2005

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ABUNDANCE AND TIDAL MOVEMENTS
OF GREEN TURTLE (*CHELONIA MYDAS*) IN B.C.S., MÉXICO

A Thesis

Presented to

The Faculty of Moss Landing Marine Laboratories

San José State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Louise B. Brooks

August 2005

UMI Number: 1429407

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ABSTRACT

ABUNDANCE AND TIDAL MOVEMENTS OF GREEN TURTLE (*CHELONIA MYDAS*) IN B.C.S., MEXICO

by Louise B. Brooks

We studied population characteristics, abundance, and tidally-oriented movements of East Pacific green turtle (*Chelonia mydas*) in Estero Banderitas, a tidal foraging area in Bahía Magdalena, Baja California Sur, Mexico. Most (98%) individuals captured were juveniles. Turtles remained in the area through seasons and years, indicating this was a developmental foraging area. A mean population size of 333 turtles was estimated using Jolly-Seber method, and turtles were denser than those found at other regional foraging areas.

We measured tidal currents with an Acoustic Doppler Profiler and tracked turtles using GPS-VHF telemetry. Turtles displayed greater vagility and faster rate of movement than at other foraging areas. Tidal speed and direction were highly correlated to turtle speed and direction. Fifteen of 19 tracks had significant vector correlation coefficients. Turtles moved with consecutive tides, indicating unselective tidal stream transport. Results indicate that Estero Banderitas is an ideal location for a community-based sea turtle sanctuary.

ACKNOWLEDGMENTS

I first visited the Baja California peninsula in June 1998 and after three weeks of fieldwork I was hooked. As a result, I enrolled at MLML to complete my master's while studying sea turtles in Bahía Magdalena. I was inspired, not only by the beauty and mystery of the land, sea and sea turtles of Baja, but also by the people who I am privileged to call friends and colleagues. This project relied on the participation of numerous people - local, national and international - who joined us in the field in Estero Banderitas to capture and track turtles. Together, we learned to navigate the intricate and ever-changing "maze" of tidal channels. We spent hours artfully cushioned in a panga, tucked in a mangrove stand or out under the stars, waiting by set turtle net. We marveled over the surreal experience of tracking a turtle by kayak during the midnight hours, when often the only sound was that of a turtle breaking the water's surface to breathe. We learned each other's language, cuisine, and culture. We are now bound by our shared experience, and by our participation in something that became full of meaning for each of us. It is through this experience that the work presented in this thesis was accomplished. I am indebted to all, including Barbara Andrews, Oakley Brooks, Alfonso Castro, Katie Cullen, Chris Detweiller, Adan Hernandez, Pam Kylstra, Pam Lawrence, Jen and Sean McKeane, Victor Mesa, Colby Moore, Nani Phillips, Juan Ramirez, Rodrigo Rangel, Rafael Riosmena, Lizzie Rosenberger, Gabriel Sarabia, Juan Sarabia, Julio Solis, Joelle Sweeney, Joel Talamantes, Marc Taylor, Erin Tennant, Will Urmston, Bill Watson, Alberto Ojeda, Marcos Vasquez, and SFS students, faculty and staff. I am grateful for our collaboration with the School for Field Studies in P.S.C. They gave constant support

in the form of email, cabin, showers, people, boats and a welcoming community in general. Terri Garland braved the roads, the garlic, and the desert to be a welcome companion, photographer and friend. Volker Koch provided sushi, hugs, a voice on the radio, and scientific advice whenever it was needed. My mom came down to ride shotgun on the last drive home with the submarine – and lived to tell about it. Very importantly, this never would have happened without J. Nichols, who picked me up at the bus station in La Paz, showed me my first sea turtle, and started me on my way. He is both a great friend, and a challenging mentor.

I benefited from the skills of the Moss Landing Marine Laboratories community, which helped me into the field, and worked to make sense of all the data when I returned. My advisor, Jim Harvey, taught me to be a scientist and offered invaluable ideas to improve this research during every stage. I feel very fortunate to have studied with him – I could ask for no better foundation. Dr. B sent his precious ADPs down with me to Baja, and then sat with me on countless Tuesdays and Thursdays (he was retired!) to wade through seemingly endless ADP data and find a use for it. His instruction added an incredible dimension to this project. Steph Flora answered so many MATLAB questions, with a smile and for only a quarter. Bill Watson took all my ideas about tags and telemetry and engineered them into reality. The No-gills, Air-breathers, Bird, Mammal and Turtle, Vertebrate Ecology Lab is truly the place to be – what a great support network and learning environment. Many thanks also to Small Boats and Diving Operations, Facilities, Kenneth Coale, Greg Cailliet, Mike Foster, Lara Ferry-Graham and Mike Graham. I remember the thrill I felt when I drove up the hill for my first day

here at MLML - how lucky I was to be studying here! MLML has met and exceeded those expectations.

Finally, this whole experience would not have been possible, nor as much fun, without the love and support of friends and family. Here at MLML, I thank Josh Adams, Sarah Connors, Heather Kerkerling, Lisa Kerr, Laurie McConnico, Hannah Nevins, Beth Phillips, Kristin Rasmussen, Wade Smith, Joelle Sweeney, and Tam Voss. Outside MLML, I am grateful for Lacey and Blayne Colmore, Oakley and Sydney Brooks, Oaks Brooks, Sam Brooks, Heather Colmore, Jen Colmore, Carson Colmore, Louis Connick, and The Nichols Family. These people gave me understanding even when they had no idea what I was talking about, unconditional love, financial backing, homes to crash in and inspiration – it was a group effort.

This work was funded by National Fish and Wildlife Foundation, Homeland Foundation, PADI Foundation, Harvey Graduate Research Fellowship, and Dr. Earl H. and Ethyl M. Myers Oceanographic Trust, the San José State University Dean's Scholarship and the John H. Martin Scholarship. Research was conducted under permit # 280499.213.03 1565 and # 280700.213.03 2619 authorized by Secretaria de Medio Ambiente Recursos Naturales y Pesca, Estado Unidos de México. Animal care protocol was approved by SJSU Animal Care and Use Committee (IACUC #805).

The chapters in this thesis are written in the format for Marine Ecology Progress Series, to which they will be submitted. I was the primary researcher and author on both papers, and acknowledge the assistance of my co-authors in this research.

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CHAPTER 1:
ABUNDANCE AND CHARACTERISTICS OF JUVENILE GREEN TURTLE
(*CHELONIA MYDAS*) IN ESTERO BANDERITAS, B.C.S., MÉXICO

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ABSTRACT

We studied the East Pacific green turtle (*Chelonia mydas*) at a tidally-influenced foraging area in Estero Banderitas, Baja California Sur, México to assess stock size, structure, and basic ecology. Field activities were from June 2000 to August 2003. One hundred eighty-four green turtles, four hawksbill turtles (*Eretmochelys imbricata*), and one loggerhead turtle (*Caretta caretta*) were captured with entanglement nets. There were 88 recaptures and 271 total captures. Time at large was 4 hours to 973 days. Recapture rate increased significantly during the years. Individual turtles were recaptured in different seasons and years. We used closed- and open-population methods to assess stock size. Estimates were 304 (95% CI = 249 – 389) to 391 (95% CI = 182 – 1333) turtles, and a density of 6.7 turtles km⁻². Green turtle straight carapace length (SCL) was 38.8 to 85.6 cm and mass was 7.0 to 80.7 kg. Of 184 green turtles captured, 181 were juveniles. Mean body condition index ($CI = (\text{body mass}/SCL^3) \cdot 10^4$) was 0.74 to 1.77, and did not vary among seasons. Few turtles had signs of injury, anthropogenic or otherwise. Eighty-four percent had at least one species of epiflora or epifauna, and presence of epibionts did not depend on turtle size or body condition index. We believe that green turtles recruit to this neritic foraging ground from their pelagic, oceanic life stage, and remain in the area until maturity. Green turtles are endangered worldwide, and are present in the Baja California region at a fraction of historical abundances. Community-based conservation efforts are promoting the establishment of a sea turtle sanctuary in Estero Banderitas, for which these data will be relevant and useful for protecting this juvenile stock in its foraging and developmental area.

INTRODUCTION

The East Pacific green turtle (*Chelonia mydas*) is the most common of five species of sea turtle off the Baja California peninsula, México. Green turtles were historically in such abundance that the area was described by Steinbeck & Ricketts (1941) as “the region of the sea turtle.” Due to more than a century of large-scale exploitation, the green turtle is presently listed as endangered by the World Conservation Union (IUCN; Hilton-Taylor 2000).

Green turtles often traverse great distances of ocean during development (Fig. 1). Green turtles off the Baja California peninsula originate at rookeries located hundreds of kilometers south in Michoacán, México, and the Revillagigedos, Tres Marias, and Galapagos Islands (Brattstrom 1982, Awbrey et al. 1984, Alvarado & Figueroa 1986, Marquez 1990, Nichols 2003). Females lay a clutch of about 70 eggs, and turtles hatch after an incubation period of 46 to 62 days (Marquez 1990). Hatchlings leave the nesting beach and disperse north and south (Cliffon et al. 1982). They enter a pelagic stage during which they probably drift passively, often associating with flotsam, before recruiting to neritic foraging areas (called developmental areas), such as those off the Baja California peninsula (Carr & Meylan 1980, Carr 1987). Juveniles may remain in these developmental areas for more than twenty years (Seminoff et al. 2002, Koch et al. in press), feeding on sea grass and algae in sheltered lagoons (Balazs et al. 1987, Bjorndal 1997). Upon maturity, green turtles make a homing migration every two or three years to their natal beach to mate and nest (Musick & Limpus 1997).

Green turtles recruit to developmental foraging areas at 25 to 40 cm straight carapace length (SCL; Felger et al. 1976, Balazs 1980, Bjorndal & Bolten 1988, Limpus et al. 1994) and remain in feeding areas year-round (Balazs 1979, Limpus 1979, Mendonça & Ehrhart 1982, Bjorndal et al. 2005) or migrate seasonally, depending on water temperature (Morreale et al. 1992, Epperly et al. 1995). At some Atlantic foraging areas green turtles originated from different source rookeries (Lahanas et al. 1998). In most regions, adult and juvenile green turtles occupy separate foraging areas (Mendonça & Ehrhart 1982, Bjorndal et al. 2005), although these areas can overlap (Seminoff et al. 2003a).

Few long-term studies have been conducted regarding abundance and density of green turtles in foraging areas. It is more difficult to study and monitor in-water activities (e.g. migration, foraging), and thus most long-term monitoring of sea turtle populations has been conducted on nesting beaches. Monitoring of juveniles at feeding grounds can provide early assessment of population trends (Bjorndal et al. 2005), complement information on turtles sampled at nesting beaches, and provide data on stock size and structure on foraging areas.

Green turtles in northwestern México have cultural, economical, and biological importance (Nichols 2003). Indigenous people, such as the Seri, used sea turtle meat and products in a sustainable way for centuries (Smith 1974). Beginning in the 1900s, commercial exploitation of sea turtles in Baja California and mainland México caused a drastic decline in the seemingly endless supply of sea turtles. East Pacific green turtles were taken from the foraging areas of the Baja Peninsula and from the mating and nesting

areas of Michoacán, México (Cliffon et al. 1982, Alvarado & Figueroa 1986). Sea turtle eggs also were taken at nesting beaches. Human coastal populations increased near Michoacán nesting beaches in response to an expanding demand for sea turtle eggs. It is estimated that 40,000 eggs were taken nightly in 1970 at Colola, the main nesting beach (Alvarado and Figueroa, 1986)

Green turtles remained numerous through 1970, when it was estimated that 25,000 females nested in Michoacán (Cliffon et al. 1982). But by 1979, this number had decreased by 50% (Alvarado & Figueroa 1995). At feeding areas off the Baja California peninsula, many areas of abundance were almost entirely depleted of sea turtles by the mid 1980s (Seminoff 2000, Nichols et al. 2002). In 1979, formal protection of nesting beaches began in Michoacán, with the goal of restoring numbers of nesting turtles to historical levels (Alvarado & Figueroa 1986). Harvest in feeding areas has hampered, and even outweighed, long-term conservation efforts on nesting beaches (Alvarado-Diaz et al. 2001). Despite national and international laws and a 1990 presidential decree banning capture and trade in sea turtles (Aridjis 1990), approximately 7,800 green turtles are killed each year on the Baja Peninsula (Gardner & Nichols 2001, Nichols 2003).

Recently, the threat of current harvest of sea turtles is recognized (Nichols 2003, Seminoff 2004, Koch et al. in review), and conservation efforts are underway throughout the region to protect juvenile and adult turtles during critical aquatic periods. The Recovery Plan for the East Pacific green turtle (NMFS-USFWS 1998) states the need to identify threats to turtles on foraging areas, to reduce take through education, and protect

and manage foraging habitat. The same plan, however, recognizes a lack of knowledge of abundance and distribution of green turtles on their foraging areas.

Green turtles were formerly abundant in Bahía Magdalena, Baja California Sur. They are still found in the lagoons and larger bay of Bahía Magdalena, although turtles often are “fished out” of an area in a given year (Nichols 2003). Observations in 2000 indicated that green turtles occurred in Estero Banderitas and catch rates indicated that they were more numerous in this area than other areas surveyed (Brooks et al. in press). Fishers confirmed that it was one of the last local areas in Bahía Magdalena in which green turtles were abundant. We investigated the population structure and ecology of green turtles at this foraging area. We hypothesized that juvenile green turtles used Estero Banderitas as a neritic, developmental feeding area, remaining in the vicinity year-round until maturity, and possibly returning after homing migrations. The characteristics of this foraging area made it ideal for formal protection. We sought to provide the scientific data and inspire the community support and stewardship necessary to establish a sea turtle sanctuary in Estero Banderitas.

METHODS

Site description. The Bahía Magdalena-Almejas complex is one of the largest Pacific coastal mangrove systems in México, enclosing an area greater than 1000 km² (Funes-Rodriguez et al. 2001; Fig. 2). It can be divided into three zones: a northern zone characterized by a network of shallow lagoons and canals (*esteros*); a central zone made up of deeper Bahía Magdalena, and a southern zone which encompasses Bahía Almejas

(Alvarez-Borrego et al. 1975). Estero Banderitas (24°50' – 25°00' N and 112°05' – 112°08' W) is an evaporative basin located in the northern zone of Bahía Magdalena (Fig. 2). The roughly 50 km² *estero* is the largest in the complex, and is heavily influenced by tidal currents, with salinity and temperature increasing northward near the head of the basin (Brooks et al. in press). Average salinity at the mouth of Estero Banderitas is between 36.9‰ and 38.7‰ (Alvarez-Borrego et al. 1975), average water temperature is from 18°C to 31°C, and depth is 1 to 9 m. Substrate consists of sand and mud with patchy algae and sea grass beds throughout.

Turtle capture and assessment. We captured turtles with ~100-m long, 25-cm mesh (50-cm stretched) nylon or cotton entanglement nets. Nets were set opportunistically at ten locations throughout Estero Banderitas, for up to 24 hours (Fig. 2). We continually monitored the net for entangled turtles, and upon capture, we transferred turtles to a padded, shaded holding area in either a boat or a nearby camp. Field activities were conducted by students and staff at Center for Coastal Studies (School for Field Studies), the Grupo Tortuguero de las Californias, and the authors.

Standard morphological data were reported for each individual. Metal forester's calipers were used to measure standard length (straight carapace length, SCL, measured as a straight line from notch to tip of distal marginal scute) to the nearest 0.1 cm. Curved carapace length (CCL, the curved distance from notch to tip) was measured using a flexible measuring tape. Tail length (total tail length, TTL, measured from posterior edge of plastron to tip of tail) was measured with smaller calipers to the nearest 0.01 cm. Turtles were weighed to the nearest 1 kg with a spring scale. A metal Inconel tag

(National Band and Tag Company, Newport, Kentucky) was applied proximal and adjacent to the first large scale on each rear flipper (Balazs 1999). Turtles were released at the capture location within ten hours of capture. We used data from initial capture for all morphological analyses. A Kruskal-Wallis test was used to test for differences in the frequency distribution of SCL among years.

There has been use of various terms to classify the life history stages of sea turtles. We use the term juvenile to refer to animals that have not reached sexual maturity and adult for those deemed mature (Musick & Limpus 1997). We assessed maturity of each animal based on a mean nesting size (MNS; Limpus et al. 1994) of 77.3 cm SCL at the Michoacán, México nesting beach (Figueroa et al. 1993). All animals less than MNS were classified as juveniles, and all animals greater than MNS were considered adults (Seminoff et al. 2003a). Mature turtles were identified as male if the tail/length index ($\lambda_t = \text{TTL}/\text{SCL}$) was > 0.38 , and considered female if λ_t was < 0.38 (Lyon et al. in press).

The general health of the animal was assessed through physical observation. Any physical abnormalities were recorded. We examined each animal closely for presence of epibionts. Species and number or percentage cover of epibiotic flora and fauna were noted. A body condition index ($\text{CI} = (\text{body mass}/\text{SCL}^3) * 10^4$) was calculated as a measure of health (Bjorndal et al. 2000). A two-way ANOVA was used to test for differences in mean CI among years and seasons.

Capture effort at one capture location, Isla Conchalita, was standardized to 24-hour effort. We classified captures as daytime if the capture occurred between sunrise

and sunset, and nighttime if the capture occurred between sunset and sunrise. We used a Chi-Square test to examine differences between day and night captures at Isla Conchalita from a 50/50 distribution during a 12-month year, assuming that day and night hours were equal during a year. Recapture rate was calculated as # of recaptures/total # of captures for a 15-day capture period. A one-way ANOVA was used to test for differences in mean recapture rates among years.

We tested all data for normality with a Kosmogorov-Smirnoff test and used a Cochran's or F-test to test for homogeneity of variances. Analyses were performed with SYSTAT Version 10 software (SPSS Inc., 2000).

We estimated population size using Schnaebel-Schumacher and Jolly-Seber methods (Krebs 1999). We grouped captures into 15-day periods for the Schnaebel-Schumacher estimate. For the Jolly-Seber estimate, we separated mark-recapture data into six periods of capture effort: June – December, 2000, January – June, 2001, July – December, 2001, January – June, 2002, July – December, 2002 and January – August, 2003. Recaptures occurring within the period of interest were not used. Standard methods of population estimation often are difficult to apply to populations of rare animals, because capture and recapture values per session are low (C. Krebs, pers. comm.). We, therefore, grouped capture periods to adhere to requirements of each estimate. We consider these periods to be independent because turtles were given enough time to disperse randomly within the area. In general, turtle movement is circatidal, meaning that tagged turtles redistributed themselves within one tidal period, or twelve

hours (Chapter 2). Population estimates were performed using Programs for Ecological Methodology, 2nd Edition (Krebs 2002).

RESULTS

Field investigations were conducted from 30 June, 2000 to 1 August, 2003. We captured 189 individual turtles of which 184 were green turtles, four were hawksbill turtle (*Eretmochelys imbricata*), and one was a loggerhead turtle (*Caretta caretta*). We captured turtles at ten different sites (Fig. 1), but 78% of captures occurred at five main sites: Isla Conchalita, Estero Estufa, Net Site #1, Net Site #2, and Campamiento Viejo. These five sites had similar bathymetric qualities. In each place the net was set over a narrow, deep channel. Substrate found at capture locations were mud, shells, sand, or rocks.

Capture effort was more intense in summer, but effort occurred throughout the year. For captures when time of capture was recorded, we caught more turtles during the night ($n = 82$) than during day ($n=59$). In most capture locations, these numbers reflect an increased effort during night. However, at Isla Conchalita, 42 turtles were captured during a 12-month period: 25 were captured during night and 17 were captured during day. There was no significant difference from an expected 50% of captures during day and 50% during night ($0.25 < P(\chi^2 \geq 1.52) < 0.10$).

Fifty-five of the 184 individual green turtles were recaptured a total of 87 times, which amounted to 271 total captures of green turtles (Table 1). We recaptured one of the hawksbill turtles once. Many individual green turtles were recaptured more than once: 35

were recaptured once, eleven were recaptured twice, six were recaptured three times, and three turtles were recaptured four times during the study period. Time before recapture was 4 hours (BMA28JUL2002-1) to 973 days (BMA29JUL2000-2). Individual turtles were recaptured in different seasons and years, indicating year-round and multiple-year residence in Estero Banderitas.

Recapture rates of green turtles increased significantly during the study period ($F = 5.940$, $df = 3$, $P = 0.002$; Table 1). In 2000, the first year of the study, there were two recaptures which resulted in a recapture rate of 4.3 %. The recapture rate increased to 33.5 % in 2001. In 2002, the rate decreased to 25.3 %, probably due to the use of new net sites. In 2003, the recapture rate was 46.8 %.

Green turtle SCL was 38.8 to 85.6 cm (mean = 53.7 ± 8.2 cm SD, $n = 184$; Fig. 2). Mass was 7.0 to 80.7 kg (mean = 22.4 ± 11.7 kg, $n = 173$; Fig. 3). Hawksbill turtle SCL was 51.0 to 63.4 cm (mean = 56.6 ± 5.9 cm, $n = 4$), and mass was 17.6 to 35.6 kg (mean = 23.4 ± 9.8 kg, $n = 4$). The one loggerhead turtle measured 65.0 cm SCL and 44.5 kg mass.

We classified 181 of the 184 green turtles as juveniles. We did not predict the sex of immature animals. Only three green turtles had standard lengths greater than the MNS of 77.3 cm. Using the tail length index, these adults were classified as females, possessing these characteristics: (1) SCL = 79.4 cm, $\lambda t = 0.22$; (2) SCL = 80.1 cm, $\lambda t = 0.33$; (3) SCL = 85.6 cm, $\lambda t = 0.22$. However, two turtles, including one previously designated as female, exhibited elongated tails and were classified as males at time of capture based on the presence of this secondary sex characteristic (SCL = 73.1 cm, tail

length = 22.8 cm; SCL = 80.1 cm, tail length = 26.5 cm). Tail length > 20 cm has been used in other studies to classify turtles as males (Seminoff et al. 2003a).

We observed a slight increase in mean SCL during the four sampling years, from 51.0 ± 4.9 cm in 2000 to 55.3 ± 11.0 cm in 2003. This increase was statistically insignificant, but is worth noting (Kruskal-Wallis, $df = 3$, $P = .096$).

Data were available on scute patterns for 148 turtles. One fifth of green turtles had irregular scute patterns, deviating from the “typical” five central scutes and four lateral scutes (Marquez 1990). Of these, 26 turtles had extra (6-9) central scutes. Five turtles had one extra right lateral scute, two of which had extra central scutes. Five turtles had one or two extra left lateral scutes, four of which had extra central scutes. One had an extra scute in all three areas. No turtles had irregular marginal scute patterns. We did not examine the head for abnormalities in scute numbers.

Mean body condition index (CI) was 0.74 to 1.77 (mean = 1.33 ± 0.16 , $n = 169$) for green turtles (Table 2). There was no difference in mean CI between summer and winter ($F = 1.969$, $df = 1$; $P = 0.162$). There was a difference in mean CI among years ($F = 11.962$, $df = 3$; $P < 0.000$), CI was greatest in 2002 and least in 2003. There was no significant interaction between season and year when assessing trends in body condition.

Few turtles had signs of injury. Nine turtles had missing pieces of rear flippers or marginal scutes. All of these had healed, indicating that injuries had been sustained earlier in life. One of these turtles was missing an entire rear flipper, but had no signs of poor health. In fact, this turtle was the second largest turtle caught, and had a body

condition index greater than the mean for the year of capture. One turtle was missing two head scutes and had signs of a contusion. One turtle had an injured front flipper.

Data on the presence of epibiotic flora and fauna were collected for 154 individuals. One hundred thirty (84%) of these individuals had at least one species of epibiont and 24 (16%) had no epibionts. Forty-two turtles had only barnacle species as epibionts, and eight turtles had only algae as epibionts; the remaining 80 turtles had epiflora and epifauna. The turtle barnacle (*Chelonibia testudinaria*) was present on 113 individuals, in quantities of one to >50. These were predominantly on the carapace and plastron, and to a lesser extent, the flippers, head, and beak. An embedding barnacle *Tubicinella cheloniae* was on eleven turtles. *Tubicinella* was most often (50%) on the leading edge of the front flippers, but also was present on the head, carapace, plastron, and trailing edge of flippers. *Tubicinella* often caused bleeding at the embedded site. Additional epifauna occurred in small numbers, including worms, leaches, isopods, mollusks, and parasites. Algae were present primarily on the carapace of turtles. Green algae were present on 34 turtles, covering 5% to 95% (mean = 46.0 ± 31.8 %) of the carapace. Red algae occurred on 19 turtles, and had a similar range of 5% - 85% cover. Red algae generally had less coverage (mean = 26.4 ± 25.8 %) than green algae, and also were found primarily on the carapace. Brown algae occurred on 15 turtles at 50% - 70% cover (mean 38.1 ± 26.7 %). Seventeen turtles had the presence of epiflora recorded simply as "algae."

Epibionts were present on turtles of all sizes. Mean SCL (53.8 ± 8.1 cm) of turtles with epibionts was not significantly different than the mean SCL (52.8 ± 7.4) of

turtles without epibionts ($t = 0.59$, $df = 153$; $P = 0.55$). Epibionts did not appear to affect the health of the turtle, nor were they an indicator of poor health. Mean body condition index was not different between those turtles with epibionts (1.33 ± 0.14) and those without epibionts (1.34 ± 0.15 ; $t = 0.35$, $df = 142$; $P = 0.73$).

We estimated there were 327 (95% CI = 280 – 420) animals in Estero Banderitas using the Schumacher method. Using the Schnabel method we estimated 304 turtles (95% CI = 249 – 389) in Estero Banderitas. We used 15-day sample periods, amounting to 49 sample periods and 83 recaptures, and estimated the size of the population at the end of sampling (August 2003). Estimated abundance using Jolly-Seber method (Table 3, 4) increased during the project time, from 78 turtles (95% CI = 24 - 477) to 391 turtles (95% CI = 182 – 1333). This method requires three or more capture occasions to calculate a population estimate (Krebs 1999), implying that the best estimates occurred after Sample 3. A mean of 332.8 turtles (using sample periods 4 and 5, rounded to 333 turtles) yields a density estimate of 6.7 turtles km^{-2} for the entire area (50 km^2).

DISCUSSION

Sea turtles were historically numerous in Bahía Magdalena and other sheltered lagoons along the Pacific coast of the Baja Peninsula (Nichols 2003). At present, however, many regional feeding areas have lesser densities of green turtles than Estero Banderitas (Mariscal Loza & Koch 2004). The presence of a relatively abundant assemblage of juvenile green turtles in Estero Banderitas indicates this is an important developmental feeding area for the East Pacific population.

Optimal capture conditions, including low light and reduced wind, were often present during night. These observations led to concentrated capture effort during night hours. Increased recaptures throughout the study period indicated that turtles were remaining in the area throughout the four years of the study. The capture of untagged individuals throughout all years indicated that turtles continued to recruit to the area, and that some individuals eluded capture. The SCL of smaller turtles did not differ considerably among years, indicating that new recruits were continually arriving at a size of ~ 40 cm SCL. Smaller turtles (23 – 25 cm SCL) have been caught using similar nets (B. Redfoot, pers. comm.) indicating that we caught all size classes of turtles present. The maximum size of untagged individuals increased by greater than 20 cm throughout the years. This could be due to variability, chance, expansion of netting locations through the years, or less likely, increased survival rates since the beginning of the project.

We could not determine sex of juvenile turtles at Estero Banderitas. Non-invasive, observational methods are useful only for adults, and even these methods can be problematic when turtles are close to maturity. For example, one mature animal in this study was classified as female using a tail-length index (λ), and classified as a male using the tail length cutoff of >20cm.

One basic assumption of mark-recapture methods is that probability of capture does not change once a turtle has been captured (Krebs 1999). We tagged 184 individuals, and estimated a mean population size (for periods 4 and 5) of 333 individuals using a Jolly-Seber estimate. Given these numbers, we would expect a 55% recapture

rate (184/333) in 2003, similar to the recapture rate of 54% in 2003. One turtle, BMA28JUL2002-1, was captured in a net in Estero Estufa, released two hours after capture, and tracked back into the same net four hours later. For turtles that were recaptured a greatest number of times (4), it was variable as to where the recaptures occurred relative to the previous capture sites. One of the three turtles, BMA29JUL2000-2, was captured at Net Site 1, Estero Estufa, and Isla Conchalita. These capture sites are up to 5.5 km away from each other. But the two other turtles, BMA21SEP2000-1 and BMA21SEP2001-2, were recaptured each time at Net Sites 1 and 3, which are separated by less than 1 km.

Two turtles were captured together during multiple capture events.

BMA23SEP2001-4 was first captured in the evening on 23 September, 2001 at Isla Conchalita. BMA24SEP2001-1 was the next turtle captured in the same net the following morning. These turtles were recaptured together on 21 May, 2002 and again on 14 January, 2003.

The sea turtles in Estero Banderitas were predominantly green turtles. The presence of juvenile hawksbill turtles, however, indicated that it might have been an historical feeding area for this species. The decline in relative abundance of hawksbill turtles on the Pacific Coast of the Baja Peninsula (Cliffon et al. 1982) has been the most dramatic of all neritic sea turtle species in the region. Bahía Magdalena is one of the last places on the Baja Peninsula where hawksbill turtles still occur. Seminoff et al. (2003b) reported captures of four hawksbill turtles along the Pacific Coast of the Baja Peninsula from 1997 to 2001. All of these turtles were from the Bahía Magdalena region, and one

was captured in Estero Banderitas. This turtle, BMA9JUL2001-2, drowned in an illegal *mantaraya* net on July 4, 2002. An additional three hawksbill turtles were captured in Estero Banderitas as part of this study. From 2001 to 2004, no hawksbill turtles were captured on the Pacific Coast at Laguna Ojo de Liebre, Laguna San Ignacio, or Punta Abreojos (Mariscal Loza & Koch 2004). Although the relative number of juvenile hawksbills in Estero Banderitas is small, their presence and persistence are important for the recovery of the regional population.

The single loggerhead captured in June 2003 was most likely an anomaly. Juvenile loggerheads are common in the oceanic environment outside Bahía Magdalena, where they feed on pelagic red crab, *Pleuroncodes planipes*, and other crustaceans for a number of years before making homing migrations to the West Pacific (Nichols et al. 2000, Nichols 2003).

The smallest green turtle (SCL = 38.8 cm) was similar in size to those recorded at other feeding areas along the Baja Peninsula. The Grupo Tortuguero de las Californias reported the smallest green turtle in Punta Abreojos was 30.0 cm in SCL, in Laguna San Ignacio it was 34.0 cm in SCL, and in Laguna Ojo de Liebre it was 38.5 cm SCL. Mean size of turtles also was similar to Estero Banderitas. These recruitment sizes are similar to those reported for other juvenile feeding areas in the Pacific, such as Hawaii (Balazs 1980) and Australia (Limpus et al. 1994), but larger than 25 cm SCL, the smallest recruitment size reported in the Atlantic (Bjorndal et al. 2000).

We expect that pre-recruit green turtles are present in the oceanic habitat off Bahía Magdalena, associated with flotsam along driftlines. Although little is known

about the pelagic stage of this population, smaller green turtles have been sighted associated with *Macrocystis pyrifera* mats kilometers off the coast of Bahía Magdalena (Nichols et al. 2001). The absence of adult turtles indicates that turtles leave the estero upon maturity and are using other habitats. We expect that they essentially “grow out of” the area, and move out into the larger, deeper Bahía Magdalena to take advantage of more space and food (Koch et al. in press). Consistent with this hypothesis, larger turtles are caught in Bahía Magdalena compared with Estero Banderitas (Nichols 2003). Adult turtles may be using different feeding areas following their homing migration to nesting beaches. Larger turtles occur in the Gulf of California compared with Pacific sites (Nichols 2003, Seminoff et al. 2003a, Mariscal Loza & Koch 2004). It also is possible that the lack of large turtles in Estero Banderitas is indicative of a recovering population. Depleted populations of green turtle in Hawaii (Balazs 1980) and Australia (Limpus et al. 1994) had similarly skewed size distributions during recovery. Protection on nesting beaches in Michoacán began almost a generation ago. It is possible that the abundance of juveniles, and the slight increase in larger turtles through the years, is indicative of the beginning of a population recovery.

Body condition of green turtles in Estero Banderitas (mean = 1.33 ± 0.16) was similar to other feeding areas in Baja California. Body index of green turtles measured in Bahía de los Angeles from June 1995 to August 2002 was 1.09 to 2.19 (mean = 1.42 ± 0.015 SD; Seminoff et al. 2003a). Green turtles at Bahía de los Angeles had a slightly greater mean, minimum, and maximum condition index than turtles in Estero Banderitas. Data on epibionts were mostly observational, and were recorded by different observers

during the four years of the project. They are intended to present a preliminary report on the presence and diversity of epibiotic flora and fauna on green turtles in Estero Banderitas. Species of epibionts were similar to those on sea turtles at other Baja California feeding areas (Seminoff 2000, Nichols 2003).

Recruitment of green turtles in Estero Banderitas is consistent with the worldwide trend of other turtles that recruit from an earlier pelagic environment to a neritic developmental habitat in their juvenile life stage (Musick & Limpus 1997). Estero Banderitas is an ideal developmental and foraging area. It is a protected, relatively shallow, warm-water lagoon with seasonally abundant algae. Turtles are transported up and down the long waterway by the tides, reducing the need to swim long distances to find food (Chapter 2). When turtles mature, they may move into the larger Bahía Magdalena system, which provides abundant space and food for larger animals (Koch et al. in press).

We estimated stock size using a closed population method, Schnabel-Schumacher, and an open population method, Jolly-Seber. Estero Banderitas is an open population, with immigration and emigration, so assumptions of the closed methods were violated. The benefit of using the closed population method was that we could divide capture events into smaller intervals of 15 days that was more similar to actual capture intervals than the 6-month intervals used in the open population model. In this way we included more recaptures in the data calculations than when using the Jolly-Seber method. Also, closed estimates allow for comparison with other studies. Mendonça & Ehrhart (1982) used the Schnabel method to predict there were 132 turtles in Mosquito

Lagoon, FL whereas using the Schumacher method there were 138 turtles. A density of 2.25 green turtles per square km in Mosquito Lagoon was one third of the density calculated for Estero Banderitas.

The Jolly-Seber method yielded a range of population estimates that included estimates from the Schumacher and Schnaebel methods. Estimates early in the project are probably less than actual because of the small number of captures during Period 2. Forty-five of the recaptures were not included in the analysis because they were multiple-recaptures within the same capture period. These results provide the first abundance estimate for green turtles at a feeding area on the Pacific Coast of the Baja Peninsula. The East Pacific subpopulation of green turtle has decreased by 89% to 94% during the past three generations, resulting in a mean of 851 nesting females per year at Playa Colola, Michoacán (Alvarado-Diaz et al. 2001, Seminoff 2004). Assuming a 50/50 sex ratio at Estero Banderitas, we estimated that 167 ($\frac{1}{2} * 333$) female turtles were resident, which is between 7 % and 10 % of the nesting females at Michoacán (assuming that females nest every two ($n = 1702$) to three ($n = 2553$) years. This indicates that Estero Banderitas may provide a significant proportion of the recruitment to the adult nesting population.

Our density estimate of 6.7 turtles km^{-2} is greater than the density predicted in Bahía de los Angeles based on mark-recapture studies conducted from 1995 to 1999 (Seminoff 2000). Seminoff (2000) reports a mean population estimate of 229 turtles in the $\sim 60 \text{ km}^2$ Bahía de los Angeles, yielding a 3.8 turtles km^{-2} density estimate. Turtles in Estero Banderitas use habitat in the deeper, center channels of the waterways, and rarely

move across shallow sand and mud flats (Fig. 3). These center channels are about 20 km² of the *estero*. A density of 16.6 turtles km⁻² is appropriate for habitats used by sea turtles in Estero Banderitas.

Conservation implications. Estero Banderitas is an ideal area for potential protection. Limited access by road, only one entrance by sea, and the narrow width of the basin allow for effective and thorough monitoring of the waters. For the most part, fishing activities have little impact on sea turtles. Fishers use the area primarily for crabbing, and this type of fishing generally has no adverse interactions with green turtles. Fish, such as California halibut (*Paralichthys californicus*), mullet (*Mugil cephalus*), corvina (Scianidae) and sandbass (Serranidae sp.) are caught using surface gill nets with small mesh size. Turtles are infrequently caught in these nets, and if they are, chances for survival are great due to short set periods. Fishing for rays, however, results in fatal interactions with sea turtles. Large-mesh nets are set and anchored below the surface of the water and are set for long periods of time, causing drowning of caught turtles. A *mantaraya* net set overnight in Estero Banderitas in July 2002 caught eight turtles, five of which drowned. It is possible to allow fishing in a sea turtle sanctuary, but practices must be turtle-safe and enforceable.

Turtles are remaining in Estero Banderitas during their developmental years. Protecting this habitat would improve their potential survival through this juvenile life stage, a stage that is critical to the recovery of long-lived, slow maturing species (Crouse et al. 1987). The nearby community of Puerto San Carlos has voiced substantial community support for a protected area, and for community involvement in the

management and monitoring of the area (Garcia-Martinez et al. 2002). Research and conservation efforts that were initiated in 2000, and continue today, have already made the area an informal sanctuary. We have involved hundreds of local, national, and international field assistants and volunteers in field work and conservation. The Grupo Tortuguero de las Californias monitors the turtle population and the area as part of a peninsula-wide, community monitoring project. At present, numerous non-profit, community and government organizations are working together to designate Estero Banderitas as a sea turtle sanctuary. We hope that Estero Banderitas becomes the first of a network of community-based, sea turtle sanctuaries in feeding areas along the coast of the Baja Peninsula.

ACKNOWLEDGMENTS

This work is a result of collaboration between Moss Landing Marine Laboratories, School for Field Studies, Wildcoast, Blue Ocean Institute, and Grupo Tortuguero de las Californias and would not have been possible without the numerous people who participated in fieldwork, especially M. Taylor, J. Solis, R. Rangel, J. Talamantes, J. Ramirez, C. Moore, W. Urmston, and SFS-CCS students and staff 2000 – 2003. We also thank the directors of Center for Coastal Studies, L. Calderon, C. de la Alba, and F. Olliverdes, for logistical support. Funding was provided by NFWF, Homeland Foundation, the Earl and Ethel Myers Oceanographic Trust, PADI Foundation, and Harvey Graduate Research Fellowship. Research was conducted under permit # 280499.213.03 1565 and # 280700.213.03 2619 authorized by Secretaria de

Medio Ambiente Recursos Naturales y Pesca, Estado Unidos de México. Animal care protocol was approved by SJSU Animal Care and Use Committee (IACUC #805).

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Table 1. Summary of mark-recapture and morphological data of East Pacific green turtle captured 2000 – 2003 in Estero Banderitas, B.C.S., México, per year, including total number captures, number of new individuals and recaptured individuals, recapture rate ($\pm$ SD) calculated for 15-day capture periods, mean straight carapace length (SCL, $\pm$ SD), and mean mass ($\pm$ SD).

Year	Total captures	New Individuals + Recaptures	Recapture Rate	Mean SCL (cm)	Mean Mass (kg)
2000	30	27 + 3	0.04 ± 0.08	51.0 ± 4.9	19.8 ± 8.7
2001	78	49 + 29	0.33 ± 0.23	52.1 ± 7.1	18.5 ± 7.5
2002	101	76 + 25	0.24 ± 0.24	55.1 ± 8.3	25.0 ± 11.5
2003	62	32 + 30	0.47 ± 0.26	55.2 ± 11.0	23.8 ± 16.7
Total	271	184 + 87	0.29 ± 0.26	53.7 ± 8.2	22.4 ± 11.7

Table 2. Mean body Condition Index [$CI = (\text{mass}/\text{SCL}^3) \cdot 10^4$] $\pm$ standard deviation (SD) of green turtles ($n = 169$) for summer, winter, and entire year of 2000, 2001, 2002, 2003; n = number of turtles.

Year	Summer			Winter			All (entire year)		
	n	Mean $CI \cdot 10^4 \pm SD$	Range	n	Mean $CI \cdot 10^4 \pm SD$	Range	n	Mean $CI \cdot 10^4 \pm SD$	Range
2000	15	1.28 $\pm$ 0.15	0.81 – 1.47	10	1.28 $\pm$ 0.15	1.10 – 1.54	25	1.28 $\pm$ 0.14	0.81 – 1.54
2001	36	1.34 $\pm$ 0.14	1.04 – 1.77	11	1.29 $\pm$ 0.12	1.11 – 1.49	47	1.33 $\pm$ 0.14	1.04 – 1.77
2002	42	1.44 $\pm$ 0.11	1.26 – 1.73	26	1.35 $\pm$ 0.14	1.15 – 1.70	68	1.41 $\pm$ 0.13	1.15 – 1.73
2003	16	1.23 $\pm$ 0.16	0.85 – 1.58	13	1.21 $\pm$ 0.19	0.74 – 1.48	29	1.22 $\pm$ 0.17	0.74 – 1.58
Total	109	1.35 $\pm$ 0.15	0.81 – 1.77	60	1.30 $\pm$ 0.15	0.74 – 1.70	169	1.33 $\pm$ 0.16	0.74 – 1.77

Table 3. Mark-recapture data for a series of six samples of green turtles captured in Estero Banderitas, B.C.S., México for analysis by the Jolly-Seber method. Capture periods: 1 = Jul – Dec, 2000, 2 = Jan – Jun, 2001, 3 = Jul – Dec, 2001, 4 = Jan – Jun, 2002, 5 = Jul – Dec, 2002, 6 = Jan – Jul, 2003, including number of marked individuals captured (m_t), number of unmarked individuals captured (u_t), total individuals caught (n_t), and total individuals released (s_t) for each capture period.

Time of last capture	Time of Capture					
	1	2	3	4	5	6
1		2	6	2	0	1
2			1	0	0	0
3				5	3	5
4					2	3
5						10
6						
Total marked (m_t)	0	2	7	7	5	19
Total unmarked (u_t)	31	4	44	28	47	32
Total caught (n_t)	31	6	51	35	52	51
Total released (s_t)	30	6	51	35	47	51

Table 4. Results of Jolly-Seber estimates for green turtles captured in Estero Banderitas, B.C.S., México, 2000 – 2003, including proportion of turtles marked (α_t), population estimate (N_t), probability of survival (Φ_t), number of turtle joining (B_t), and standard errors of N_t , Φ_t and B_t . Sample times are six month periods representing July 2000 – July 2003.

Sample	Proportion	Population	Probability	Number	<u>Standard errors of</u>		
	Marked α_t	estimate N_t	of survival Φ_t	joining B_t	N_t	Φ_t	B_t
1	--	--	1.117	80.1	--	1.044	--
2	0.429	78.2	0.484	158.7	82.9	0.446	46.2
3	0.154	117.9	0.982	254.5	50.2	0.473	120.8
4	0.222	274.5	0.497	254.5	154.2	0.249	186.2
5	0.113	391.1	--	--	209.6	--	--
6	0.385	--	--	--	--	--	--

Figure 1. Simplified life history model of East Pacific green turtle (*Chelonia mydas*), emphasizing three primary habitats (nesting beach, pelagic waters and neritic waters) that are used over the life cycle of the green turtle.

Figure 2. Study site. (A) The Baja California Peninsula. (B) The Bahía Magdalena – Almejas Complex. (C) Estero Banderitas, Baja California Sur, México, capture locations are marked by circles (⊙).

Figure 3. Histogram of straight carapace length (SCL) of 184 green turtles caught in Estero Banderitas, BCS, México from July 2000 – August 2003. Mean Nesting Size (MNS) of females at Michoacán, México was 77.3 cm (Figuerola et al. 1993).

Figure 4. Histogram of mass (kg) of 173 green turtles caught in Estero Banderitas, BCS, México from July 2000 – August 2003.

A.

B.

Figure 5. Irregular (A) and normal (B) scute pattern observed on East Pacific green turtle (*Chelonia mydas*) caught in Estero Banderitas, Baja California Sur, México. Area of interest for (A) is boxed in black; scutes in normal pattern (B) have been outlined in white. Photos by T. Garland (A) and L. Brooks (B).

CHAPTER 2:
TIDAL MOVEMENTS OF EAST PACIFIC GREEN TURTLE (*CHELONIA MYDAS*)
AT A FORAGING AREA IN BAJA CALIFORNIA SUR, MÉXICO

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ABSTRACT

We tracked East Pacific green turtle (*Chelonia mydas*) using GPS-VHF telemetry in Estero Banderitas, a tidal foraging area in Bahía Magdalena, Baja California Sur, México. We measured tidal currents with a bottom-mounted Acoustic Doppler Profiler (ADP) and predicted tidal current speed and direction at the location and time during which turtles were tracked. Thirty turtles were tracked in the summers of 2000 – 2003. Vagility (mean = 18.6 ± 11.4 km d⁻¹) and speed (mean = 0.83 ± 0.47 km h⁻¹) of turtles was the greatest reported for green turtles at foraging areas. Turtles displayed highly linear movements, and activity patterns were circatidal. Vector correlation was used to compare turtle speed and direction with tidal speed and direction. Correlation coefficients were significant for sixteen out of twenty tracks, indicating significant linear interdependence between turtles and tides. Both speed and direction contributed equally to the correlation. Results indicate a new paradigm for green turtles in feeding areas, where turtles are transported on continual tides which allows them to exploit a patchy and seasonal distribution of algae, their main diet component. This tidal transport is markedly different than Selective Tidal Stream Transport, in which animals use either the ebb or flood tide for transport. Tidal currents may be an accurate indicator of turtle movement in tidal areas, and this transport system has implications for foraging ecology, energetics, and growth. Tracks also indicated that turtles do not leave Estero Banderitas during their juvenile years, making this developmental area an ideal candidate for a sea turtle sanctuary.

INTRODUCTION

The East Pacific green turtle (*Chelonia mydas*), like many sea turtle species and sub-populations worldwide, has experienced a dramatic decrease in numbers in the last century. As a result, it is currently listed as endangered by the World Conservation Union (Hilton-Taylor 2000) and is protected by international and national law (Aridjis 1990). Although nesting beaches in the eastern Pacific (e.g. Colola and Maruata, Michoacán, México) are well protected, the sub-population continues to suffer from direct and incidental take at feeding areas in northwestern México (Alvarado & Figueroa 1995, Alvarado-Diaz et al. 2001, Seminoff 2004). An estimated 7,800 green turtles die each year at northern feeding areas off the Baja California peninsula (Gardner & Nichols 2001, Nichols 2003).

Green turtles that occur in northwestern México hatch from eggs on nesting beaches located hundreds of kilometers south in Michoacán, México, Islas Revillagigedos, Islas Tres Marias, and Galapagos Islands (Awbrey et al. 1984, Alvarado & Figueroa 1986, Marquez 1990, Whiting & Miller 1998). Hatchlings spend their first years in the pelagic environment, drifting with currents, associating with flotsam, and maintaining an omnivorous diet (Carr & Meylan 1980, Carr 1987, Nichols et al. 2001, Bolten 2003). After an estimated five to seven years, juveniles recruit to neritic, foraging areas to develop and feed in sheltered coastal lagoons containing sea grass and algae (Balazs et al. 1987, Bjorndal 1997). Green turtles may reside in these developmental areas for more than twenty years (Seminoff et al. 2002c, Koch et al. in press). Upon

maturity, they migrate every one to three years to their natal beach to mate and nest (Alvarado & Figueroa 1986).

Less is known about the ecology of green turtles at feeding areas than on nesting beaches (Mortimer 1981, Bjorndal 1997). Recent studies of feeding ecology have provided new information on diet, activity, movement, and home range. Environmental factors, such as water temperature, time of day, and location of food affect activity and movement patterns of green turtles in feeding areas (Bjorndal 1980, Mendonça 1983, Ogden et al. 1983, Seminoff et al. 2002b). In general, green turtles exhibit a bimodal pattern of movement, feeding in the early morning and late afternoon, and resting in deeper waters during midday and night (Bjorndal 1980, Mendonça 1983, Ogden et al. 1983, Seminoff et al. 2002b).

Numerous foraging areas for green turtles are found off the Baja California peninsula due to its abundance of coastal habitat and nutrient-rich waters (Nichols 2003). Bahía Magdalena is an important foraging area for juvenile and adult green turtles (Nichols 2003, Chapter 1). The green turtle is the only sea turtle that is primarily herbivorous, and those in the region feed on algae (Seminoff et al. 2002a) and sea grass (Felger & Moser 1973). Green turtles inside Bahía Magdalena consume mainly algae, including Gracilariaceae, *Codium* spp. and *Hypnea* spp., whereas those outside the bay eat primarily surfgrass, *Phyllospadix torreyi* (Hilbert et al. 2000, Lopez-Mendilaharsu 2002). The macroflora in Bahía Magdalena, consisting of more than 219 species, is dominated by Rhodophytes, and species composition is seasonally variable (Sanchez Rodriguez et al. 1989, Hernández-Carmona et al. in press). Forty-one species of algae

are documented in Estero Banderitas, a tidal lagoon in northern Bahía Magdalena, and species abundance and distribution is seasonal (Ramos & Santos 2005). Diet of sea turtles in Estero Banderitas is seasonally variable (Lopez-Mendilaharsu 2002).

Ocean currents affect the movements of turtles undergoing large scale migrations (Luschi et al. 2003a). But rarely have oceanographic phenomena such as tides, which act on a smaller spatial scale, been considered an important environmental factor affecting sea turtle behavior and movement. Use of Selective Tidal Stream Transport (STST) is well documented in fishes and invertebrates (Forward & Tankersley 2001). For animals using STST, “horizontal transport is accomplished by vertically migrating into and out of the water column synchronously with changes in the direction of the tidal transport” (Forward & Tankersley 2001). Animals use either ebb-tide or flood-tide transport, and might make use of both strategies on different occasions or stages of their life history. At all stages, such transport is considered energetically beneficial (Forward & Tankersley 2001).

Tidally-oriented movements have been observed for sea turtles. Green turtles in Moreton Bay, Australia moved into and out of intertidal feeding areas with the tide (Limpus et al. 1994). Byles (1988) noticed that loggerhead turtles (*Caretta caretta*) drifted with the tide in foraging areas in Chesapeake Bay, MD, and suggested this behavior might be energetically advantageous. Schmid et al. (2002) found that mean bearing of Kemp’s ridley turtle (*Lepidochelys kempii*) movement was oriented with the mean direction of tidal flow and that rate of movement of turtles was affected by tidal velocity. However, this movement was different than STST. The “selective” component

of the behavior associated with STST was absent, and animals instead moved with the ebb and flood tide in sequential and continuous fashion. Additionally, several species of fish exhibit similar movement patterns (Teaf 1980, Almeida 1996, Ackerman et al. 2000).

Previous studies on foraging ecology were conducted in non-tidal habitats, although tidally influenced lagoons or bays are an important habitat (Bjorndal & Bolten 1996). In non-tidal foraging areas, food availability is the main determinant of green turtle activity (Bjorndal 1980, Ross 1985, Balazs et al. 1987). But areas where tidal currents are a dominant environmental force, it is possible that tides become an important determinant of activity.

Preliminary data indicated that strong tidal currents affected the diel movement of green turtles in Estero Banderitas (Brooks et al. in press b). Tides had not been formally measured in the area, and tidal predictions for Bahía Magdalena were historically made from offsets of San Diego. The purpose of this study was to investigate the extent to which tidal currents affected the foraging ecology and daily activities of green turtles. We hypothesized that (1) daily movements and foraging activities would be strongly affected by tidal currents, (2) the direction and speed of turtle movement would be directly related to the direction and speed of the tidal currents, and (3) turtles would exhibit circatidal rhythms. We deployed Acoustic Doppler Profilers to obtain quantitative local tide data. We tracked turtles with GPS-VHF telemetry, and compared data on turtle speed and direction with tidal speed and direction as measured by the ADPs.

METHODS

Study Area. The Bahía Magdalena-Almejas complex is located on the Pacific Coast of Baja California Sur, México (Fig. 1). The area of the coastal lagoon system is greater than 1000 km² (Funes-Rodriguez et al. 2001), and is separated from the Pacific Ocean by Isla Margarita and Isla Magdalena. Estero Banderitas (24°50' – 25°00' N and 112°05' – 112°08' W) is an evaporative basin located in the northern zone of Bahía Magdalena. The roughly 42 km² lagoon is the largest in the complex. Three species of mangroves (*Avicennia germinans*, *Laguncularia racemos*, and *Rhizophora mangle*) line the main waterway and the curving side lagoons, which are characterized by deeper channels in the center and shallower mud and sand flats on the edges. Substrate consists of sand and mud with patches of algae and sea grass beds. The area is heavily influenced by tidal currents, with salinity and temperature increasing near the head of the basin (Brooks et al. in press a). Average salinity at the mouth of Estero Banderitas is between 36.9‰ and 38.7‰ (Alvarez-Borrego et al. 1975), average water temperatures are 18°C to 31°C, and depth is 1 to 9 m. Green turtles are the most abundant species of sea turtle in the area, although loggerhead and hawksbill (*Eretomochelys imbricata*) turtles also are encountered.

Tides. We measured tidal currents with a bottom-mounted SONTEK Acoustic Doppler Profiler (ADP). Water motion was measured every 0.25 cm (cell depth) within the water column. Profiling intervals were 240 seconds with averaging intervals of 120 seconds, thus reducing Doppler noise to less than 1 cms⁻¹. Data were recorded every 4 minutes. Tides were sampled at ten systematically-selected locations (stations) throughout the

study site for a minimum of 48 hours at each location (Fig. 1). We divided Estero Banderitas into geographic areas based on the location of stations.

We determined the direction, height, and speed of tidal currents during ADP deployment at each station using a program written in MATLAB Version 6.5 (The MathWorks Inc. 2002). Along-channel current direction was determined by corroborating ADP-measured angles of flow with known channel orientations on a chart of the region. Direction of flow ($\pm 1^\circ$) was calculated for ebb and flood currents for each of five levels of current speed, (divided in 0.2 ms^{-1} increments, from $0.0 - 1.0 \text{ ms}^{-1}$).

We estimated tide height by counting the number of 0.25 m cells sampled from the ADP to the surface signal. We used harmonic regression to correct for the measurement error ($\pm 0.25 \text{ m}$) in these heights. We regressed observed heights with two harmonic tidal constituents, M2 (principal lunar semi diurnal, N_1 (speed number) = $28.9841042 \text{ deg hr}^{-1}$) and K1, (luni-solar diurnal, $N_2 = 15.0410686 \text{ deg hr}^{-1}$). This yielded the regression coefficients $A_{1,2}$, the tidal amplitude, and $L_{1,2}$, the local phase lags. We used the regression equation (Equation 1) to predict tidal height (H) at time (t). Msl is the average water height above the ADP.

$$(1) \quad H = msl + A_1 * \cos(N_1 t + L_1) + A_2 * \cos(N_2 t + L_2)$$

We calculated the change in height vs. the change in time ($\Delta H / \Delta t$) for each measured tidal transition (low to high, high to low).

Tidal currents were separated into along-channel (V) and across-channel (U) velocity components using a program written in MATLAB. Velocity measurements ($\pm 0.01 \text{ ms}^{-1}$) for each cell were averaged for the water column. We determined an along-channel maximum speed (V_{max}) for each measured tidal period. These calculations were performed for each ADP station.

Times for high and low tides, based on San Diego tide predictions, were corrected for the study site using published offsets of - 37 min for high tide and - 22 min for low tide. Height for the San Diego tides was predicted by a program developed at Moss Landing Marine Laboratories in MATLAB. We calculated $\Delta H/\Delta t$ for San Diego for each tidal transition during the time that the ADP was deployed.

Our goal was to predict the speed of the tidal current where a tracked turtle was swimming, therefore, at a station of interest. The velocity of a tidal current through a basin depends on the surface area (A), the cross sectional area of the opening to the basin (S), and the tidal range, (h). The current in the center of a channel is 1/3 larger than the average current. The maximum velocity (V_{max}) through a channel connecting the open sea to a basin over one-half (6 hours) of a tidal cycle (T) can be described by Equation 2 (Sverdrup et al. 1947), where V_{max} is proportional to change in height during the change in time.

$$(2) \quad V_{\text{max}} = \frac{4 \pi A}{3 T S} 2h$$

Linear regression was used to compare San Diego $\Delta H/\Delta t$ with $\Delta H/\Delta t$ at a station in Estero Banderitas during measured tides. We used the resulting regression equation to predict Station $\Delta H/\Delta t$ using San Diego $\Delta H/\Delta t$ during times when the ADP was not

deployed at the same station. We used linear regression to analyze the relationship between Station $\Delta H/\Delta t$ and Station $V_{\max}$, and used the regression equation to predict Station $V_{\max}$ for any tidal transition during tracking.

Once $V_{\max}$ was predicted, we used sine interpolation (Equation 3) to interpolate the along-channel current speed at any particular time between the times of known current velocities of zero, or slack tides (T_1 and T_2). Using these calculations, we predicted the along channel tidal current speed (V_i) at a desired location (Station 1-10) and time (T_i).

$$(3) \quad V_i = V_{\max} * \sin\left(180 \frac{(T_i - T_1)}{(T_2 - T_1)}\right)$$

Current speed was predicted for the time midway through each half hour interval of turtle movement, for each turtle track. Once the speed of the tide was predicted, the corresponding direction of flow was determined. These estimates resulted in a tidal vector, consisting of speed and direction, predicted for each half hour interval during each turtle track, and at the corresponding geographical area of the turtle. We compared these tidal vectors to turtle vectors, as explained in the next section. We used the U and V components of tidal vectors to construct virtual displacement diagrams. The diagrams model the virtual displacement of a particle of water subjected to the predicted tidal velocities. A virtual displacement diagram was modeled for tidal conditions corresponding to each turtle track.

Tidal current velocities were averaged in one-hour intervals to examine vertical profile of the velocity throughout the water column. Profiles for one ebb tide and one flood tide were constructed for each tidal station.

Turtles. We captured and tracked sea turtles in Estero Banderitas for the summer seasons of 2000 to 2003. We captured turtles using entanglement nets (100 m long, 25 cm mesh) set at eight locations throughout the study site (Fig. 1). Nets were set day and night, and monitored continuously for captured turtles. Turtles were removed from the net and placed in the shade in a boat or a padded holding box (1.5 m x 1.5 m). We recorded mass ($\text{kg} \pm 1 \text{ kg}$), standard length [straight carapace length (SCL), measured notch to tip of longest marginal scute, $\pm 0.1 \text{ cm}$], and curved length [curved carapace length (CCL), measured with flexible tape along longest line, $\pm 0.1 \text{ cm}$]. We measured tail length (TTL) from the posterior edge of the plastron to the tip of the tail using calipers ($\pm 0.1 \text{ cm}$). Turtles were tagged on each rear flipper with metal Inconel tags (National Band and Tag Company, Newport, Kentucky), adjacent to the first large scale (Balazs 1999). All turtles were released at the location of capture within ten hours of capture.

We determined the maturity of the animal based on a mean size of nesting females of 77.3 cm SCL at the Michoacán, México nesting beach (Figueroa et al. 1993). All animals greater than 77.3 cm SCL were considered mature. Sex of mature turtles was determined according to a tail/length index ($\lambda_t = \text{TL}/\text{SCL}$) with a threshold $\lambda_t > 0.38$ indicating a male (Lyon et al. 2005).

A two-sample t test was used to compare the mean SCL of turtles tracked to the mean SCL of all turtles captured in Estero Banderitas. We used a one-way ANOVA to test for differences in mean SCL of tracked turtles among years. For these and all subsequent statistical analyses, $\alpha = 0.05$.

We tracked turtles using GPS-VHF telemetry. The telemetry unit consisted of a floating, PVC plastic cylinder (15 cm long, 7 cm diameter) containing a VHF transmitter, a 10 m monofilament line as a tether, and a carapace attachment (Brooks et al. in press a). VHF transmitters were 3 to 5 cm in length and 2 to 3 cm in width, and transmitted at 164-165 MHz. For the first three years, a kayaker followed each tagged turtle for the duration of tracking. Turtle positions were recorded every fifteen minutes, by the kayaker, using a Garmin Geko or Mariner handheld Global Positioning System (GPS).

In 2003, a GPS was housed in the tracking float and GPS locations (± 3 m) were recorded every 2 minutes. A VHF transmitter was attached to the top of the cylinder and monitored to locate the unit. A 5.2-m Boston Whaler was used to monitor the turtles regularly throughout the tracking period. We observed the location, behavior, and condition of the turtle and the telemetry unit using VHF and binoculars. Care was taken to remain at a monitoring distance of >50 m so as not to affect the behavior of the turtle. Closer and unobtrusive observations were conducted by swimmers and kayakers. When GPS batteries were low, the float was changed by detaching the existing float from the tether and attaching a new tracking float, thus allowing continuous position data. Termination of the tracking period occurred when either the attachment broke under

natural conditions, or the unit was removed from the turtle by pulling the monofilament line until it broke at the carapace attachment point.

GPS positions were downloaded from the handheld unit using Waypoint+ (Hildebrand 2000) and analyzed with MATLAB. We wrote MATLAB programs to determine speed and course of turtle movement and length of the track. We divided tracks into thirty minute segments, and calculated the mean speed and course of the turtle for each segment. Mean, maximum, and minimum speeds of each turtle were calculated for each track. Duration of time at zero speed, or rest duration, also was calculated. We mapped the tracks using MATLAB and ArcView.

Tracks were designated as neap or spring tide tracks if they fell on the day of neap or spring tide, or one day preceding or following that tide. Track segments were designated as “day” if they occurred from 0800 to 1800h, and “night” if they occurred from 2100 to 0500h. We used two-sample t tests to compare mean kilometers traveled per day (vagility), mean speed, and maximum speed between tracks at neap and spring tides, and to compare mean speed between day and night tracks. We used linear regression to analyze whether mean speed and vagility were dependent on turtle size (SCL).

We estimated home range using protocols described by (Seminoff et al. 2002b). We used minimum convex polygon (MCP) and fixed kernel density (FKD, 95% utilization distribution) methods to estimate home range area. FKD with a 50% utilization distribution was used to estimate activity centers. We analyzed data using the animal movement analyst extension (U.S. Geological Survey, Anchorage, Alaska;

www.absc.usgs.gov/glba/gistools/animal_mvmt.htm) for ArcView version 3.2

Geographic Information Software (GIS, Environmental Research Systems Institute). We tested for differences in mean home range among years with a one-way ANOVA.

Auto- or serial correlation of telemetry data has traditionally been a concern when estimating home range (Swihart & Slade 1985, Schmid et al. 2002, Seminoff et al. 2002b). Recently, researchers reported that data taken at predefined and short time intervals, such as GPS locations, were not affected by autocorrelation, and that intensive sampling improved range estimates (Reynolds & Laundré 1990, Otis & White 1999, Girard et al. 2002). Also, Blundell et al. (2001) agreed with other researchers that autocorrelation was inherent in biological data and independence was biologically impossible. To reduce the effects of autocorrelation, we recorded GPS locations at two minute intervals, and sub-sampled at a rate of one location per hour for home range analysis.

We compared mean speed of turtles and tides using a two-sample t test. Speed and direction were averaged for turtles and tides during half-hour intervals. Tidal current speed and direction were predicted for the midpoint of the half hour interval. We plotted the resultant vectors, one for each half hour of each track, using stick plots to show magnitude (speed) and direction (course of travel) for turtles and tides. Vectors for turtle and tide were analyzed using vector correlation as defined by Crosby et al. (1993) and Breaker et al. (1994). This technique allowed us to analyze the vector quantity, inclusive of magnitude and direction, rather than the two scalar (x and y) components separately, which provided a more comprehensive analysis of the relationship. The sample

correlation coefficient, R^2 , is a measure of linear interdependence, and ranges from 0.0 for no correlation to 2.0 for perfect correlation. To assess significance of the correlation, 95th percentile limits were determined using cumulative frequency distributions for two-dimensional vectors for the sample size of interest (n = number of vectors; Breaker et al. 1994).

RESULTS

Tides. Tides were measured at each station for 48.7 to 117.1 hours. Data from eight stations were used to compare with turtle tracks in 2003. Station 6 was not used due to its proximity with Station 7. Station 8 was located at the corner of an island where tidal currents were confounding; therefore, data were of limited use.

Direction of along-channel flow varied among the stations depending on the orientation of the main channel (Fig. 3). Flow in the main channel was generally to the north-northeast on flood tides, and to the south-southwest on ebb tides. Flow direction also depended on speed of the tide, and varied as much as 32° within a tidal phase (ebb or flood, Table 1). In Estero Estufa, the winding shape of the lagoon caused the direction of flow to change frequently, making direction at one location an inaccurate proxy for the entire station. We determined direction of flow by observations of channel direction on a map for the two branches of this lagoon. Tidal range, or change in height, was 2.8 m at full moon spring tide and 1.1 m at quarter moon neap tide (Fig. 4).

Along-channel current speeds were greater, by an order of magnitude, than across-channel speeds at all locations (Fig. 5). Mean along-channel speed per station was

0.29 ± 0.13 SD ms^{-1} (range: 0.11 ms^{-1} - 0.46 ms^{-1}). The greatest mean along-channel speed, $0.43 \pm 0.22 \text{ ms}^{-1}$, occurred during spring tide. The along-channel mean speed measured at neap tide was $0.16 \pm 0.09 \text{ ms}^{-1}$. The mean across-channel current speed was $0.03 \pm 0.02 \text{ ms}^{-1}$ (range: 0.01 ms^{-1} to 0.05 ms^{-1}).

The maximum along-channel current speed, 0.93 ms^{-1} , occurred during the full moon spring tide at Station 2. All of the stations in the main channel had greater along-channel speeds during ebb tide compared with flood tide. Stations 9 and 10, located in Estero Estufa, had greater flood speeds than ebb speeds. Maximum along-channel speeds also were almost an order of magnitude greater than across-channel maximum speeds. The maximum across-channel speed (0.15 ms^{-1}) was at Station 1, but across-channel speeds at other stations were considerably less than this maximum. Maximum across-channel speeds were greater during flood tides than ebb tides at all stations.

Vertical profiles of currents during ebb and flood tides indicated that velocities varied with depth (Fig. 6). Current velocities were greater at the surface and lesser near the benthic boundary layer, with a difference as great as 0.3 ms^{-1} . Water column differences were more pronounced when the current velocities were greater.

Linear regression indicated a significant relationship between San Diego $\Delta H/\Delta t$ and Station $\Delta H/\Delta t$ and V_{max} and Station $\Delta H/\Delta t$, illustrating the relationship described in Equation 2 (Table 2). Regression lines for V_{max} vs. $\Delta H/\Delta t$ at stations in Estero Banderitas revealed geometric characteristics of the embayment (Fig. 7). Stations situated in narrower sections of the channel, such as Station 5, had regression lines with greater slopes. This is because as cross-sectional area of the channel decreases, velocity

increases. The opposite was true for stations in wider sections of the channel. Noise due to local seiches and acceleration of water through the curved channel is indicated by the scattering of data points for each station. Greater regression coefficients and lesser standard error for the estimate indicated, however, that the relationship between $V_{\max}$ and $\Delta H/\Delta t$ was well described.

Turtles. Thirty turtles were tracked during the study period: five in 2000, three in 2001, nine in 2002, and thirteen in 2003 (Table 3). Twenty-nine of these turtles were green turtles and one was a hawksbill turtle. Tracks were analyzed for 29 turtles. One of the turtles swam back into the net four hours after release, and its track was not used. SCLs of tracked turtles were 43.9 to 68.9 cm (mean = 54.5 ± 5.8 cm SD). Recapture rate increased during the years of the study. In 2003, greater than half of turtles captured were captured at an earlier date. Recaptured turtles were at large for a maximum of 372 days. Turtles were caught at all eight netting locations and tracked in June, July, and August. Turtles were caught in day and night, and during slack and flowing tides. Substrate at capture locations were rocks, mud, and sand. Turtles were tracked for 5.2 to 53.0 hours and traveled 1.4 to 65.3 km. All telemetry units were recovered successfully at termination of tracking and all turtles were safely released.

There was no significant difference in the SCL of turtles tracked among years ($F = 0.90$, $P = 0.45$, $df = 3$). The mean SCL of turtles tracked (54.5 ± 5.8 cm) also did not differ significantly from the mean SCL of all 184 turtles captured during the project (53.7 ± 8.2 cm; $t = 0.53$, $P = 0.600$, $df = 182$). All turtles tracked were juveniles, therefore, sex was undetermined.

Area of use, indicated by tracks, was similar among years (Figs. 8, 9, 10). Turtles were tracked in the main channel and side lagoons. They used the entire length of Estero Banderitas, but no turtle was ever tracked outside the *estero*. Turtles used the deeper, center channel of waterways, and rarely were tracked over shallow mudflats. Movements were dependent somewhat on where the turtle was captured. For example, those turtles captured in Estero Estufa used this lagoon more than those captured outside the area.

Turtles traveled at speeds of 0 to 1.45 ms^{-1} (0 to 5.22 kmh^{-1}). Mean speed for all turtles tracked was $0.23 \pm 0.13 \text{ ms}^{-1}$ ($0.83 \pm 0.47 \text{ kmh}^{-1}$). Vagility, or distance traveled per day, was 3.3 to 38.9 kmd^{-1} (mean = $18.6 \pm 11.4 \text{ kmd}^{-1}$). Speed did not differ between day and night ($t = 1.54$, $P = 0.13$, $df = 29$). Speed and vagility were independent of turtle SCL (speed: $F = 0.47$, $P = 0.50$, $df = 27$; vagility: $F = 0.30$, $P = 0.64$, $df = 27$).

We tracked six turtles during neap tide and nine turtles during spring tide. Turtles traveled a greater distance during spring tide ($28.9 \pm 11.3 \text{ km day}^{-1}$) than during neap tide ($9.8 \pm 8.3 \text{ km day}^{-1}$; $t = -3.55$, $P = 0.004$, $df = 13$). Turtles maintained a greater mean speed during spring tide ($0.35 \pm 0.13 \text{ ms}^{-1}$) than during neap tide ($0.12 \pm .01 \text{ ms}^{-1}$; $t = -3.81$, $P = 0.002$, $df = 13$). Mean maximum speeds also were significantly greater during spring tide ($1.12 \pm 0.35 \text{ ms}^{-1}$) compared with neap tide ($0.50 \pm 0.25 \text{ ms}^{-1}$; $t = -3.9$, $P = 0.003$, $df = 13$).

Periods of rest, or zero movement, were infrequent. From 2000-2002, there were two tracks containing speeds of zero, indicating single, fifteen minute periods of no movement. In 2003, positions were determined more frequently (every two minutes), and eighteen tracks had speeds of zero at some point during the track. During 2003,

maximum duration of zero speed was sixteen minutes. If turtles were resting, it was not in the conventional method of remaining in one place for an extended (> 1 hour) amount of time. Investigative dives at these locations found no significant cover of algae or seagrass, indicating that turtles were not feeding at these locations.

Home ranges were calculated for 29 turtles tracked during the four years of the project: five in 2000, three in 2001, eight in 2002, and 13 in 2003. Minimum convex polygon estimates of home range were 5 to 2230 ha (mean = 621 ± 586 ha, Fig. 9,10). Fixed kernel density estimates were 5 to 5216 ha (mean = 2097 ± 1766 ha), and were significantly greater than MCP estimates ($t = 2.38$, $P = 0.021$, $df = 56$). Whereas both estimates are not perfectly suited for estimates in a narrow, linear habitat, FKD areas included greater portions of land and shallow water habitat where turtles were not found. Inspection of MCP and FKD estimates and corresponding tracks indicated that MCP estimates were more appropriate because they did not extrapolate outside recorded locations to the extent of FKD estimates. Although MCP estimates occasionally crossed land masses, they were better suited to the habitat and the turtle behavior found in Estero Banderitas. For this reason we did not consider FKD estimates further. Although the greatest mean estimate for MCP occurred in 2002, there was no significant difference of mean MCP among years ($F = 0.57$, $P = 0.639$, $df = 3$).

Activity centers also were not appropriate. The linear and tidal movement of turtles in Estero Banderitas were not consistent with the traditional use of an activity "center."

Stick plots indicated a similarity between tidal speed and direction and turtle speed and direction through time (Fig. 10). There was no significant difference between mean turtle speeds and mean current speeds measured during the same time period ($t = 0.44$, $P = 0.666$, $df = 14$). There was a significant vector correlation between movements of turtles and tidal currents for sixteen of the twenty turtle tracks for which data were available (Fig. 10). Correlation was significant during all tidal phases, and for tracks occurring throughout the length of the Estero Banderitas. Correlations for tracks A, H-1, I-2, and K were insignificant.

Virtual displacement diagrams of water motion were similar to turtle tracks in shape (Fig. 11). Predictably, the tracks with greater vector correlation had the most analogous virtual displacement diagrams. Estimated distance traveled in the models was an overestimate of the distance of most tracks, but closely predicted distance traveled (within 20%) for six tracks. Virtual displacement diagrams better predicted the general shape of tracks, rather than exact displacement.

DISCUSSION

Tides. Physical environmental factors, such as tides, affect the ecology of marine animals but rarely are quantitative methods applied to evaluate this relationship. This study represents one of the first in which tides and tidal currents were quantitatively measured and compared with movements of a large marine vertebrate, in this case sea turtles. Tides in Estero Banderitas had not been measured before this study.

The direction of tidal flow followed the bathymetric orientation of the channels, but changed with the speed of the current, as the tide changed phases. The transition from ebb direction to flood direction occurred gradually, and this transition was also reflected in turtle direction. Additionally, direction of ebb and flood flow were not 180° opposed. This was a result of shear, and is characteristic of flow in winding embayments where currents will accelerate due to the curvature of the channel. These characteristics were important to consider when predicting directional components of the tidal vector that were compared with turtle movements.

Our recorded tidal range of 2.8 m maximum and 1.1 m minimum was within reported and predicted ranges in the region. Tidal ranges of 1.46 m, 1.19 m, and 1.13 m were recorded at other locations in the Bahía Magdalena-Almejas complex during transitional tides (Obeso Nieblas et al. 1999, Robinson & Gomez-Aguirre 2004). We expected that tidal range in Estero Banderitas would be greater due to the long, narrow shape of the embayment, and its relatively shallow depth. Harmonic regression provided a more accurate estimate of tidal height than was available using estimates based only on the ADP. A greater sample duration would allow the use of additional tidal constituents to increase the accuracy of tidal height estimates. However, the use of level loggers or other pressure gauges is more desirable for measuring tidal heights. Also, one month of tidal data is generally recommended for generating reliable prediction models. Our tidal heights, therefore, must be interpreted with caution. They were sufficient to predict tides within the month that tides were measured and turtles were tracked, but they have limited applicability outside this time frame.

Tidal stations do not exist within Bahía Magdalena to our knowledge. As a result, previous researchers predicted tides using a published offset from San Diego or tidal prediction programs, such as Jtides (Lutus 2003) and Predicción de mareas en México (Gonzalez et al. 2005). Discrepancies existed between predicted and measured times and heights of tides in this and aforementioned studies. Research efforts throughout the region would benefit from the presence of a tidal station.

Maximum tidal current speeds of 0.93 ms^{-1} in Estero Banderitas also were similar to the 0.5 ms^{-1} measured by (Robinson & Gomez-Aguirre 2004) and 1.1 ms^{-1} measured by (Obeso Nieblas et al. 1999). Maximum speeds at all stations occurred during ebb tides rather than flood tides. In Estero Banderitas, the highest high tide is almost always followed by the lowest low tide, resulting in a maximum height change and maximum tidal speed of the day during this ebb tide.

Previous researchers comparing animal movement with tidal movement have used less precise measurements of tidal direction and speed, such as handheld compass, flowmeter, visual observation, and tide predictions (Teaf 1980, Ackerman et al. 2000, Schmid et al. 2002). Arnold et al. (1994) measured tidal currents with current meters and Savonius rotors, and presented resultant tidal vectors with mapped movements of cod (*Gadus morhua*) tracked with acoustic tags in the North Sea to show that cod moved by STST and passive drift.

Vector correlation, to our knowledge, has not been used to assess the similarity between tidal and animal movement. Vector correlation was used previously to analyze wind and current samples in a time series (Breaker et al. 1994), but is applicable to any

analysis in which two vectors are compared. By comparing quantities as vectors, rather than scalars, we avoided problems associated with correlating circular, or directional data, and allowed the effects of both scalar quantities to be compared as a single entity (Crosby et al. 1993). As with all statistical measures, a greater sample size affords greater confidence in the results, and correlation for small sample sizes (<10) can be due to chance. For example, results for BMA-A, where eleven samples were obtained, should be interpreted with caution.

A greater sample size, or longer time series, also allows for analysis through time. We calculated a single value to obtain a correlation coefficient for the entire record. This was meaningful, but with greater sample sizes, one could observe the variation in correlation through the duration of the record by using a moving window. For example, we might have determined where in the tidal cycle vector correlation was the greatest, during mid-tide or slack tide, or ebb or flood tide.

Telemetry. Tracking of marine turtles has increased in recent years with the improvement of telemetry technology. Satellite telemetry, the most highly evolved technique, is used worldwide, and it is well suited for recording large-scale migrations on the order of hundreds of kilometers. Due to limitations in scale and accuracy of the position fixes, it is generally unsuitable for tracking in a local foraging habitat where fine-scale data (error < 1km) are needed (Godley et al. 2003). Tracking in foraging areas has been undertaken using acoustic and VHF telemetry (Mendonça 1983, Ogden et al. 1983, Brill et al. 1995, Schmid et al. 2002, Seminoff et al. 2002b, Schmid et al. 2003). This method can be somewhat inaccurate, time-consuming, and yield a relatively small

amount of fixes. Our study represents the first known use of a tethered GPS-VHF device for tracking marine turtles. GPS telemetry application in marine vertebrates has been limited because of the required acquisition time, as diving animals rarely spend enough time at the surface to achieve a fix by the GPS unit. We overcame this by using a buoyant housing with the GPS unit at the surface most of the time. Location of the turtle and GPS positions were recorded throughout the tracking period. The technique yielded greater than 10,000 high-quality data points, with an error of ± 3 m. The failsafe design allowed for safe detachment and release of the floating housing and the tether if accidental entanglement occurred, or when we terminated tracking. A 10-m long connection between the turtle and the buoyant housing was chosen because water depth was usually < 10 m throughout Estero Banderitas. This length was chosen so that the turtle did not drag the housing under water and so there was minimal extra line in the water.

We measured the force imposed by the telemetry unit with a Multiscale Flow Analysis System (Brooks et al. in press a). Force ranged from < 1 g (9.8×10^{-3} N) at currents < 0.34 ms⁻¹ (0.7 knots) to 265.0 g (2.6 N) at currents of 0.92 ms⁻¹ (~ 2 knots). We calculated the percentage of turtle biomass equivalent to tag forces by comparing tension (grams) with the mean turtle mass (22.3 kg $\pm$ 1.86 SE). Forces represented 0% to 1.2% of mean turtle biomass. This compares favorably with other studies on telemetered animals. Seminoff et al. (2002b) reported the maximum mass of their radio and sonic telemetry unit was 1.2% of body mass for tagged green turtles. The 0 to 1.2% of tag vs.

body mass for our study was less than the maximum tag/mass ratio of 2% recommended from studies on telemetered fish (Mellas & Haynes 1985).

We propose the telemetry unit had minimal effect on turtle behavior because: (1) we observed non-telemetered turtles exhibiting similar behavior to telemetered turtles, (2) turtles tracked were recaptured in similar locations at a later date, and (3) one turtle tracked swam directly into the net in which it had been captured hours earlier.

Our two-minute sampling interval followed recommendations for GPS telemetry studies. Ryan et al. (2004) suggested using a sampling interval that allowed the animal to move at least 4 m between fixes to reduce error and noise in data. Turtles in Estero Banderitas moved at a mean rate of $0.23 \pm 0.14 \text{ ms}^{-1}$, or 13.9 m min^{-1} . Our sampling interval was sufficiently conservative, and allowed for a high level of accuracy during movement, even if turtles were traveling at rates of 0.03 ms^{-1} . At this and lesser speeds, movement was negligible.

The greatest limitation of the telemetry device was battery life. Batteries required changing every ten to twelve hours by either a kayaker or swimmer. This necessitated extra devices and made for complicated switching episodes. Longer and dependable battery life would improve the ease of tracking turtles.

Movement patterns of turtles in this area made them well suited for this tracking technique. Our preliminary observations indicated that turtles moved, and possibly drifted, with tidal currents. Considerable drag of the tag and tether might have occurred had the turtles swam against the current for sustained periods of time. Though this tag

does not provide a force greater than those used in other studies, reducing the effect of the tag is of some concern.

Turtles. Turtles tracked in Estero Banderitas were representative of the juvenile stock found in the area. All turtles tracked were juveniles, and their size range represented 87.5% of all individuals captured in Estero Banderitas. Few (<2%) mature turtles have been found in Estero Banderitas. Green turtles recruit to Estero Banderitas at about 38 cm SCL, similar to other neritic feeding grounds on the Pacific coast of the Baja Peninsula (Mariscal Loza & Koch 2004) and in the Pacific Basin (Balazs 1980, Limpus et al. 1994). We believe they remain in Estero Banderitas year round to feed and develop to maturity, at which point they move into Bahía Magdalena, a larger bay with greater food availability. Turtles have been recaptured in different seasons and years, with recapture rate increasing to greater than 50% during four seasons. No turtles tracked vacated the area, and none of the 184 individuals first captured in Estero Banderitas have been recaptured at outside locations (V. Koch, pers. comm.).

Recent work by Seminoff et al. (2002b) provided the first estimates of home range for green turtles in the East Pacific. Mean MCP estimates in Estero Banderitas were considerably less than those in Bahía de los Angeles (1,662 ha), but were greater than those reported for green turtles at other feeding grounds: 46 – 506 ha for sub-adults in Florida (Mendonça 1983), 22 – 311 ha for juveniles in Texas (Renaud et al. 1995), and 84 – 850 ha for adults in Australia (Whiting & Miller 1998). Fifteen of the twenty-nine turtles (52%) in Estero Banderitas had lesser MCP values than the minimum reported in Bahía de los Angeles. Though green turtles moved greater distances in Estero

Banderitas, the shape of their movements was more linear than the polygonal movements in Bahía de los Angeles.

Green turtles in Estero Banderitas traveled further and faster than those found in other feeding areas. Vagility measured during spring tides is the greatest reported for green turtles on any feeding areas (Mendonça 1983, Ogden et al. 1983, Brill et al. 1995, Renaud et al. 1995, Seminoff 2000; Table 4). Mean vagility measured at neap tide in Estero Banderitas is comparable with maximum vagility reported at other sites. This is understandable, as it is during neap tides when tidal influence is minimal and Estero Banderitas is most similar to non-tidal habitats.

Speed, or rate of movement, is less frequently reported. Speed of green turtle movements in Estero Banderitas was the greatest reported for sea turtles in feeding areas, as compared with $0.33 \pm 0.09 \text{ kmh}^{-1}$ for green turtles in Bahía de los Angeles (Seminoff & Jones in review), 0.4 to 1.4 kmh^{-1} for loggerhead turtles in the Gulf of México (Renaud & Carpenter 1994), and $0.44 \pm 0.33 \text{ kmh}^{-1}$ (range: 0.004 – 1.758 kmh^{-1}) for Kemp's ridley turtles in Cedar Keys, Florida (Schmid et al. 2002). It is of note that Kemp's ridley turtles, which moved at the next greatest speeds, also moved with tidal currents.

We do not expect that turtles in Estero Banderitas were swimming faster than turtles in other feeding areas. Rather, we believe that the greater vagility and speed of Banderitas turtles was due to transport by tidal currents. Other sea turtles move quickly within currents. Leatherback turtles traveled at maximum speeds of 6 kmh^{-1} in the Agulhas Current in the Indian Ocean, a current with water speeds up to 7.2 kmh^{-1} (Luschi et al. 2003b).

Tides were the greatest determinant of movement and activity patterns in Estero Banderitas. Greater tidal currents resulted in greater distances traveled, greater mean speeds, and greater maximum speeds than lesser, neap currents. Transport distance and speed did not depend on size of turtle, as for juvenile green turtles in Texas (Arms 1996), or time of day. Turtle tracks were mostly linear, and replicated the inward and outward movement of the tide. Stick plots provided a unique way to observe the similarity between the movement of turtles and tides, and to visually analyze the effects of the two scalar components, direction and speed, on one figure. Vector correlation provided a quantitative measurement of this similarity, and the majority of turtle movements were significantly correlated with tidal movements. Differences in direction of turtles and currents were observed as a lag between when the tide changed directions and when the turtle changed directions. Differences in speed may have been due to the vertical position of the turtle in the water column. We used a mean velocity for the entire water column to determine tidal vectors, but turtles on feeding grounds dive from the surface to the bottom in regular intervals. Vertical profile diagrams illustrate the variation in velocity throughout the water column. Also, we expected that turtles would not always act as passive drifters and would swim either with, against, or perpendicular to the currents.

Movements in Estero Banderitas were unlike the tracks reported at non-tidal feeding areas, where turtles followed a diel pattern and poygonal movements were suited to their bay-like habitats. Speed and direction, the two scalar components of vector

correlation, were similar between turtle and water movement, indicating there was not one controlling scalar factor causing significant vector correlation.

The paucity of periods of no movement indicates that turtles in Estero Banderitas were not resting while being transported with the tide. Data collected underwater, such as that from a carapace-mounted camera, might indicate whether turtles were actively moving their flippers (i.e. swimming) during movement, or whether they were drifting and essentially motionless. If they were not swimming for substantial periods throughout the day, resting during tidal transport might be sufficient to satisfy energetic needs. Turtles also maintained themselves in the center of the channel, which corresponds to the fastest currents along the width of the channel. We are unsure whether dynamics of flow keep turtles entrained within the strongest currents, or whether turtles actively steer themselves so they remain in the greatest current speed in the center of the channel. Further research on the location of the turtle within a three-dimensional scale would help answer these questions.

Green turtles in Estero Banderitas have a mostly herbivorous diet, composed primarily of algae, with invertebrates, sea grass, and mangrove seed pods also present (Hilbert et al. 2000, Lopez Mendilaharsu 2002). In Estero Banderitas, researchers conducting benthic surveys identified 41 species of marine algae (Ramos & Santos 2005). Diet samples retrieved by lavage in 2002 indicated that turtles fed selectively and primarily on three algae: *Codium amplivesiculatum*, *Gracilaria textorii*, and *Gracilaria pacifica* (Lopez Mendilaharsu 2002). However, diet items and their relative importance changed due to season and year. Qualitative lavage samples (n = 6) collected in July

2003 had different species composition than samples from 2002. Three samples were dominated by a single alga: two by *Hypnea johnstonii* and one by *Zostera marina*. Three samples were heterogeneous, containing *Cladophora columbiana*, *Caulerpa sertularoides*, *G. textorii*, *Polysiphonia sp.*, *Gracilariopsis andersonii*, *H. johnstonii*, *Risoclonium sp.* and *C. amplivesiculatum*. At the same time, benthic algal cover in Estero Banderitas, measured by wet weight and in order of abundance, was dominated by *C. sertularoides*, *C. columbiana*, *Amphiroa beauvoisii*, *H. johnstonii* and *G. pacifica* (Ramos & Santos 2005). These data indicate that sea turtles are feeding selectively, but also alter their diet to accommodate the seasonal and yearly availability of algae.

Most feeding studies of green turtles describe the presence of large pastures of dense sea grass or algae in the foraging habitat (Bjorndal 1980, Mendonça & Ehrhart 1982, Ogden et al. 1983, Seminoff et al. 2002a). In Estero Banderitas, algae distribution and abundance is patchy (Ramos & Santos 2005, Brooks and Harvey, unpubl. data). The lack of persistent pastures on which to feed means that turtles cannot depend on a food source in one particular place. Whiting & Miller (1998) proposed that widely distributed food in Repulse Bay, Australia, resulted in greater movements of foraging green turtles. Similarly, green turtles in Estero Banderitas must travel long distances to find food items. The local environment is ideally suited to this need by providing strong tidal currents by which to transport turtles at low energetic cost.

Our study is the first to investigate the influence of tides on green turtles, but tidal currents affected movements of loggerhead turtles in Chesapeake Bay, MD (Byles 1988) and Kemp's ridley turtles in Cedar Keys, FL (Schmid et al. 2002). Researchers in both

studies noted the potential benefit of this behavior for conserving energy. If turtles in Estero Banderitas swim less than turtles in other feeding areas, we would expect the consequential conservation of energy, therefore increased growth. Mean growth rate of turtles in Estero Banderitas, at large for at least twelve months, was $1.7 \pm 0.6 \text{ cm yr}^{-1}$, with growth rates three times greater in summer than in winter (Koch et al. in press). This rate is greater than growth rates reported in the Galápagos Islands (Green 1993, Seminoff et al. 2002c). Researchers in previous studies have suggested that growth is density dependent, which might explain the slower growth of the protected Galápagos stock (Bjorndal et al. 2000, Seminoff et al. 2002c). However, growth rates in the Atlantic are consistently greater than those in the Pacific, even at sites that have been heavily exploited (Bjorndal et al. 2000).

At present, growth rates in Estero Banderitas and Bahía de los Angeles are comparable (Seminoff et al. 2002c). Perhaps dominant environmental factors in each site act to cancel out possible negative effects. Though turtles in Bahía de los Angeles must swim between feeding and resting sites, they have an abundance of food and short travel distances. Turtles in Estero Banderitas must travel long distances to encounter sufficient food, but tides provide energetically advantageous transport. Both stocks might also be experiencing similar decrease in food availability and/or foraging activity in winter as water temperatures decrease. This is evidenced by slow winter growth at Estero Banderitas. Green turtles at other sites in the Gulf of California and Pacific lagoons go into torpor, a type of hibernation, during winter months (Felger et al. 1976, Nichols 2003). Winter growth in Bahía de los Angeles has not been investigated.

We can use data on growth and recruitment size to estimate duration of life history stages of green turtles in Estero Banderitas. The estimated age at maturity (at MNS) for East Pacific green turtles is 33.3 years (Seminoff 2004). If green turtles are an average 38 cm SCL when they arrive at Estero Banderitas, it will take 23 years to grow, at a rate of 1.7 cm yr^{-1} , to MNS. Green turtles probably spend close to 10 years as pelagic juveniles, growing at a faster rate of $\sim 3.8 \text{ cm yr}^{-1}$ before recruiting to neritic feeding grounds. These values are estimates, but provide an approximation of duration of life stages for the East Pacific green turtle. Growth rates at other Pacific feeding areas are non-monotonic functions: greater growth rates in juveniles that decrease for subadults (Balazs 1982, Green 1993, Limpus & Chaloupka 1997). However, Limpus & Chaloupka (1997) reported maximum growth at $\sim 60 \text{ cm SCL}$, and we expected greatest growth of East Pacific green turtles at smaller sizes, when they are in their pelagic stage.

A critical component of STST is vertical migration of the animal in the water column to control the direction of horizontal movement. Species of invertebrates and fish use STST at larval and/or adult stages to leave nursery areas and to return to them (Forward & Tankersley 2001, Robinson & Gomez-Aguirre 2004). Our data indicated a similar but notably new transport pattern. Green turtles in Estero Banderitas were transported continuously, with sequential ebb and flood tides, throughout the tidal cycle, rather than traveling selectively upstream or downstream. They experienced tides in their home habitat, areas in which they persist during seasons and years. Other marine animals, including Atlantic stingray (*Dasyatis sabina*) in Florida (Teaf 1980), leopard shark (*Triakis semifaciatis*) in California (Ackerman et al. 2000), thin-lipped grey mullet

(*Liza ramada*) in Portugal (Almeida 1996), and sea turtles (Byles 1988, Schmid et al. 2002) move unselectively with tidal currents. But similar species, such as the lemon shark (*Negaprion brevirostris*) and bat ray (*Myliobatis californica*) did not drift with tides (Gruber 1982, Matern et al. 2000). If planktonic animals, such as larvae, can avoid undesirable tidal currents, we would expect green turtles to have the same ability, and to demonstrate it on a regular basis, as needed. However, turtles are not being displaced unfavorably by tidal transport, therefore, they have no reason to avoid it. Instead, we argue, they probably need the transport to effectively exploit food resources in Estero Banderitas.

We anticipate that these data are applicable to behavior of turtles in other tidally-dominated areas worldwide, and to potential management plans for these areas. In habitats with strong tidal currents, turtles probably are moving with the tides. Conducting studies of turtle movement can be costly, in time and money, but tidal information often is more readily available. Displacement of water by tidal flow during a half tidal period (6 hours) can be explained by a non-dynamic equation that incorporates $V_{\max}$, or the maximum speed of the current, and T, or tidal period (12 hours):

$$(4) \quad Disp = V_{\max} \left(\frac{T}{\pi} \right).$$

Displacement predicted by this equation, using mean $V_{\max}$ from tide stations, was 0.2 to 0.6 kmh^{-1} , whereas movements of turtles were 0.2 to 1.6 kmh^{-1} . Our virtual displacement diagrams were constructed from a more complex method in an effort to predict turtle movement with greater accuracy. We predicted cumulative displacement by using U and

V components of our tidal vectors calculated through sine interpolation, with $V_{\max}$ from each geographic area, or station, through which the turtle was traveling. While distance of displacement was usually greater than distance traveled by the turtle, the general shape of movements was similar to turtle tracks. The displacement closely predicted the most highly linear turtle tracks, such as BMAD2 and BMAL. In areas with more information on tides than turtles, turtle movement potentially can be predicted using tidal data. However, it is obvious that turtle movement and transport is far more complex than the displacement, or transport, of a particle of water.

The number of female green turtles nesting on the main nesting beach in Michoacán, México, has decreased 94% since 1970 (Seminoff 2004). Harvest of juveniles at foraging habitats is one of the greatest threats to this sub-population (Alvarado & Figueroa 1995, Seminoff 2000, Alvarado-Diaz et al. 2001, Nichols 2003). Although nesting beaches for this population are effectively protected and laws prohibit the take of sea turtles, there is, in practice, little protection for sea turtles on feeding areas off the Baja Peninsula. Conservation efforts are underway, and successes have been rooted in community participation and support. Recently, non-profit, community and government organizations have collaborated to propose the establishment of a sea turtle sanctuary in Estero Banderitas. This study will provide the technical data on sea turtles in this area, and will provide information on boundaries for management plans of the sanctuary. Data indicate that a sanctuary in Estero Banderitas could provide effective protection for this stock of juvenile sea turtles until maturity. Community support for this effort has been documented (Garcia-Martinez et al. 2002). Estero Banderitas would serve

as the first of a network of sanctuaries on the coast of the Baja California peninsula, and the sanctuary would signify the beginning of formal protection for sea turtles in critical foraging and developmental habitat in northwestern México.

Our data indicate a new paradigm for green turtles in tidal foraging areas, and a newly described transport system for animals in high energy tidal systems. Long-term monitoring will continue to provide information on residence times, population size, and habitat use. Future studies will investigate turtle transport on a three-dimensional scale, flow dynamics within a tidal current, algal density and distribution, and energetics and feeding activity to create a more complete assessment of the foraging ecology of green turtles in this, and other, tidally-dominated habitats.

ACKNOWLEDGMENTS

Thanks to W. Watson for invaluable engineering in tag construction; S. Flora for MATLAB help; L. Breaker for vector correlation instruction; V. Koch, R. Rangel, J. Solis, Grupo Tortuguero de las Californias, SFS students and staff for field assistance; J. Adams, H. Nevins and MLML Vertebrate Ecology Lab. Funding was provided by NFWF, Homeland Foundation, Myers Oceanographic Trust, PADI Foundation, and Harvey Graduate Research Fellowship. Research was conducted under permit # 280499.213.03 1565 and # 280700.213.03 2619 authorized by Secretaria de Medio Ambiente Recursos Naturales y Pesca, Estado Unidos de México. Animal care protocol was approved by SJSU Animal Care and Use Committee (IACUC #805).

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Table 1. Direction (in degrees) of flow for ebb and flood tide at each ADP Station, according to speed of the tidal current, and binned in speed increments of 0.2 ms^{-1} .

Station	Speed	Flood	Ebb
St. 1	$\leq 0.2 \text{ ms}^{-1}$	42°	155°
	to ≤ 0.4	18°	181°
	to ≤ 0.6	15°	186°
	to ≤ 0.8	13°	187°
	> 0.8	---	---
St. 2	$\leq 0.2 \text{ ms}^{-1}$	17°	161°
	to ≤ 0.4	4°	176°
	to ≤ 0.6	2°	178°
	to ≤ 0.8	---	181°
	> 0.8	---	179°
St. 3	$\leq 0.2 \text{ ms}^{-1}$	29°	197°
	to ≤ 0.4	30°	205°
	to ≤ 0.6	---	205°
	to ≤ 0.8	---	205°
	> 0.8	---	---
St. 4	$\leq 0.2 \text{ ms}^{-1}$	39°	185°
	to ≤ 0.4	33°	203°
	to ≤ 0.6	30°	207°
	to ≤ 0.8	---	209°
	> 0.8	---	---
St. 5	$\leq 0.2 \text{ ms}^{-1}$	16°	172°
	to ≤ 0.4	4°	178°
	to ≤ 0.6	3°	178°
	to ≤ 0.8	3°	181°
	> 0.8	---	180°
St. 7	$\leq 0.2 \text{ ms}^{-1}$	20°	152°
	to ≤ 0.4	7°	165°
	to ≤ 0.6	---	168°
	to ≤ 0.8	---	---
	> 0.8	---	---
St. 9	$\leq 0.2 \text{ ms}^{-1}$	94°	262°
	to ≤ 0.4	85°	263°
	to ≤ 0.6	88°	---
	to ≤ 0.8	---	---
	> 0.8	---	---

Table 2. Regression equations and R^2 values for $\Delta H/\Delta t$ San Diego vs. $\Delta H/\Delta t$ Station, and $\Delta H/\Delta t$ Station vs. $V_{\max}$ at ADP Stations in Estero Banderitas, B.C.S., México.

Station	$\Delta H/\Delta t$ San Diego vs. $\Delta H/\Delta t$ Station	$\Delta H/\Delta t$ Station vs. $V_{\max}$
1	$y = 0.8466x + 0.0002$ $R^2 = 0.9601$	$y = 32.174x - 0.0329$ $R^2 = 0.9760$
2	$y = 0.7804x + 0.0002$ $R^2 = 0.9906$	$y = 30.305x - 0.1356$ $R^2 = 0.9874$
3	$y = 0.6783x - 0.0003$ $R^2 = 0.9906$	$y = 30.807x - 0.1282$ $R^2 = 0.9895$
4	$y = 0.8622x - 0.00008$ $R^2 = 0.9800$	$y = 37.401x - 0.0524$ $R^2 = 0.9965$
5	$y = 0.8694x - 0.0001$ $R^2 = 0.9848$	$y = 37.555x - 0.0644$ $R^2 = 0.9952$
7	$y = 0.6619x - 0.00008$ $R^2 = 0.9765$	$y = 34.935x - 0.0221$ $R^2 = 0.9566$
9	$y = 0.8041x + 0.00004$ $R^2 = 0.9925$	$y = 23.811x + 0.0711$ $R^2 = 0.9895$
10	$y = 0.7382x - 0.0001$ $R^2 = 0.9883$	$y = 16.112x + 0.0985$ $R^2 = 0.9473$

Table 3. Morphological and tracking data for green turtles captured and tracked in Estero Banderitas, B.C.S., México, 2000 – 2003.

Year	# turtles tracked	# locations captured	% re-captures	SCL (cm $\pm$ sd)	SCL Range (cm)	Mass (kg $\pm$ sd)	Duration of tracks (hr)	Distance of tracks (km)
2000	5	2	0	50.8 $\pm$ 3.6	46.2 – 55.3	14.8 $\pm$ 1.9	16.3 – 46.9	4.5 – 65.3
2001	3	2	33	56.8 $\pm$ 8.0	52.0 – 66.1	25.1 $\pm$ 12.9	10.0 – 45.3	8.8 – 11.7
2002	9	4	22	55.0 $\pm$ 4.8	50.0 – 64.0	24.0 $\pm$ 6.6	6.9 – 24.6	10.0 – 38.6
2003	13	7	54	55.1 $\pm$ 6.7	43.9 – 68.9	20.4 $\pm$ 5.2	5.2 – 53.0	1.4 – 46.7
Total	30	8	33	54.5 $\pm$ 5.8	43.9 – 68.9	21.3 $\pm$ 6.9	5.2 – 53.0	1.4 – 65.3

Table 4. Summary of vagility (distance traveled per day) reported by this and other studies on green turtle (*Chelonia mydas*) at foraging areas.

Research study	Location of study	Vagility (distance per day)
This study	Estero Banderitas, B.C.S., Mexico	29.9 ± 11.3 km (spring tide, summer) 9.8 ± 9.3 km (neap tide, summer)
Mendonça 1983	Mosquito Lagoon, FL, USA	8.2 ± 1.75 km (winter) 2.62 ± 0.96 km (summer)
Ogden et al. 1983	St. Croix, USVI, USA	~ 2 km
Brill et al 1995	HA, USA	3 km ² area for 13 days
Renaud et al 1995	TX, USA	1.2 km
Seminoff 2000	Bahía de los Angeles, B.C., Mexico	9.54 ± 3.2 km (summer)

Figure 1. Study area. (A) The Baja California Peninsula. (B) The Bahía Magdalena – Almejas Complex. (C) Estero Banderitas, Baja California Sur, Mexico. Capture locations are marked by triangles, ADP locations and stations are marked by circles and numbers.

Figure 2. Schematic drawing of (A) GPS-VHF telemetry unit and (B) the telemetry unit attached to a green turtle.

Figure 3. Direction ($^{\circ}$) and speed (ms^{-1}) of tidal currents measured by Acoustic Doppler Profilers (ADP) at numbered stations (1-10) in Estero Banderitas, B.C.S., México.

Figure 4. Height of water at stations (1-10) during ADP deployment as predicted for San Diego (---), as measured by ADP (red), and resulting from harmonic regression of ADP heights (black).

Figure 5. Along-channel (blue) and across-channel (red) current speeds (ms^{-1}) over time as measured by ADP at numbered stations (1-10) in Estero Banderitas, B.C.S., México.

Figure 6. Vertical profiles of tidal current velocity (ms^{-1}) averaged over 1 hour intervals, from 1 m above the bottom (due to ADP height and 0.4 m blanking distance) to surface in 0.25 m bins, at Station 1. Numbers within the figures represent chronological sequence, in hours, of sampling. This station shows patterns typical of all others.

Figure 7. $V_{\max}$ vs. $\Delta\text{Height} / \Delta\text{time}$ at Stations located in the main channel of Estero Banderitas, B.C.S., México. Points (•) were calculated for each change in tidal phase; lines result from linear regression. Stations are numbered beginning south and moving north. Steeper lines represent station location where the channels were most narrow.

Figure 8. All turtle tracks from GPS locations obtained from green turtles tracked Summer 2000 – 2003 (n = 29) in Estero Banderitas, B.C.S., México

Turtle 2.

Turtle 3.

Figure 9. Turtle tracks from 2000 – 2002 ($n = 16$) in Estero Banderitas, B.C.S., México. Black flag indicates release location, turtle track is in red, MCP outer limits are in black.

Turtle 4.

Turtle 5.

Figure 9. (cont.)

Turtle 6.

Turtle 7.

Figure 9. (cont.)

Turtle 8.

Turtle 10.

Figure 9. (cont.)

Turtle 11.

Turtle 12.

Figure 9. (cont.)

Turtle 13.

Turtle 14.

Figure 9. (cont.)

Turtle 15.

Turtle 16.

Figure 9. (cont.)

Turtle 18.

Turtle 19.

Figure 9. (cont.)

Turtle A.

Figure 10. Track, minimum convex polygon, and stick plot for individual turtles tracked using GPS-VHF telemetry in Estero Banderitas, B.C.S., México, in 2003. On map: black flag indicates release location, turtle track is in red, MCP outer limits in black. On stick plot: resultant vectors composed of speed (ms^{-1}) and direction (north points up) representing tidal current movement (blue) and turtle movement (red), plotted in $\frac{1}{2}$ hour intervals. Correlation coefficient (r^2) results from vector correlation, * indicates significant vector correlation based on 95th % limits.

Turtle B.

Figure 10. (cont.)

Turtle C.

Figure 10. (cont.)

Turtle D.

Figure 10. (cont.) Stick plot corresponds to track beginning at black arrow on map and all southern portions.

Turtle E.

Figure 10. (cont)

Turtle F.

Figure 10. (cont.)

Turtle G.

Figure 10. (cont.)

Turtle H.

Figure 10. (cont.) Black arrow on stick plot indicates a time break in tracking.

Turtle I.

Figure 10. (cont.) Black arrow on stick plot indicates a time break in tracking.

Turtle J.

Figure 10. (cont.) Black arrow on stick plot indicates a time break in tracking.

Turtle K.

Figure 10. (cont.)

Turtle L.

Figure 10. (cont.) Stick plot is for track designated in red; second half of track is in black.

Turtle M.

Figure 10. (cont.) Black arrow on stick plot indicates a time break in tracking.

Figure 11. Virtual displacement diagrams modeling the theoretical displacement of a particle of water subjected to identical tidal current vectors as predicted for turtle tracks. Each letter indicates the analogous turtle track.

Figure 11. (cont.).

Appendix 1. Capture, morphological and track data of green turtles tracked in Estero Banderitas, B.C.S., México, July – August, 2000-2003.

Field ID	Track ID	Capture Date	Recap?	SCL (cm)	CCL (cm)	Mass (kg)	TTL (cm)	Track hours*	Track km*	MCP (ha)
BMA6JUL2000-1	2	6 Jul 2000	N	48.8	52.0	15.9	8.7	33.7	28.9	1094.3
BMA7JUL2000-2	3	7 Jul 2000	N	53.2	55.5	n/a	n/a	16.3	8.8	127.2
BMA7JUL2000-3	4	7 Jul 2000	N	55.3	59.0	13.6	n/a	19.1	4.5	6.0
BMA23JUL2000-1	5	23 Jul 2000	N	46.2	49.5	12.7	6.3	46.7	52.8	914.7
BMA23JUL2000-2	6	23 Jul 2000	N	50.3	53.7	16.8	8.8	46.9	65.3	1064.9
BMA9JUL2001-2	7	9 Jul 2001	N	52.4	56.7	17.2	9.5	10.0	9.0	157.3
BMA21SEP2000-2	8	12 Jul 2001	Y	66.1	70.1	39.9	12.6	11.2	11.7	778.7
BMA25JUL2001-1	10	25 Jul 2001	N	52.0	55.5	18.1	9.5	45.3	8.9	5.0
BMA21SEP2001-3	11	7 Jul 2002	Y	50.4	53.1	17.7	9.1	24.6	28.8	1223.6
BMA10JUL2002-1	12	10 Jul 2002	N	50.0	53.4	17.7	8.7	22.1	32.9	953.9
BMA3JUL2001-2	13	10 Jul 2002	Y	51.5	n/a	19.1	6.4	23.0	26.5	1492.9
BMA28JUL2002-1	14	18 Jul 2002	N	56.3	61.2	25.9	10.9	23.9	10.0	60.9
BMA23JUL2002-1	15	23 Jul 2002	N	53.5	56.6	20.4	11.2	23.7	35.8	713.1
BMA24JUL2002-1	16	24 Jul 2002	N	55.4	61.1	24.2	11.1	23.8	38.6	1035.0
BMA28JUL2002-2	18	28 Jul 2002	N	60.8	65.0	32.7	12.7	6.9	10.9	378.3
BMA29JUL2002-3	19	29 Jul 2002	N	64.0	68.5	36.3	11.0	12.9	17.6	637.9
BMA13SEP2002-3	A	1 Jul 2003	Y	55.9	58.1	21.8	12.9	5.2	4.7	46.7
BMA3JUL2003-1	B	3 Jul 2003	N	47.3	55.0	12.5	8.5	25.5	29.1	865.5
BMA12NOV2002-1	C	3 Jul 2003	Y	53.6	57.0	22.0	7.4	18.7	11.2	192.9
BMA7JUL2003-1	D	7 Jul 2003	N	53.6	56.7	21.0	8.2	51.3	47.7	2229.6
BMA12APR2003-2	E	8 Jul 2003	Y	68.9	n/a	n/a	n/a	22.5	12.1	105.1
BMA23OCT2001-1	F	11 Jul 2003	Y	58.6	63.2	25.9	9.8	28.3	13.4	369.0
BMA13SEP2002-2	G	14 Jul 2003	Y	59.0	63.5	24.4	10.8	12.0	46.7	1443.9
BMA10MAR2003-1	H	22 Jul 2003	Y	53.1	56.5	21.0	11.2	53.0	2.6	21.5
BMA24JUL2003-1	I	24 Jul 2003	N	54.8	59.6	19.8	9.7	17.3	38.4	1367.0
BMA24JUL2003-2	J	24 Jul 2003	N	56.4	61.1	23.8	10.9	54.3	17.7	52.2
BMA28JUL2003-1	K	28 Jul 2003	N	48.1	50.8	17.6	5.8	20.7	2.8	5.5
BMA20MAR2002-6	L	1 Aug 2003	Y	63.5	67.0	26.3	16.6	45.8	38.6	571.1
BMA1AUG2003-1	M	1 Aug 2003	N	43.9	45.5	9.1	6.1	33.0	11.9	73.8

* Several turtles (D, H, I, J, L, and M) were tracked for non-consecutive segments separated by >1 hour. Track hours and kilometers are combined for these turtles in this table.