Changes in flipper beat frequency, body angle and swimming speed of female green turtles *Chelonia mydas*

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ABSTRACT: Data loggers were utilized to record depth, temperature, biaxial motion and swimming speed for female green turtles *Chelonia mydas* between nesting events in Thailand. The present study demonstrated clear alternations in swimming effort with depth. Both resident and maximum dive depths significantly affected flipper beat frequency, suggesting that turtles change flipper beat frequency with current buoyancy in ways similar to other diving mammals and birds. Body angles became steepest during the initial phases of descent and ascent, but were <60°. Swimming speeds were related to flipper beat frequency and current buoyancy. Swimming speeds based on the dominant stroke frequency during the inter-nesting period (0.18 to 0.21 Hz) were estimated at 0.52 to 0.60 curved carapace lengths s^{-1}. These values are similar to the modal speeds of the leatherback turtles *Dermochelys coriacea* and the mean speeds during the initial descent of the loggerhead turtles *Caretta caretta*. We calculated the dynamic body acceleration (DBA) as the index of activity during the descent and ascent phases and found a relationship between maximum dive depth and DBA. Although active stroking during deeper dives may result in a shorter dive duration, daytime dives (ca. 16 to 26 m) were deeper than those observed during the night (ca. 9 to 13 m). This result suggests a beneficial reproductive strategy for females that involves changes in vertical space, for example, to obtain refuge from energy-consuming encounters with males or predators.

KEY WORDS: Diving behaviour · *Chelonia mydas* · Sea turtles · Flipper beat frequency · Swimming speed · Body angle

INTRODUCTION

As air-breathing vertebrates descend during a dive, the buoyancy varies due to the compression of gas in the lungs and/or the plumage (for birds), in accordance with Boyle's law. Such changes in buoyancy may aid or impede swimming efficiency (Wilson et al. 1992). In this situation, some deep-diving mammals exhale prior to submergence. Alternatively, they use oxygen in their blood and tissues during the dive (Butler & Jones 1997). The costs of swimming for these animals are also affected by drag forces, which increase exponentially with swimming speed (Schmidt-Nielsen 1984, Williams et al. 1993). Therefore, these diving vertebrates are likely to tactically use both an active stroke swimming and passive

glide swimming, as the situation demands (e.g. Williams et al. 2000, Sato et al. 2003, Watanuki et al. 2003). In fact, a narrow range of swimming speeds during a dive (Williams et al. 1993, Boyd et al. 1995) and the decline in thrust or stroke frequency have been demonstrated to parallel changes in buoyancy with depth (Lovvorn et al. 1999, Watanuki et al. 2003, 2005).

To date, few studies have investigated the swimming effort of hard-shelled sea turtles during a dive compared to those of diving mammals and birds. Hays et al. (2007) examined the flipper beat frequency and amplitude of green turtles *Chelonia mydas* using an animal-borne video camera (CRITTERCAM; Marshall 1998) and found that these parameters decreased as the descent or ascent continued, suggesting that a gen-

eral rule applies across a diverse range of mammalian, avian and reptilian divers. Similar flipper beat frequencies were recorded for a single green turtle equipped with an IMASEN data logger (Hays et al. 2004a). However, there is no empirical evidence of changes in swimming effort in relation to instantaneous (i.e. resident) depth or maximum dive depth. In addition, the diving behaviour of gravid female turtles differs from that of these animals in at least one fundamental respect: female sea turtles of a number of species, including green turtles, loggerhead turtles *Caretta caretta* and hawksbill turtles *Eretmochelys imbricata*, which have a low metabolic rate compared to other non-reptilian diving animals (e.g. Hays 2008), may fast during the nesting period (Limpus & Reed 1985, Starbird et al. 1999, Hays et al. 2002, T. Yasuda unpubl. data), with the exception of some populations (e.g. Hochscheid et al. 1999). Alternatively, they spend much of the inter-nesting periods on the seabed or at a distinct depth performing U-shaped (Hochscheid et al. 1999, Hays et al. 2000, Houghton et al. 2002, 2008) or S-shaped (Minamikawa et al. 2000; also see Hochscheid et al. 1999) resting dives to conserve energy for reproduction. It is expected that the most efficient depth is the shallowest depth at which the turtle is allowed to establish neutral buoyancy. If turtles dive considerably deeper than the depth at which neutral buoyancy is attained, travelling costs may decrease the resting duration. Therefore, selecting the depth at which turtles attain close to neutral buoyancy, in accordance with pre-submergence inspiration, may be important for conserving energy for reproduction (Minamikawa et al. 1997, 2000, Hays et al. 2004b).

In the present study, to bridge the gap in our understanding of swimming effort between sea turtles and other non-reptilian diving animals, we deployed acceleration data loggers to record stroke frequency, body angle, swimming speed and ambient water temperature for gravid female green turtles. The aim of the present study was to determine if flipper beat frequency, body angle and swimming speed are regulated by both the resident and maximum dive depths and to examine the relationship between dive depth and dive duration using an index of activity level calculated based on accelerations.

MATERIALS AND METHODS

Study site, field survey and instrument deployment. Field surveys were conducted in 2006 at Huyong Island (8° 29′ N, 97° 38′ E), Thailand. Huyong Island is a small oceanic remote island (area: 1.62 km²) that has a sandy beach for year-round nesting populations of green turtles *Chelonia mydas* (Yasuda et al. 2006).

Nesting females were found by night patrols on the beach. The instrument was attached and curved carapace length (CCL) was measured after nesting. Two types of accelerometers were used separately (i.e. W380L-PD2GT and UME190L-D2GT; Little Leonard Ltd.), with 12-bit resolution, to obtain the depth, ambient temperature, biaxial acceleration and swimming speed of turtles. The D2GT and PD2GT were 15 and 27 mm in diameter and 53 and 128 mm in length and had masses of 16 and 73 g in the air, respectively. The full recording range depth was 380 m, with a resolution of 0.093 m for PD2GT, and 190 m, with a resolution of 0.046 m for D2GT. The measuring ranges were ±49 m s^{-2}, with a resolution of 0.02 m s^{-2} for acceleration, and -20 to 50°C, with a resolution of 0.018°C for temperature. We measured the surge acceleration along the long axis of the body and the heave acceleration along the orthogonal axis of the surge acceleration. Swimming speed was only obtained by PD2GT. The swimming speed was converted from the rotation of an external propeller by a calibration experiment using a water circulation tank. The rotation of the propeller was unstable at water flow speeds of <0.2 m s^{-1}. However, at water flow speeds of >0.2 m s^{-1}, linear relationships between the rotation number of the propeller and water flow speed were obtained with a high coefficient of determination that was >0.9 for all data loggers. This enabled us to compare the swimming speeds of the green turtles. Sampling intervals were 1 Hz for depth and swimming speed, 0.1 Hz for temperature and 16 Hz for acceleration. The data logger was attached to the top of the carapace using a quick-setting epoxy resin (Quick-5, Konishi Ltd.) in accordance with the Japan Ethological Society guidelines for the experimental use of animals. Total attachment durations were <30 min. Turtles with instruments returned to the same beach approximately 12 d later for the next nesting, and data loggers were retrieved from the turtles after the subsequent nestings were completed.

Diving behaviour. Recently, accelerometers have been utilized to analyse the locomotion of both terrestrial and aquatic animals (Yoda et al. 2001, Watanabe et al. 2005, Tsuda et al. 2006, Wilson et al. 2006). The accelerometers can measure both dynamic acceleration (e.g. propulsive activities) and static acceleration (e.g. gravity). High-frequency components of the surge acceleration were used to calculate the flipper beating of the turtles. In contrast, low-frequency components of the longitudinal acceleration along the long axis of the body were used to calculate the pitch angle of the turtles (see Sato et al. 2003). The low-frequency component of the acceleration was obtained using an Igor Filter Design Laboratory (IFDL) Version 2.0 (WaveMetrics), which removed the high-frequency component based on flipper strokes measured by the 0.1 Hz low-pass filter.

The diving behaviour of the turtles was divided into 6 different dive types. A generalized time-series of the depth profile has been published by Seminoff et al. (2006). In the present study, we focused on the flat-bottom U-shaped dive (Type 1), which is the dive most commonly performed by female green turtles during the inter-nesting period (Hochscheid et al. 1999, Hays et al. 2000, 2004b). Dive data were automatically analysed using a macro in Igor Pro Version 5.0 (WaveMetrics). A dive was defined as a depth of >3 m for at least 30 s to extract dive parameters for each dive.

We detected all individual flipper movements during each dive. Flipper movements were defined as high-frequency components of acceleration >0.01 m s^{-2} for at least 1 s. We defined the time of the flipper beat as the time of maximum acceleration during each flipper movement. Using the intervals between consecutive flipper beats, we then calculated the instantaneous flipper beat frequency. The U-shaped resting dive was defined as the turtle remaining within 50 cm of the maximum depth for >80% of the dive duration to account for the resolution of the loggers. The start and end of the bottom phase were defined as those times associated with successive flipper beats, which had the longest flipper beat frequency, since both landing and take-off from the seabed were accompanied by flipper beats. The maximum dive depth was defined as the maximum depth during the bottom phase. Visual analysis of individual dive profiles and statistical values obtained for each parameter confirmed that the macro successfully captured the dives and each parameter. If these items were not successfully captured by the macro, they were corrected manually.

Dominant stoke cycle frequency during the monitoring period. To determine the dominant stroke cycle frequency of the turtles from the time-series data, the periodic properties of the acceleration signal were analysed. Power spectral density (PSD) was calculated from the high-frequency component of the entire surge acceleration dataset for each turtle using a fast Fourier transform (FFT) with a computer programme package in Igor. The dominant stroke cycle frequency was defined as the value obtained at the peak power spectral density for each turtle. Diving mammals and birds employ both active stroke swimming and passive glide swimming, according to the situation. As an index of the depth at which turtles begin to conduct passive glide swimming, the instantaneous depth when flipper beat frequency was below the dominant stroke cycle frequency (hereafter, the instantaneous depth is termed DFBD) was calculated. To determine the beginning of the glide swimming, 0.18 Hz, which was the lowest value associated with each turtle, was used as the dominant stroke cycle frequency (Table 1). If the flipper beat frequency of a turtle was continuously above the dominant stroke cycle frequency throughout the descent and ascent phases, the DFBD was considered to be the maximum dive depth.

Dynamic body acceleration (DBA). Recent studies suggest that acceleration can serve as a proxy for the rate of energy expenditure in free-living animals (Wilson et al. 2006, Halsey et al. 2008, Green et al. 2009). In the present study, we calculated the DBA as the index of activity during the descent and ascent phases. High-frequency components of the surge and heave accelerations were converted into absolute positive units, and the resulting values from both channels were added to obtain an overall value for the biaxial acceleration. We summed the total amount of DBA for the whole of the descent or ascent phase in any single dive. These values were used in regressions of DBA versus the maximum dive depth for turtles.

Statistical analyses. To examine whether both resident and dive depths affect flipper beat frequency, body angle and swimming speed, we applied the generalized linear mixed model (GLMM; Schall 1991) with restricted maximum likelihood (REML) analysis. The mixed model allows both fixed and random terms to be fitted, while random terms take into consideration repeated sampling. The resident and maximum dive depths were defined as the fixed effects, and an interaction between these variables was also considered. We fitted the identity of individuals as the random effect and ran separate statistical analyses on the descent and ascent phases. Before application of the model, we calculated the mean values of the flipper beat frequency, body angle and swimming speed at depths ranging from 0 to 5, 5 to 10, 10 to 15 m, etc.,

Table 1. *Chelonia mydas.* Summary of the diving data for female green turtles during the inter-nesting period at Huyong Island, Thailand, in 2006. CCL: curved carapace length

Turtle	Loggers	Recording period	Dive depth (m)	Dive duration (min)	Dominant stroke cycle frequency (Hz)	CCL (cm)	No. of U-dives	Total no. of dives
CM1	PD2GT	6–11 Mar	13.21 ± 5.75	45.01 ± 8.33	0.19	99	93	193
CM2	PD2GT	9–15 Mar	10.10 ± 4.37	38.31 ± 15.23	0.18	90	132	348
CM3	D2GT	14–17 Mar	23.62 ± 7.42	58.27 ± 12.73	0.18	103	65	137
CM4	D2GT	14–18 Mar	14.48 ± 13.38	29.61 ± 10.04	0.21	101	58	229

for each individual. Statistical analyses were performed using SPSS Version 15.0 J for Windows (SPSS). We included all likely independent terms and possible interactions in the maximal model and excluded terms sequentially until the model included only those terms whose elimination would significantly decrease the Akaike's information criterion (AIC) of the model.

RESULTS

Diving behaviour

A total of 348 (58 to 132) U-shaped dives was obtained from 4 female green turtles *Chelonia mydas*

during the inter-nesting periods (Table 1). The mean bottom depth at which the turtles rested on the seabed ranged from 13.21 ± 5.75 m (n = 93 dives) to 23.62 ± 7.42 m (n = 65 dives). Mean dive duration ranged from 29.61 ± 10.04 min (n = 41 dives) to 58.27 ± 12.73 min (n = 65 dives). Although the flat-bottom dives were observed during both the day and at night, there was a significant difference in maximum dive depth between daytime and nighttime over the recording period (Fig. 1, Table 2). In contrast, no apparent pattern was detected between daytime and nighttime dive durations (Table 2). Dive duration was affected by the bottom depth (Fig. 2), and the relationships between these variables for each turtle were typically explained by a quadratic curve (Table 3).
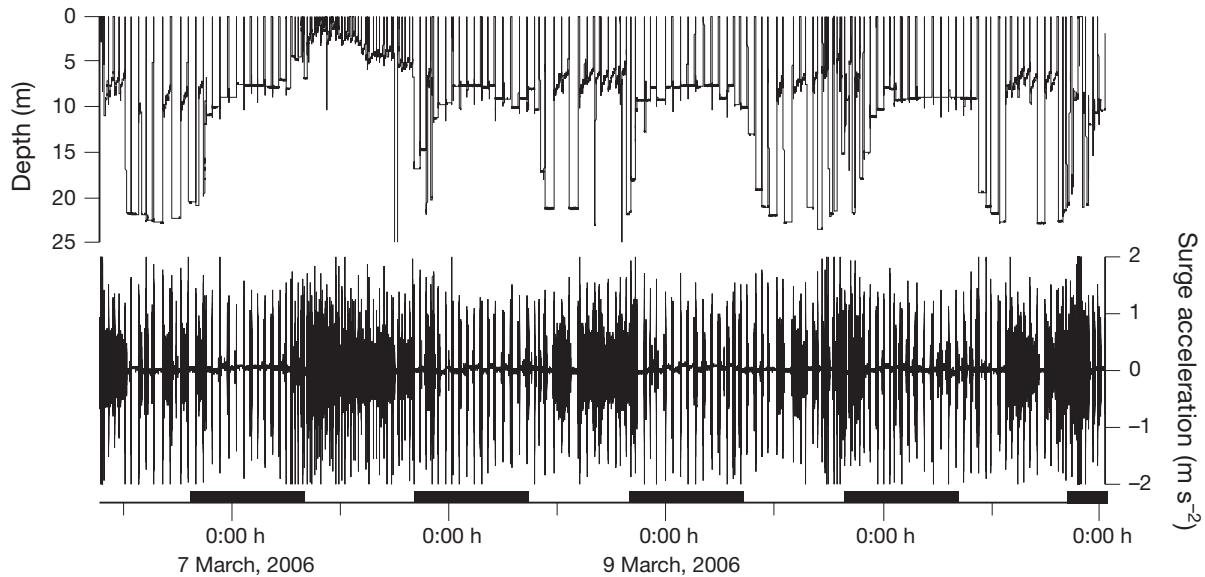

Fig. 1. *Chelonia mydas.* An example (Turtle CM1) of diel alternations in the maximum dive depth and high-frequency component of surging acceleration during the inter-nesting period for female green turtles, nested at Huyong Island, Thailand. Black bars indicate nighttime (19:00 to 06:59 h)

Table 2. *Chelonia mydas.* Results of Student's *t*-test and Wilcoxon test for comparison between day (D; 07:00 to 18:59 h) and night (N; 19:00 to 06:59 h) in the diving parameters

| Turtle	Parameters	Day (mean ± SD)	Night (mean ± SD)	n (D vs. N)	t or χ^2	df	p
CM1	Resident depth (m)	10.36 ± 7.65	9.45 ± 4.75	255 600 vs. 220 226 (point)	47.91	475 824	<0.001
	Dive depth (m)	16.89 ± 5.92	10.43 ± 3.76	40 vs. 53 (dive)	25.215	1	<0.001
	Duration (min)	47.27 ± 8.10	43.30 ± 8.17	40 vs. 53	4.118	1	0.0424
CM2	Resident depth (m)	20.57 ± 9.00	8.15 ± 3.00	256 800 vs. 223 875	623.487	480 673	<0.001
	Depth (m)	22.45 ± 7.23	9.23 ± 2.09	58 vs. 74	88.961	1	<0.001
	Duration (min)	46.16 ± 17.58	32.13 ± 9.31	58 vs. 74	28.112	1	<0.001
CM3	Resident depth (m)	21.43 ± 10.47	19.80 ± 8.13	172 800 vs. 155 986	49.255	328 784	<0.001
	Depth (m)	26.31 ± 7.91	20.49 ± 5.40	35 vs. 30	7.821	1	0.0052
	Duration (min)	58.55 ± 12.01	57.91 ± 13.7	35 vs. 30	0.014	1	0.9057
CM4	Resident depth (m)	11.50 ± 12.26	9.99 ± 8.20	172 800 vs. 180 959	43.075	353 757	<0.001
	Depth (m)	16.43 ± 20.16	13.29 ± 6.62	22 vs. 36	6.33	1	0.0121
	Duration (min)	23.10 ± 10.37	33.57 ± 7.53	22 vs. 36	16.7	1	<0.001
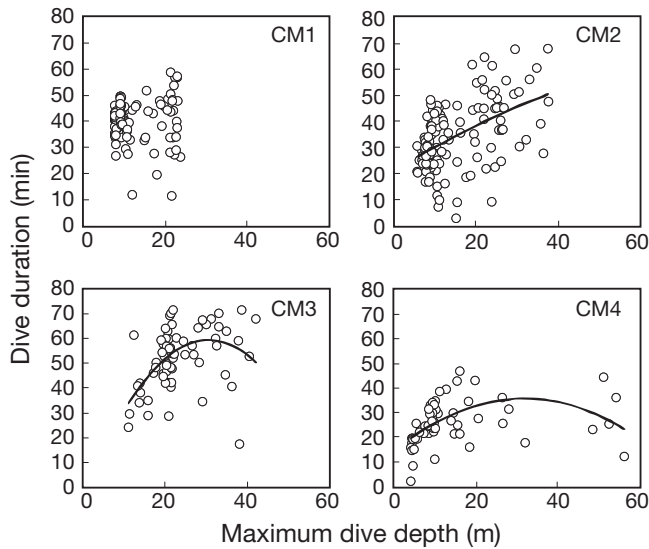
Fig. 2. *Chelonia mydas*. Relationships between maximum dive depth and dive duration during the inter-nesting period for 4 female green turtles nested at Huyong Island, Thailand. Bottom depth is the maximum dive depth of a U-shaped dive. A regression curve is shown in each graph for significant relationships. Statistical analysis is described in Table 3

Behaviour during descent

A distinct alternation in flipper beat frequency, body angle, and swimming speed was observed during a U-shaped dive (Fig. 3). At the initial phase of descent, a high frequency of flipper beating at 0.3 to 0.6 Hz was observed (Fig. 4A). The flipper beat frequency during deep dives was higher than that during shallow dives (Fig. 4), such that the bottom depth of a dive significantly affected the flipper beat frequency (Table 4). There was a significant effect of resident depth on flipper beat frequency (Fig. 4A, Table 4). However, the decline in flipper beat frequency stopped at 0.1 to 0.2 Hz, when turtles reached a depth of 15 to 20 m, and the flipper beat frequency was approximately constant despite changes in depth. The depth at which the frequency of flipper beating significantly decreased (i.e. DFBD) was affected by the bottom depth (Fig. 5), and the relationship between the bottom depth and DFBD could be described by a logistic curve (Table 3).

No vertical body angles of the turtles were observed, but the angles were steepest (approximately $-60°$) at depths of 5 to 10 m (Fig. 4B). Subsequently, the body angles became significantly shallower as turtles descended the water column, although body angles were generally steeper during deeper dives (Table 4, Fig. 4B).

Swimming speeds were highest at the start of the descent (Figs. 3 & 4C), and varied in an alternating fashion in accordance with the flipper beating during

Table 3. *Chelonia mydas*. Results from regression analysis of the dive parameters during the inter-nesting period for green turtles nested at Huyong Island, Thailand. DFBD: instantaneous depth when flipper beat frequency was below the dominant stroke cycle frequency; DBA: sum of the total amount of dynamic body acceleration for the whole of the descent or ascent phase in any single dive; ns: not significant

|	$y =$	r^2	p
CM1 (n = 93, max. depth range = 7.6 to 23.6 m)			
DFBD descent (m) vs. max. dive depth (m)	$-0.2 + 3.4 \ln(x)$	0.51	<0.0001
DFBD ascent (m) vs. max. dive depth (m)	$2.6 + \ln(x)$	0.16	<0.0001
Dive duration (min) vs. max. dive depth (m)	ns	ns	ns
Dive duration (min) vs. mean temp. (°C)	ns	ns	ns
DBA during descent vs. max. dive depth (m)	ns	ns	ns
DBA during descent vs. max. dive depth (m)	$-8.5 + 6.0x$	0.49	<0.0001
CM2 (n = 132, max. depth range = 5.8 to 37.2 m)			
DFBD descent (m) vs. max. dive depth (m)	$-9.4 + 7.6 \ln(x)$	0.77	<0.0001
DFBD ascent (m) vs. max. dive depth (m)	$-7.5 + 5.1 \ln(x)$	0.66	<0.0001
Dive duration (min) vs. max. dive depth (m)	$20.8 + x - 0.005x^2$	0.25	<0.0001
Dive duration (min) vs. mean temp. (°C)	ns	ns	ns
DBA during descent vs. max. dive depth (m)	$42.2 + 3.9x$	0.11	<0.0001
DBA during descent vs. max. dive depth (m)	$14.5 + 2.7x$	0.48	<0.0001
CM3 (n = 65, max. depth range = 11.2 to 42.1 m)			
DFBD descent (m) vs. max. dive depth (m)	$-12.7 + 9.2 \ln(x)$	0.61	<0.0001
DFBD ascent (m) vs. max. dive depth (m)	$-10 + 6.7 \ln(x)$	0.51	<0.0001
Dive duration (min) vs. max. dive depth (m)	$-3.7 + 4.1x - 0.1x^2$	0.23	0.0002
Dive duration (min) vs. mean temp. (°C)	$-2629.9 + 191.9x - 3.4x^2$	0.1	0.0380
DBA during descent vs. max. dive depth (m)	$338.7 - 7.6x$	0.2	0.0003
DBA during descent vs. max. dive depth (m)	$1.6 + 2.6x$	0.57	<0.0001
CM4 (n = 58, max. depth range = 3.8 to 54.2 m)			
DFBD descent (m) vs. max. dive depth (m)	$-6.9 + 6.3 \ln(x)$	0.87	<0.0001
DFBD ascent (m) vs. max. dive depth (m)	$-9.5 + 5.8 \ln(x)$	0.81	<0.0001
Dive duration (min) vs. max. dive depth (m)	$-14.8 + 1.3x - 0.02x^2$	0.23	0.0005
Dive duration (min) mean temp. (°C)	$-983.9 + 75.9x - 1.4x^2$	0.17	0.0057
DBA during descent vs. max. dive depth (m)	$51.8 + 3.6x$	0.27	<0.0001
DBA during descent vs. max. dive depth (m)	$9.5 + 2.8x$	0.79	<0.0001
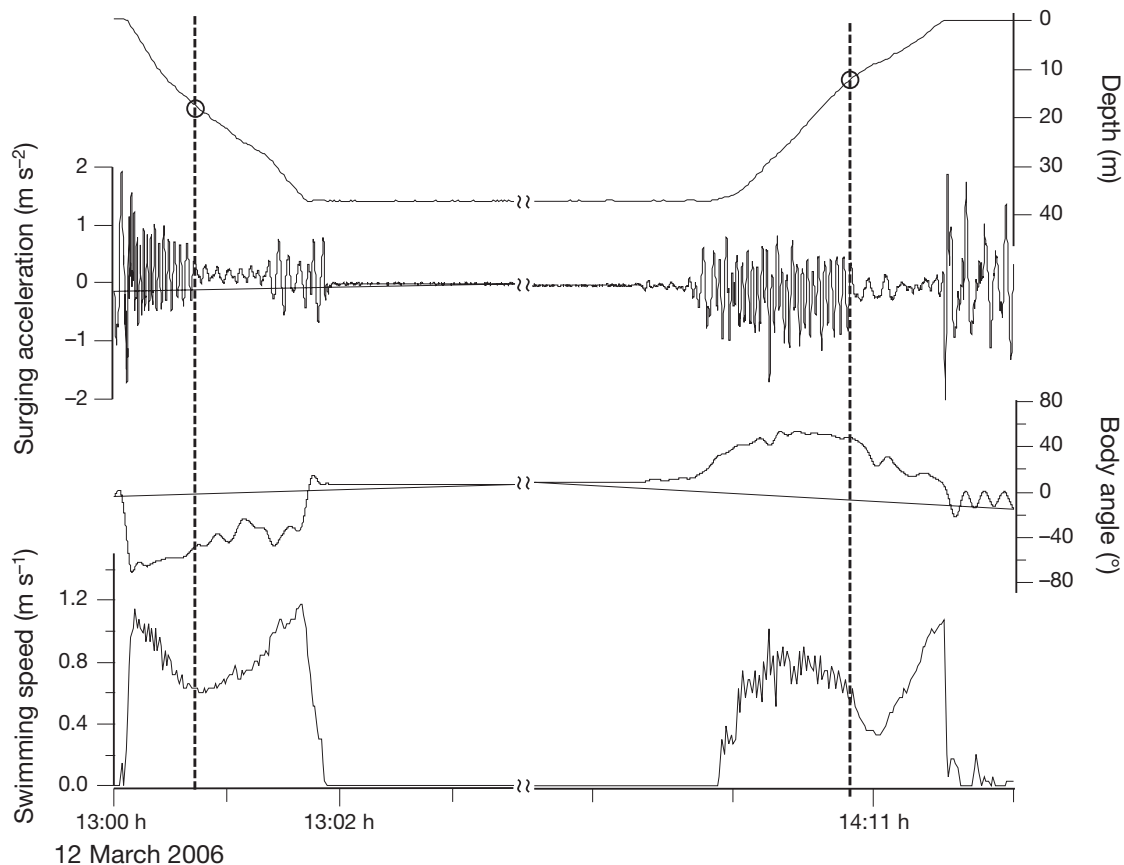
Fig. 3. *Chelonia mydas*. Time-series of depth, high-frequency components of surging acceleration, body angle and swimming speed during a U-shaped dive of a female green turtle (CM2), during the inter-nesting period at Huyong Island, Thailand. ○: Depth where the flipper beat frequency was below the dominant stroke cycle frequency (DFBD); dashed vertical lines: DFBD time. Note that the bottom phase is omitted in this figure, since the diving parameters rarely varied during the bottom phase in the U-shaped dive, when the green turtles typically rested on the seabed

the initial phase (Fig. 3). The swimming speeds and flipper beat frequency decreased as depth increased (Fig. 4C). There was also a significant effect of flipper beat frequency on swimming speed (Fig. 6). When the turtles reached depths of 15 to 20 m, the decline in swimming speeds halted at 0.6 to 0.8 m s^{-1}. However, swimming speeds subsequently increased despite less flipper stroking (Figs. 3 & 4A, C).

Relationships between maximum dive depth and DBA were detected during the descent phase for only 3 individuals, but the correlation coefficients (r^2) were low (Fig. 7, Table 3).

Behaviour during ascent

The pattern of changes in flipper beat frequency, body angle and swimming speed during the ascent was generally similar to that during the descent (Figs. 3 & 4). Thus, there were also significant effects of current and

bottom depth on these parameters (Table 4). However, turtles did not beat their flippers strongly at the end of the ascent, as they did at the end of the descent (Fig. 3). The maximum dive depth also significantly affected DFBD, but this depth was shallower than during the descent (paired *t*-test, p < 0.05; Fig. 5). Maximum dive depth significantly affected DBA during the ascent phase (Fig. 7, Table 3).

Behaviour and temperature in the bottom phase

Dynamic acceleration indicated that turtles rested during the bottom phase in the analysed U-shaped dives (Figs. 1 & 3). Mean ambient water temperature during the bottom phase ranged from 28.23 ± 1.54°C (n = 93 dives) to 29.31 ± 0.69°C (n = 132 dives). Relationships existed between ambient water temperature and dive duration for only 2 individuals, but the correlation coefficients (r^2) were very low (Table 3).
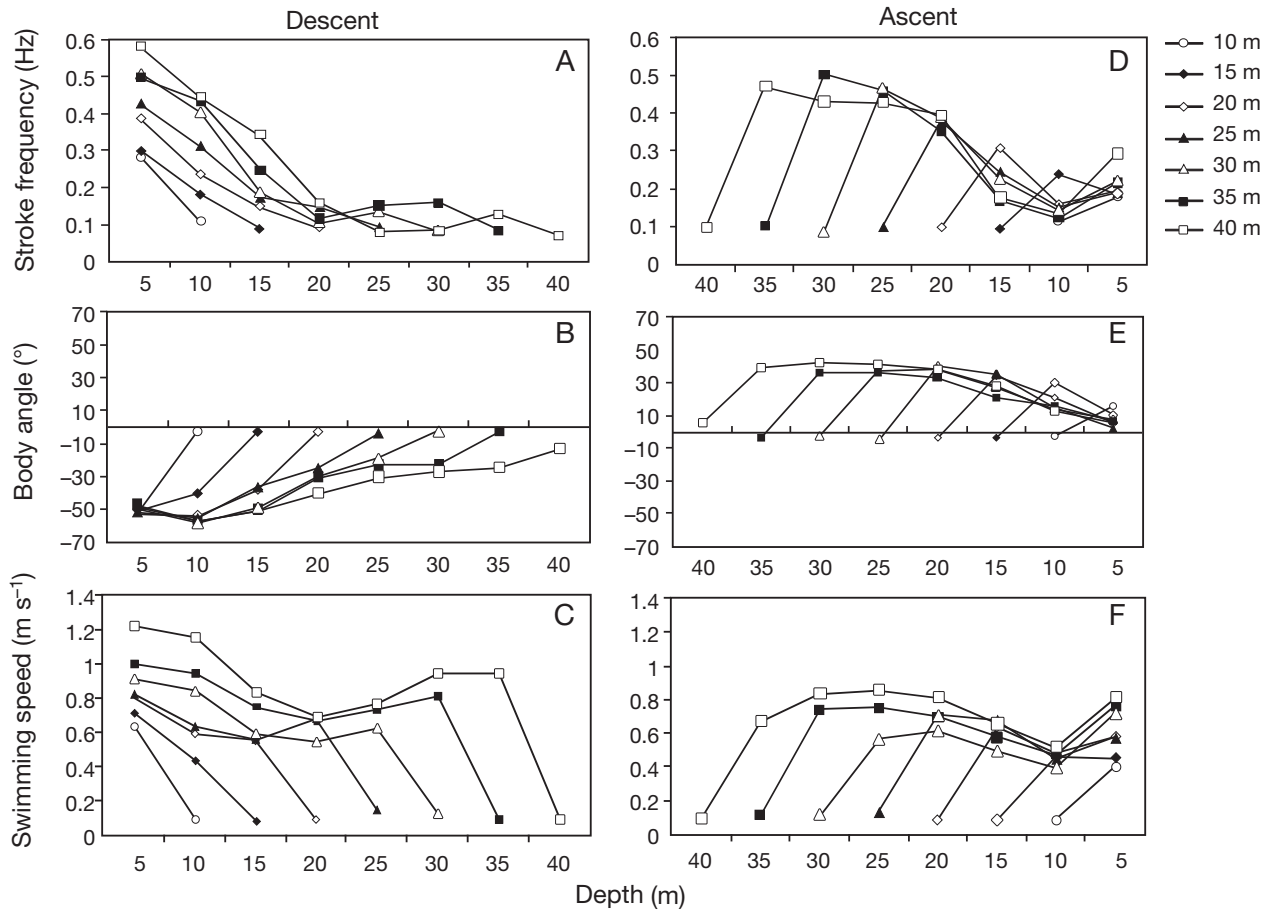
Fig. 4. *Chelonia mydas*. Changes in (A,D) stroke frequency, (B,E) body angle and (C,F) swimming speed with resident depth while descending and ascending. To show the general trends of the parameters, mean values are indicated over depth ranges, e.g. for 0 to 5, 5 to 10 and 10 to 15 m, based on 331 flat-bottom dives of 4 green turtles. Shallow dives (less than 6 m, n = 17) were excluded in the analysis. Data from dives with bottom depths of each depth rank are shown separately. Different symbols indicate different maximum dive depths. Accompanying statistical analysis is shown in Table 4

Table 4. *Chelonia mydas*. Results of generalized linear mixed model (GLMM) with restricted maximum likelihood (REML) analysis performed during the descent and ascent phases

| Phase	Dependent variable	Fixed effect	No. of turtles	No. of dives	No. of records	F	p
Descent	Stroke frequency	Depth	4	331	1208	115.403	<0.0001
		Bottom depth	4	331	1208	66.494	<0.0001
		Depth × Bottom depth	4	331	1208	16.995	<0.0001
	Body angle	Depth	4	331	1208	305.136	<0.0001
		Bottom depth	4	331	1208	225.82	<0.0001
		Depth × Bottom depth	4	331	1208	114.477	<0.0001
	Swimming speed	Depth	2	221	754	124.733	<0.0001
		Bottom depth	2	221	754	223.402	<0.0001
		Depth × Bottom depth	2	221	754	50.666	<0.0001
Ascent	Stroke frequency	Depth	4	331	1208	32.196	<0.0001
		Bottom depth	4	331	1208	42.741	<0.0001
		Depth × Bottom depth	4	331	1208	73.555	<0.0001
	Body angle	Depth	4	331	1208	65.505	<0.0001
		Bottom depth	4	331	1208	35.807	<0.0001
		Depth × Bottom depth	4	331	1208	158.921	<0.0001
	Swimming speed	Depth	2	221	754	446.3	<0.0001
		Bottom depth	2	221	754	4048.683	<0.0001
		Depth × Bottom depth	2	221	754	33.969	<0.0001
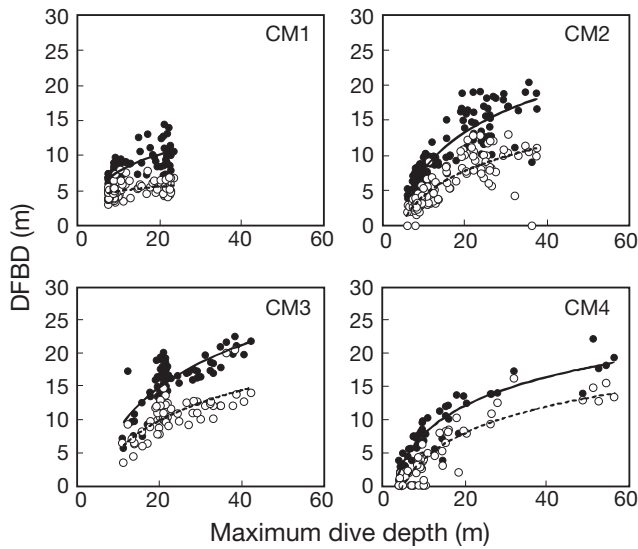
Fig. 5. *Chelonia mydas*. Relationships between maximum dive depth and the depth at which the flipper beat frequency was below the dominant stroke cycle frequency during the inter-nesting period (DFBD) for 4 female green turtles nested in Huyong Island, Thailand. ○: ascent; ●: decent; solid and dashed curves: regression curves for the descent and ascent, respectively. Accompanying statistical analysis is described in Table 3
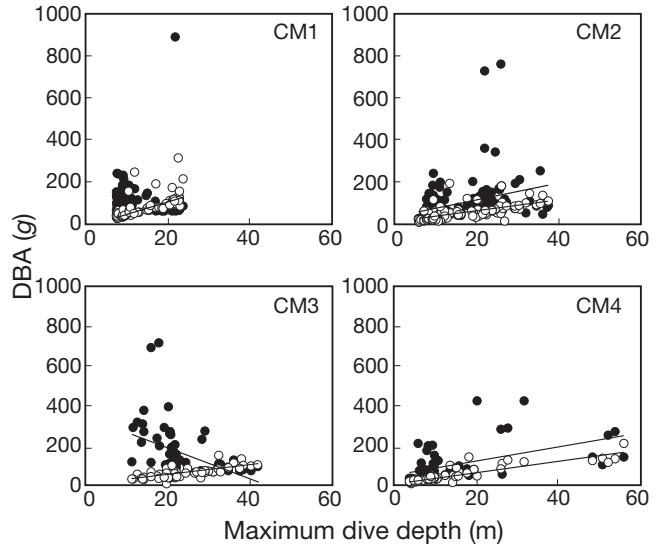

Fig. 7. *Chelonia mydas*. Relationships between maximum dive depth and dynamic body acceleration (DBA) during the descent phase (●) and the ascent phase (○) of U-shaped dives of 4 female green turtles. Solid lines: regression lines. Accompanying statistical analysis is described in Table 3
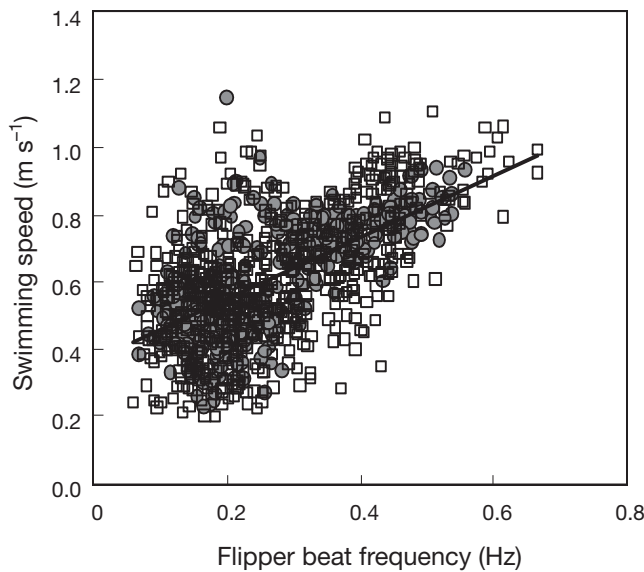

Fig. 6. *Chelonia mydas*. Relationships between flipper beat frequency and swimming speed for U-shaped dives during the inter-nesting period of female green turtles nested in Huyong Island, Thailand. The data on 2 individuals were pooled. Shaded circles and open squares indicate CM1 and CM2, respectively (see Table 1). The regression line was significant; $r^2 = 0.51$, $F_{1,1030} = 609.6812$, p < 0.0001, swimming speed (m s^{-1}) = 0.37 + 0.92 flipper beat frequency (Hz)

DISCUSSION

Effect of resident depth

An apparent, consistent pattern of flipper stroking, body angle and swimming speed in green turtles *Chelonia mydas* was detected with an alternation in the current depth during a dive (Fig. 3). In the initial phases of both descent and ascent, turtles performed active stroke swimming with a steep body angle. Swimming speed occurred in a zigzag pattern during the initial phases in accordance with flipper beating, suggesting that turtles might swim against buoyancy during the initial phases. Subsequently, swimming effort shifted and glide swimming was performed instead of active stroke swimming when turtles reached the DFBD. Despite less active stroking, swimming speed smoothly increased after the DFBD. This passive glide swimming of turtles indicated that residual buoyancy was exhausted and that the buoyancy then aided the swimming of the turtles. The acceleration loggers used in the present study were not attached to the flipper, but instead to the top of the carapace of turtles for simultaneous recording of both body angle and flipper beating. Therefore, the attack angle of the flippers, which may cause a reduction in thrust (e.g. Watanuki et al. 2003), was not considered in the present study and merits further examination. Regardless of the flipper angle, it was clear that the

stroke frequency of turtles declines in parallel with changes in buoyancy with depth, similar to those of other diving animals (Williams et al. 2000, Watanuki et al. 2005, Hays et al. 2007).

Evaluation of DFBD

The maximum depth at which neutral buoyancy is attained (MDNB) is related to individual body size and weight (Minamikawa et al. 2000). Recently, Hays et al. (2004b) calculated the MDNB for green turtles at Ascension Island with approximately 120 cm CCL to be approximately 17 m. In the present study, asymptotic DFBD was typically 20 m for descent and 12 m for ascent (Fig. 5). If turtles change stroke frequency based on the buoyancy at the current depth, then the DFBD during descent would be deeper than the true depth at which neutral buoyancy is attained, and vice versa. Therefore, the MDNB for the green turtles investigated is considered as the depth between 12 and 20 m. The DFBD of the turtles studied was similar to the MDNB for green turtles at Ascension Island (Hays et al. 2004b) and may serve as an index for the depth at which turtles nearly attain neutral buoyancy.

Effect of maximum dive depth

In the present study, turtles rested on the seabed within a wide range of depths, although there seemed to be a preference in resting depth for each turtle (Table 1, Fig. 2). Maximum dive depth was found to significantly affect the swimming effort of turtles, since these organisms exerted greater effort during deeper dives (Fig. 4). These results imply that larger pre-submergence inspiration during deeper dives results in high positive or negative buoyancy and active stroking in both the descent and ascent phases (Fig. 7). However, we could not find a clear positive relationship between the maximum dive depth and DBA during the descent of some turtles (Fig. 7). The reason for this result is unknown. By observing the time-series data, we speculate that they swam at a depth near the seabed, implying that they were searching for a resting point. In contrast, the turtles went directly to the surface for breathing, and a clear relationship was found between maximum dive depth and DBA during the ascent phase. These results must be addressed by further experimental study (e.g. Wilson et al. 2006, Halsey et al. 2008, Green et al. 2009) of sea turtles.

The dive duration of green *Chelonia mydas* and loggerhead *Caretta caretta* turtles is a result of the depth obtained during the bottom phase, which may be regulated by the amount of oxygen stored in the lungs as well as by the metabolic rate (Minamikawa et al. 2000, Hochscheid et al. 2003, Hays et al. 2004b), if resting depth is not a result of active habitat selection as a consequence of lung volume, e.g. geographic condition regulates the depth selection of turtles (Seminoff et al. 2006). Therefore, our data agree with previous studies indicating that an increase in metabolic rate during the descent and ascent of deeper dives can potentially result in shorter dive durations (Figs. 2 & 7) and suggest that selection of resting depth, in accordance with pre-submergence inspiration, plays an important role in the conservation of energy for reproduction.

Body angle and swimming speed

The body angles of turtles were steepest at the start of the descent and were related to maximum dive depth. This supports the hypothesis that turtles should initially descend at a steep angle in order to travel through the zone of highest buoyancy as efficiently as possible. However, unlike diving birds (e.g. Watanuki et al. 2005), turtles were not vertical (less than –60°), even at the start of descent, as previously shown by Glen et al. (2001). The reason for these results is uncertain. However, shallow body angle during descent is consistent with findings for other diving animals (Le Boeuf et al. 1992, Chappell et al. 1993, Sato et al. 2003). One possibility is that body angle is restricted by the shape of the slope around the nesting site (Sato et al. 2003) or that a shallow angle allows the animals to scan for suitable foraging or resting areas (Glen et al. 2001). Body angles might be restricted due to morphological traits, since the body of hard-shelled green turtles is clearly flat and not fusiform in shape like diving animals.

There are few data available regarding direct measurements of swimming speed for adult sea turtles. Therefore, the swimming speeds of turtles were previously estimated on the basis of the results of a tagging–recapture and satellite-tracking study (see the summary by Wyneken 1997). Recently, data loggers have emerged as tools to measure aquatic animal locomotion, including swimming speed. For loggerhead turtles, which may rest mid-water and on the seabed during the inter-nesting period (Minamikawa et al. 1997, 2000), the mean swimming speed during the initial descent of mid-water resting dives is 0.27 to 0.60 SCL s^{-1} (SCL: standard carapace length in meters, n = 6 individuals; Minamikawa et al. 2000). For leatherback turtles *Dermochelys coriacea*, which may swim continuously and forage or attempt foraging during the inter-nesting period (Eckert et al. 1989, Eckert 2002, Myers & Hays 2006, Fossette et al. 2008), modal speeds are 0.33 to 0.51 CCL s^{-1}, with a maximum speed range

of 1.19 to 1.65 CCL s^{-1} (n = 5 individuals; Eckert 2002). In our initial investigation of female green turtles, which mainly rest on the seabed, the swimming speed obtained for the estimated dominant stroke frequency (i.e. 0.18 to 0.21 Hz) was 0.52 to 0.60 CCL s^{-1} (n = 4 individuals). We may need to interpret this result with caution, as carapace length may not be a good indicator of sea turtle swimming speed capacity. Nonetheless, this result suggests that sea turtles may have a distinct speed preference, which is related to organism size, even if habitat utilization differs amongst species or populations.

Effect of ambient water temperature on dive duration

While the green turtle is endothermic, it is capable of raising its body temperature through swimming activity, maintaining a body temperature slightly higher than water temperature while swimming and resting (Spotila et al. 1997). In the present study, there was no measurable importance of the effect of mean water temperature during the bottom phase of the dive (Table 3). Nesting colonies of green turtles generally occur in the tropics (Pritchard 1997). Therefore, the thermal range during dives may be narrow, since female green turtles are shallow divers during the inter-nesting period (Hochscheid et al. 1999, Hays et al. 2000). In contrast, over a wide range of temperatures, dive duration has been shown to vary robustly with water temperature in loggerhead turtles with, for example, dive durations of >6 h during the cold midwinter temperatures encountered at high latitudes (Hochscheid et al. 2005).

Diel changes at resting depth

The present study indicates that depth selection during a dive affects the performance of resting (Figs. 2 & 4). Previous studies suggested that green and loggerhead turtles seem to select resting depth within a range in which the lungs can be utilized to achieve close to neutral buoyancy (Minamikawa et al. 2000, Hays et al. 2004b). Since the range of asymptotic DFBDs was about 12 to 20 m in the present study (Fig. 5), turtles resting at this depth range do so efficiently. In the present study, mean resting depths ranged from 9.23 ± 2.09 to 13.29 ± 6.62 m for night dives and from 16.43 ± 20.16 to 26.31 ± 7.91 m for daytime dives (Table 2). Therefore, the gravid female turtles investigated in our study seemed to be resting around the depth near the range of asymptotic DFBDs, and deep dives that exceeded the upper threshold of

the depth range were rare. However, there was an apparent alternation in dive depth between daytime and nighttime, as daytime dives and resident depth were deeper than those observed during the night (Fig. 1, Table 1).

A previous satellite-tracking study and home range analysis suggested that horizontal utilization by female green turtles was within a 7 km buffer area around Huyong Island (Yasuda 2007). The diel alternation in the observed resting depth might indicate a reproductive strategy for females. One possibility is a beneficial change in vertical space to obtain refuge from energy-consuming encounters with males (Lee & Hays 2004, Schofield et al. 2006) or predators (e.g. large sharks; Fergusson et al. 2000, Hays et al. 2001). In fact, females commonly suffer from the superfluous mating and copulation that arises from male coercion in nature (Lee & Hays 2004). These behaviours are likely to be observed in daytime (Booth & Peters 1972, Schofield et al. 2006). In addition, Hays et al. (1991, 1999) found that there was a systematic change in diel patterns in diving behaviour between the start and end of an interval, suggesting that turtles may not be simply employing an energy conservation strategy. Recording of the behaviour during the overall inter-nesting interval and an intensive analysis, including other diving patterns, are needed to achieve a better understanding of female reproductive strategies.

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