated from the nearest foraging concentration of immatures (25–65 cm SCL) at Mooney Harbor.

RELATIVELY HIGH GENETIC DIVERSITY: Turtles on foraging grounds are drawn from multiple genetic populations. However, the data available for *C. mydas* in the West Atlantic indicate that aggregations occupying benthic developmental habitats ($n = 4$) show higher genetic diversity than the one studied adult foraging range in Nicaragua (Bass et al., 2006: table 2). Lahanas et al. (1998) described the pooling effect of the "lost year" stage of sea turtle life history whereby turtles from multiple nesting beaches become mixed in the pelagic environment. This pooled diversity is clearly maintained into the extended pelagic stage of Atlantic *Caretta* (Bolten et al., 1998). It also appears to be maintained into the benthic developmental habitat stage at other benthic developmental foraging aggregations studied so far (Bass et al., 2006: table 2; Sears et al., 1995; Engstrom et al., 2002; Blumenthal et al., 2009; Velez-Zuazo et al., 2008). When turtles of varying genotypes depart from benthic developmental habitats for adult foraging habitat, there may be geographic sorting that results in individuals occupying adult foraging range with better proximity to nesting beaches for the population to which they belong.

DEVELOPMENTAL MIGRATIONS LONGER THAN REPRODUCTIVE MIGRATIONS: The work at Bermuda reported here has led to the realization that green turtles and hawksbills must travel long distances to reach benthic developmental habitat there and likewise to move to adult foraging habitat assuming that is the next destination after leaving Bermuda. Extensive developmental migrations for *Caretta* are well documented (Bolton et al., 1998; Polovina et al., 2004) and consist of tens of thousands of kilometers of travel in some cases. But other species also appear to be capable of traveling long distances during developmental migrations. For example, green turtles hatched at Tortuguero, Costa Rica, are represented in benthic developmental foraging habitats as far away as Barbados, North Carolina, and Bermuda (Bass et al., 2006; BTP, unpubl. data). These sites are about 2600, 2800, and 3000 km straight-line distance from the nesting beach, respectively. Migration from these sites to Nicaragua, the most likely adult foraging range for this population, would be nearly as long, resulting in a total developmental migration of well over 5000 km. As adults, most of these turtles are likely to make their reproductive migrations between Nicaragua and Costa Rica (500 km). The single international tag return in Grenada for a hawksbill tagged in Bermuda and transatlantic movements of Brazilian hawksbills (see above) suggest that some individuals of this species are making developmental migrations of similar magnitude.

### FACTORS OBFUSCATING THE DEVELOPMENTAL HABITAT STAGE

Not all authors writing about sea turtle foraging aggregations recognize the benthic developmental habitat stage as it is considered here (Lanyon et al., 1989; Miller, 1994). The spatial overlap of life history stages, either on a temporary or permanent basis, is a frequent obfuscating factor. The data on green turtles at Zapatilla Cays, Panama, presented above suggest that developmental habitat that is occupied by large immature green turtles year-round is shared annually with migratory adults from May to September (fig. 23A). A different type of overlap appears to exist for *Caretta* on the east coast of Florida. Henwood and Ogren (1987) described an immature assemblage of *Caretta* that dissipates annually when adults arrive to use nesting beaches. Any remaining immature *Caretta* must share their foraging grounds with internesting adult females and with adult males looking for mates (fig. 23B). Similar overlap appears to occur for both hawksbills and green turtles at American Samoa (Grant et al., 1997). The hawksbills of Mona Island, Puerto Rico (van Dam and Diez, 1998a, 1998b, and references therein), provide another example where developmental habitat overlaps with internesting habitat and, to some extent, with adult foraging grounds.

Certain sampling methods may not be sensitive enough to detect details of distribution that might be required to recognize differences in habitat use by adult and immature individuals that live in proximity to one another. Among these methods might be rodeo, trawling with long tow times, and collection of data from strandings or certain fisheries.

A major complicating factor in the recognition of the benthic developmental stage along the eastern seaboard of the United States is that occupation of certain benthic developmental habitats is strictly seasonal. A number of studies cited above confirm that *Caretta, Lepidochelys*, and to a smaller extent, *C. mydas*, move up the eastern seaboard as the water warms each summer and then either move back south or seaward into warmer waters in the fall as water temperatures drop. Thus, although certain sounds and bays from Georgia to Massachusetts have predictable use by immature cheloniids, sometimes in fairly large numbers, year-round residency at these latitudes is limited by climatic factors.

A frequent reason for the failure to recognize a benthic developmental stage as separate from adult foraging stage is the assumption of the presence of mature animals because some individuals observed are above the minimum reproductive size for that species. Attainment of sexual maturity in sea turtles in not based on size alone. Limpus (1992) provided excellent evidence of the impact of this problem on the understanding of foraging ground "population" structure and the utility of laparoscopy in correcting it. In his sample of 152 *Eretmochelys* from the southern Great Barrier Reef, 20 animals were larger than the minimum size at sexual maturity (based on minimum size of nesting females). If only these data had been available, one might have assumed that this is a mixed adult and immature foraging aggregation. However, of 109 animals for which maturity status was assessed (including 16 of the "adult-sized" individuals), only one adult (0.9%) was identified. This suggests the alternative possibility that immature-dominated, benthic developmental habitat exists for *Eretmochelys* in the southern Great Barrier Reef. In the Limpus (1992) study, the largest immature female was 3.5 cm larger than the average size of nesting females. This is a pointed example of the problem of using size at sexual maturity to extrapolate maturity status in a population of turtles.

Limpus et al. (1994a) provided another example of this phenomenon in their study of green turtles at Moreton Bay, Queensland, where they calculated that the number of mature females in the sample would have been overestimated by 42% if maturity status were based on size alone. They pointed out that, on average, *C. mydas* does not mature at a minimum breeding size but rather at a size approaching the average breeding size for the population (average nesting size for females, average mating size for males). It seems clear that using the minimum size of sexual maturity to recognize "sexually mature" individuals will always greatly overestimate the number of mature individuals in the sample.

Finally, there is geographic variation within species in the degree to which a separate benthic developmental habitat stage exists. *C. mydas* in the Atlantic system provides some of the best evidence for the existence of a separate stage. However, in the Pacific there are few, if any, discrete all-immature, postpelagic foraging assemblages for this species. Similarly, *Caretta* in the Atlantic has a prolonged stage at sea in their early lives, but most individuals eventually enter benthic foraging habitats at sizes of about 45–50 cm (Panama: this study; Indian River: Ehrhart et al., 1996, 2007; Chesapeake Bay: Lutcavage and Musick, 1985; etc.). However, no near shore developmental habitat has been reported for *Caretta* in the Pacific (Limpus et al., 1994b). Individuals as large as 83 cm are present in the open North Pacific (Polovina et al., 2004), suggesting that in the Pacific, *Caretta* may remain pelagic until it is ready to enter the adult foraging range. This would agree with observations of recruitment of *Caretta* to Australian foraging grounds. Limpus (1994) and Limpus et al. (1994b) reported that *Caretta* recruits to two different foraging grounds at about 80 cm CCL, matures over the next 8–14 years, and then remains resident at these sites.

## EVOLUTION OF A BENTHIC DEVELOPMENTAL STAGE

Why does a separate benthic developmental stage in the life history exist in this set of four cheloniid sea turtles (*Chelonia mydas, Eretmochelys imbricata, Lepidochelys kempii*, and *Caretta caretta*)? Congdon et al. (1992) suggested that differential habitat use associated with age or size in turtles may result from changes in diet, distributions of food resources of appropriate size, size-specific risks of predation, or a combination of these factors. A shift in resource use is associated with the change from the epipelagic to the benthic developmental stage but not from the latter to the adult foraging range. For *Chelonia, Eretmochelys,* and *L. kempii*, there is no known shift in diet between these stages (Bjorndal, 1997). Thus, a change in resource use can explain the shift from epiplegic to benthic foraging but does not explain why, in many cases, benthic developmental foraging sites are separate from adult foraging habitat.

Size-specific risk of predation appears to be an important factor that keeps smaller aquatic organisms of many species in shallower water. Congdon et al. (1992) reported that for certain freshwater turtles, there is a tendency for smaller individuals to use shallower water. Thus, an alternative reason for the existence of benthic developmental habitat separate from adult foraging range is that it offers enhanced refuge from predators to immatures that they do not enjoy in adult foraging habitat. Sharks are probably the single most important predator of sea turtles of all sizes (Heithaus et al., 2002, 2005). Perhaps the shallower inshore areas that typically serve as benthic developmental habitat offer some additional protection from sharks. Estuarine foraging areas may provide a refuge from shark predation because of lower salinity. This is believed to be the case for the Chesapeake Bay (J. Musick, personal commun.) However, a study of tiger sharks in Western Australia showed that these known turtle predators prefer foraging in shallow waters and forage in shallows ($< 4$m) more frequently than expected based on several measures (Heithaus et al., 2002). Thus, shallow waters alone may not serve to protect sea turtles from their predators.

Another possible explanation for the existence of geographically separate benthic developmental habitat is resource partitioning by size (or age or maturity status). Because the diets of immature green turtles, hawksbills, Kemp's ridleys, and loggerheads do not differ significantly from those of the adults, intraspecific competition with adults is possible and, in fact, likely. Classic Lotka-Volterra theory suggests that the ability of a local population ($N_1$) to increase is negatively affected by the number of individuals of that species already present, plus the number of competitors present, times their respective coefficients of competition. For species of the same approximate body size, if there is no significant ontogenetic shift in diet, it is likely that intraspecific competition will have a larger effect than interspecific competition. Thus, any reduction in $N_1$ will be an advantage to the population, but only if that reduction is not permanent and those individuals that leave are not lost from the population.

Intraspecific competition can be reduced by geographic partitioning of the habitat. If members of a population can use resources at a distant location (benthic developmental habitats) from the primary residence of a population (adult resident habitats), then the effect on population growth could be favorable. Natural selection should favor populations in which this partitioning takes place. If immatures can delay their return to the adult foraging range, more resources will be available for resident adults to invest in future generations of that population. Furthermore, immatures may be able to occupy habitats that do not contain sufficient resources to support larger adults. In any case, staying away from adult resident habitats may increase their own growth rate by reducing intraspecific competition with adults. Increased growth rate is an added benefit, as it should lead to higher rates of survivorship; most turtles show type III survivorship, with high mortality at the earliest stages that diminishes rapidly as the turtles grow (Iverson, 1991). Bjorndal et al. (2000b) provided evidence for density-dependent growth in *C. mydas,* which indicates that intraspecific competition can limit growth rate in this species.

For most sea turtles species, geographic displacement to distant foraging areas is favored by the presence of the epipelagic stage. It is interesting to note that *Natator*, which is clearly primitive relative to other sea turtles in other life history traits (Van Buskirk and Crowder, 1994), should apparently also lack both an open-ocean pelagic stage and the benthic developmental stage of the life history. This suggests that an epipelagic stage may be a prerequisite for the evolution of an immature-dominated, benthic developmental stage of the life history.

## RESEARCH AND MANAGEMENT SIGNIFICANCE OF THE BENTHIC DEVELOPMENTAL STAGE

Developmental habitat is a useful biological concept. Recognition of a separate benthic developmental stage further elucidates the complexity of the life cycle of cheloniid sea turtles and promotes discussion of why this complexity exists. It is also important for research and conservation efforts because each stage of a species' life history needs to be identified and studied. As pointed out by Bjorndal and Bolten (1996) and illustrated by the fieldwork discussed here, turtles in benthic developmental habitats are easily captured and, with the continual replenishment due to recruits, might be harvested over time with no notable decline. The impact on nesting populations of the harvest of turtles at benthic developmental sites may not be seen at the nesting beach for several decades.

Recognition that life history stages overlap could help to explain unexpected results such as those of Godley et al. (2003). In this case, *C. mydas* from a single foraging ground showed two very different patterns of movements when satellite tracked. Laparoscopy might have shown that the smaller, more resident individuals were immature, and the large individuals that showed migratory tendencies were mature. Recognition of this stage also may be important in research design. For example, precautions should be taken in genetic studies when attempting to characterize the genetic diversity of an immature foraging aggregation that might be inflated by inclusion of transient adults (Wood, Hardy, Meylan, and Meylan, in prep.).

Recognition of the benthic developmental stage may also be important for the explanation of variance in genetic diversity among "foraging grounds" (see above). It appears likely that genetic diversity in adult resident habitat may be less than that in developmental habitat. The genetic diversity seen in benthic developmental habitats also suggests that losses at a single developmental site may impact multiple genetic populations.

Large immature sea turtles that are ready to depart from developmental habitat have survived the most dangerous years of their lives, and monitoring their numbers could provide a mechanism for predicting demographic shifts in a population. Turtles that complete this stage are demographically important because sea turtles appear to have type III survivorship. But before they can become reproductive adults they have to make a final developmental migration to the adult resident habitat. In some cases, this may be thousands of kilometers away. Tag-return data from this study suggest that this may be a dangerous time for these turtles, and protection of subadults as they move into adult foraging ranges could be a productive objective of policy change for effective marine turtle conservation.

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