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Migration of green turtles *Chelonia mydas* from Tortuguero, Costa Rica

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Abstract During 1955–2003, flipper tags were attached to 46,983 green turtles and ten turtles were fitted with satellite transmitters at Tortuguero, Costa Rica. Eight satellite-tracked turtles stayed within 135 km of the beach and probably returned to nest after release. The interesting area is more extensive than previously documented. Post-nesting migration routes of satellite-tracked turtles varied. Seven turtles swam close to the coast and three turtles swam through oceanic waters before moving toward nearshore areas. Sea surface height anomaly maps indicate that oceanic movements were consistent with the southwestern Caribbean gyre. Circling and semi-circling turtles could have been disoriented but submergence and surface times suggest they may have been feeding in *Sargassum* sp. concentrations. Rapid post-nesting migrations (mean 2.2 km hr^{-1}) ended on benthic feeding grounds in shallow waters ($<20 \text{ m}$) off Belize ($n=1$), Honduras ($n=1$) and Nicaragua ($n=8$). The spatial distribution of migration end points ($n=10$) and tag returns ($n=4,669$) are similar. Fishermen in Nicaragua target green turtles along migratory corridors and on foraging grounds. Management efforts are urgently needed in Nicaragua, particularly in the high-density feeding areas south and east of the Witties (N14°09 W82°45). The proximity of foraging grounds to the nesting beach

(mean 512 km) may permit female turtles to invest more energy in reproduction and hence the Tortuguero population may have greater potential for recovery than other green turtle nesting populations. Recovery of the Tortuguero green turtle population will benefit countries and marine ecosystems throughout the Caribbean, especially Nicaragua.

Introduction

Patchy food resources and complex life cycles contribute to heterogeneous distribution of individuals for many species of marine fauna. Geographical separation of habitats used during distinct life stages represents a logistical challenge to scientific studies. Detailed research into the behavior of marine turtles has been conducted for five decades but the majority of studies have focused on land-based life stages (Carr and Giovannoli 1957; Hendrickson 1958; Hirth 1997). However, the time spent on land by hatchlings and nesting females only represents a small fraction of the potential lifespan of a marine turtle. Marine turtles spend most of their time in oceanic and coastal waters where frequent access is a limiting factor to studies based on direct observations. Instead, indirect methods have been employed to elucidate habitat utilization and migration behavior, including external and internal tagging, sonic, radio and satellite telemetry (Addison et al. 2002; Balazs 1999; Bentivegna 2002; Cheng 2000; Godley et al. 2002; Hays et al. 1999, 2001a, 2001b, 2002a; Luschi et al. 1998; Polovina et al. 2000; Seminoff et al. 2002).

The behavior and movements of marine turtles have broad ecological and management implications. Marine turtles fulfill important ecological roles through energy transport (Bouchard and Bjorndal 2000), nutrient cycling and through affecting community structure (Bjorndal 1997). Interactions between anthropogenic activities such as fisheries and tourism, and marine turtle

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populations have both ecological (Bjorndal and Jackson 2003) and economic consequences (Troëng and Drews 2004). Identifying the geographic location and size of habitats used by marine turtles for migrations and foraging are needed in order to determine their ecosystem roles. Also, identification of priority areas for protection and restricted resource use is needed to ensure marine turtles fulfill their ecological roles.

The green turtle *Chelonia mydas* is classified as endangered and a recent evaluation estimated that the global population has declined between 48% and 67% over the last three generations (Seminoff 2004). The largest remaining green turtle rookery in the Atlantic is at Tortuguero Beach, Costa Rica (N10°35.51 W83°31.40 to N10°21.46 W83°23.41) (Troëng and Rankin 2005). This green turtle population is important as an income and protein source through extractive use in Nicaragua (Lagueux 1998) and other neighboring countries and through ecotourism to watch nesting turtles (Troëng and Drews 2004).

At Tortuguero, tagging of green turtles was historically conducted during the main nesting season from July until mid-September and since 1998 from mid-June to the end of October (Carr et al. 1978; Caribbean Conservation Corporation (CCC) unpublished data). Recaptures of tagged individuals provide information on the green turtles' impressive migratory abilities (Carr et al. 1978). Information from tag returns, however, is limited to two temporally and spatially defined moments—the time and place of tagging and recapture. Satellite telemetry provides more detailed information about migratory behavior and routes. This paper aims to summarize post-nesting movements of adult female green turtles from Tortuguero as documented by tag returns and satellite telemetry and discuss management and ecological implications.

Materials and methods

Recapture of tagged individuals

In 1955, Dr. Archie Carr began flipper tagging green turtles at Tortuguero and tagging has continued every year since through the CCC. From 1955 to 2003, 46,983 green turtles were tagged predominately with monel#49 metal tags and since 1998 with inconel#681 tags (<http://www.nationalband.com>) because they have shown to have a longer retention time (Troëng et al. 2003) and to be less prone to corrosion (Bellini et al. 2001). Tag return data for 1,110 international green turtle recaptures during 1956–1976 were reported by Carr et al. (1978). Each tag has a unique number, a return address (University of Florida, USA), and advises the finder of a reward (US\$5.00) for returning the tag. Tags are returned with varying amounts of information about the recapture. For recaptures without exact locations, we

estimated a position based on the description of the recapture site.

Satellite telemetry

Since 2000, the CCC and the Ministerio del Ambiente y Energia (MINAE, Ministry of Environment and Energy), Costa Rica have implemented the Tortuguero Sea Turtle Tracking Project. Between July 2000 and September 2002, seven female green turtles (Table 1) were fitted with ST-14 satellite transmitters from Telonics, Inc. (<http://www.telonics.com>) and in September 2001, three additional females were fitted with KiwiSat 101 satellite transmitters from Sirtrack Ltd. (<http://www.sirtrack.com>) after the nesting process was completed. Transmitters were attached to the carapace according to the methods described by Balazs et al. (1996), with the exception that the ST-14 transmitters were positioned with the antenna orientated posteriorly and a roll of kevlar or fiberglass cloth placed on top of the transmitter immediately anterior to the antenna to protect its base. Location and time data were provided by the Argos satellite system (<http://www.argos-inc.com>). ST-14 transmitters had sensors that provided mean submergence time during the previous 12 h. Only submergence events exceeding 10 s were recorded. The sensors on the only refurbished ST-14 transmitter failed to provide any useful submergence data (Table 1). KiwiSat 101 transmitters provided time spent at the surface during the previous 24 h.

Data were filtered to ensure that only high quality information was used for analyses. Prerelease location data were sorted by location class (LC) to determine the accuracy of each LC (3, 2, 1, 0, A, B and Z) according to Hays et al. (2001c). Only LC 3, 2, 1 and A data were used in calculations of travel speed and bearing. All location data points indicating unrealistic travel speeds of $> 5 \text{ km h}^{-1}$ (Luschi et al. 1998) were removed from further analysis.

Location, submergence and surface data points were divided into four activity categories based on turtle movements. Internesting began when the turtle was released into the water and continued until the final nesting event was observed or location data indicated that nesting had occurred. Pelagic circle is when turtles took a post-nesting circular or semicircular route through oceanic waters after the final nesting event, without moving in the direction of benthic foraging grounds. Post-nesting return migration began after the final nesting event, or for turtles moving in pelagic circles when the turtles began moving rapidly ($> 1.2 \text{ km h}^{-1}$) in the direction of benthic foraging grounds. Post-nesting return migrations were considered completed once the turtle remained within a 20 km diameter area for more than 24 h. Shallow water feeding/resting is defined as restricted movements following

Table 1 Summary data for *Chelonia mydas* tracked by satellite

| Release date | 18 July 2000 | 20 July 2000 | 17 September 2000 | 18 September 2000 | 19 September 2000 | 20 September 2000 | 11 September 2001 | 12 September 2001 | 13 September 2001 | 27 September 2002 |
|--|--------------------|--------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|-------------------------|
| Turtle identification | A | B | C | D | E | F | G | H | I | J |
| Curved carapace length minimum (cm) | 106.1 | 101.1 | 108.1 | 103.7 | 99.3 | 107.9 | 99.1 | 95.5 | 110.9 | 103.2 |
| PTT | ST-14 | ST-14 | ST-14 | ST-14 | ST-14 | ST-14 | KiwiSat101 | KiwiSat101 | KiwiSat101 | ST-14 ^b |
| Interesting (days) | 33 | 12 | 14 | | 22 | 20 ^a | 15 | 8 | | 21 |
| Pelagic circle (days) | | | | | | 22 | | | 38 | 3 |
| Post-nesting return migration (days) | 27 | 25 | 15 | 11 | 16 | 13 | 11 | 22 | 15 | 15 |
| Shallow water feeding/resting (days) | 197 | 114 | 302 | 236 | 384 | 283 | 146 | 242 | 91 | 281 |
| Total time tracked (days) | 257 | 151 | 331 | 246 | 423 | 338 | 172 | 272 | 144 | 319 |
| Distance traveled beach—foraging ground (km) | 747 | 1,152 | 411 | 437 | 441 | 1,325 | 410 | 513 | 1470 | 630 |
| Direct distance beach—foraging ground (km) | 639 | 1,089 | 397 | 397 | 398 | 412 | 398 | 473 | 506 | 409 |
| Ratio traveled/direct distance | 1.17 | 1.06 | 1.04 | 1.10 | 1.11 | 3.22 | 1.03 | 1.08 | 2.91 | 1.54 |

^a Observed nesting on the night of September 29, 2000 and during a non-nesting emergence on October 9, 2000;

^b PTT refurbished

post-nesting migrations and continued until the transmitters stopped sending information.

Remote sensing data

Bathymetric information at a resolution of 0.03 decimal degrees was obtained from the NOAA National Geophysical Data Center (<http://www.ngdc.noaa.gov/mgg/bathymetry/relief.html>). ESRI ArcView 3.3 software with the spatial analyst extension (<http://www.esri.com>) was employed to map 10 m bathymetry contour lines. Sea surface height anomaly maps were generated from 10-day averages of TOPEX/Poseidon satellite data and downloaded from the Colorado Center for Astrodynamics Research Real-Time Altimetry Project website (http://e450.colorado.edu/realtime/gsfcr_global-real-time_ssh/). These maps provide information on temporal variation in the direction and speed of currents and the location of oceanographic mesoscale features such as eddies and gyres (Luschi et al. 2003b).

Results

Recapture of tagged individuals

Since 1955, a total of 4,669 green turtles (including the 1,110 recaptures reported by Carr et al. 1978), representing 9.9% of tagged individuals have been recaptured and reported. The recapture country was

unknown for two of the records. The remaining recaptures ($n=4,667$) demonstrate a wide distribution of Tortuguero adult green turtles throughout Costa Rica and 19 other countries (Fig. 1). The largest proportion of recaptures (0.82) came from Nicaragua. The most distant recapture was a green turtle found on the coast of the Municipality of Fortaleza, Ceará, Brazil at a straight-line distance of 5,200 km from Tortuguero (Lima and Troëng 2001).

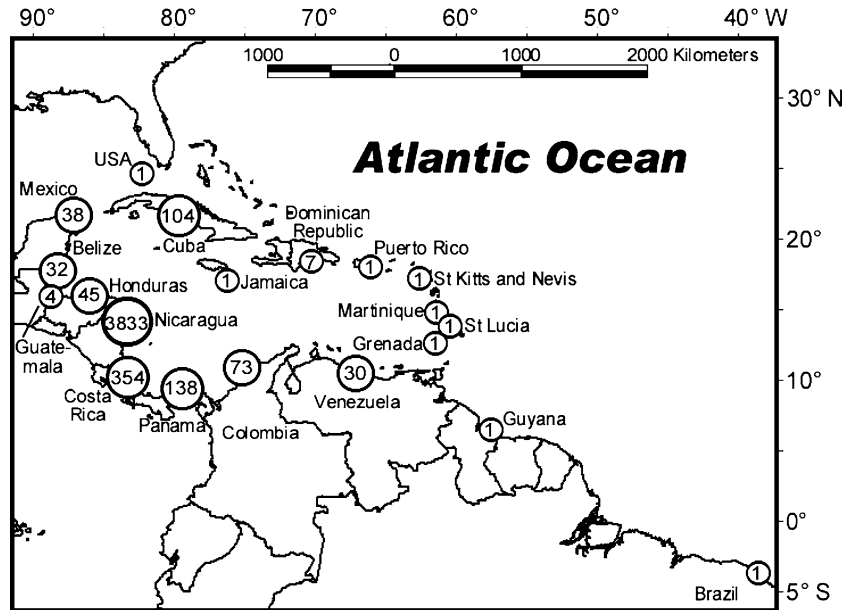
Data quality and filtering from satellite transmitters

Data in LCs 3, 2 and 1 were most accurate with a mean total deviation of less than 1.1 km, followed by LC A with a mean total deviation of 3.1 km (Table 2). After deleting data points from LCs 0, B and Z, a mean 23.4% (range: 15.7–28.2%) of location data points were analyzed.

Interesting behavior

Eight of the turtles are believed to have returned to nest after release (Table 1), but only six generated information on interesting submergence ($n=4$) or surface times ($n=2$). Mean submergence times varied (mean 7.8 min, range 5.0–16.2 min for individual turtles), with 5–10 min submergences, the most common mode during interesting (Fig. 3a). All green turtles remained within 12 km NNW–120 km SE of the release location and within

Fig. 1 Tortuguero green turtle recaptures by country from 1955 to 2003



30 km of the coastline with the exception of Turtle E which swam 135 km to the north during the internesting period (Fig. 2). Mean travel speed for periods of 1.2–232.7 h (mean 33.0 h) was 0.9 km hr^{-1} (SD ± 1.0).

Pelagic circle

Upon completing nesting, seven green turtles (turtles A, B, C, D, E, G and H) immediately swam north in post-nesting migrations. Three turtles (turtles F, I and J) made large circular or semicircular movements in oceanic waters before initiating migration toward benthic foraging areas (Fig. 4). The three turtles swam as far as 150 km offshore in waters $>1,000 \text{ m}$ deep. During the circular movements, Turtle F made short duration submergences, most of the mean submergence times (89%) were less than 5 min (Fig. 3a). Turtle I spent considerable time at the surface during the circular movements. The most common mode was 20–40 min surface time over 24 h periods (Fig. 3b). Movements during the pelagic circles greatly increased,

for Turtle I more than tripling, the distance traveled between the nesting beach and the benthic feeding grounds (Table 1). All three turtles moved in counterclockwise circles or semicircles consistent with the anticyclonic surface current of the oceanic gyre present offshore (Fig. 4). The three turtles initiated post-nesting migrations toward benthic feeding grounds after spending 3–38 days making pelagic circles or semicircles (Table 1).

Post-nesting migrations

Post-nesting return migrations had a mean speed of 2.2 km hr^{-1} (SD ± 1.1 , range $0.9\text{--}2.5 \text{ km hr}^{-1}$ for individual turtles) until the turtles reached benthic foraging grounds off the coasts of Nicaragua, Honduras and Belize (Fig. 2). Location data indicate that all ten green turtles (with the possible exception of Turtle C) traveled within 15 km of the Nicaragua mainland at Pearl Cay Point ($N^{\circ}12.24 \text{ W}83^{\circ}30$), but Turtles F, I and J traveled relatively far offshore until coming within 60 km of Pearl Cay Point. The direct distance between the nesting beach and the shallow water feeding/resting areas ranged from 397 to 1,089 km (mean 512 km).

Shallow water feeding/resting

At completion of post-nesting return migrations, green turtles remained resident in shallow waters (Fig. 5). Seven of the turtles that remained in Nicaragua stayed in the vicinity (within 40 km) of the Witties and the eighth remained in waters north of Deadman's Cay (Fig. 5). All eight took up residence in waters less than 20 m deep

Table 2 Estimated mean accuracy for transmitter location classes (LC)

| LC | N locations | Mean latitude deviation (km) | Mean longitude deviation (km) | Mean total deviation (km \pm SD) |
|----|-------------|------------------------------|-------------------------------|------------------------------------|
| 3 | 4 | 0.10 | 0.22 | 0.41 ± 0.26 |
| 2 | 3 | 0.14 | 0.83 | 0.48 ± 0.48 |
| 1 | 4 | 0.65 | 0.81 | 1.06 ± 0.63 |
| 0 | 3 | 6.66 | 5.66 | 6.66 ± 5.76 |
| A | 3 | 1.40 | 2.91 | 3.11 ± 3.41 |
| B | 6 | 4.79 | 25.95 | 17.88 ± 12.05 |

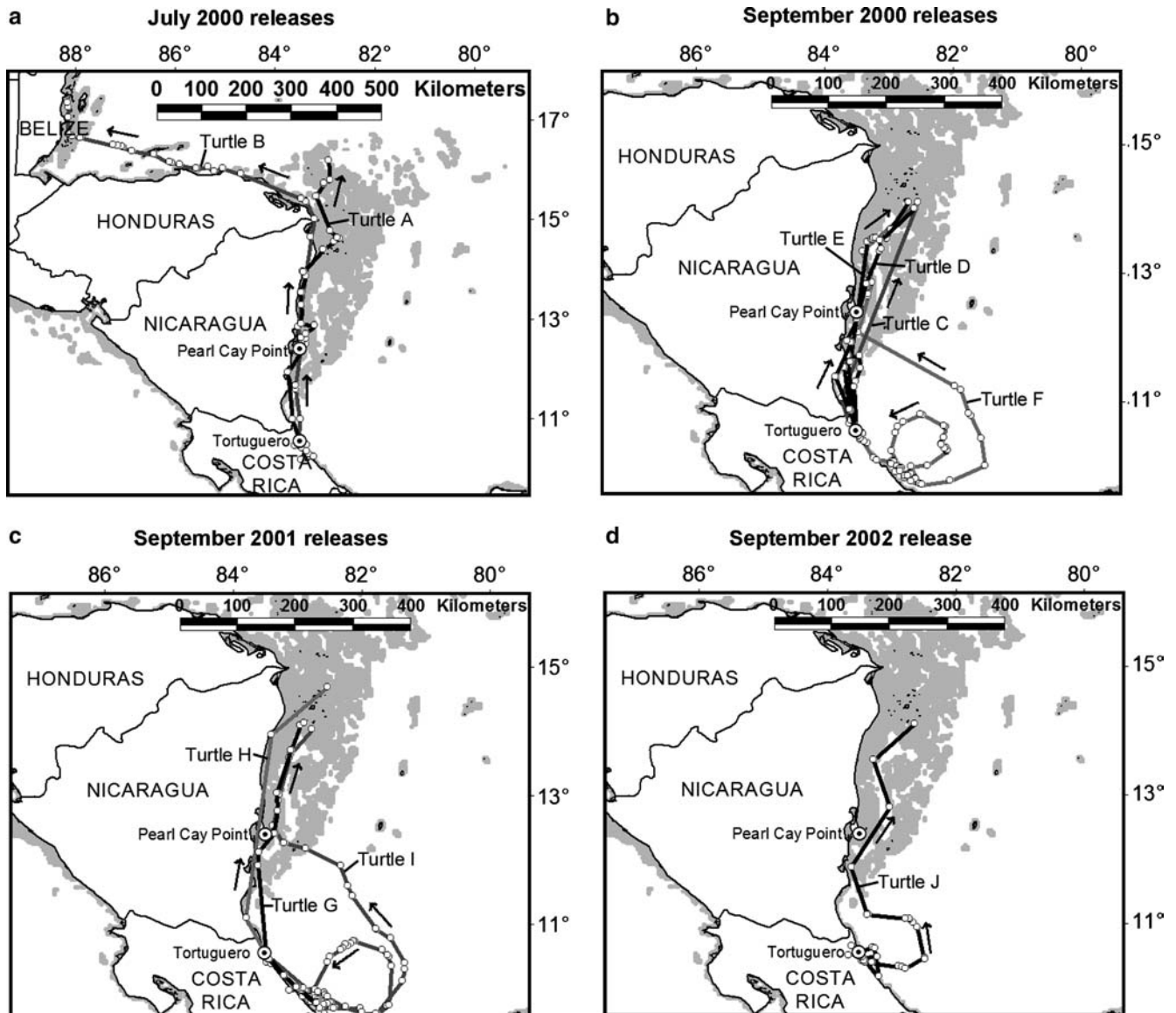


Fig. 2 Green turtle interesting, pelagic circle and post-nesting migration movements from Tortuguero, Costa Rica. *Open circles* indicate location data points, shallow water (<20 m) is shaded gray

(Fig. 5). Turtles A and B migrated to shallow waters <10 m deep, located south of Belize City and near Cajones Cays, Honduras.

The green turtles displayed longer submergence and surface times during the shallow water feeding/resting phase than during interesting and post-nesting migrations (Fig. 3a, b). Mean submergence times were shorter (independent samples *t*-test, $p < 0.001$) for the green turtles residing in the very shallow waters off Belize and Honduras (mean 6.2 min) than for green turtles residing on the Nicaragua feeding grounds (mean 12.2 min).

Total tracking time ranged from 144 to 423 days with a mean 265 days (Table 1). One of the turtles (Turtle F) was caught and killed by turtle fishermen in Nicaragua in August 2001 and the satellite transmitter was recovered. The flipper tags from Turtle I were

returned by a fisherman from Nicaragua in October 2003, but there was no information regarding the fate of the transmitter. Turtles C and D were observed nesting at Tortuguero during the 2002 and 2003 seasons, respectively, but both turtles had lost the transmitters prior to nesting.

Discussion

The satellite telemetry study provided new detailed information on the migratory routes of Tortuguero green turtles from the nesting beach to benthic foraging areas. In our study, LC A data were found to be slightly less accurate than LCs 3, 2 and 1. This observation may be a result of small sample size as a similar study (Hays et al. 2001c) with a larger sample size ($n = 18$ compared to $n = 3$ in our study) found LC A data to be equally accurate as LC 1 data. Although the proportion of useful location data points (3, 2, 1, A)

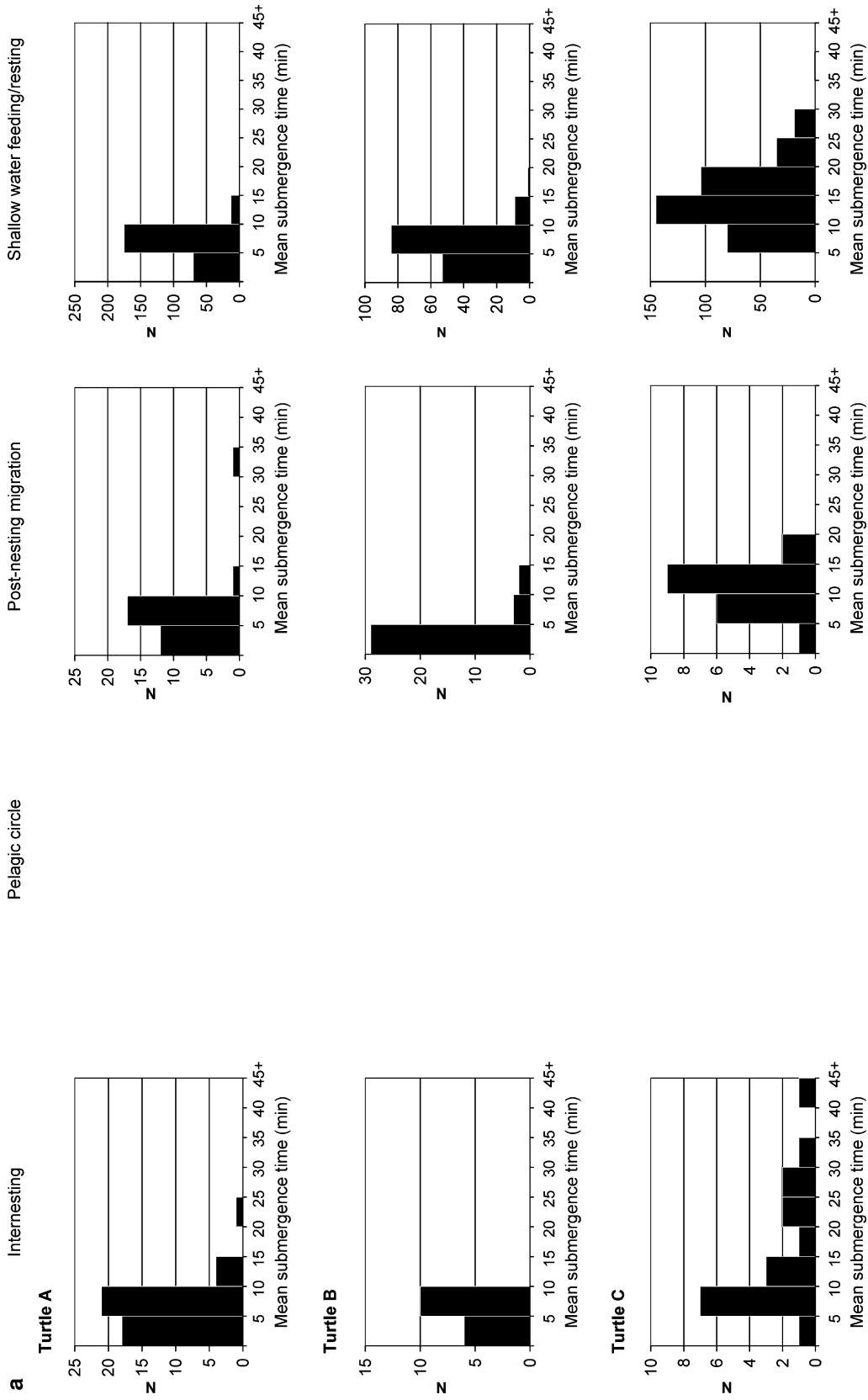


Fig. 3 a Green turtle interesting, pelagic circle and post-nesting migration submergence times. b Green turtle interesting, pelagic circle and post-nesting migration surface times

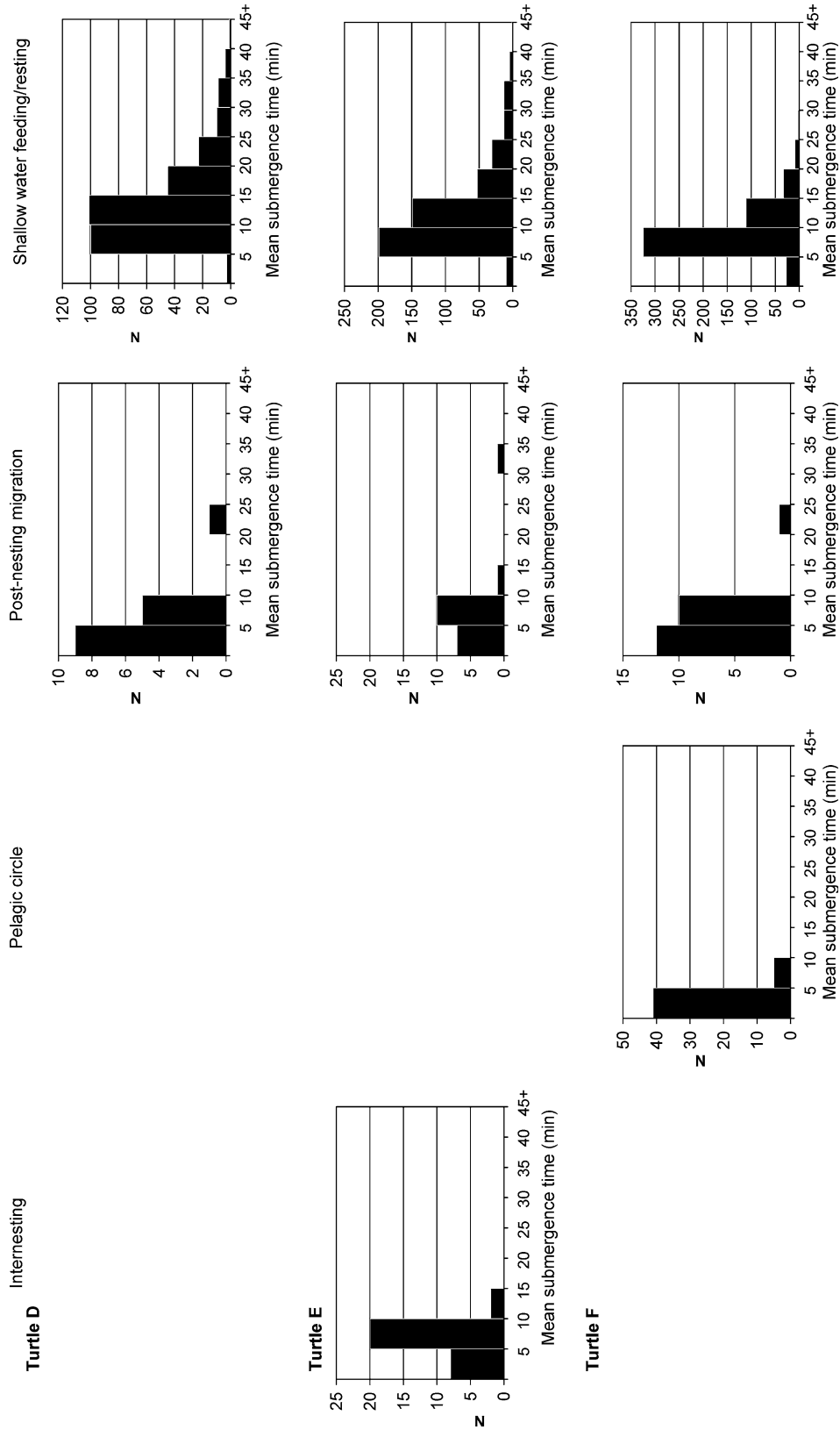


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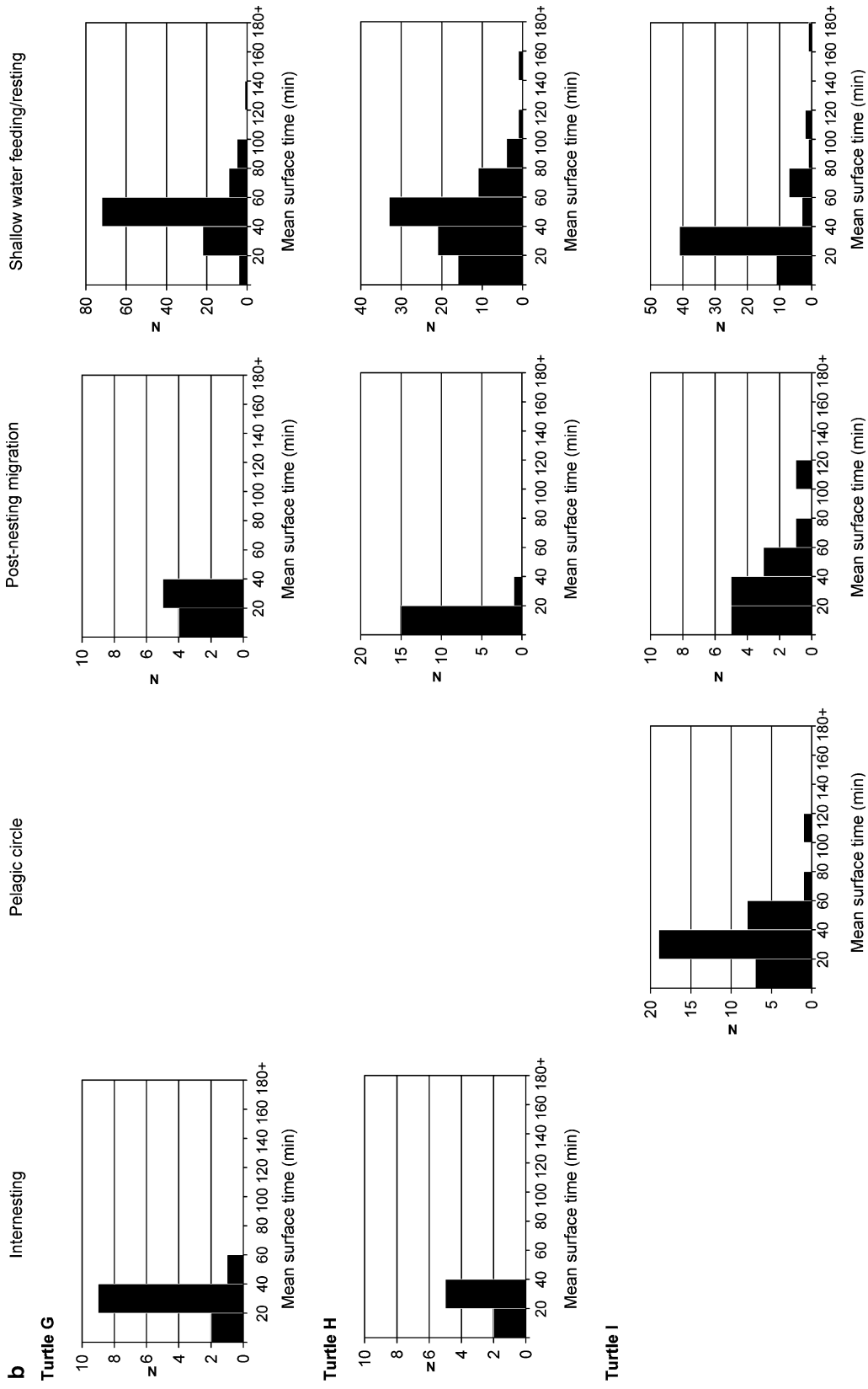


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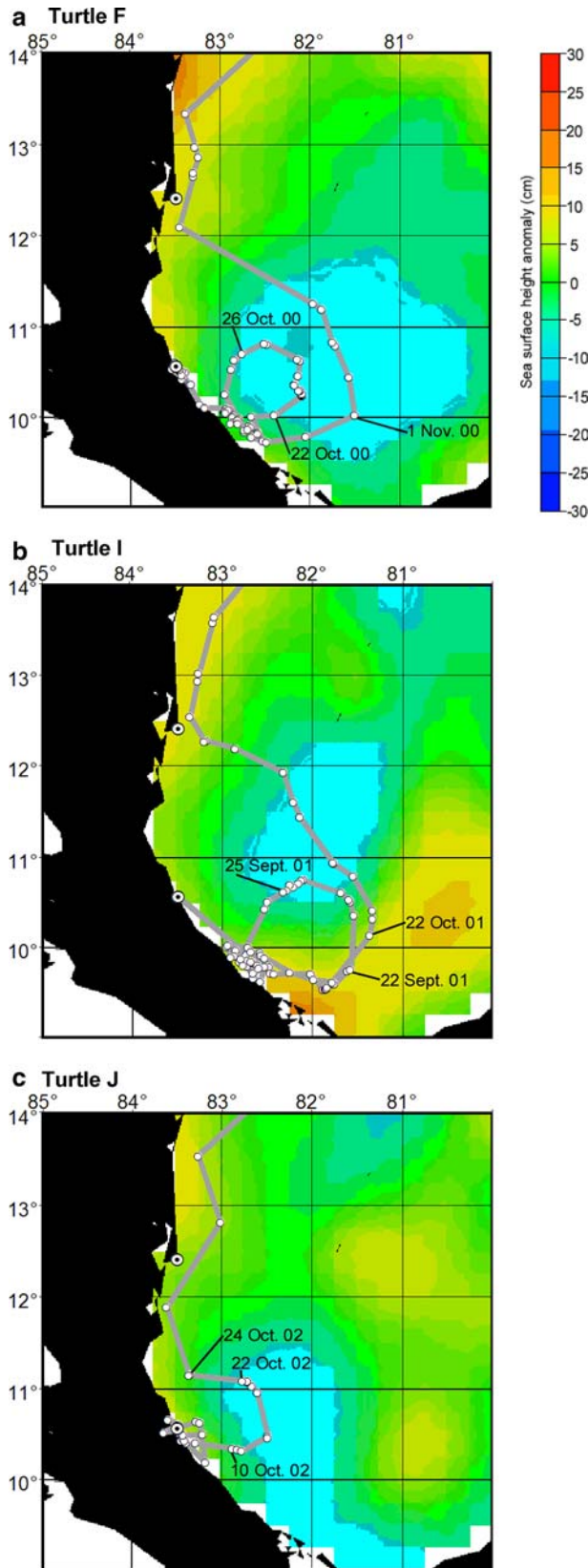


Fig. 4 Green turtle movements during pelagic circles superimposed over sea surface height anomalies (*open circles* indicate location data points). Negative anomalies are associated with cyclonic (counterclockwise) gyres. Dates for anomalies are: a October 19–28, 2000; b September 18–27, 2001; and c October 18–27, 2002

location of the transmitter antenna means that it may not clear the water as often as an anterior antenna but the protection afforded the base of the antenna may extend the lifespan of the transmitter. Future satellite telemetry studies should consider the trade off and chose the antenna location that best meets research objectives.

Carr et al. (1978) estimated a mean interesting period of 12.8 days for Tortuguero green turtles. Interesting periods for satellite-tracked turtles varied from 8 to 33 days and suggest females may have returned to nest as many as three times after release (Table 1). During the interesting period, female turtles are mainly resting (Hays et al. 1999). Green turtles may feed during the interesting period when there are foraging grounds close to the nesting beach (Hays et al. 2002b). Tortuguero green turtles do not appear to forage extensively during the interesting period (Mortimer 1981) because there are no sea grass beds in the vicinity of the beach. Mean interesting submergence times were shorter in our study than for green turtles at Ascension Island (Hays et al. 1999). It could be that the Tortuguero green turtles bask at the surface rather than rest at the sea floor. A direct observation study of interesting green turtles at Tortuguero suggested that female turtles remain within 10 km N and 10.1 km S of the previous nesting location and within 14.5 km of the coast (Meylan 1995), a much more restricted area than what was recorded in our satellite telemetry study. Meylan (1995) also reported mean travel speeds during the interesting period of $0.7\text{--}2.7\text{ km hr}^{-1}$ which are greater than those observed in our study. Logistical limitations to direct observations may explain the different estimates of the interesting area and the greater travel speeds are also likely an artifact of different methodologies. Meylan (1995) measured travel speed over shorter time intervals of 0.5–3.8 h. We calculated travel speed over much longer time periods (1.2–232.7 h, mean 33.0 h). The conclusion by Meylan (1995) that interesting turtles undertake longshore travel along the prevailing southward current with periodic correction by active up-current swimming explains the different estimates of travel speeds in the two studies. Rapid swimming may occur over short time periods but over longer periods the net changes in geographic position are small.

The circular and semicircular oceanic movements made by three turtles are inconsistent with previous records of open ocean travel in straight lines (Godley et al. 2002; Papi and Luschi 1996), but similar to a post-nesting green turtle from Taiwan that followed surface currents and moved in a large circle before swimming to benthic foraging grounds (Cheng 2000). Looping behavior has

was lower in this study than for previous green turtle satellite telemetry studies (Cheng 2000; Godley et al. 2002), total tracking time was longer. The posterior

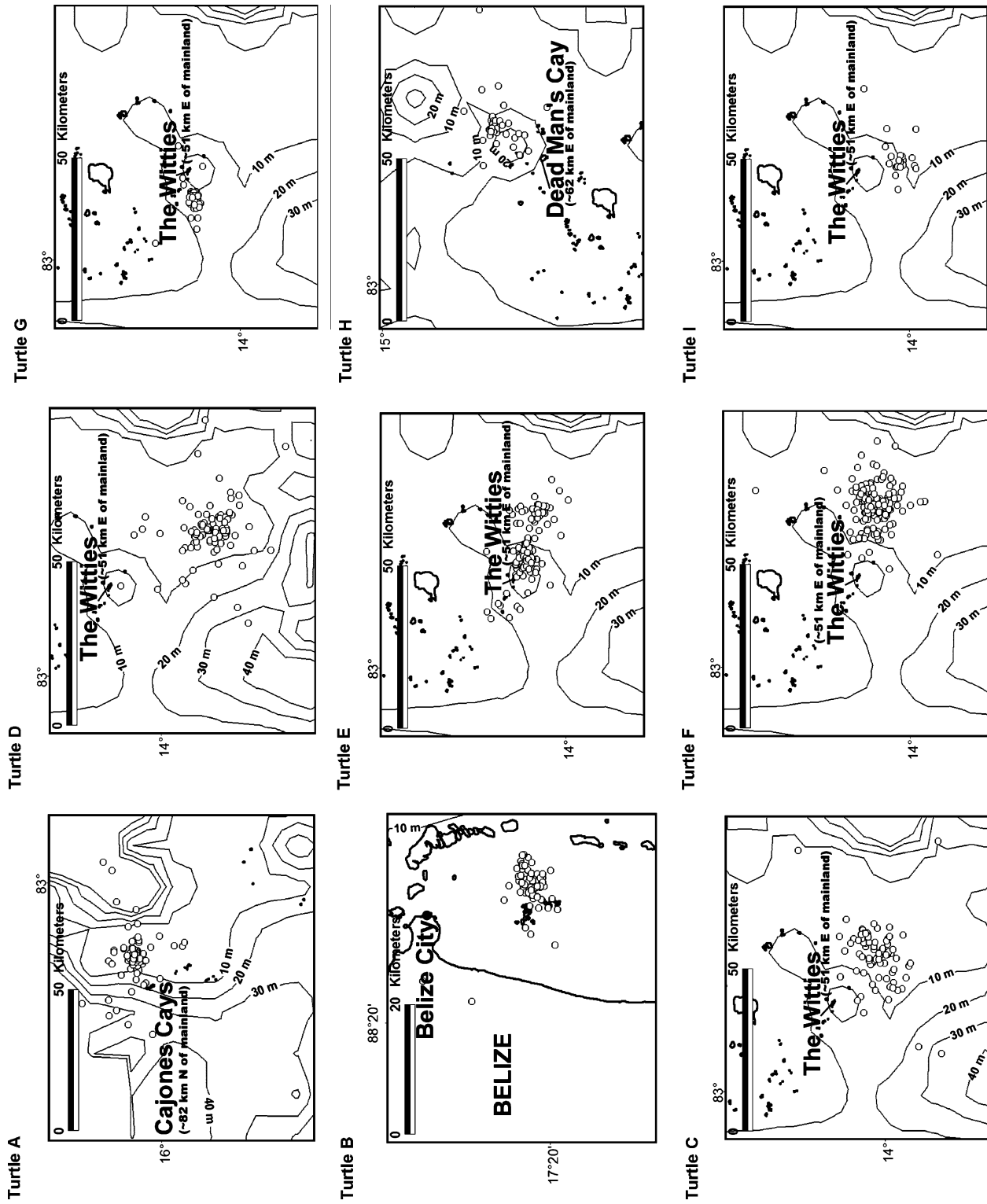


Fig. 5 Green turtle benthic foraging ground location data (open circles indicate location data points)

Turtle J

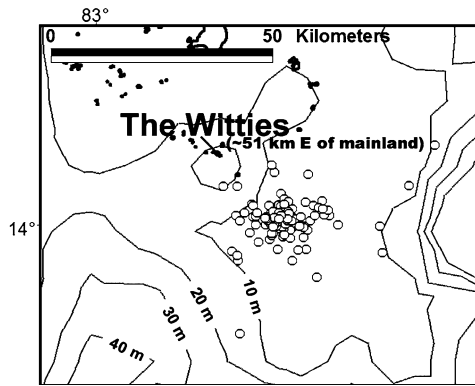


Fig. 5 (Contd.)

been described in disoriented green turtles (Luschi et al. 2001). Another possibility is that circling turtles are foraging in oceanic waters. Adult green turtles are benthic herbivores (Bjørndal 1997), hence they are not expected to feed actively in oceanic waters but biphasal migrations consisting of rapid straight-line open ocean travel followed by slower coastal migrations possibly associated with benthic feeding have been reported for green turtles (Cheng 2000; Godley et al. 2002; Hays et al. 2002a). Also, green turtles display behavioral plasticity (Hays et al. 2002b). When food items are available in oceanic waters close to the migratory routes, green turtles would benefit from utilizing these resources. The ocean section where the circular and semicircular movements were undertaken coincides with the southwestern Caribbean gyre (Andrade et al. 2003). This area hosts large rafts of *Sargassum* sp. which are utilized by post-hatchling green turtles for shelter and food from associated fauna (Carr and Meylan 1980; Carr 1987a; S. Troëng personal observation). Adult green turtles can feed on *Sargassum* sp. (Hirth 1997; Mortimer 1981) and may also use associated food items. In Nicaragua, Mortimer (1981) found that a small number of green turtles ($n=8$) had ingested *Sargassum vulgare*. Three of four green turtles captured in the Set Net Cays (also known as Pearl Cays) ($N^{\circ}12.27$ $W83^{\circ}24$), located to the north of where green turtles undertaking pelagic circles entered into coastal waters, had ingested *S. vulgare* (Mortimer 1981). Adult green turtles utilizing *Sargassum* sp. or associated food resources would be expected to engage in shallow dives, consistent with the very short submergence times of Turtle F, and stay close to or within the oceanic gyre to remain with the food resource. The southwestern Caribbean gyre is highly variable (Sheng and Tang 2003), which explains the variation between years in the location and extent of oceanic turtle movements. Oceanographic processes such as fronts, currents and eddies are known to influence the movements of loggerhead (Polovina et al. 2000) and leatherback turtles (Luschi et al. 2003a). Our study suggests that adult green turtles may be similarly influenced, at least over short time periods. Unfortu-

nately, the surface currents that concentrate *Sargassum* sp. also carry floating plastic materials and other contaminants to the same zones (Carr 1987a). Such materials are known to have lethal and sublethal effects on turtles (Carr 1987b; Lutcavage et al. 1997; McCauley and Bjørndal 1999) and may represent a threat to Tortuguero green turtles. Direct observations of adult green turtles feeding in *Sargassum* sp. concentrations and stomach content analysis are needed to confirm the hypothesis that green turtles are foraging during the oceanic movements rather than being partly or completely disoriented.

Migratory corridors have been described for marine turtles (Hays et al. 2001b; Morreale et al. 1996). For Tortuguero green turtles, the first part of the post-nesting migration (south of $N12^{\circ}24$) was either along a narrow migratory corridor close to shore or through oceanic waters. The two travel paths joined at $N12^{\circ}24$ where all ten green turtles (with the possible exception of Turtle C) passed within 15 km of Pearl Cay Point.

Adult Caribbean green turtles feed mainly on turtle grass *Thalassia testudinum* (Mortimer 1981), which is the most abundant seagrass in the region (Creed et al. 2003). Turtle grass grows on sandy and muddy substrates from lower intertidal areas to a maximum of 10–12 m, although it has been reported below 20 m depth (Creed et al. 2003). Detailed maps of Caribbean seagrass distribution are not available but the location and depth of the areas where Tortuguero green turtles took up residence suggest that they most likely correspond to turtle grass pastures. Only 2 of the 4,669 green turtle tag recaptures ($n=1$ in Guyana and $n=1$ in Brazil) were from locations outside the turtle grass species range (Green and Short 2003).

Distribution of tag recaptures probably does not reflect an unbiased distribution of post-nesting female turtles. Capture and reporting can be biased by fisheries effort and the willingness or likelihood of people reporting tagged turtles (Bjørndal et al. 2003). The different sample sizes for tag recaptures and satellite-tracked turtles prevent detailed comparison of the two datasets. However, both the methods indicate that a large proportion (0.82 and 0.8, respectively) of tagged Tortuguero green turtles forage in Nicaragua waters. This is consistent with previous studies which suggest that the Nicaraguan continental shelf with its extensive seagrass beds is the major foraging area for adult Tortuguero green turtles (Carr et al. 1978; Mortimer 1981). It appears that the area to the south and east of the Witties hosts high-density adult green turtle foraging.

The distance between the nesting beach and benthic foraging grounds documented in satellite telemetry studies was 1,968 km for the Ascension Island rookery (some turtles may not have reached foraging grounds) (Luschi et al. 1998), 1,076 km for Cyprus (Godley et al. 2002) and 1,073 km for Hawaii green turtles (Balazs 1994). The distance between the Tortuguero nesting beach and the foraging areas is much shorter at a mean distance of 512 km. Therefore, female green turtles from Tortuguero should spend less energy on migrations and

invest more energy in reproduction (Bjorndal 1995). If so, the Tortuguero green turtle population may have greater potential for recovery than other populations and the proximity of the foraging grounds could be a contributing factor to the increasing nesting trend (Bjorndal et al. 1999; Troëng and Rankin 2005).

The study results have multiple management implications. We establish that the interesting area for Tortuguero green turtles is greater than previously thought. To protect green turtles in the interesting habitat, enforcement efforts are needed not only in waters adjacent to the nesting beach in Tortuguero National Park but along the entire coast of Costa Rica and southern Nicaragua. In addition, coastal migrations may increase the probability of capture by fishermen (Hays et al. 2002a; Mortimer 1981; Pritchard 1973). Mortimer (1981) reports that fishermen in Nicaragua consider green turtle fishing to be good between Prinzapolka (N13°24.6 W83°34.8) and Pearl Cay Point in spring and late summer. The capture area and timing coincides with the migratory routes and time of green turtle migration between Nicaragua foraging grounds and Tortuguero. Clearly, the migratory corridors and major foraging grounds should be priority areas for active management. In total, more than 10,000 green turtles are caught by fishers in Nicaragua waters each year (Lagueux 1998). Although tag returns show that adult turtles are taken, the majority of captured turtles are of size classes corresponding to large juveniles (Lagueux 1998). The annual survivorship rates calculated for Tortuguero green turtles using tag recoveries (0.82, Campbell 2003; Campbell and Lagueux 2005) and a re-migration model (0.80, Solow et al. 2002) are lower than the 0.95 survivorship rate estimated for adult green turtles in Australia (Chaloupka 2002). So far, the large take has not resulted in decreased nesting at Tortuguero (Bjorndal et al. 1999; Troëng and Rankin 2005). Based on a recent population modeling study the Tortuguero population is likely already in decline, although it may not be detected on the nesting beach for several years due to the late age to maturity of green turtles (Campbell 2003). Given the importance of the Nicaragua feeding grounds, successful green turtle conservation efforts in Nicaragua are crucial to ensure continued nesting increases at Tortuguero.

From an ecosystem perspective, green turtles fill an important role in seagrass communities by cropping seagrass, speeding up nutrient cycling and preventing sediment build-up (Bjorndal and Jackson 2003; Jackson et al. 2001). The Tortuguero green turtle population is one of the largest in the world (Seminoff 2004), but green turtle abundance in the Caribbean remains relatively low in comparison with historical levels (Bjorndal et al. 2000; Jackson 1997). Restoring green turtle abundance will have positive effects on Caribbean marine ecosystems. Our study suggests that marine ecosystems in many Caribbean countries, and particularly in Nicaragua, will benefit from a restored green turtle population.

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References

- Addison DS, Gore JA, Ryder J, Worley K (2002) Tracking post-nesting movements of loggerhead turtles (*Caretta caretta*) with sonic and radio telemetry on the southwest coast of Florida, USA. *Mar Biol* 141:201–205
- Andrade CA, Barton ED, Mooers CNK (2003) Evidence for an eastward flow along the central and south American Caribbean coast. *J Geophys Res* 108:16-1–16-11
- Balazs GH (1994) Homeward bound: satellite tracking of Hawaiian green turtles from nesting beaches to foraging pastures. In: Schroeder BA, Witherington BE (eds) Proceedings of the 13th annual symposium on sea turtle biology and conservation. US Dep. Commer. NOAA Tech Memo NMFS-SEFSC-341:205–208
- Balazs GH (1999) Factors to consider in the tagging of sea turtles. In: Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M (eds) Research and management techniques for the conservation of sea turtles. IUCN/SSC marine turtle specialist group Publication No 4:101–109
- Balazs GH, Miya RK, Beaver SC (1996) Procedures to attach a satellite transmitter to the carapace of an adult green turtle, *Chelonia mydas*. In: Keinath JA, Barnard DE, Musick JA, Bell BA (Compilers) Proceedings of the 15th annual symposium on sea turtle biology and conservation. US Dep. Commer. NOAA Tech Memo NMFS-SEFSC-37:21–26
- Bellini C, Godfrey MH, Sanches TM (2001) Metal tag loss in wild juvenile hawksbill sea turtles (*Eretmochelys imbricata*). *Herp Rev* 32:172–174
- Bentivegna F (2002) Intra-Mediterranean migrations of loggerhead sea turtles (*Caretta caretta*) monitored by satellite telemetry. *Mar Biol* 141:795–800
- Bjorndal KA (1995) The consequences of herbivory for the life history pattern of the Caribbean green turtle, *Chelonia mydas*. In: Bjorndal KA (ed) Biology and conservation of sea turtles revised edition. Smithsonian Institution, Washington, pp 111–116
- Bjorndal KA (1997) Foraging ecology and nutrition of sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC, Boca Raton, pp 199–231
- Bjorndal KA, Jackson JBC (2003) Roles of sea turtles in marine ecosystems: Reconstructing the past. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles Volume II. CRC, Boca Raton, pp 259–273
- Bjorndal KA, Wetherall JA, Bolten AB, Mortimer JA (1999) Twenty-six years of green turtle nesting at Tortuguero, Costa Rica: An encouraging trend. *Conserv Biol* 13(1):126–134
- Bjorndal KA, Bolten AB, Chaloupka MY (2000) Green turtle somatic growth model: evidence for density dependence. *Ecol Appl* 10(1):269–282

- Bjorndal KA, Bolten AB, Chaloupka MY (2003) Survival probability estimates for immature green turtles *Chelonia mydas* in the Bahamas. *Mar Ecol Prog Ser* 252:273–281
- Bouchard SS, Bjorndal KA (2000) Sea turtles as biological transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology* 81(8):2305–2313
- Campbell CL (2003) Population assessment and management needs of a green turtle, *Chelonia mydas*, population in the western Caribbean. PhD dissertation, University of Florida, Gainesville
- Campbell CL, Lagueux CJ (2005) Survival probability estimates for large juvenile and adult green turtles (*Chelonia mydas*) exposed to an artisanal marine turtle fishery in the western Caribbean. *Herpetologica* 61(2):91–103
- Carr A (1987a) New perspectives on the pelagic stage of sea turtle development. *Conserv Biol* 1(2):103–121
- Carr A (1987b) Impact of nondegradable marine debris on the ecology and survival outlook of sea turtles. *Mar Pollut Bull* 18:352–356
- Carr A, Giovannoli L (1957) The ecology and migrations of sea turtles. 2. Results of field work in Costa Rica, 1955. *Am Mus Novit* 183:1–32
- Carr A, Meylan AB (1980) Evidence of passive migration of green turtle hatchlings in sargassum. *Copeia* 1980(2):366–368
- Carr A, Carr MH, Meylan AB (1978) The ecology and migrations of sea turtles, 7. The west Caribbean green turtle colony. *Bull Am Mus Nat Hist* 162:1–46
- Chaloupka M (2002) Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. *Ecol Modell* 148:79–109
- Cheng IJ (2000) Post-nesting migrations of green turtles (*Chelonia mydas*) at Wan-An Island, Penghu Archipelago, Taiwan. *Mar Biol* 137:747–754
- Creed JC, Phillips RC, Van Tussenbroek BI (2003) The seagrasses of the Caribbean. In: Green EP, Short FT (eds) *World atlas of seagrasses*. University of California, Berkeley, pp 234–242
- Godley BC, Richardson S, Broderick AC, Coyne MS, Glen F, Hays GC (2002) Long-term satellite telemetry of the movements and habitat utilisation by green turtles in the Mediterranean. *Ecography* 25:352–362
- Green EP, Short FT (2003) *World atlas of seagrasses*. University of California, Berkeley
- Hays GC, Pusi P, Papi F, del Seppia C, Marsh R (1999) Changes in behavior during the inter-nesting migration for Ascension Island green turtles. *Mar Ecol Prog Ser* 189:263–273
- Hays GC, Åkesson S, Broderick AC, Glen F, Godley BJ, Luschi P, Martin C, Metcalfe JD, Papi F (2001a) The diving behavior of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution. *J Exp Biol* 204:4093–4098
- Hays GC, Dray M, Quaife T, Smyth TJ, Mironnet NC, Luschi P, Papi F, Barnsley MJ (2001b) Movements of migrating green turtles in relation to AVHRR derived sea surface temperature. *Int J Remote Sens* 22(8):1403–1411
- Hays GC, Åkesson S, Godley BJ, Luschi P, Santidrian P (2001c) The implications of location accuracy for the interpretation of satellite-tracking data. *Anim Behav* 61:1035–1040
- Hays GC, Broderick AC, Godley BJ, Lovell P, Martin C, McConnell BJ, Richardson S (2002a). Biphase long-distance migration in green turtles. *Anim Behav* 64:895–898
- Hays GC, Glen F, Broderick AC, Godley BJ, Metcalfe JD (2002b) Behavioral plasticity in a large marine herbivore: contrasting patterns of depth utilisation between two green turtles (*Chelonia mydas*) populations. *Mar Biol* 141:985–990
- Hendrickson JR (1958) The green sea turtle, *Chelonia mydas* (Linn.) in Malaya and Sarawak. *Proc Zool Soc Lond* 130(4):455–535
- Hirth HF (1997) Synopsis of the biological data on the green turtle *Chelonia mydas* (Linnaeus 1758). USFWS Biological Report 97(1)
- Jackson JBC (1997) Reefs since Columbus. *Coral Reefs* 16(Suppl):S23–S32
- Jackson JBC, Kirby MX, Berger WG, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Lagueux CJ (1998) Marine turtle fishery of Caribbean Nicaragua: human use patterns and harvest trends. PhD dissertation, University of Florida, Gainesville
- Lima EHSM, Troëng S (2001) Link between green turtles foraging in Brazil and nesting in Costa Rica? *Mar Turtle News* 94:9
- Luschi P, Hays GC, Del Seppia C, Marsh R, Papi F (1998) The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proc R Soc Lond B Biol Sci* 265:2279–2284
- Luschi P, Åkesson S, Broderick AC, Glen F, Godley BJ, Papi F, Hays GC (2001) Testing the navigational abilities of ocean migrants: displacement experiments on green sea turtles (*Chelonia mydas*). *Behav Ecol Sociobiol* 50:528–534
- Luschi P, Hays GC, Papi F (2003a) A review of long-distance movements by marine turtles, and the possible role of ocean currents. *Oikos* 103:293–302
- Luschi P, Sale A, Mencacci R, Hughes GR, Lutjeharms JRE, Papi F (2003b) Current transport of leatherback sea turtles (*Dermochelys coriacea*) in the ocean. *Proc R Soc Lond B Biol Sci* 270(Suppl):S129–S132
- Lutcavage ME, Plotkin P, Witherington B, Lutz PL (1997) Human impacts on sea turtle survival. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*. CRC, Boca Raton, pp 387–409
- McCauley SJ, Bjorndal KA (1999) Conservation implications of dietary dilution from debris ingestion: sublethal effects in post-hatchling loggerhead sea turtles. *Conserv Biol* 13(4):925–929
- Meylan AB (1995) Behavioral ecology of the west Caribbean green turtle (*Chelonia mydas*) in the inter-nesting habitat. In: Bjorndal KA (ed) *Biology and conservation of sea turtles revised edition*. Smithsonian Institution, Washington DC, pp 67–80
- Morreale SJ, Standora EA, Spotila JR, Palandino FV (1996) Migration corridor for sea turtles. *Nature* 384:319–320
- Mortimer JA (1981) The feeding ecology of the west Caribbean green turtle (*Chelonia mydas*) in Nicaragua. *Biotropica* 13(1):49–58
- Papi F, Luschi P (1996) Pinpointing 'Isla Meta': the case of sea turtles and albatrosses. *J Exp Biol* 199:65–71
- Polovina JJ, Kobayashi DR, Parker DM, Seki MP, Balazs GH (2000) Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997–1998. *Fish Oceanogr* 9:71–82
- Pritchard P (1973) International migrations of South American sea turtles (Cheloniidae and Dermochelidae). *Anim Behav* 21:18–27
- Seminoff J (2004) Marine turtle specialist group *Chelonia mydas* assessment. IUCN Marine Turtle Specialist Group
- Seminoff JA, Resendiz A, Nichols WJ (2002) Home range of green turtles *Chelonia mydas* at a coastal foraging area in the Gulf of California, Mexico. *Mar Ecol Prog Ser* 242:253–265
- Sheng J, Tang L (2003) A numerical study of circulation in the Western Caribbean Sea. *J Phys Oceanogr* 33:2049–2069
- Solow AR, Bjorndal KA, Bolten AB (2002) Annual variation in nesting numbers of marine turtles: the effect of sea surface temperature on remigration intervals. *Ecol Lett* 5:742–746
- Troëng S, Drews C (2004) Money talks: economic aspects of marine turtle use and conservation. WWF-International, Gland, Switzerland
- Troëng S, Rankin E (2005) Long-term conservation of the green turtle *Chelonia mydas* nesting population at Tortuguero, Costa Rica. *Biol Conserv* 121:111–116
- Troëng S, Mangel J, Reyes C (2003) Comparison of monel#49 and inco#681 tag loss in green turtles *Chelonia mydas* nesting at Tortuguero, Costa Rica. Proceedings of the twenty-second annual symposium on sea turtle biology and conservation. U.S. Dep. Commer. NOAA Tech Memo NMFS-SEFSC-503:121–122