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RESEARCH ARTICLE

Changes of loggerhead turtle (*Caretta caretta*) dive behavior associated with tropical storm passage during the inter-nesting period

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ABSTRACT

To improve conservation strategies for threatened sea turtles, more knowledge on their ecology, behavior, and how they cope with severe and changing weather conditions is needed. Satellite and animal motion datalogging tags were used to study the inter-nesting behavior of two female loggerhead turtles in the Gulf of Mexico, which regularly has hurricanes and tropical storms during nesting season. We contrast the behavioral patterns and swimming energetics of these two turtles, the first tracked in calm weather and the second tracked before, during and after a tropical storm. Turtle 1 was highly active and swam at the surface or submerged 95% of the time during the entire inter-nesting period, with a high estimated specific oxygen consumption rate (0.95 ml min^{-1} kg$^{-0.83}$). Turtle 2 was inactive for most of the first 9 days of the inter-nesting period, during which she rested at the bottom (80% of the time) with low estimated oxygen consumption (0.62 ml min^{-1} kg$^{-0.83}$). Midway through the inter-nesting period, turtle 2 encountered a tropical storm and became highly active (swimming 88% of the time during and 95% after the storm). Her oxygen consumption increased significantly to 0.97 ml min^{-1} kg$^{-0.83}$ during and 0.98 ml min^{-1} kg$^{-0.83}$ after the storm. However, despite the tropical storm, turtle 2 returned to the nesting beach, where she successfully re-nested 75 m from her previous nest. Thus, the tropical storm had a minor effect on this female's individual nesting success, even though the storm caused 90% loss nests at Casey Key.

KEY WORDS: Activity level, Climate change, Animal motion tags, Satellite tags, Loggerhead turtle, Tropical storm

INTRODUCTION

The rising temperatures of the oceans caused by global warming are expected to increase the intensity and frequency of tropical storms and hurricanes (Mann and Emanuel, 2006). Understanding how increased storm activity may affect marine animals is important to improve conservation strategies for threatened species and it has been identified as a key question concerning marine megafauna (Hays et al., 2016). Hurricanes can cause significant destruction to coral reefs, with corresponding changes in the reef fish population (Woodley et al., 1981). In an estuarine environment, a significant change in fish assemblages was observed after the passage of a cyclone, with reduction in species diversity and variation in the seasonal pattern of abundance (Mukherjee et al., 2012). A satellite tracking study on manatees in southwest Florida showed no significant effect on movement patterns before and during hurricane passages, and it was therefore concluded that the hurricanes had a minor effect on this species (Langtimm et al., 2006). Juvenile blacktip sharks left an estuary during barometric pressure drops from an impending hurricane (Heupel et al., 2003). Thus, marine vertebrates can respond differently to storm passages.

The loggerhead turtle (*Caretta caretta*) is listed as threatened under the US Federal Endangered and Threatened Species Act of 1977 and the North West Atlantic subpopulation is International Union for Conservation of Nature (IUCN) red-listed as Least Concern (http://dx.doi.org/10.2305/IUCN.UK.2015-4.RLTS.T84131194A84131608.en). Some of the biggest threats against sea turtles are human activities and fishery bycatch, which might have played a significant role in declines in the loggerhead population (Finkbeiner et al., 2011; McDaniel et al., 2000; Witherington et al., 2009). Other major threats are loss of eggs as a result of nest predation and human disturbances (Engeman et al., 2016). Naturally occurring threats like tropical storms and hurricanes may also have a major damaging effect on the nests (Hillis and Phillips, 1998; Milton and Leone, 1994; Starbird et al., 1991), but our knowledge about how juvenile and adult sea turtles are affected by severe weather conditions is limited (Limpus and Reed, 1985), mainly because of difficulties in studying sea turtles after they leave the nesting ground. Storms may have profound impacts on the oceanic stages of juvenile loggerhead turtles, blowing them to unexpected locations with potential impact on their fitness (Monzon-Arguello et al., 2012). After hatching, males never return to land. Thus, tagging studies involving male sea turtles are difficult and must be done by capture at sea (Schofield et al., 2010). Mature female loggerheads only return to the beach every 2–7 years to nest (Plotkin, 2003). Loggerheads deposit multiple clutches of eggs at 10- to 21-day inter-nesting intervals across a nesting season (Hays et al., 2002; Sato et al., 1998; Schroeder et al., 2003). When a female has found a nesting beach, she often shows strong nest site fidelity and will tend to nest within 5 km of the previous nest (Tucker, 2010). However, a small percentage of turtles have weak nest site fidelity and will utilize more distant nesting sites in the general area (Bjorndal et al., 1983; Schofield et al., 2010). Because of the strong site fidelity, loggerhead sea turtles are susceptible to negative impact from development and destruction of beach areas, but it also gives opportunities to study the inter-nesting behavior of female loggerhead sea turtles.

The use of advanced technical equipment (archival and satellite tags) makes it possible to collect important information about sea

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turtle diving behavior, their ecology and habitat use (Eckert and Martins, 1989; Eckert et al., 1986; Hays et al., 1991, 2004a; Houghton et al., 2002; Minamikawa et al., 1997, 2000; Sakamoto et al., 1990a,b; Sato et al., 1995; Wilson et al., 2006). Studies show that loggerhead turtles exhibit plasticity in behavior during the inter-nesting period, and their behavior can be linked to the local environment and how close they are to the next nesting event (Tucker et al., 1996; Houghton et al., 2002; Schofield et al., 2009; Fossette et al., 2012). In areas where food is abundant, both green (*Chelonia mydas*) (Hochscheid et al., 2010) and loggerhead turtles may opt to forage during the inter-nesting period (Sakamoto et al., 1990b), whereas, if food is limited, they may save energy for reproduction and rest on the seabed (Hays et al., 1999; Minamikawa et al., 1997). At the end of an inter-nesting period, both green and loggerhead turtles spend less time resting on the seabed and more time near the surface (Hays et al., 1991, 1999; Houghton et al., 2002). It would therefore seem that sea turtles tend to optimize energy reserves in a way best suited to local environmental conditions (Houghton et al., 2002) and, when inter-nesting sea turtles are exposed to storms or hurricanes, it could be expected to cause changes in their behavior to cope with the severe oceanographic conditions. Two studies have examined the effect of severe weather conditions on the behavior of a loggerhead turtle (Sakamoto et al., 1990b) and a hawksbill turtle (Storch et al., 2006). Both studies found changed swimming behavior by turtles during the storm passage. The hawksbill encountering hurricane George in the Caribbean made shorter dives and spent less time at the surface (Storch et al., 2006). A loggerhead turtle encountering a typhoon made more dives and increased the dive depth and time spent at depth to avoid the wave action (Sakamoto et al., 1990b). However, after the passage of the severe weather, both turtles resumed their normal behavior.

Florida's coasts are significant nesting grounds for loggerhead sea turtles, with the number of annual nests in recent years ranging from 77,975 to 122,706 (http://myfwc.com/research/wildlife/sea-turtles/nesting/statewide/, 2017). Florida is annually hit by hurricanes and tropical storms, and there is close overlap of the tropical storm/hurricane season and turtle nesting season. Hurricanes and tropical storms are therefore potential threats to the loggerhead turtle population because of beach erosion and nest losses. We used Argos satellite tags and high-speed multi-channel animal motion datalogging tags to study the behaviors of inter-nesting female loggerhead turtles. One deployment took place during the passage of a tropical storm in the Gulf of Mexico, which gave us a unique opportunity to conduct a detailed analysis of how the inter-nesting behavior of a loggerhead sea turtle is altered during severe weather conditions.

MATERIALS AND METHODS
Animals
We attached Argos satellite tags (Wildlife Computers, SPOT5, WA, USA) to six female loggerhead turtles [*Caretta caretta* (Linnaeus 1758)] during the 2012 nesting season between May and July at Casey Key, Florida. Five females were co-instrumented with an animal motion tag (OpenTag, Loggerhead Instruments, Sarasota, FL, USA). Transmitters were glued to the carapace using a two-part epoxy resin and covered in antifouling paint. The Argos tag transmitted approximate location (accuracy from 0.1 to 2.0 km), whereas data from the motion tags were stored to a microSD card (4 GB Amazon Basics) and retrieval of the motion tags was necessary to access the data. Four of the six satellite-tracked females spread their subsequent nests widely, and two departed without laying an additional nest. However, motion tag recoveries were only

possible if the turtles returned to a cooperative tagging project for the SW Florida coast at either Casey Key, Manasota Key or Keewaydin Island. One turtle bearing a motion tag was intercepted within the 6 km patrolled area at Casey Key and a second turtle's motion tag was recovered at Keewaydin Island 140 km to the south. The two recovered motion tags provided continuous recordings from 31 May 2012 to 14 June 2012 (tag 1) and from 14 June 2012 to 29 June 2012 (tag 2). Turtle 1 had a curved carapace length (CCL) of 95.7 cm (estimated weight 102 kg, based on Ehrhart, 1976) and carried PTT 115649 (Archival Pop-up Tag, Microwave Telemetry, Inc., Columbia, MD 21045, USA); turtle 2 was 109.0 cm CCL (estimated weight 136 kg, based on Ehrhart, 1976) and carried PTT 115650.

Tagging and instrument attachment was conducted with animal ethics approval and permits from Florida Fish and Wildlife Conservation Commission Permits MTP126 and MTP155 and IACUC permits at Mote Marine Laboratory.

Argos satellite tag
The Argos satellite tags were programmed to be continuously on, and a salt water switch prevented signal transmission during submergence. Locations were retrieved and analyzed using the Satellite Tracking and Analysis Tool (Coyne and Godley, 2005). Locations used for turtle movements were Argos Location Classes for expected accuracy (3, 2, 1, 0, A, B) and filtered to remove unrealistic swimming speeds exceeding 10 km h^{-1} and positions inland (Witt et al., 2010).

Animal motion tag
The animal motion tags contain a 3-axis accelerometer, 3-axis gyroscope, 3-axis magnetometer (each sampled at 100 Hz), and temperature and pressure sensors (each sampled at 1 Hz). The gyroscope data of rotational velocity around the vertical plane were used to calculate flipper beats min^{-1}. The gyroscope signal was high-pass filtered to remove DC offset (defined as the mean amplitude displacement from zero). The flipper beats were estimated based on a 8192-point fast Fourier transform (FFT) analysis of the high-pass-filtered gyroscope signal with a calculated rate for every 2 s (Fig. 2). Wave action close to the surface interfered with the flipper beat signal and therefore the flipper beat rate was only estimated at depths >0.5 m. Based on accelerometer data in the three orthogonal planes (heave: dorso-ventral acceleration, sway: lateral acceleration, and surge: anterior-posterior acceleration) the dynamic body acceleration (DBA) can be calculated (Shepard et al., 2008; Wilson et al., 2006). The influence of gravitational acceleration was reduced by subtracting the running mean over 1 s from the raw accelerometer signal independently in all three dimensions. A vector of the dynamic body acceleration (VDBA) was then calculated from the remaining dynamic x, y and z acceleration values as the norm $(x^2+y^2+z^2)^{1/2}$ in 2 s time intervals. DBA can be used as a proxy for energy consumption (Enstipp et al., 2011; Fossette et al., 2012). A recent study on captive green turtles found a strong correlation between partial dynamic body acceleration (PDBA) and oxygen consumption with the equation used by Enstipp et al. (2011):

$$S v_{O_2} = 12.17 \text{PDBA} + 0.03 T_w - 0.46 \, ,$$

where $S v_{O_2}$ is the mixed venous oxygen saturation in ml min^{-1} kg$^{-0.83}$, PDBA is in **g** and T_w is water temperature in °C. In addition to VDBA, we therefore also calculated PDBA from heave and sway accelerometer signals (PDBA=$|x|+|y|$) to
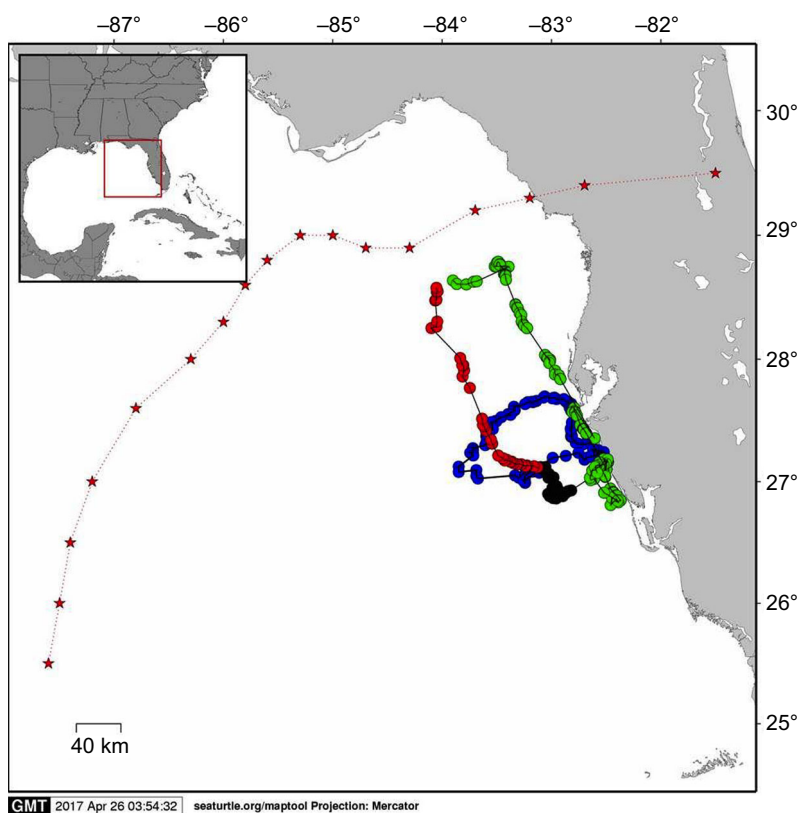
Fig. 1. Swimming tracks of the two loggerhead turtles. The turtles were equipped with an animal motion tag and a satellite tag and satellite positions tracked from 31 May 2012 to 6 April 2012 (turtle 1: blue circles, unaffected by storm) and 14 June 2012 to 4 July 2012 (turtle 2: black/red/green circles delineate before/during/after storm passage, respectively). Red stars indicate the track of tropical storm Debby in the Gulf of Mexico. The strongest winds are on the right side of the storm in counterclockwise circulation of hurricanes in the Northern Hemisphere. Despite the fact that Debby never achieved hurricane strength, the slow movement of the system and prolonged period of onshore flow allowed a moderate storm surge to move into the Florida Big Bend. Maximum wind speed was 55 knots from a southerly direction over the period when the turtle drifted northward (red circles).

estimate the daily oxygen consumption of loggerheads. The use of PDBA to estimate oxygen consumption has, to our knowledge, only been conducted on green turtles and no calibration exists on loggerhead. However, the values we calculated with this equation are similar to the values measured for green turtles (Hays et al., 2000). Even if the calculated estimate is off with loggerhead turtles, the values are still useful for comparing estimated energy expenditure of swimming versus energy required for egg production. The estimated oxygen consumption for a green turtle of a comparable size (150 kg) to turtle 2 was 0.63 ml min^{-1} kg$^{-0.83}$ during resting dives (Hays et al., 2000; Enstipp et al., 2011). The estimated oxygen consumption for turtle 2 was 0.62 ml min^{-1} kg$^{-0.83}$ during resting dives.

Dive classification

Depth and temperature data were retrieved from the accelerometer tag and analyzed. Dives had to be longer than 60 s and deeper than 3 m to be classified as a dive or else it was categorized as swimming or resting close to the surface. Classification of the different dives followed the classification of Minamikawa et al. (1997, 2000). Dives were assigned into five different categories based on their profile characteristics (Fig. 2A). Type 1 dives consist of a descent phase, a flat bottom phase (longer than 60 s) and an ascent phase. The bottom phase is often associated with a resting period (Hochscheid, 2014). Type 2 dives are often a short dive, consisting of only a descent and an ascent phase. These dives are observed when turtles are traveling away from shore, for example during the first 24 h after a nesting event (Hochscheid, 2014). Type 3 dives consist of three phases: a descent, a gradual ascent (longer than 60 s) and a final ascent. Type 4 dives consist of four phases: a rapid descent to maximum depth, followed immediately by ascent to a certain depth (often where the turtles are believed to be neutrally buoyant), a gradual ascent and lastly a final rapid ascent. The last

categories of dives are type 5. When a dive did not have a profile that fitted into one of the first four categories, it was placed in the type 5 category.

Tropical storm Debby

Tag 2 was deployed just before tropical storm Debby passed through the Gulf of Mexico on June 23–27, 2012. The tropical storm caused extensive flooding in Florida after it developed from a low-pressure cell in the central Gulf of Mexico on June 23. The storm slowly strengthened to peak intensity with maximum sustained winds of 65 mph (100 km h^{-1}) at 18:00 UTC on June 25. On June 26 at 21:00 UTC, the storm made landfall near Steinhatchee, Florida with winds of 40 mph (65 km h^{-1}). Once inland, the system weakened and crossed Florida to the Atlantic on June 27 (Kimberlain, 2012).

Statistics

Statistical analyses were performed using MATLAB 8.2 (MathWorks Inc.) and PAST3 (version 1.0.0.0) (Hammer et al., 2001). We used a non-parametric Mann–Whitney test for matched pairs to test for differences in the temperature experienced by the two turtles, because temperature data were not normally distributed. A non-parametric Spearman's rank correlation was used to test for the relation between the two estimated activity measures: flipper beats min^{-1} and VDBA (g). To evaluate the effect of the tropical storm on the swim behavior of turtle 2, a non-parametric Kruskal–Wallis test was performed to test for significance in the difference in medians between the daily energy estimate, amount of time swimming, amount of time submerged, and kilometers traveled before, during and after the tropical storm. If a significant difference in median values was found, a Dunn's non-parametric multiple comparison test was conducted to test for pairwise differences ($\alpha=0.05$ for the tests). Non-parametric tests were used because data was not normally distributed (Bagdonavicius et al., 2011).
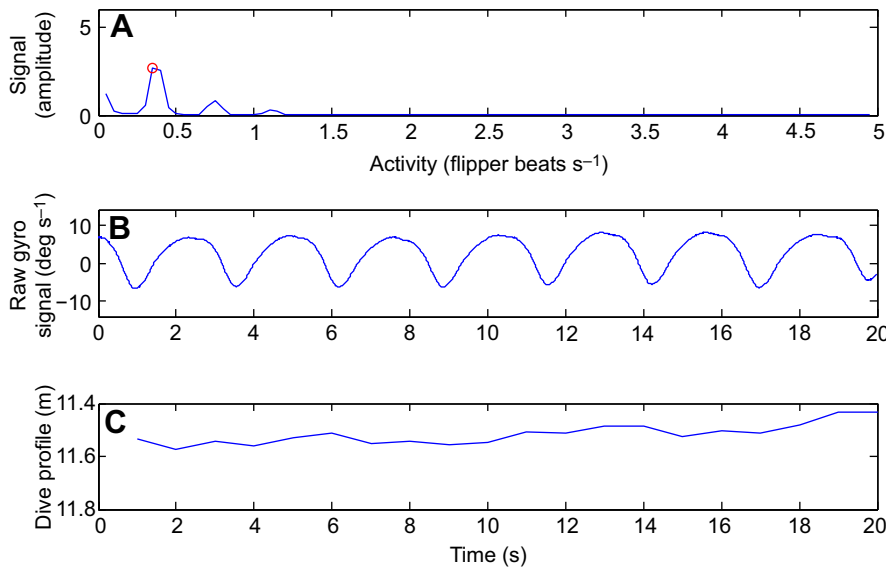
Fig. 2. Illustration of estimation of flipper beat rate based on an 8192-point fast Fourier transform (FFT) analysis of the gyroscope signal with a calculated rate for every 2 s. (A) FFT of the gyro signal in the vertical plane. Red circle indicates peak energy of the signal and gives the flipper beats s^{-1}. (B) The high-pass-filtered gyro signal in the vertical plane. (C) Corresponding dive profile.

RESULTS

The two recovered animal motion tag (OpenTags) contained continuous recordings for 15 days, a total of 347 h and 57 min (tag 1: turtle 1), and 16 days, a total of 379 h and 42 min (tag 2: turtle 2). Tag 1 was operating during a period of relatively calm weather from May 31, 2012 to June 14, 2012, whereas tag 2 was operating from June 14–29, 2012, while tropical storm Debby passed through the Gulf of Mexico (June 23–27, 2012). Both tags were recovered as the two turtles re-nested; turtle 1 at Keewaydin Island on June 18, 2012 (inter-nesting period: 18 days) >140 km from her previous nest, and turtle 2 at Casey Key on July 5, 2012 75 m from her previous nest (inter-nesting period: 21 days).

The total distance traveled for turtle 1 was 675 km (45 km day^{-1}) and for turtle 2 it was 613 km (38 km day^{-1}). Before the tropical storm, turtle 2 traveled a total of 177 km (20 km day^{-1}), during the storm 285 km (57 km day^{-1}) and after the storm 151 km (75 km day^{-1}) (Fig. 1B).

Turtle 1 spent 94% of the entire time actively swimming, whereas turtle 2 spent 54% of the time actively swimming. An overview of the dive activities, distance traveled per day and amount of time swimming per day are given in Table 1A and Fig. 3A (turtle 1) and Table 1B and Fig. 3B (turtle 2).

Turtle 1 spent 42% (146 h) of the total time at depths deeper than 3 m [6% conducting type 1 dives, 0% type 2, 19% type 3, 7% type 4 and 9% type 5 (Fig. 4B)]. Examples of diving behavior for turtle 1 are given in Fig. S1A–D. During 7 out of the 37 type 1 dives, turtle 1 was resting at the bottom (defined as no flipper beat activity in at least 75% of the bottom phase). Mean (±s.d.) duration of type 1 dives was 50±22 min (max. 87 min), type 2 dives was 7±2 min (max. 10 min), type 3 dives was 15±9 min (max. 38 min) and type 4 dives was 22±13 min (max. 57 min).

Turtle 2 spent 69% (262 h) at depths deeper than 3 m [42% conducting type 1 dives, 4% type 2, 5% type 3, 17% type 4 and 15% type 5 (Fig. 4C)]. Examples of the diving behavior for turtle 2 are given in Fig. S1E–H. In contrast to turtle 1, turtle 2 spent 135 out of 176 of the type 1 dives resting at the bottom. Mean duration of type 1 dives was 33±20 min (max. 90 min), type 2 dives was 5±4 min (max 15 min), type 3 dives was 19±8 min (max 43 min) and type 4 dives was 23±10 min (max 45 min).

Fig. 4 gives typical examples of type 3 dives (A,B: turtle 1; F,G: turtle 2) and type 4 dives (C,D: turtle 1; H,I: turtle 2). Both turtles

swam during the gradual ascent phase (Fig. 4E,J). For turtle 2, type 3 and 4 dives were mainly conducted during and after the tropical storm [type 3: 35 dives out of 56 (63%); type 4: 71 of 97 (73%)]. Median flipper beat of the different dive phases for the two turtles is shown in Fig. S2.

VDBA and oxygen consumption

We used data from the rotational velocity gyroscope signal in the vertical plane to estimate the direct flipper beat rate. Furthermore we used data from the tri-axial accelerometer to calculate the VDBA (Enstipp et al., 2011). Both measures reflect the activity level of the turtles, and a Spearman's correlation was performed to determine the relationship between the flipper beat rate and VDBA values. There was a strong, positive correlation between flipper beat rate and VDBA (r_s=0.64, n=2301, P<0.001) (Fig. S3).

The daily oxygen consumption was estimated for both turtles and the average daily oxygen consumption (for the entire period) was slightly higher for turtle 1 [median 0.953 ml min^{-1} $kg^{-0.83}$ (lower quartile: 0.899; upper quartile: 1.029)] compared with turtle 2 [median 0.803 ml min^{-1} $kg^{-0.83}$ (lower quartile: 0.614; upper quartile: 0.991)]. However, there was no significant difference in the overall daily amount of oxygen used for the two turtles during the tagged periods (Mann–Whitney signed-rank test, $|z|$=1.70, $n_{turtle1}$=15, $n_{turtle2}$=16, P=0.088) (Fig. 6).

Temperature

The two turtles were exposed to relatively high water temperatures, with a median of 28.1°C (min.: 23.1°C, max.: 31.1°C) for turtle 1 and a median of 27°C (min.: 25.3°C, max.: 30.5°C) for turtle 2 during the entire deployment periods (Fig. 6). There was a significant difference between the median temperatures (Mann–Whitney signed-rank test, $|z|$=−3.76, n=15, P<0.001).

Tropical storm Debby

We obtained storm tracking data from a NASA summary report on Tropical Debby (tables 1 and 2 in Kimberlain, 2013). There was a significant change in the behavior of turtle 2 when she encountered the tropical storm. Table 2 summarizes changes in daily median oxygen consumption, amount of time spent swimming, amount of time submerged and distance traveled before, during and after the storm with supportive statistical tests. Oxygen consumption was

Table 1. Overview of the daily activity for each turtle

| Date | No. dives | Time submerged (%) | Time swimming (%) | Distance traveled (km) | Temperature (°C) | | | Max. depth (m) | Mean VDBA (g) | O$_2$ consumption (ml min^{-1} kg$^{-0.83}$) |
					Mean	Min.	Max.			
(A) Turtle 1										
31 May	51	55	96	20	28.6	25.7	30.3	12.8	0.04	0.87
1 June	49	68	83	28	27.9	27.6	28.2	14.7	0.03	0.79
2 June	42	54	99	39	28.0	27.3	29.7	20.5	0.04	0.87
3 June	26	63	90	38	27.0	24.7	29.2	40.0	0.04	0.83
4 June	26	66	80	57	26.3	24.0	29.1	50.9	0.04	0.84
5 June	17	30	97	40	27.0	23.1	28.2	57.0	0.05	0.97
6 June	7	10	99	39	27.1	24.5	27.5	47.4	0.06	1.11
7 June	8	13	99	59	27.2	25.4	27.8	41.0	0.06	1.08
8 June	22	28	98	55	27.4	24.9	30.2	45.6	0.05	0.98
9 June	16	36	85	41	27.1	24.3	28.9	47.1	0.05	0.95
10 June	41	67	99	43	28.2	27.2	30.2	31.2	0.04	0.89
11 June	43	51	97	51	29.1	28.1	30.9	16.8	0.04	0.92
12 June	37	49	97	60	28.9	28.3	30.8	21.1	0.04	0.95
13 June	6	5	100	54	29.2	28.5	31.1	23.1	0.05	1.06
14 June	23	36	100	51	29.5	28.7	31.1	22.8	0.05	1.05
(B) Turtle 2										
14 June	73	75	85	40	28.7	26.7	30.5	29.1	0.05	0.99
15 June	38	94	24	25	26.8	25.9	29.3	33.7	0.02	0.56
16 June	24	94	12	17	26.2	25.9	29.4	34.8	0.01	0.51
17 June	21	92	11	12	26.2	25.7	28.8	36.1	0.01	0.50
18 June	22	88	13	12	26.4	25.8	29.2	36.9	0.02	0.53
19 June	24	82	27	16	26.8	26.1	28.2	35.9	0.02	0.64
20 June	20	75	24	15	26.8	26.0	28.3	36.4	0.02	0.64
21 June	20	83	16	18	27.4	26.3	28.2	35.6	0.02	0.61
22 June	26	76	30	22	27.5	26.7	28.1	37.5	0.03	0.71
23 June	19	50	72	35	27.1	25.3	27.5	48.9	0.04	0.89
24 June	14	41	88	71	26.8	25.4	27.3	49.5	0.06	1.07
25 June	16	38	90	69	26.7	25.5	27.1	45.3	0.06	1.02
26 June	18	46	89	52	26.9	26.4	27.7	40.8	0.05	0.99
27 June	52	57	98	58	27.2	26.6	28.1	31.4	0.05	0.95
28 June	60	47	92	94	27.5	26.7	29.9	22.8	0.05	0.91
29 June	85	66	95	57	27.4	26.8	28.5	22.1	0.04	0.87

All dates are from 2012. VDBA, vector of the dynamic body acceleration.

significantly higher during the storm (0.97 ml min^{-1} kg$^{-0.83}$) compared with before the storm (0.62 ml min^{-1} kg$^{-0.83}$). After the storm, the oxygen consumption was also higher compared with

before, but not significantly (0.99 ml min^{-1} kg$^{-0.83}$) (Fig. 6B). The amount of time swimming was significantly higher during the storm (91%) compared with before the storm (20%), and also after the
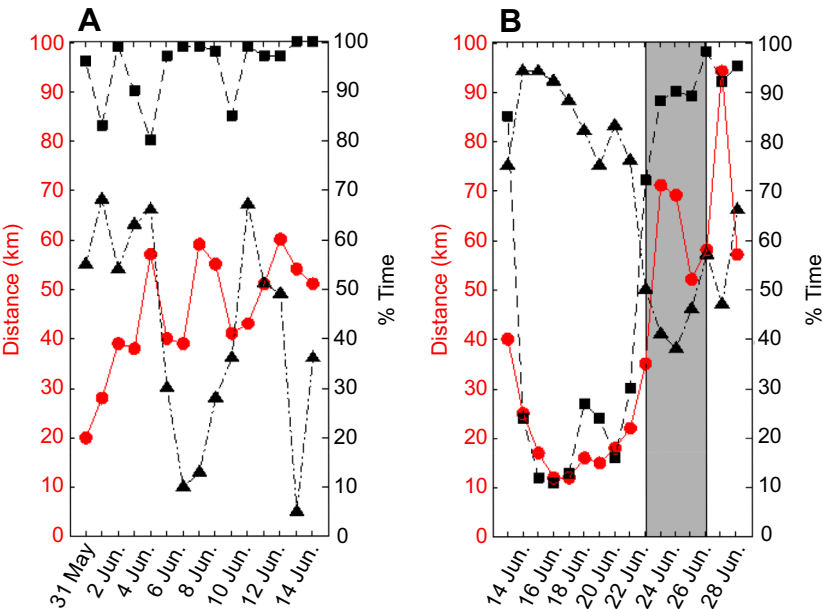

Fig. 3. Activity budget of the two loggerhead sea turtles. Overview of distance traveled per day, amount of time spent submerged per day and amount of time spent swimming (A: turtle 1; B: turtle 2). Red circles are distance traveled (km day^{-1}), black triangles are percent of the time submerged and black squares are percent of time swimming. Gray shaded area in B indicates the passage of the tropical storm. All dates are from 2012.
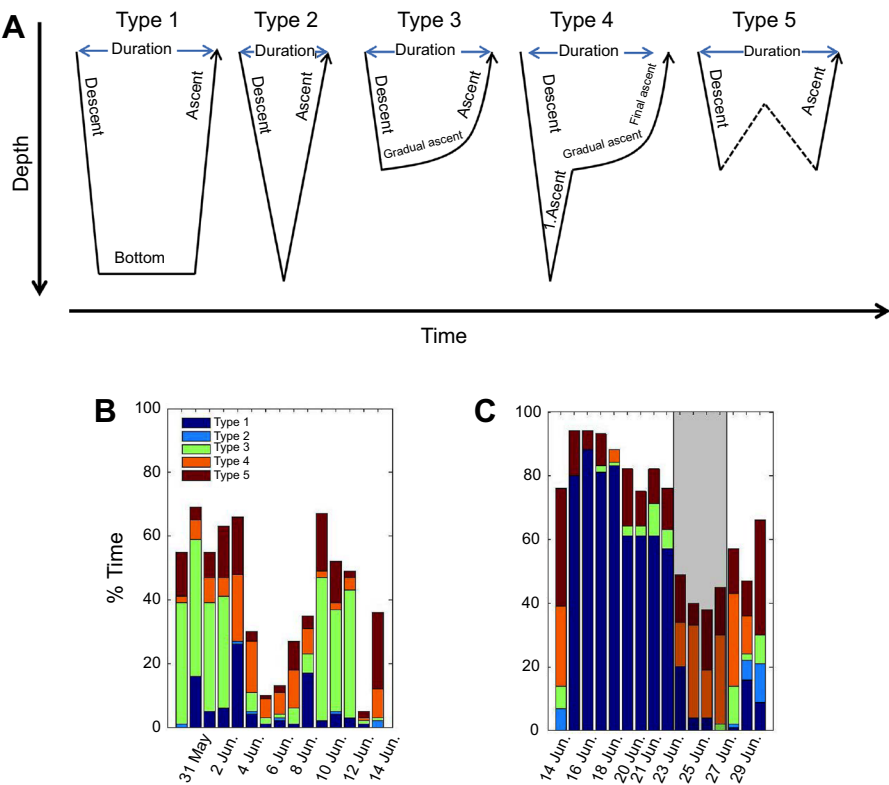
Fig. 4. Different dive categories. (A) Classic dive categories and illustration of the dive profiles of each dive type conducted by the female loggerhead turtles during the inter-nesting period (modified from Minamikawa et al., 1997). Dashed lines in type 5 indicate a variable phase. (B,C) Histograms illustrating the proportion of time spent conducting different dive types during the inter-nesting period for (B) turtle 1 and (C) turtle 2. Gray shaded area in C indicates the passage of the tropical storm. All dates are from 2012.

storm (86%) versus before. The amount of time submerged (86%) was significantly higher before the storm compared with during the storm (44%), but there was no significant difference before the storm compared to after the storm (57%). Daily distance traveled was significantly higher during the storm (57 km) compared with before the storm (17 km), and also after the storm (70 km) compared with before.

DISCUSSION
Sea turtles exhibit plasticity in behavior during inter-nesting periods (Hochscheid, 2014) and the present study supports previous findings. We documented different behaviors by two female loggerheads nesting at the same rookery. Both turtles were instrumented early in the nesting season. The entire period where turtle 1 was tagged and the first 9 days where turtle 2 was tagged were periods with calm and warm weather. Despite the same weather conditions, the turtles displayed different inter-nesting strategies; this complicates a direct comparison between females even without the tropical storm.

A fundamental factor affecting inter-nesting behavior is water temperature (Fossette et al., 2012; Hays et al., 2002; Sato et al., 1998; Schofield et al., 2009). Sea turtles are ectotherms and the maturation of eggs is therefore dependent on the surrounding water temperature (Schofield et al., 2009). Active maintenance of a high and stable body temperature is a clear benefit; however, both of the turtles in the present study experienced water temperature above 23°C and water temperature therefore seems an unlikely reason why different inter-nesting strategies were observed.

Another explanation for higher activity by turtle 1 could be that food was available. Instead of resting and saving energy, females may invest energy into foraging to supplement their body reserves and maximize reproduction outcomes. This type of behavior has been observed in both a Greek loggerhead population (Schofield et al., 2009) and in Japan, where pelagic feeding took place during the inter-nesting period (Narazaki et al., 2013). Pelagic feeding events were mainly observed during the gradual ascent phase of type 3 and type 4 dives (Narazaki et al., 2013). Of the 335 dives turtle 1 conducted during the inter-nesting period,

Table 2. The effect of the tropical storm on the behavior of turtle 2

	Before (n=9)	During (n=3)	After (n=4)	Kruskal–Wallis test (d.f.=2)	Dunn's multiple-comparison test		
					Before vs during	Before vs after	During vs after
Median daily O_2 consumption (ml min^{-1} kg$^{-0.83}$)	0.62	0.97	0.99	$P<0.05$* $H_c=10.76$	$Q=2.78$ $P<0.05$*	$Q=1.61$ $P>0.05$	$Q=0.78$ $P>0.05$
Daily amount of time swimming (%)	20	91	86	$P<0.01$** $H_c=10.5$	$Q=2.74$ $P<0.05$*	$Q=2.48$ $P<0.05$*	$Q=0.0$ $P>0.05$
Daily amount of time submerged (%)	84	44	57	$P<0.001$*** $H_c=11.23$	$Q=3.20$ $P<0.05$*	$Q=1.93$ $P>0.05$	$Q=0.85$ $P<0.05$
Daily distance traveled (km)	17	57	70	$P<0.01$** $H_c=10.5$	$Q=2.70$ $P<0.05$*	$Q=1.56$ $P<0.05$*	$Q=0.34$ $P>0.05$

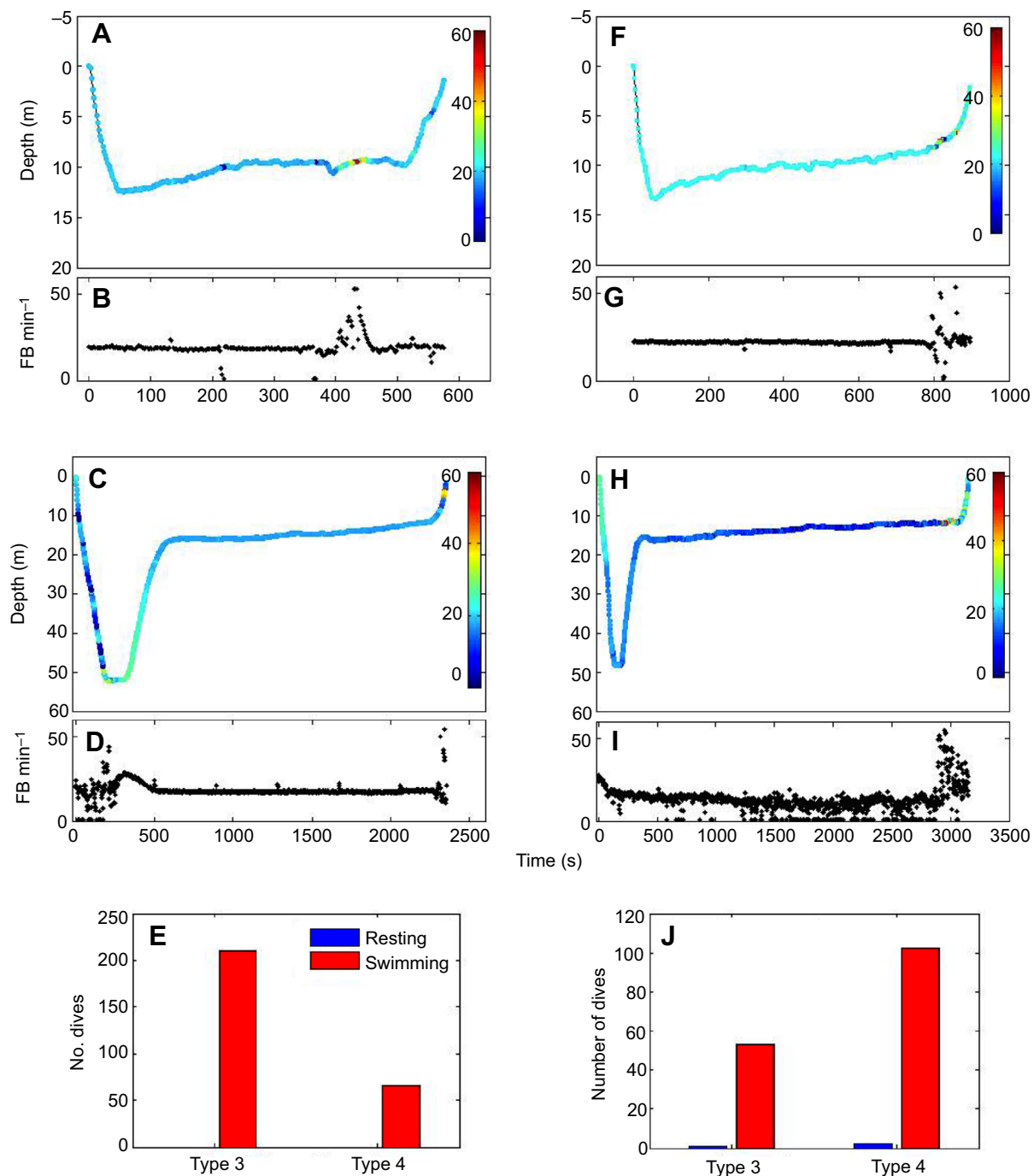*n*, number of days. *$P<0.05$, **$P<0.01$, ***$P<0.001$.

Fig. 5. Type 3 and type 4 dives. Examples of a type 3 (A: turtle 1; F: turtle 2) and a type 4 (C: turtle 1; H: turtle 2) dive. Color code gives flipper beats min⁻¹ (FB min⁻¹). (B,D,G,I) Flipper beats of the dives in A, C, F and H, respectively. (E,J) The number of type 3 and type 4 dives in which the turtles are swimming more than 95% of time at the gradual ascent phase (red) or resting (blue) (E: turtle 1; J: turtle 2).

276 of the dives were either type 3 or type 4, and it is therefore possible that turtle 1 encountered waters with a high concentration of gelatinous food items and that she was foraging. There were no video corroborations of feeding in the present study of neritic Gulf of Mexico loggerheads to uncover whether she was feeding or not. However, decades of systematic necropsies find negligible or empty gastrointestinal tracts in gravid female loggerheads during Florida's nesting season (A. Foley, Florida Fish and Wildlife Conservation Commission, personal communication; G. Lovewell, Mote Marine Laboratory, personal communication).

Dive types and estimated aerobic dive limit

Both turtles conducted relatively long type 1 dives, with maximum durations of 90 min and 87 min for turtles 1 and 2, respectively. By using the estimated resting oxygen consumption of 0.62 ml min⁻¹ kg⁻⁰·⁸³ and the approximate oxygen store of a loggerhead turtle of 22.2 ml O_2 kg⁻¹ (Hochscheid et al., 2005), the aerobic dive limit would be 89 min, corresponding to the maximum length of type 1 dives in the present study. Our study supports previous findings that loggerheads very rarely make anaerobic dives (Hochscheid et al., 2005).

Both turtles conducted type 3 and type 4 dives, with a gradual ascent phase to between 10 and 20 m, where turtles are neutrally
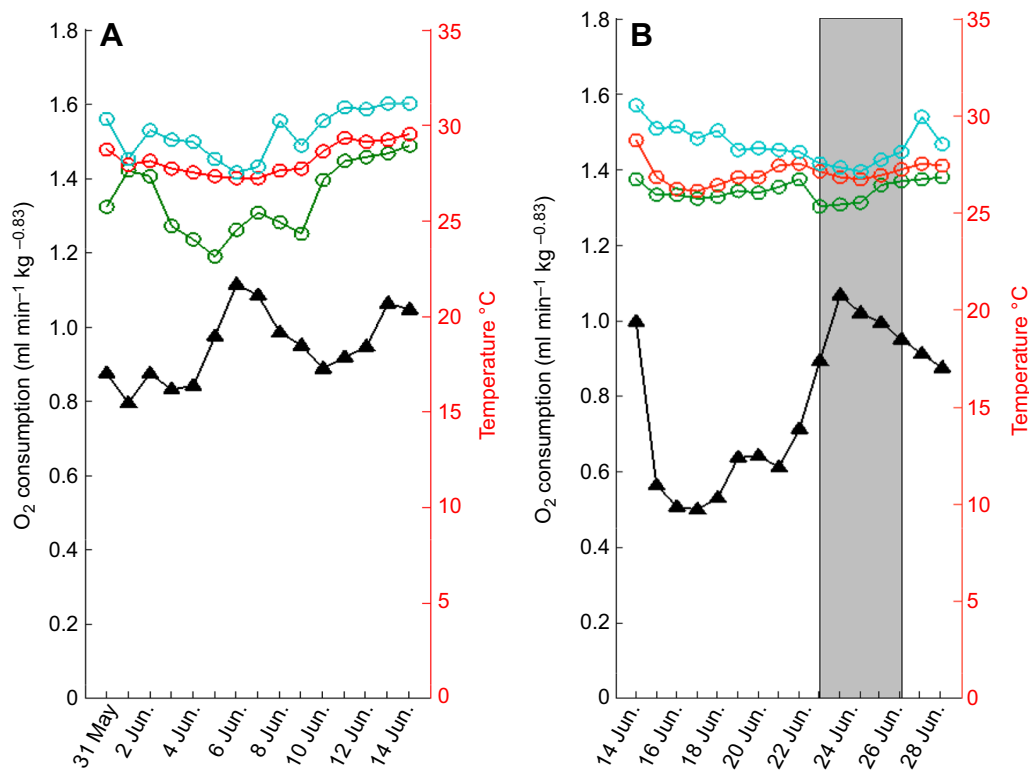
Fig. 6. Oxygen consumption and water temperature. Mean daily estimated oxygen consumption (black line) and mean daily temperature (red: mean temperature; turquoise: maximum temperature; green: minimum temperature). (A) Turtle 1; (B) turtle 2. Gray shaded area in B indicates the passage of the tropical storm. All dates are from 2012.

buoyant (Hays et al., 2004b; Minamikawa et al., 2000). Studies on loggerhead turtles in Japan (Minamikawa et al., 1997, 2000) and Cyprus (Houghton et al., 2002) found that type 3 and 4 dives are used for midwater resting by females during the inter-nesting period. However, loggerhead dive types might also have different purposes than in green turtles, which travel by swimming or gliding during type 3 and 4 dives (Hochscheid et al., 1999; Rice and Balazs, 2008) or conduct pelagic foraging on gelatinous prey during these dives (Narazaki et al., 2013). For both turtles in the present study, we found that they were swimming during most of type 3 and type 4 dives (Fig. 5) and not resting as previously observed in other female loggerheads during the inter-nesting period. Turtle 2 conducted the main part of the type 3 and 4 dives during or after the tropical storm (Fig. 4), where she also moved relatively long distances (Fig. 3). Swimming at a depth of neutral buoyancy is energetically efficient because turtles would not have to allocate energy to remain at a certain depth nor struggle with surface waves. Some of the type 4 dives were quite long, with a maximum duration of 57 min and 45 min for turtle 1 and turtle 2, respectively. By using the estimated active oxygen consumption of 0.95 ml min^{-1} kg$^{-0.83}$ for turtle 1 and 0.97 ml min^{-1} kg$^{-0.83}$ for turtle 2, active dives will become anaerobic after 58 and 56 min for the two turtles. None of the active dives exceeded the estimated aerobic dive limit.

Tropical storm Debby

Turtle 2 encountered changing weather conditions during the 16 days she was instrumented. Before the storm she was resting, which is common for sea turtles between nesting events and agrees with previous data recorded for loggerheads (Sakamoto et al., 1993; Minamikawa et al., 1997; Houghton et al., 2002), green turtles (Hochscheid et al., 1999; Rice and Balazs, 2008; Cheng et al., 2013)

and hawksbill turtles (Storch et al., 2006). During the storm, the behavior of turtle 2 changed significantly and she became highly active, moving in a northern direction, consistent with surface currents generated by the storm (Kimberlain, 2013). We interpreted the displacement as passive storm-generated drift rather than active directed movement by the turtle (Fig. 1). During the storm, she spent more time close to the surface as opposed to the two former studies that found that turtles spend less time at the surface when encountering severe weather (Sakamoto et al., 1990b; Storch et al., 2006). The dominant dive type during the storm was type 4 (Fig. 2), in which the turtle descended to the bottom but shortly afterwards ascended to the neutral buoyancy zone between 10 and 20 m (Hays et al., 2004b; Minamikawa et al., 2000), where she swam during the gradual ascent phase. After the storm, most dives were short dives while she traveled south back to the nesting beach (Figs 1 and 4G). She returned to the same nesting beach (Casey Key), where she successfully re-nested only 75 m from her previous nest. According to Sato et al. (1998), there is a negative correlation between the time span between nesting attempts and the temperature of the surrounding water in loggerhead sea turtles. A surrounding water temperature of 22°C will cause an inter-nesting period of approximately 21.7 days, whereas, if the temperature is 27°C, the inter-nesting period decreases to approximately 14.9 days. Turtle 2 was exposed to an average water temperature of 27°C; thus, according to the study by Sato et al. (1998), the predicted inter-nesting period would be 15 days. The actual inter-nesting period was 21 days, 6 days longer than the predicted value. Twenty-one days is still within the normal range of loggerheads and the longer inter-nesting interval could be explained by individual variation. An equally parsimonious explanation is displacement from the tropical storm.

The question is how much energy did the tropical storm cost? If we assume that the turtle is metabolizing fat (Schmit-Nielsen, 1997), the daily energy expenditure based on the oxygen consumption estimate would be 1029 kJ before the tropical storm, whereas during and after the storm the daily energy consumption would be 1608 kJ, more than a 50% increase. Is this much compared to the energy used during a nesting event? Energy expenditure for a nesting event is very high (Jackson and Prange, 1979). Hays and Speakman (1991) estimated the mean oxygen consumption by nesting loggerhead turtles on the beach to be 0.23 ml kg^{-1} h^{-1}, which corresponds to an energy expenditure of 4.52 kJ kg^{-1} h^{-1}. Egg production is, however, by far the most energy consuming process in the nesting event. Assuming the volume-specific energy content of loggerhead eggs is the same as for green turtles, the energy content of a loggerhead egg would be 165 kJ (Hays and Speakman, 1991). Clutch size depends on turtle size and her carrying capacity. For turtle 2, the estimated clutch size would be approximately 150 eggs (Hays and Speakman, 1991), corresponding to 24,750 kJ per clutch. A nesting event depositing a clutch size of 150 eggs takes approximately 100 min (Hays and Speakman, 1991). Based on these values, the total energy expenditure of the entire nesting event for turtle 2 would be 25,777 kJ. If turtle 2 did not encounter the tropical storm and she rested during the entire inter-nesting period, she would expend 1994 kJ less energy, corresponding to the energy content in 12 eggs. Therefore, the significant change in turtle 2's behavior during the tropical storm would likely have had a minor effect on the overall energy budget.

The overall estimated oxygen consumption for the tracked time span was actually lower for turtle 2 compared with turtle 1, which encountered calm weather. Consequently, the tropical storm effects on a single sea turtle appear to have a negligible effect on site fidelity of the turtle and her ability to nest, despite any behavioral changes at sea for the dive profile. The same tropical storm had a more severe effect on the beach itself, where almost 90% of the incubating nests at Casey Key were destroyed (Tucker et al., 2012). Thus, in terms of conservation priorities, focus should be on securing the incubating nest from beach erosion.

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