Diel foraging behavior of gravid leatherback sea turtles in deep waters of the Caribbean Sea

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SUMMARY

It is generally assumed that leatherback turtles (*Dermochelys coriacea*), like other species of sea turtle, do not feed while offshore from nesting beaches, and rely instead on fat reserves to fuel reproductive activities. Recent studies, however, provide evidence that leatherbacks may forage during the internesting interval while offshore in the Western Atlantic Ocean and Caribbean Sea. Bio-logging technology was used to investigate the foraging behavior of female leatherback turtles at St Croix, US Virgin Islands. Leatherback gastrointestinal tract temperatures (T_{GT}) were analyzed for sudden fluctuations indicative of ingestions, and laboratory ingestion simulations were used to characterize temperature fluctuations associated with ingestion of prey *versus* seawater. Dive patterns associated with prey ingestion were characterized and the proportion of prey ingestion during the day (05:00–18:59 h) and night (19:00–04:59 h) were compared. A combined total of 111 prey ingestions for seven leatherback turtles were documented during the internesting interval. The number of prey ingestions ranged from six to 48 for individual turtles, and the majority (87.4%) of these events occurred during the daytime. Prey ingestions were most frequently associated with V-shaped dives, and the mean (±1 s.d.) maximum dive depth with prey ingestion ranged from 154±51 to 232±101 m for individual turtles. Although leatherbacks were found to opportunistically feed during the internesting interval, the low prey ingestion rates indicate that energy reserves acquired prior to the breeding season are critical for successful reproduction by leatherbacks from the St Croix, USVI nesting population.

Key words: diving, energetics, prey ingestion, stomach temperature telemetry, body temperature, *Dermochelys coriacea*, jellyfish, siphonophores, capital breeders.

INTRODUCTION

Leatherback turtles (*Dermochelys coriacea* L.) undertake long-distance oceanic migrations, sometimes across entire ocean basins, and travel seasonally between high and low latitudes (e.g. Keinath and Musick, 1993; Hays et al., 2004a; Hays et al., 2004b; James et al., 2005a; Eckert, 2006; Shillinger et al., 2008). During the summer and fall, leatherbacks in the Atlantic Ocean are found in temperate waters off the coast of Europe and North America, including Ireland, the United Kingdom, Canada and the US (Hays et al., 2004a; Hays et al., 2004b; James et al., 2005a; James et al., 2005b; Eckert, 2006; Houghton et al., 2006; James et al., 2006a; James et al., 2006b; Witt et al., 2007). These sites are known to be valuable foraging grounds for leatherback turtles where they exploit seasonally high concentrations of prey, such as the jellyfish species *Aurelia aurita*, *Rhizostoma octopus*, *Rhizostoma pulmo* and *Cyanea capillata* (James and Herman, 2001; James and Mrosovsky, 2004; Hays et al., 2004a; Houghton et al., 2006; Jonsen et al., 2007; Witt et al., 2007). Leatherbacks leave high latitude foraging grounds in the North Atlantic during the fall and winter to begin southerly migrations, with some turtles heading to breeding and nesting areas in the tropics and subtropics (James et al., 2005a; James et al., 2005b; Eckert, 2006), and others utilizing low latitude open ocean foraging areas (James et al., 2005a; Eckert, 2006).

Until recent years, leatherback turtles were assumed to be capital breeders, relying on energy stores accrued at foraging grounds to fully support all activities associated with reproduction (Miller, 1997;

Hays et al., 2004a; James et al., 2005b; Reina et al., 2005). Eckert et al. (Eckert et al., 1986) was the first to suggest that leatherbacks may not be capital breeders, based on internesting dive patterns of leatherbacks from the St Croix, US Virgin Islands (USVI) nesting population. Dives by gravid leatherbacks offshore St Croix, USVI were deeper and less frequent during the daytime than at nighttime; a dive pattern reflective of foraging on vertically migrating prey associated with the deep scattering layer (DSL) (Eckert et al., 1986). The organisms in the DSL typically migrate from deep waters during the day to shallow depths at night, a processed referred to as diel vertical migration (reviewed by Hays, 2003). Thus, a diel dive pattern by leatherbacks may reflect a strategy to improve foraging success on gelatinous organisms as they migrate closer to the surface at night. Subsequent studies have confirmed that leatherback turtles in the Caribbean Sea conduct longer, deeper dives during the day and shorter, more frequent dives during the night (Eckert et al., 1989b; Hays et al., 2004a; Myers and Hays, 2006), and provided additional information on potential prey ingestion events during the nesting season (Eckert et al., 1989b; Myers and Hays, 2006; Fossette et al., 2008). Eckert et al. (Eckert et al., 1989b) reported a decrease in mass of female leatherbacks over the course of the nesting season at St Croix, USVI that was much lower than expected, based on measurements of egg clutch mass and the assumption that internesting mass loss for females should account for approximately 50% of egg clutch mass (Eckert et al., 1989b). Myers and Hays (Myers and Hays, 2006) and Fossette et al. (Fossette

et al., 2008) used inter-mandibular angle sensors (IMASENs) to record beak-mouth opening movements by free-swimming leatherbacks during the internesting period offshore from Grenada and French Guiana, respectively. Despite short monitoring periods with IMASENs in these studies (maximum monitoring period with IMASENs was 56.1 h), numerous movements were documented that could be indicative of prey ingestion.

Under a capital breeding strategy, leatherbacks must acquire sufficient energy stores at foraging grounds to fuel long-distance migrations (3000–5000 km) from high latitude foraging areas to low-latitude nesting areas (James et al., 2005a; James et al., 2005b). In addition, they must have enough energy stores to support all further activities associated with successful reproduction once they arrive at their breeding and nesting areas. Given the high energetic demands associated with reproduction for leatherback turtles (see Wallace et al., 2006), it seems likely that leatherback turtles would forage opportunistically during the nesting season to take advantage of locally available food sources and augment energy reserves. Although previous studies have provided intriguing evidence to support this idea, long-term monitoring of leatherback feeding behavior during the internesting interval are lacking in the literature.

A popular technique for investigating foraging patterns of marine endotherms over the course of several days to weeks is stomach temperature telemetry (Wilson et al., 1992; Wilson et al., 1995; Ancel et al., 1997; Kuhn and Costa, 2006; Horsburgh et al., 2008). With this technique, the study organism is fed an instrument capable of detecting stomach temperature and transmitting the temperature data to an externally mounted receiver. The use of stomach temperature telemetry to monitor feeding behavior of marine predators relies on temperature differences between the study animal and its prey, and thus is typically employed with endothermic marine predators that prey on ectothermic marine animals. Ingestion of prey at ambient temperature (T_A) by animals that have warm core body temperatures results in a rapid decrease in stomach temperature. The animal's stomach temperature gradually rises back to previous levels as the animal's metabolic heat warms the prey contents inside the stomach (Wilson et al., 1995). Thus, a rapid fall and rise in stomach temperature may be used to identify prey ingestion. An investigation of leatherback feeding behavior using stomach temperature telemetry is feasible because adult leatherback turtles maintain a significant thermal gradient between core body temperatures and T_A (range: 1.2–4.3°C) (Southwood et al., 2005), primarily because of their massive size (300–600 kg) and circulatory adjustments (Paladino et al., 1990), and because they forage exclusively on ectothermic gelatinous prey.

We used a combination of stomach temperature telemetry and archival data logging technology to investigate the internesting foraging and diving behavior of female leatherback turtles nesting at Sandy Point National Wildlife Refuge (SPNWR), St Croix, USVI (64°50′00″ W, 17°40′12″ N; Fig. 1). This site was chosen because previous studies had provided behavioral and circumstantial evidence supporting the idea that turtles from this nesting population feed during the internesting interval (Eckert et al., 1989b). Opportunistic foraging by leatherback turtles during the internesting interval may be best served by adopting the most energetically efficient dive pattern that would result in contact with prey. In particular, targeting vertically migrating prey while it is at shallow depth at night would provide a 'cheap' method of foraging that would allow energy to be conserved for reproduction. We hypothesized that leatherback turtles would concentrate foraging efforts at shallow depths during the night and would therefore display a higher frequency of feeding events during nighttime compared
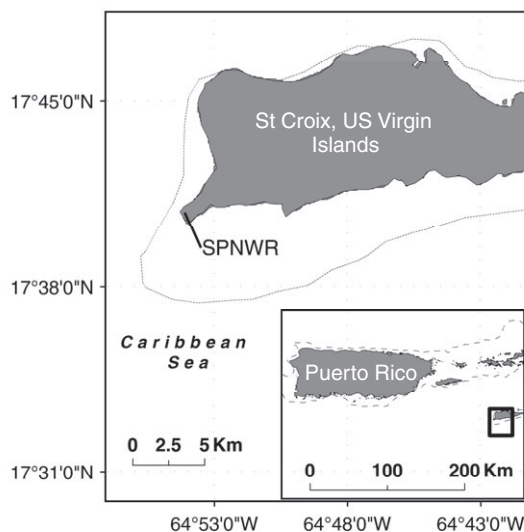

Fig. 1. Sandy Point National Wildlife Refuge (SPNWR), St Croix, US Virgin Islands. The dotted line delineates the 200 m isobath.

with daytime. In this paper, we report the findings from our field study, as well as results from laboratory simulations that provide criteria for distinguishing prey and seawater ingestions based on characteristics of temperature fluctuations obtained through stomach temperature telemetry.

MATERIALS AND METHODS
Field procedures

The primary leatherback nesting area on SPNWR was patrolled nightly (20:00 h to 05:00 h) to intercept nesting turtles. Turtles were selected based on their nesting history at SPNWR, with preference given to turtles that had at least a 3-year nesting history at SPNWR and had already laid two to four nests at the time of instrument deployment. Long-term tagging records show that leatherbacks usually return to SPNWR to nest every 2–5 years, lay an average of four to eight clutches in a nesting season, and spend 8–10 days at sea between each nesting event (Boulon et al., 1996). The nesting behavior of leatherbacks at SPNWR provided the opportunity to deploy instruments on nesting turtles and to retrieve the instruments when turtles returned to nest again.

Archival platform transmitter terminals (model Mk10-AL, Wildlife Computers, Redmond, WA, USA) and pre-calibrated stomach temperature pills (model STP3, Wildlife Computers; please see the Instruments section) were deployed on gravid leatherback turtles at SPNWR in 2007 (N=9) and 2008 (N=10). The Mk10-AL was attached directly to the turtle's carapace during oviposition. The attachment site was cleaned with isopropyl alcohol (70%) followed by application of betadine antiseptic. A cordless drill (DC728 14.4 V, DeWalt) with a 4 mm surgical drill bit (model QC 4.0 mm 195/40 mm, Apiary Medical, Inc., West Milford, NJ, USA) was used to drill holes in the carapace for attachment of the Mk10-AL.

The Mk10-ALs deployed in 2007 were attached to the leading edge of the carapace between the medial and first lateral ridge (Fig. 2A). Four holes were drilled into the turtle's carapace to a depth of <20 mm and at an angle perpendicular to the surface of the carapace. The spacing of the drill holes matched the spacing of holes in the Mk10-AL arm-plates. Orthopedic mini-anchors (OMAs) were inserted into the pre-drilled holes to a depth of <15 mm, leaving
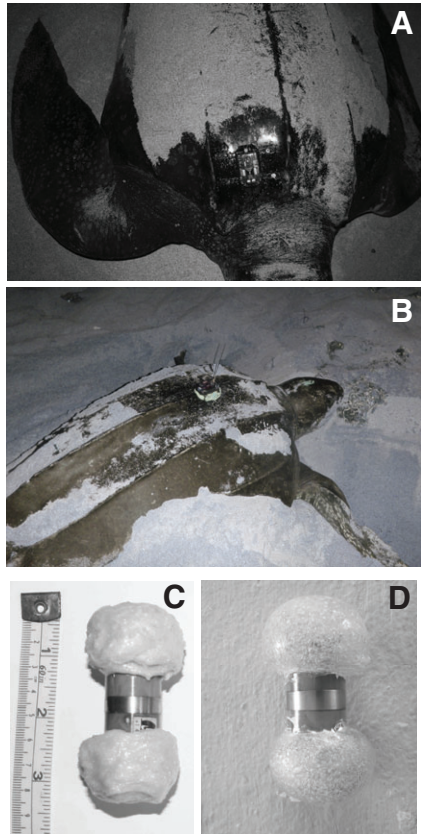
Fig. 2. Photographs of MK10-AL deployments on leatherback turtles at St Croix, USVI in 2007 (A) and 2008 (B). (C,D) The STP3 stomach temperature pills used in the 2007 study (C), which were enlarged using layers of gelatin coated with ethylcellulose, and in the 2008 study (D), which were only coated in ethylcellulose, as the retention matrix.

~15 mm of the OMA shaft protruding from the turtle's carapace. The holes were treated with an antibacterial ointment (Furacin, Squire Laboratories, Revere, MA, USA) prior to and after the insertion of the OMAs. The Mk10-AL was placed onto the turtle's carapace with the external shafts of the OMAs passing through holes on the Mk10-AL arm-plates. Stainless steel washers were threaded onto the OMA shaft so that they lay flat across the Mk10-AL arm-plates, and a stainless steel hairpin was inserted into a hole at the top end of each OMA shaft to secure the Mk10-AL to the OMA.

The Mk10-ALs deployed in 2008 were attached directly to the dorsal medial ridge of the carapace, posterior to the turtle's scapulae (Fig. 2B). Two holes were drilled through the dorsal medial ridge and the holes were spaced evenly to match the spacing of the Mk10-AL arm-plates. Tygon-coated flexible stainless steel wire was passed through the drill holes in the medial ridge and the Mk10-AL arm-plates. A biocompatible two-part cold-curing putty (Equinox™ Silicone Putty, Smooth-On, Inc., Easton, PA, USA) was molded to the turtle's medial ridge prior to securing the Mk10-AL to provide a stable and flat surface for the Mk10-AL to rest on. The Mk10-AL was positioned on top of the putty as the putty was setting, and the ends of the stainless steel wire were then twisted together to secure the Mk10-AL to the turtle's carapace. An STP3 was inserted into the turtle's esophagus once ovipositing was complete and the turtle was covering her nest. Two pieces of flat nylon webbing (width 1.9 cm) were placed into the turtle's mouth and used to open the turtle's mouth and to keep the jaws agape (~15–20 cm) during STP3

insertion. The STP3 was placed inside the lumen of a lubricated, flexible, braided PVC tube (inner diameter 3.9 cm; outer diameter 4.7 cm), which was inserted into the turtle's esophagus to a depth of approximately 40 cm. The STP3 was then pushed out of the PVC tube and into the turtle's esophagus using a plastic, rigid PVC trocar, threaded through the flexible PVC tube. The handle of the rigid trocar had a rubber stopper to limit its extension to 2 cm beyond the insertion end of the flexible PVC tube.

Mk10-ALs were removed from the carapace when turtles returned to nest again at SPNWR and archival data was downloaded to a computer. The OMAs used to attach Mk10-ALs to the carapace during the 2007 field season were not removed, but the Tygon-coated stainless steel wires used to attach Mk10-ALs to the dorsal medial ridge during the 2008 field season were clipped and removed with the Mk10-ALs. The attachment site was carefully examined and treated with betadine antiseptic and anti-bacterial ointment after Mk10-AL removal. The STP3s were not retrieved, as they pass through the gastrointestinal tract of the turtle and are ultimately excreted into the ocean. All field procedures were approved by Institutional Animal Care and Use Committee (IACUC) of the University of North Carolina Wilmington (UNCW; Protocol #2006-011) and the USFWS (Permit #SPNWR-41526-2007-03 and Permit #SPNWR-41526).

Instruments

The STP3 (30 g in air, 63×24 mm) detected temperature (range: 0–50°C, resolution: 0.1°C) with an arrangement of four thermistors evenly spaced along a titanium ring that encircled the middle portion of the pill, and emitted pulse-coded acoustic signals corresponding to the coldest temperature detected at 10-s intervals (battery life: ~22 days). Prior to field deployments, each STP3 was calibrated using a temperature-controlled water bath (Haake DC10-V26/B, Thermoscientific, Inc., Waltham, MA, USA) and a NIST-traceable mercury precision thermometer (VWR International LLC, Batavia, IL, USA). The STPs were coated with dissolvable, biocompatible materials to temporarily increase pill diameter to approximately 40 mm and thereby increase pill retention time in the leatherback's stomach (Fig. 2C,D). As the coating material dissolved, the overall diameter of the STP3 decreased until the pill was small enough to pass through the pyloric sphincter and into the small intestine. In 2007, alternating layers of gelatin (Knox Gelatin, Kraft Foods, Inc., Chicago, IL, USA) and ethylcellulose (Ethocel; Dow Chemical Company, Midland, MI, USA) were used to increase pill diameter. Ethylcellulose is an organic compound commonly used in pharmaceutical industry formulations for time-release medicine capsules. The combination of gelatin and ethylcellulose used in 2007 resulted in low pill retention times (<60 h), so in 2008 we used only ethylcellulose to coat pills. The coated STP3s weighed 48-60 g in air, with a volume displacement of 45–60 ml^3.

Internal temperature data transmitted by the STP3 were intercepted, interpreted and archived by the externally mounted Mk10-AL (175 g in air, 93 mm$\times$52 mm$\times$26 mm; data resolution: 12-bit, memory size: 64 Mb) as time-series data at 10-s intervals. The effective range for communication between the STP3 and the Mk10-AL was ≤2 m. Temperature data transmitted by the STP3 were broadly interpreted as representing gastrointestinal tract temperature (T_{GT}) because the exact location of the STP3 inside the turtle was not known while it was within range of the Mk10-AL. The Mk10-AL also archived depth (range: 0–1000 m, resolution: 0.5 m, accuracy: 1.0 m) and T_A (range: –40°–+60°C, resolution: 0.05°C, accuracy: 0.1°C) data at 10-s intervals that coordinated with the T_{GT} readings, and was capable of transmitting location data to the Argos

satellite system [results reported in Casey (Casey, 2010)]. Depth, T_A and T_{GT} data were downloaded from the Mk10-AL upon retrieval using Wildlife Computers instrument software (MK-Host v1.23.1011).

Laboratory simulations of ingestions

A series of laboratory ingestion simulation trials were performed with different masses and combinations of jellyfish and artificial seawater (salinity 33–36 p.p.t.) in order to allow us to distinguish prey and water ingestions in the field data. An empty plastic bag (700 ml volume), representing a leatherback's stomach, was suspended in a temperature controlled 26-liter water bath set to 28.1°C to simulate core body temperature in a leatherback turtle (Casey, 2010). An STP3 was placed in the bag, and an Mk10-AL was placed within 1 m of the water bath to log STP3 transmissions during the simulation trial. An equilibration period of ≥5 min was followed by the introduction of a known mass of diced jellyfish (*Aurelia aurita*; 500 g, $N=4$), seawater (650 g, $N=6$), or different combinations of diced jellyfish and seawater (200 g jellyfish: 300 g seawater, $N=6$; 300 g jellyfish: 200 g seawater, $N=5$) to simulate an ingestion event by a leatherback with an empty stomach. Ingesta were cooled to 24.4–26.4°C prior to trials. Ingestion simulation trials lasted between 45 and 90 min and were ended when the temperature of contents inside the bag was equal to the temperature of the water bath. A mercury precision thermometer was used to check the temperature of the bag contents at 15-min intervals beginning at 45 min into the simulation. Temperature data were downloaded from the Mk10-AL to a computer at the end of each simulation and analyzed using OriginPro software (OriginLab Corporation, Northampton, MA, USA).

The speed at which an animal transfers heat from its body to stomach contents depends on many factors, such as stomach volume, ingesta fluidity, and degree of mixing that occurs in the stomach. We attempted to account for all of these factors in our laboratory simulations. We estimated stomach volume for the range of sizes of our study turtles based on the limited available data from necropsies (Casey, 2010), and used this approximate volume (700 ml) for our laboratory simulations. Jellyfish were diced prior to simulation based on the assumption that gelatinous prey would be shredded by the sharp papillae lining the leatherback's esophagus prior to reaching the stomach. Finally, we assumed that some degree of prey churning would occur in the stomach based on the very thick, muscular morphology of leatherback stomachs obtained from necropsies (Casey, 2010). Accordingly, contents of the bag were squeezed with tongs at 1-min intervals to simulate stomach churning during laboratory ingestion simulations.

Temperature fluctuations due to simulated ingestions were characterized by a rapid drop in temperature (ΔT_D) followed by a gradual temperature rise (ΔT_R). The temperature rise integration method (TRIM) was used to analyze the integral below the asymptote for temperature fluctuations recorded in both laboratory simulations and field data (Grémillet and Plös, 1994; Wilson et al., 1995) (Fig. 3). The shape of the curve below the asymptote can provide important information on characteristics of the ingestion that would be lost by looking solely at the TRIM integral value. For example, ingestion of a cold, semi-solid prey item resulting in a small ΔT_D with a prolonged ΔT_R may have a TRIM integral value similar to the ingestion of a bolus of cold seawater resulting in a large ΔT_D with a rapid ΔT_R event (Fig. 3) (Wilson et al., 1992; Catry et al., 2004; Grémillet and Plös, 1994; Wilson et al., 1995). In order to account for this type of variation and make comparisons between temperature fluctuations of different magnitudes, the TRIM integral values were divided by their
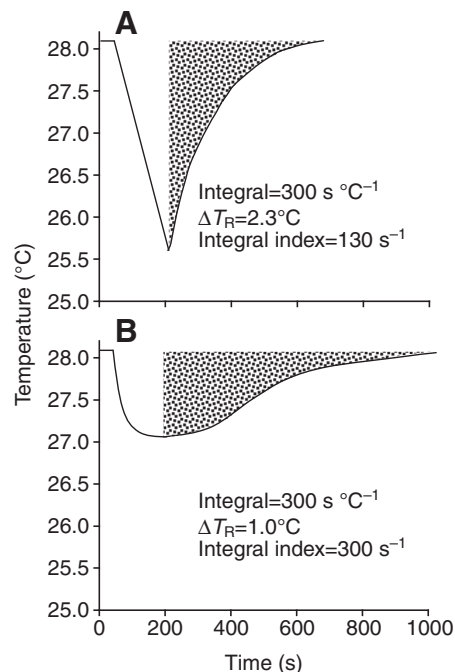

Fig. 3. Theoretical stomach temperature fluctuations caused by ingestion of cold seawater (A) and prey (B). Integral values (shaded region) were measured from the minimum temperature of the fluctuation to when the temperature returned to the asymptote. Integral index values were determined by dividing the integral by the magnitude of the temperature rise (ΔT_R).

associated ΔT_R to produce an integral index value. The integral index value represents the recovery time of an ingestion event corrected for the magnitude of its associated ΔT_R, and may be used to characterize prey and seawater ingestions.

The non-parametric Kruskal–Wallis test in combination with *post-hoc* Mann–Whitney U-tests were used to test for significant difference between the integral index values of jellyfish, seawater, and jellyfish–seawater combinations. Significance level for the Kruskal–Wallis test was set at $P<0.05$. A Bonferroni-corrected significance level of $P<0.017$ was set for each pair-wise comparison in the Mann–Whitney U-test to reduce the potential for type I errors. A minimum integral index value for distinguishing prey ingestions from seawater ingestions was established based on the statistical differences that existed between ingestion simulation groups. All statistical tests were performed using OriginPro (v.8.0) graphing and data analysis software.

Analysis of feeding and diving patterns

The archival time-series data for T_{GT} were imported into OriginPro (v.8.0) software and manually filtered for irregular spikes of ±6–25°C and erroneous data due to malfunctions in STP3-Mk10-AL communication. Descriptive statistics were calculated for T_{GT} and comparisons between mean T_{GT} and mean T_A were made using the paired *t*-test. The T_{GT} data were visually inspected to identify all fluctuations that could be interpreted as ingestions (Grémillet and Plös, 1994; Southwood et al., 2005). Ingestions were broadly defined as a ΔT_D of ≥0.3°C (three times the STP3 accuracy) at a minimum rate of ≥0.033°C min^{-1} followed by a ΔT_R. The time at which the ΔT_D began was designated as the initial temperature (T_I) of the ingestion event. To minimize error in identifying ingestions and to account for long-term fluctuations in T_{GT} of leatherbacks

(Southwood et al., 2005), specific criteria were adopted for determining the final temperature (T_F) of the ingestion (i.e. when the ingestion event ended): (1) an ingestion event ended and T_F was attained when T_{GT} returned to T_I; (2) an ingestion event ended and T_F was attained when T_{GT} returned to within 0.1–0.2°C of the T_I and remained stable for >25 min or was followed by the start of another ingestion event; and (3) the T_F of a sequence of multiple ingestions was attained when T_{GT} returned nearest to and within 0.1–0.2°C of the T_I of the first ingestion in the sequence and remained stable for >25 min or was followed by the start of another ingestion event.

The TRIM integrals and integral index values were calculated for all ingestions that resulted in a steady rise between the minimum temperature and T_F, and a critical integral index value established in laboratory simulations was used to identify prey ingestions. Ingestions that did not meet the criteria for prey were designated as unidentified ingestions, which could represent drinking or ingestion of a mixture of prey and seawater. A paired *t*-test was used to test for a significant difference between the proportion of daytime (05:00–18:59 h) and nighttime (19:00–04:59 h) prey ingestions.

Archival depth data were imported into Wildlife Computers Instrument Helper (v 1.0.100) software for dive analysis. A zero-offset correction function was performed on the depth data to correct for possible drift during data recording. A dive was defined as a submergence of ≥3.0 m with a starting and ending depth of 1.0 m. Maximum depth, dive duration, post-dive surface time, and the number of 'wiggles' (i.e. a rapid change in depth >1 m) were determined for each dive. The bottom phase of a dive was defined as the period during which depth was greater than 90% of the maximum depth of a dive. Dives with a bottom phase <30% the dive duration were classified as V-shaped and dives with a bottom phase >30% of the dive duration were classified as U-shaped (Fossette et al., 2007; Fossette et al., 2008b). The paired *t*-test was used to make diel comparisons in dive frequency, maximum depth, dive duration, and post-dive surface times for all dives combined

and for dives associated with prey ingestions. Prey ingestion dives were also characterized in terms of the presence or absence of a wiggle, dive shape, dive phase in which ingestion occurred, and the T_A at maximum depth.

RESULTS

Eleven of nineteen turtles returned to SPNWR to nest following instrument deployments. All turtles that returned to nest at SPNWR displayed normal nesting behavior, and all but one had retained the Mk10-AL (Table 1). Eight turtles returned to nest after 8.1–10 days, but three turtles (turtle nos. L08, P08 and R08) had extended internesting intervals and returned to nest after a period of 16.0–30.8 days (Table 1). Interestingly, each turtle with extended internesting intervals had prior records of 15–29.0 days separating consecutive nesting attempts at SPNWR. It is possible that these turtles nested elsewhere in the Caribbean Sea prior to returning to SPNWR, since leatherbacks display interseasonal nesting shifts between SPNWR and Manchenil Bay, St Croix, Isla Culebra, Puerto Rico (Eckert et al., 1989a; Boulan et al., 1996), and beaches on the Federation of St Kitts and Nevis (WIMARCS, Inc., personal communication). An additional Mk10-AL was recovered 166 days after deployment, in Fairhaven, MA, from a scallop fisherman who dredged the shed instrument from the ocean floor approximately 60 km offshore from Long Island, NY, USA. Six of nine turtles tagged during the 2007 field season nested again at SPNWR during the 2009 (*N*=5) or 2010 (*N*=1) nesting season (WIMARCs, Inc., personal communication). Two of ten turtles tagged during the 2008 field season had 2-year remigration intervals and nested at SPNWR during the 2010 nesting season. The instrument attachment sites had healed and were in good condition for all remigrants (the WIMARCs, Inc., personal communication), providing evidence that the direct attachment technique is safe for use with leatherbacks and does not cause lasting damage to the carapace. Of the 11 Mk10-ALs that were ultimately retrieved, usable time-series T_{GT} data was obtained from eight instruments (Table 2).

Table 1. Summary of recording information for leatherback turtles monitored at St Croix, USVI in 2007 and 2008

Turtle ID no.	CCL (cm)	Mk10-AL deployment date	Mk10-AL recovery date	Internesting interval (days)	Most recent nesting date at St Croix
A07	163.4	18 May 2007	26 May 2007	8.9	
B07	156.5	19 May 2007	–	–	
C07	157	20 May 2007	–	–	
D07	158.5	21 May 2007	31 May 2007	9.1	21 July 2009
E07	163	22 May 2007	–	–	27 May 2009
F07	172.5	22 May 2007	1 June 2007	9.1	15 July 2009
G07*	162.5	23 May 2007	–	–	07 June 2009
H07	160.5	24 May 2007	2 June 2007	9	18 May 2010
I07	155.8	24 May 2007	2 June 2007	8.1	28 June 2009
J08	153.1	12 May 2008	21 May 2008	10	27 May 2010
K08	156.9	14 May 2008	–	–	
L08	164.3	14 May 2008	12 June 2008	28.9	
M08	167.7	15 May 2008	–	–	
N08	161.4	16 May 2008	–	–	24 May 2010
O08	151.2	17 May 2008	–	–	
P08†	155.8	18 May 2008	17 June 2008	30.8	
Q08	150.1	18 May 2008	28 May 2008	9.1	
R08	158.3	19 May 2008	4 June 2008	16	
S08	155.4	20 May 2008	28 May 2008	8.0	

CCL, curved carapace length; *N*=9 (2007) and 10 (2008).
*Turtle's Mk10-AL was recovered by a scallop dredger approximately 60 km offshore of Long Island, NY, USA.
†The Mk10-AL was shed at sea before the turtle returned to Sandy Point to nest again.

Table 2. Summary of ingestions, foraging behavior and gastrointestinal tract temperature recorded for seven leatherback turtles monitored at St Croix, USVI during one of their internesting intervals

| Turtle ID no. | Duration of T_{GT} data (h) | | | No. of ingestions | No. of prey ingestions | | | Prey ingestion integral index value (s^{-1}) | T_{GT} (°C) | T_A (°C) |
	Total	Day	Night		Total	Day	Night			
A07	57.9	37.7	20.2	9	6	6	2	1004±623	28.1±0.3	26.6±2.0
D07	23.1	13.8	9.4	20	9	8	1	795±388	28.1±0.4	25.4±3.3
G07	27.2	14	13.15	0	0	0	0	–	28.2±0.4	27.4±1.2
J08	202.8	117.9	84.9	21	10	10	0	1340±565	28.5±0.4	26.5±1.7
L08	644.3	381.2	263.1	65	48	43	5	1294±650	28.2±0.4	27.0±1.3
Q08	207.1	125.5	81.6	31	15	12	3	1107±446	28.3±0.4	25.7±2.2
R08	317.4	200	117.4	34	15	14	1	932±340	28.5±0.3	26.1±2.0
S08	157.4	93.6	63.7	11	8	6	2	998±402	28.7±0.5	26.9±1.7
All turtles	1637.2	1043.7	653.8	191	111	97	14	1067±195	28.3±0.2	26.5±0.7

Data are presented as mean ± 1 s.d.
T_{GT}, gastrointestinal tract temperature; T_A, ambient temperature; day, 05:00–18:59 h; night 19:00–04:59 h.

Prey ingestion during the internesting interval

The T_{GT} data were not contiguously recorded throughout the entire internesting interval because of periodic loss of communication between the STP3 and Mk10-AL (Fig. 4). The first 6 h of T_{GT} recordings were excluded from analysis, because of the steady decline in T_{GT} as turtles cooled down after leaving the beach (Southwood et al., 2005) which prevented us from establishing a baseline for analysis of temperature fluctuations. For periods after the turtles were at sea for 6 h, the total duration of T_{GT} recordings for individual turtles ranged from 23.1 to 644.3 h (1.0 to 26.8 days; Table 2). The mean T_{GT} of turtles (28.3±0.2°C) was significantly higher than mean T_A (26.5±0.7°C) during the T_{GT} monitoring periods (t=7.77, d.f.=7, P<0.001; Table 2). Sudden fluctuations in T_{GT} indicative of ingestion occurred for seven of the eight turtles (Table 2; Fig. 4). A total of 191 ingestions were identified, and the total number of ingestions for individual turtles ranged from 9 to 65.

Results of the laboratory simulations allowed us to develop criteria for distinguishing prey ingestions from seawater ingestions in the field data, as the Kruskal–Wallis test detected significant differences between simulation groups ($H_{2,35}$=21.2, P<0.001; Fig. 5). Integral index values for simulations with 200 g jellyfish plus 300 g seawater were not distinguishable from ingestions of 650 g seawater, but integral index values for simulations with 300 g jellyfish plus 200 g seawater and 500 g jellyfish were significantly higher than integral index values for simulations with 650 g seawater (P<0.017; Fig. 5). The mean integral index value of the 300 g jellyfish plus 200 g seawater group was 482 s^{-1}, so this value was used as a cut-off point to identify leatherback prey ingestion in the field data. Ingestions with integral index values higher than 482 s^{-1} were classified as prey ingestions and those with integral index values lower than 482 s^{-1} were classified as unidentified ingestions.

A total of 111 prey ingestion were identified during the T_{GT} monitoring period (Table 2). The mean number of prey ingestions for individual turtles was 15.9±14.6 (range: 6 to 48). The mean integral index value of prey ingestion was 1067±195 (range: 795±388 to 1294±650). The mean rate of prey ingestion by turtles was 0.11±0.12 ingestions h^{-1} (range: 0.05 to 0.37). The majority of the prey ingestions occurred during the daytime, and paired t-test found a statistically significant difference between the proportion of daytime (85.1±10.6%) and nighttime (14.9±10.7%) prey ingestions (t=8.0, d.f.=6, P<0.001; Table 2). Sixty-nine percent of
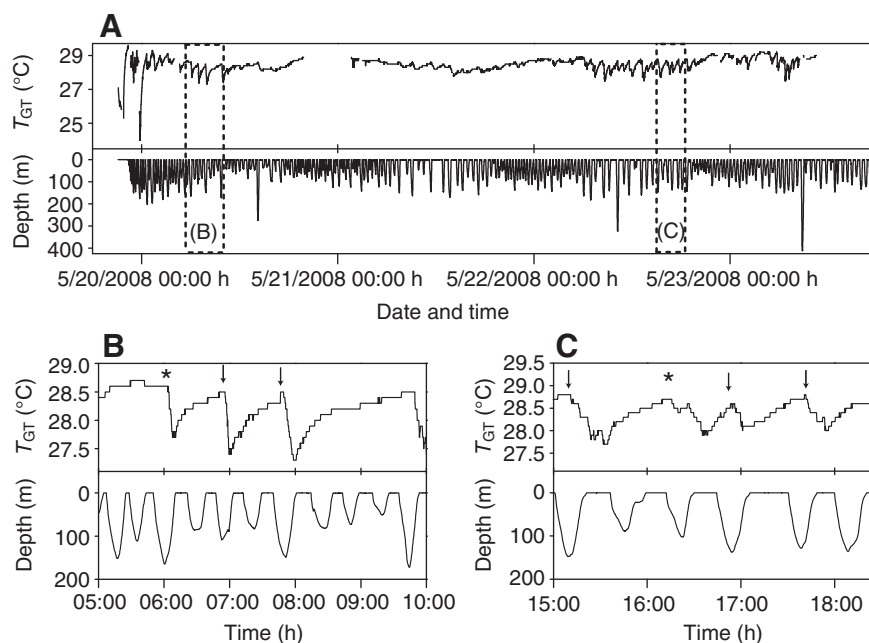

Fig. 4. (A) Archival time-series gastrointestinal tract temperature (T_{GT}) and dive profile recorded for turtle no. R08 between 5/19/2008 21:00 h and 5/23/2008 18:00 h. (B,C) Expanded sections of the time-series in A. There were sudden fluctuations in the T_{GT} that were indicative of ingestions. The arrows indicate the start of an ingestion identified as a prey ingestion, based on laboratory ingestion simulations, and the asterisk indicates the start of an unidentified ingestion (B,C).
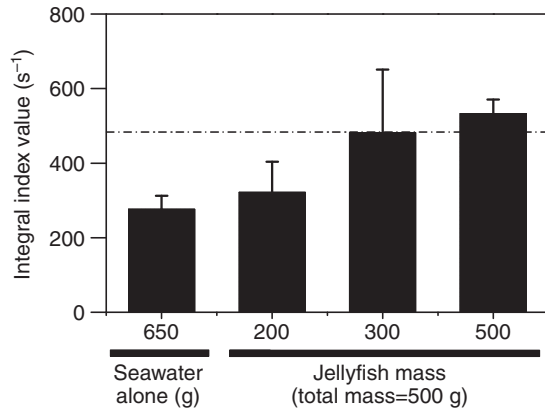
Fig. 5. Integral index values of various combinations of jellyfish and artificial seawater used for laboratory ingestion simulations. The integral index values for the ingestion simulation group consisting of 300 g of jellyfish with 200 g seawater and 500 g of jellyfish were significantly greater ($P<0.017$) than the group consisting of 650 g of seawater alone (Mann–Whitney U-test). The dotted line delineates the minimum integral index value ($482\,s^{-1}$) for identifying leatherback prey ingestions in this study. All jellyfish ingestion simulation groups had a total mass of 500 g – the difference in mass was accounted for by seawater (e.g. 300 g jellyfish with 200 g of seawater equals 500 g).
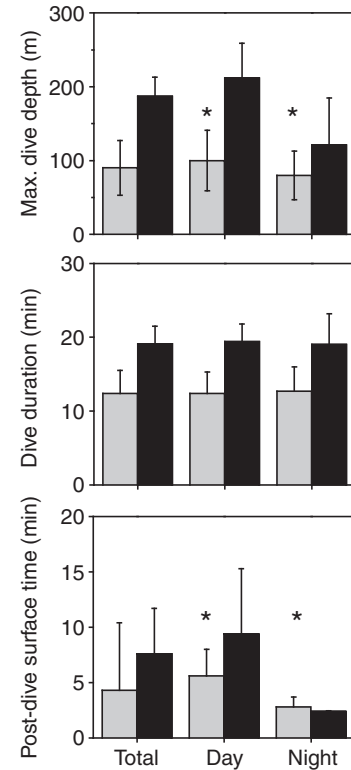

Fig. 6. Diel dive behavior for leatherback turtles ($N=7$) from the St Croix, USVI nesting population during the internesting interval. Values are means with error bars indicating ±1.s.d. Gray bars, all dives; black bars, dives with prey ingestions. Asterisks mark dive groups (e.g. All Dives) with a significant difference ($P<0.05$) between day (05:00–18:59 h) and night (19:00–04:59 h).

prey ingestions occurred during the first 4 days of the internesting interval.

Dive patterns associated with prey ingestion

The total number of dives conducted during the period when T_{GT} was being monitored ranged from 56 to 2006 for individual turtles, and the mean dive frequency was 3.6 ± 0.6 dives h^{-1}. The mean maximum dive depth was 90 ± 37 m, mean dive duration was 12.4 ± 3.1 min, and the mean post-dive surface time was 4.3 ± 6.1 min (Fig. 6). The mean percent frequency of V-shaped and U-shaped dives was $85.8\pm5.9\%$ and $14.1\pm5.9\%$, respectively ($t=7.2$, d.f.=7, $P<0.001$). Turtles exhibited a diel diving pattern during the T_{GT} monitoring period, with fewer dives conducted during the daytime (3.2 ± 0.9 dives h^{-1}) compared with nighttime (4.0 ± 1.3 dives h^{-1}; $t=2.5$, d.f.=7, $P=0.04$) and daytime dives that were deeper (100 ± 41 m) than nighttime dives (80 ± 33 m; $t=4.1$, d.f.=7, $P=0.004$; Table 2; Fig. 6). In addition, post-dive surface times were longer during the daytime (5.6 ± 2.3 min) compared with nighttime (2.8 ± 0.8 min; $t=4.5$, d.f.=6, $P=0.003$). There was no significant difference in dive duration between daytime (12.4 ± 2.9 min) and nighttime (12.7 ± 3.4 min, $t=0.5$, d.f.=7, $P=0.62$).

The dive patterns observed specifically for prey ingestion dives were somewhat different from patterns observed for all dives combined. The mean maximum dive depth of prey-ingestion dives was 187 ± 26 m, mean dive duration was 19.1 ± 2.4 min, and the overall mean post-dive surface time of prey-ingestion dives was 7.6 ± 4.1 min (Fig. 6). The mean percent frequency of V-shaped and U-shaped prey ingestion dives was $92.1\pm11.5\%$ and $7.9\pm11.5\%$, respectively ($t=15.0$, d.f.=6, $P<0.05$). The prey ingestion dives that occurred during the daytime (212 ± 47 m) were typically deeper than those that occurred during the nighttime (121 ± 64 m), but this difference was not statistically significant ($t=2.49$, d.f.=3, $P=0.08$; Fig. 6). Likewise, daytime prey ingestion dive durations (20.0 ± 3.1 min) were not statistically different from nighttime prey ingestion dive durations (19.0 ± 4.2 min, $t=0.66$, d.f.=3, $P=0.55$; Fig. 6). Post-dive surface times following prey-ingestion dives were typically longer

during the daytime (9.4 ± 5.9 min) compared with nighttime (2.4 ± 0.4 min), but the difference was not statistically significant ($t=1.9$, d.f.=3, $P=0.15$; Fig. 6).

Prey ingestion typically started between 1.0 min prior to and 5.0 min after the maximum dive depth was reached. The overall mean T_A at the maximum depth of prey-ingestion dives was 21.2 ± 0.9°C. No significant difference was detected between the mean T_A at the maximum depth of prey ingestion dives that occurred during daytime (20.8 ± 1.4°C) and nighttime (23.2 ± 2.4°C; $t=1.79$, d.f.=3, $P=0.17$). The mean ΔT_D for prey ingestion ranged from 0.5 ± 0.1°C to 1.0 ± 0.1°C. Twenty-nine percent of prey-ingestion dives contained a wiggle. The mean lapse in time between a wiggle and detection of prey ingestion based on temperature recordings was 3.6 ± 3.5 min (mean range: 0.3 ± 8.1 to 8.6 ± 11.6 min). The majority of wiggles associated with prey ingestion dives were documented during V-shaped dives (84.3%), but the proportion of the total number of V-shaped prey ingestion dives that contained a wiggle event was lower than the proportion of U-shaped prey ingestion dives that contained a wiggle event ($t=7.8$, d.f.=3, $P=0.004$).

DISCUSSION

In this study, data obtained from remote monitoring instruments and laboratory ingestion simulations revealed that leatherback turtles forage during the nesting season while offshore St Croix, USVI. We initially predicted that leatherbacks would adopt an energetically efficient strategy of foraging primarily at night, since

their prey would be closer to the surface at this time because of the normal pattern of diel vertical migration by DSLs (Hays, 2003). Surprisingly, and despite the adoption of the expected diel dive pattern, the percentage of prey ingestions that occurred during the daytime (range: 66.7–100%) was significantly higher than the percentage of prey ingestions that occurred during the nighttime (range: 0–33.3%). These findings did not support the hypothesis that gravid leatherbacks forage primarily at nighttime.

The tendency towards diurnal foraging and a shift to shallow diving at night may reflect a reliance on ambient light to locate and capture suitable prey in deep water (<100 m) offshore of St Croix, USVI. Under this assumption, adoption of an interesting dive pattern with consistently shallow nighttime dives and deeper daytime dives may be an effective strategy for conserving energy resources when light availability and chances of detecting and capturing prey are low (i.e. nighttime). Interestingly, a similar diel dive pattern displayed by several species of penguins, such as King (*Aptenodytes patagonicus*) and Adelie (*Pygoscelis adeliae*), was found to be dependent on light availability rather than the normal diel vertical migration of their pelagic prey (Wilson et al., 1993). Wilson et al. (Wilson et al., 1993) suggest that pelagic prey, such as Antarctic krill (*Euphausia superba*) and laternfish (Family *Myctophidae*), vertically migrate to shallow waters when ambient light and predation risk from penguins is low. Although the majority of prey ingestion occurred during the day in our study, we did document successful nocturnal foraging by leatherbacks at depths >100 m. Houghton et al. (Houghton et al., 2008) support the idea that leatherbacks have a 'heightened visual acuity' (Oliver et al., 2000) that aids in nocturnal foraging, although anatomical studies do not provide strong support for enhanced nocturnal vision (Brudenall et al., 2008). Leatherbacks have small eyes relative to body size, and the size of the pupil in relation to the lens suggests that leatherbacks have low sensitivity to light, particularly in comparison with fishes that utilize similar habitat (Brudenall et al., 2008). It has been proposed that waterborne chemical cues may also play an important role in prey detection (Constantino and Salmon, 2003; Myers and Hays, 2006). Chemical cues may be particularly important in low light conditions.

Recent work has demonstrated the presence of vertically migrating DSLs near the interesting habitat occupied by turtles from the St Croix population (Rovira-Peña, 2006). Data collected by acoustic Doppler current profiler (ADCP) and Trucker trawl nets detected a persistent DSL between Puerto Rico and the Dominican Republic at the Central Mona Passage station, as well as at insular slope waters of Puerto Rico (Rovira-Peña, 2006). The DSLs detected west of Puerto Rico, which consisted primarily of copepods, euphausiids and myctophids, ascended from deep waters around dusk, and descended from shallow waters around dawn. Maximum depths for nighttime prey ingestions dives in our study (121±64 m) correlate with the depths occupied by the DSL at the Mona Passage at night (0–150 m) (Rovira-Peña, 2006), but there are discrepancies between maximum depths of daytime prey ingestion dives (212±47) and the daytime location of the DSL at the Mona Passage (~400 m). This may be due to the nature of the prey targeted by leatherbacks. Observations at other locations show that siphonophores, a known prey item of leatherbacks (den Hartog, 1980), maintain daytime depths that are 100–200 m shallower than DSLs comprising myctophids (Barham, 1963). A similar partitioning of habitat may exist in the Caribbean. Siphonophores were collected at depths of up to 180 m during trawls at the Mona Passage, indicating that they are present in this area. Unfortunately, the ADCP frequency used for DSL detection in Mona Passage study (76.8 kHz) (Rovira-Peña, 2006) was higher than the most useful frequency for detecting

siphonophores (24.5 kHz) (Warren et al., 2001), and so acoustic documentation of siphonophore vertical movement patterns are not available at this site. Other potential gelatinous prey for leatherbacks in the Eastern Caribbean Sea include the white-spotted jellyfish (*Phyllorhiza punctata*) (Garcia and Durban, 1993), pink meanie (*Drymonema dalmatinum*) (Williams et al., 2001) and moon jellyfish (*Aurelia aurita*) (Iverson and Skinner, 2006). Detailed information on the spatial patterns of abundance of the aforementioned prey and other gelatinous zooplankton are scant (e.g. Richardson et al., 2009). Future studies would benefit from simultaneously recording of leatherback turtle behavior while mapping their prey distribution.

Short T_{GT} monitoring periods (<2.5 days) for three turtles (e.g. turtle nos. A07, D07 and G07) was of concern in this study, but T_{GT} monitoring periods for the other five turtles lasted for 95–100% of their time at sea (7.6–28.0 days; Table 1). Prey ingestion occurred primarily during the first several days of the interesting interval (0–4 days) for leatherback turtles at St Croix. The decrease in prey ingestion towards the end of the interesting interval may reflect a shift from foraging to reproductive activities in the final days at sea prior to a nesting attempt. Previous studies have reported significant changes in leatherback diving behavior toward the end of the interesting interval, such as a decrease in dive effort and increase in dive variability at French Guiana (Fossette et al., 2007), consistently shallower and shorter dives at Costa Rica (Southwood et al., 2005), and lower variability in swim speeds at St Croix (Eckert, 2002). There was no apparent shift in interesting dive patterns in our study to suggest a major change in feeding behavior or energy expenditure. It is possible that the decline in detection of prey ingestions towards the end of the interesting interval is not due to a decrease in feeding, but rather due to the STP3 moving from the stomach into the small intestine after a period of several days (Southwood et al., 2005). Under this scenario, the STP3 would be unable to detect ingestions but would continue to transmit T_{GT} data to the Mk10-AL.

V-shaped dives are often interpreted as representing exploration or travel (Eckert et al., 1989b; Thompson et al., 1991; Hochscheid et al., 1999; Ropert-Coudert et al., 2000; Schreer et al., 2001; Houghton et al., 2008), whereas U-shaped dives are interpreted as a reflection of foraging by air-breathing predators at a depth where prey are assumed to be located (Thompson et al., 1991; Le Bouf et al., 2000; Schreer et al., 2001; Fossette et al., 2007; Fossette et al., 2008b). Nevertheless, pelagic V-shaped foraging dives have recently been confirmed or suggested for several species of seabirds (Schreer et al., 2001; Elliott et al., 2008), as well as marine mammals (Lesage et al., 1999). In our study, foraging by leatherbacks was most commonly documented during dives that were deep (>100 m), long (19.2±2.5 min), and V-shaped. U-shaped dives associated with foraging were also deep (>100 m) and long (16.9±4.1 min), but were less frequently (7.9±11.5%) associated with foraging compared with V-shaped dives. Previous investigations of the interesting diving behavior of leatherbacks at St Croix have led other researchers to suggest that V-shaped dives by leatherbacks were foraging dives (Eckert et al., 1986; Eckert et al., 1989b), and results from this study support this conclusion.

In contrast to the dive pattern associated with foraging by leatherbacks in this study, foraging dives by gravid leatherbacks at French Guiana are typically shallow (18.1±6.3 m), short (7.5±2.8 min), and either U-shaped or W-shaped (Fossette et al., 2007; Fossette et al., 2008b). Differences in local bathymetry, prey distribution and prey concentration can explain disparities between leatherback diving patterns at different sites. At French Guiana, leatherback movements were restricted to the coastal shelf and U-

shaped and W-shaped dives resulted in increased time spent at shallow depths (<50m) in highly productive areas where leatherback prey, such as *Stomolophus* sp. and *Aurelia* sp. (Eisenberg and Frazer, 1883; Grant et al., 1996), have been documented in great numbers (Fossette et al., 2009). In contrast, leatherbacks from the St Croix nesting population were monitored in deep waters (depth range: 200–4000m) where they appear to target and capture vertically migrating prey associated with the DSL. Based on phytoplankton studies in the Caribbean Sea (Hargraves et al., 1970; Marshall, 1973) and trophic relationships and interactions between phytoplankton, zooplankton and gelatinous organisms, gelatinous prey abundance in the oceanic waters of the Eastern Caribbean Sea is likely to be sparse compared with coastal areas of north eastern South America. Under these circumstances, an exploratory V-shaped dive pattern with diel variation in depth that mirrored behavior of local DSLs could provide the best opportunities for encountering prey.

Although leatherbacks in this study were found to have wiggles associated with feeding, they occurred in less than one-third of all documented prey-ingestion dives and typically as single events. By contrast, leatherbacks at French Guiana exhibit wiggles during the majority of foraging dives (62.7%) and foraging dives typically contain multiple wiggles (2.4 ± 1.0 wiggles per dive) (Fossette et al., 2008b). The multiple wiggles by leatherbacks during foraging dives at French Guiana may be the result of them locating prey slightly above and below their swimming depth as they move horizontally along the seafloor. There was a time lag of 3.6 ± 3.5min between the wiggles and the detection of the foraging events by the STPs in this study. This time lag seems reasonable because the leatherbacks have a long (>2m) esophagus. To our knowledge, however, no information exists on the passage time of food through the alimentary canal, specifically from the mouth to the stomach, of adult leatherback turtles. This makes it problematic to determine the specific depth and T_A for prey ingestion when using T_{GT} to detect foraging events.

Captive feeding trials to determine the relationships between the mass of food ingested, energy invested in heating ingested food, and the integral of stomach temperature fluctuations have proved useful in stomach temperature telemetry studies with birds (e.g. Wilson et al., 1992; Grémillet and Plös, 1994; Wilson et al., 1995) and mammals (e.g. Gales and Renouf, 1993; Kuhn and Costa, 2006). If these relationships are known, the integrals of stomach temperature fluctuations recorded from free-swimming animals can be used to estimate the mass of the prey ingested. Controlled feeding trials with leatherbacks were not feasible, since this species is extremely difficult to care for in captivity (see Jones, 2009), and the size of STP instruments precluded use with smaller species of sea turtle. As an alternative to captive feeding trials, we used laboratory simulations to characterize ingestions of prey and seawater (Wilson et al., 1992; Wilson et al., 1995). The use of laboratory simulation-derived data to estimate prey mass for our field data was complicated by a lack of information on the actual temperature of prey ingested, which is a necessary component to determine energy invested in heating the prey to predator body temperature. As previously mentioned, transit time in the ~2m long esophagus led to a lag time between ingestion of prey and detection by the STP3, so the actual temperature of prey was not known. An additional problem was that the fluidity of ingested prey was not known, and fluidity can have strong effects on the relationship between the integral of a stomach temperature fluctuation and energy invested to heat prey to predator body temperature. For these reason, we did not use laboratory simulations to estimate the mass of ingested prey from field data.

A salient finding of our laboratory simulations was that jellyfish (300–500g) and seawater ingestions could be distinguished from each other based on the integral index values of temperature fluctuations (Grémillet and Plös, 1994). The critical integral index value established by our laboratory simulations ($482\,s^{-1}$) was conservative, since we do not account for differences in stomach retention times for prey and seawater. Seawater ingestion simulations may slightly overestimate the integral values for free-living animals due to rapid passage of seawater from the animal's stomach to the small intestine (Wilson et al., 1992). If seawater passes from the leatherback's stomach to small intestine prior to the stomach returning to pre-ingestion temperatures, the critical integral index value for identifying prey ingestions is conservatively high and prey ingestion rates documented in this study are slightly underestimated.

Ingestions that did not meet criteria for prey ingestion were characterized as 'unidentified' and may represent ingestion of seawater or a combination of prey and seawater. Ingestion of seawater during the breeding season in the tropics may serve as a means for the giant leatherback to thermoregulate (i.e. lower body temperature). One argument against this is that leatherbacks are capable of altering their body temperatures (T_B) by changes in behavior and blood circulation in the absence of ingestions (Paladino et al., 1990; Southwood et al., 2005; Wallace et al., 2005). For example, leatherback T_B transiently decreases during square-shaped resting dives at depths >20m in the tropics (Southwood et al., 2005). It is likely that exposure to cooler temperatures at deeper depths, in combination with circulatory adjustments and use of the elongate, poorly insulated front flippers as thermal windows, allows leatherbacks to exchange heat effectively without the need to ingest seawater and incur a salt load. Use of the lachrymal glands to excrete salts and maintain water and ion balance requires energy (Lutz, 1997; Reina et al., 2002). It seems unlikely that leatherbacks would choose to thermoregulate through a behavior that requires the use of additional energetic resources when they have demonstrated the ability to thermoregulate by energetically cheap methods, such as lowering activity levels and resting in relatively cool waters at depth (Southwood et al., 2005; Wallace et al., 2005). In our study, the unidentified ingestions resulted in only small, evanescent changes to the T_{GT} and were typically followed by extended periods in warm surface waters (<3m), which does not lend strong support to the proposal that drinking seawater serves a thermoregulatory purpose.

A second reason for leatherbacks to ingest seawater during the nesting season is to re-hydrate. Recently, Wallace et al. (Wallace et al., 2006) reported that water constituted 67% of the total wet mass of a leatherback egg. Based on the average wet mass of leatherback eggs (~76g) (Wallace et al., 2006) and the average number of eggs in a clutch (~80eggs) (Miller, 1997), the amount of water invested by leatherbacks into a single clutch is 4.1kg or 4.1liters. This amounts to 16.3–32.6l of water invested by leatherbacks into egg formation during a nesting season, based on leatherbacks laying four to eight clutches. The maximum estimate for water investment by leatherbacks accounts for 6.5–10.9% of the typical leatherback mass (300–500kg). Water requirements for egg formation could be provided by drinking, body water reserves, energy stores (i.e. metabolic water) or, if they are feeding, gelatinous prey (Doyle et al., 2007).

Wallace et al. (Wallace et al., 2006) estimated that leatherbacks from the St Croix, USVI nesting population require 6.3×10^6kJ of energy to fuel activities associated with reproduction, including the round-trip migration to the nesting site, and assumed that leatherbacks did not feed and relied solely on fat stores to fuel all activities during the nesting season (i.e. egg production, nesting

activities and internesting activities). We were unable to accurately estimate prey mass from our T_{GT} data, but we may assume that individual prey items ingested by leatherbacks at St Croix weighed a minimum of 300 g based on our laboratory simulations (Fig. 5). Given a gelatinous prey energy content of 0.18 kJ g^{-1} (Doyle et al., 2007), energy assimilation of 80% (Wallace et al., 2006), and an average ingestion rate of 0.11 prey ingestions h^{-1} (this study) over a nesting season of 45–63 days (average internesting interval of 9 days with five to seven internesting intervals per season), the amount of energy gained by foraging during the internesting interval amounts to less than 1% of the energy necessary for leatherback reproduction. Rates of prey intake for our study may be underestimated, given our conservative criteria to distinguish between prey and water ingestion and the possibility that the STP3 had passed into the small intestine before the end of the recording period. Nevertheless, feeding during the nesting season by leatherbacks offshore of St Croix, USVI appears to provide a very small amount of energy to leatherbacks. The low number of prey ingestion observed in this study may be the result of limited availability of suitable prey and/or low prey encounter rates for leatherbacks at their internesting habitat.

For other species of sea turtle, evidence of a capital breeding strategy comes from turtles resting for prolonged periods (e.g. Hays et al., 2000; Schofield et al., 2007), having empty stomachs (e.g. Hays et al., 2002), and not moving far from the nesting beach (e.g. Schofield et al., 2007). There is now an accumulation of evidence from this study and others that leatherbacks nesting in the Caribbean move long distances, dive frequently and with a diel pattern, and ingest material during the internesting interval. All these lines of evidence point to active foraging. Nevertheless, our results indicate that energy reserves procured prior to the breeding season are crucial for successful reproduction by leatherbacks from the St Croix, USVI nesting population. This conclusion is supported by models of leatherback turtle foraging behavior that are based on analyses of travel speeds and path straightness (Fossette et al., 2010), as well as evidence of changes in body mass of female leatherbacks during the remigration period and nesting season (James et al., 2005b).

LIST OF ABBREVIATIONS

DSL	deep-scattering layer
OMA	orthopedic-mini-anchors
T_A	ambient temperature
T_a	asymptotic temperature
T_B	body temperature
T_F	final temperature
T_f	temperature of food
T_{GT}	gastrointestinal tract temperature
T_I	initial temperature
T_R	temperature rise
TRIM	temperature rise integration method
ΔT_D	drop in temperature

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