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Dive and beak movement patterns in leatherback turtles *Dermochelys coriacea* during internesting intervals in French Guiana

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Summary

1. Investigating the foraging patterns of free-ranging species is essential to estimate energy/time budgets for assessing their real reproductive strategy. Leatherback turtles *Dermochelys coriacea* (Vandelli 1761), commonly considered as capital breeders, have been reported recently to prospect actively during the breeding season in French Guiana, Atlantic Ocean. In this study we investigate the possibility of this active behaviour being associated with foraging, by studying concurrently diving and beak movement patterns in gravid females equipped with IMASEN (Inter-MAndibular Angle SENsor).

2. Four turtles provided data for periods varying from 7·3 to 56·1 h while exhibiting continuous short and shallow benthic dives. Beak movement ('b-m') events occurred in 34% of the dives, on average 1·8 ± 1·4 times per dive. These b-m events lasted between 1·5 and 20 s and occurred as isolated or grouped (two to five consecutive beak movements) events in 96·0 ± 4·0% of the recorded cases, and to a lesser extent in series (> five consecutive beak movements).

3. Most b-m events occurred during wiggles at the bottom of U- and W-shaped dives and at the beginning and end of the bottom phase of the dives. W-shaped dives were associated most frequently with beak movements (65% of such dives) and in particular with grouped beak movements.

4. Previous studies proposed wiggles to be indicator of predatory activity, U- and W-shaped dives being putative foraging dives. Beak movements recorded in leatherbacks during the first hours of their internesting interval in French Guiana may be related to feeding attempts.

5. In French Guiana, leatherbacks show different mouth-opening patterns for different dive patterns, suggesting that they forage opportunistically on occasional prey, with up to 17% of the dives appearing to be successful feeding dives.

6. This study highlights the contrasted strategies adopted by gravid leatherbacks nesting on the Pacific coasts of Costa Rica, in the deep-water Caribbean Sea and in the French Guianan shallow continental shelf, and may be related to different local prey accessibility among sites. Our results may help to explain recently reported site-specific individual body size and population dynamics.

Key-words: alternative reproductive strategy, Atlantic Ocean, foraging, hall sensor, sea turtle

Introduction

The resources (water, nutrients, energy) acquired by organisms in the wild are limited and cannot be allocated simultaneously to survival, growth and reproduction (Stearns 1992). Organisms are thus predicted to adopt strategies for facing trade-offs between these competing life-history traits (Stearns 1992). For instance, organisms compensate for the high energy demands of reproduction by increasing the amount of total food resources available through two main strategies: schematically, capital breeders store body reserves prior to reproduction and rely exclusively on them during breeding; conversely, income breeders show limited storage capacities and adjust their food intake during reproduction (Jönsson 1997). However, in some cases where body reserves do not fulfil reproductive

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requirements, certain organisms considered commonly as capital breeders may refuel by feeding during the breeding season. Several examples of this intermediate strategy have been reported in birds (Durant, Massemin & Handrich 2004), ungulates (Byers & Moodie 1990), pinnipeds (Boness, Bowen & Oftedal 1994) and sea turtles (Hays *et al*. 2002; Myers & Hays 2006).

Assessing real reproductive strategy by investigating the foraging patterns during and outside the breeding season is essential for the reliable estimation of energy and time budgets in order to establish ultimately how organisms ensure their reproduction and their own survival optimally (e.g. Boyd, Lunn & Barton 1991; Challet *et al*. 1994; Hochscheid *et al*. 1999; Georges & Guinet 2000). This has obvious consequences in terms of conservation in the case of species that feed on sites overlapping with human activities (e.g. Delord *et al*. 2005; Fossette *et al*. 2007b). Accordingly, there has been a general impetus to investigate in much greater detail the foraging behaviour of free-ranging species during their life cycle. In the case of marine species, where foraging occurs mainly underwater during dives, investigating foraging behaviour (i.e. diving pattern and actual feeding activity) is particularly difficult due to the limited accessibility of marine environments (Kooyman *et al*. 1992). Consequently, foraging behaviour in marine vertebrates has been explored in different ways based on two-dimensional time–depth dive profiles and three-dimensional compass (e.g. Schreer & Testa 1996; Le Boeuf *et al*. 2000; Mitani *et al*. 2003), echolocation buzzes in sperm whales *Physeter macrocephallus* (e.g. Miller *et al*. 2004; Watwood *et al*. 2006), stomach/oesophageal/gastrointestinal temperature (e.g. Ancel, Horning & Kooyman 1997; Southwood *et al*. 2005) or underwater video (e.g. Reina *et al*. 2005; Watanabe *et al*. 2006). One of the most recent techniques is the recording of dive depth in conjunction with beak-opening events (e.g. Wilson *et al*. 2002; Wilson *et al*. 2003; Hochscheid *et al*. 2004; Myers & Hays 2006; Liebsch *et al*. 2007). This latest approach uses a magnet/Hall sensor combination connected to a data-logger that records changes in the inter-mandible angle with a high frequency [Inter-MAndibular Angle SENsor (IMASEN), see Wilson *et al*. 2002].

IMASENs have been proved to be a reliable system to investigate fine-scale ingestion and/or respiratory patterns in relation to diving behaviour. Given the relative difficulty of IMASEN deployment, this technique has been used mainly in captive animals (e.g. Ropert-Coudert *et al*. 2002, 2004; Wilson *et al*. 2002, 2003; Hochscheid *et al*. 2004; Liebsch *et al*. 2007). Data on free-living individuals concern only four different species of marine animals: *Leptonychotes weddellii* (the Weddell seal, $n = 7$ individuals, Plötz *et al*. 2001; Liebsch *et al*. 2007), *Spheniscus magellanicus* (the Magellanic penguin, $n = 19$ individuals, Wilson *et al*. 2002, 2003; Simeone & Wilson 2003), *Pygoscelis antarctica* (the Chinstrap penguin, $n = 1$ individual, Takahashi *et al*. 2004) and *Dermochelys coriacea* (the leatherback turtle, $n = 1$ individual, Myers & Hays 2006).

In sea turtles, reproduction consists of successive ovipositions on land separated by internesting intervals of a few days, during which turtles remain at sea for egg maturation. Sea turtles are considered commonly to be capital breeders, i.e. they ensure reproduction by relying on body reserves stored prior to reproduction during migration (Miller 1997). However, previous studies suggest that leatherbacks nesting in the Atlantic Ocean may forage during the nesting season (Eckert *et al*. 1989; Hays *et al*. 2004; Fossette *et al*. 2007b; Georges *et al*. 2007). This suggestion has been supported by Myers & Hays (2006), who reported some rhythmic beak movements in a single leatherback equipped with an IMASEN during the nesting season on Grenada Island (Atlantic Ocean). These rhythmic beak movements occurred as the animal was descending to depth and have been interpreted as potential attempts to detect prey by relying on gustatory cues to sense the surrounding waters (Myers & Hays 2006). Such putative foraging behaviour in Atlantic leatherbacks may help to compensate for particularly high reproductive costs. However, in the Pacific Ocean leatherbacks nesting in Costa Rica appear to compensate for high reproductive costs (Wallace *et al*. 2007) by reducing their activity (Reina *et al*. 2005) and their metabolic rate (Wallace *et al*. 2005) during internesting intervals. These two different strategies may be linked with different reproductive outputs, i.e. fewer nests and fewer eggs in Pacific populations (Wallace *et al*. 2006) and/or with different oceanographic conditions and local food availability (Hays *et al*. 2002; Saba *et al*. 2007).

The Atlantic Ocean hosts the world's two largest leatherback nesting populations, found within the large estuary of the Maroni river at the border between French Guiana and Suriname (South America) and on the coasts of Gabon (western Africa, review in Fossette *et al*. in press). In the Guianas region, the leatherback's nesting season coincides with the peak of Amazonian influence where rich and turbid water masses cross off the continental shelf, enhancing biological production (Froidefond *et al*. 2002; Baklouti *et al*. 2007; S. Fossette, T. Bastian, F. Blanchard, C. Girard, Y. Le Maho, P. Vendeville & J.-Y. Georges, unpublished data). This is illustrated by massive stranding of jellyfish on the leatherback rookery of Awala-Yalimapo beach (French Guiana) and by the presence of large amounts of gelatinous plankton near the seabed in shallow waters during the leatherback nesting season (S. Fossette, T. Bastian, F. Blanchard, C. Girard, Y. Le Maho, P. Vendeville & J.-Y. Georges, unpublished data). As leatherbacks feed primarily on jellyfish (James & Herman 2001), this suggests favourable local trophic conditions for gravid females feeding during the nesting season in French Guiana. Consistently, leatherbacks have been reported to disperse widely across the Guiana continental shelf (Georges *et al*. 2007) and to dive continuously day and night, concentrating mainly on the area close to the seabed where they perform numerous vertical excursions of several metres of amplitude at the bottom of the dives (hereafter called 'wiggles'; Fossette *et al*. 2007b). Wiggles are interpreted commonly as prospecting and foraging behaviour (e.g. Schreer, Kovacs & O'Hara Hines 2001; Simeone & Wilson 2003), so it has been suggested that leatherbacks may attempt to feed on the Guiana continental shelf (Fossette *et al*. 2007b). This hypothesis is supported further by the fact that leatherbacks

nesting in French Guiana are larger and heavier compared to those present on other nesting sites, suggesting either that they forage during the nesting season and/or that there is a site-specific growth strategy in this species (Georges & Fossette 2006). However, there is no direct evidence to date of leatherbacks actually feeding in French Guiana.

Here, we test the hypothesis that in French Guiana gravid leatherbacks do forage during the nesting season by jointly investigating the fine-scale diving and beak movement patterns. We predict that if leatherbacks in French Guiana attempt to forage during the nesting season, mouth-openings should occur at least during the descent phase of dives for detecting prey (as reported by Myers & Hays 2006), but also during wiggles performed at the bottom of benthic dives (as suggested by Fossette *et al.* 2007b).

Materials and methods

Fieldwork was conducted during the leatherback's nesting season in May–June 2006 at Awala-Yalimapo beach (5·7° N–53·9° W), French Guiana, South America.

INSTRUMENT DEPLOYMENT

Twelve turtles were selected opportunistically during our night patrolling on the beach and equipped with an IMASEN (Terralog, JUV Elektronic; Borstel, Germany). The IMASEN consisted of a three-channel data logger (70 × 50 × 20 mm, 55 g in air, data resolution: 16 bit, memory size: 128 Mbit), sampling at the same frequency (8 Hz for six turtles and 4 Hz for six other turtles) depth (range: 0–200 m) and strength of the magnetic field from which jaw movements can be extrapolated. The logger was cast in resin and powered by a lithium 3·6-V battery (Sonnenschein Lithium GmbH, Büdingen Germany). Theoretically, these sampling protocols allow 92 and 184 h of recording for 8 and 4 Hz sampling frequency, respectively, the total amount of data stored being limited by instrument memory capacity rather than by the battery.

The devices were attached at night during oviposition which took approximately 10 min. The logger was fixed on the pseudo-carapace using 4·5 mm wide plastic nylon ties introduced in 6 mm diameter holes drilled in a lateral dorsal ridge (similar to Fossette *et al.* 2007a). The logger was connected with a 1 m cable to a Hall sensor (15 × 5 × 3 mm), highly sensitive to magnetic field, set in epoxy and glued onto the upper jaw directly onto the skin (see Myers & Hays 2006). A small, rare earth magnet (10 × 10 × 2 mm) also set in epoxy was glued onto the lower jaw face to the Hall sensor, directly onto the skin using cyanoacrylite glue (see Myers & Hays 2006). Dimensions of the Hall sensor and the magnet set in epoxy were approximately 30 × 15 × 3 mm, necessitating a minimum distance of 2·5 cm between sensor and magnet locations.

IMASENs are based on the Hall effect, where an increase in the distance between the Hall sensor and the magnet (as the beak opened) results in a decrease in the magnetic field strength, recorded by the logger as a drop in voltage. The Hall sensor output can thus be related theoretically to the intermandible distance by calibrating the logger before deployment once fixed on the turtle. For each logger, an exponential relationship was obtained between the magnetic field strength and the intermandible distance, with differences noted among loggers due to different sensitivity and position of the sensor relative to the magnet. However, for all loggers, the magnetic field strength did not vary for intermandible distances larger than 3·5 cm. According to the narrow reading window (2·5–3·5 cm), most (> 95%) of the recorded data could not be used for quantitatively estimating mouth-opening amplitude. In addition, the baseline of the Hall signal was affected highly by pressure and changed parallel to the diving profile (Fig. 1). Simple mathematical high-pass filtering (butter-high and filtfilt functions in MATLAB version 6, > 6 s) was used to smooth the voltage baseline (Fig. 1). However, due to the above-mentioned patterns, we did not investigate the amplitude change patterns of the Hall signal. Consequently, this study is based on the pattern of beak-opening event occurrence.

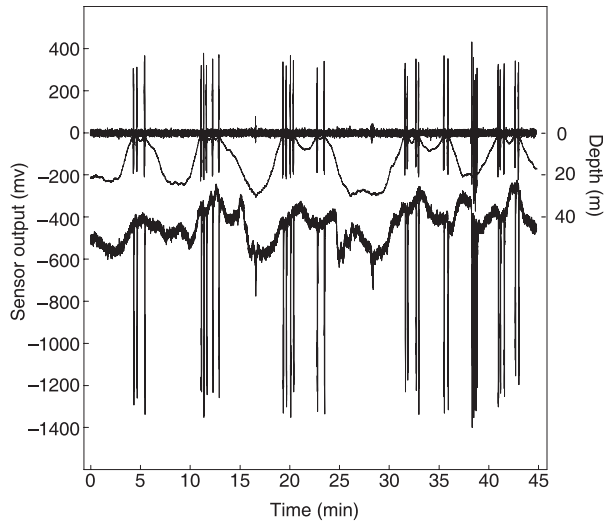


Fig. 1. Example of a record of pressure and Hall signal obtained in a leatherback turtle concurrently equipped with a time depth recorder and an Inter-MAndibular Angle SENsor (IMASEN) during one internesting interval in French Guiana in 2006. Note that the raw Hall signal (bottom) was highly affected by pressure (middle), which implied to filter Hall data (top). Consequently, beak movement patterns were investigated in terms of occurrence rather than quantitatively (see Methods).

DATA ANALYSIS

IMASENs data were analysed using MT Dive software (Jensen Software Systems 2006, Laboe, Germany). Individual dives were defined as any depth exceeding 3 m. For each dive, the program calculated the start and end time, the maximum depth reached during the dive, dive duration, the post-dive surface interval, time spent at the bottom of the dive, the number of wiggles and the number of dive steps. The bottom phase was defined as the period during which (a) depth was greater than 70% of maximum depth of a given dive and (b) the vertical speed was less than 0·3 ms^{-1}. Wiggles were defined for any event involving a rapid opposite change in depth > 1·2 m (equivalent to *c.* twice the maximum ventro-dorsal height of a leatherback turtle; Georges & Fossette 2006) during the bottom phase of the dive. 'Dive steps' were defined as any events where vertical rate was less than 0·3 ms^{-1} during the descent or ascent phase of the dive (Hochscheid *et al.* 1999). Dives were then classified into three types according to their profiles (see Fossette *et al.* 2007b) – 'V-type' and 'U-type' dives – where bottom phase duration was < 30% and > 30% of dive duration, respectively, and 'W-type' (U-type dive showing at least one wiggle with an amplitude of 40% of the maximum wiggle amplitude recorded for a given turtle).

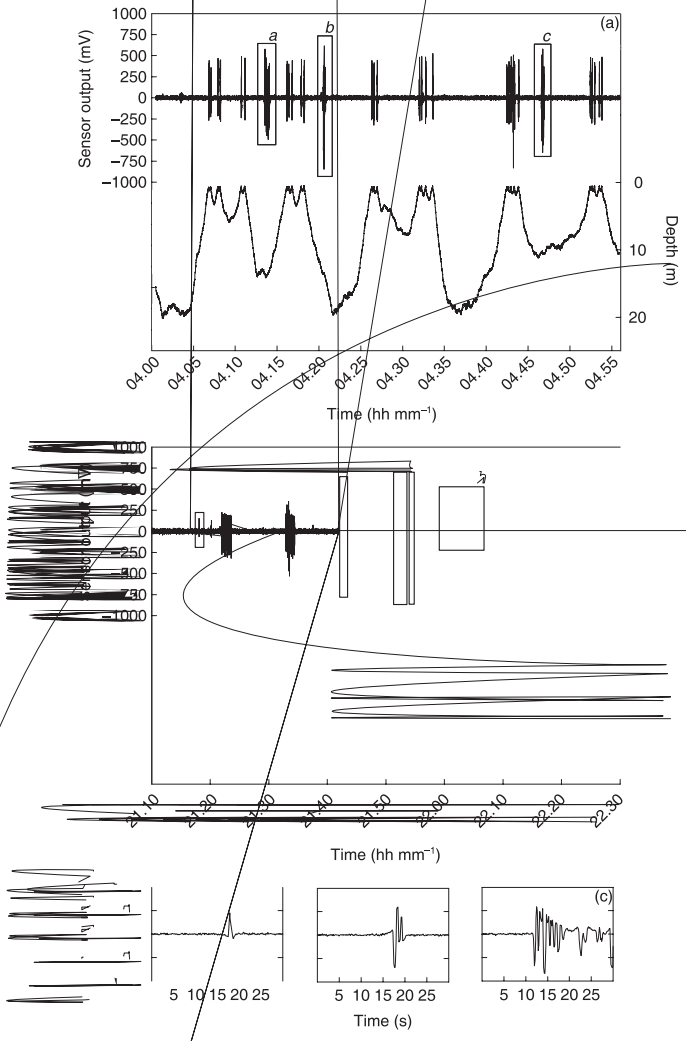


Fig. 2. Example of Hall signals and dive profiles for two leatherbacks during their internesting interval in French Guiana in 2006; (a) turtle no. 1; (b) turtle no. 2. Note that most beak movement events occurred at the surface (breath) but beak movement events eventually occurred underwater either as isolated events (*d*, *h*), grouped events (*b*, *c*) or in series (*a*, *f*) during either the descent, bottom or ascent phase of the dives. (c) Enlarged profiles of isolated, grouped and series of beak movements (from left to right).

Filtered IMASEN sensor output was used to detect beak movements (Figs 1 and 2). A preliminary visual inspection of the filtered Hall and diving data permitted the distinction of beak movements occurring at the surface from those occurring during dives. Their similar shape and amplitude indicated that underwater beak movement events recorded in this study were actual biological events rather than artefacts. For each dive, we then identified beak movements visually, defined as any drop in voltage with at least twice the amplitude of the background noise. For each dive, we recorded manually the number of beak movement events, the dive phase (descent, bottom or ascent phase) during which they occurred, and also noted if they were associated or not with either wiggles or dive steps.

Statistical analyses were carried out using Minitab® statistical software. Values in percentage were arcsin-transformed. Values are given as means ± standard deviation (SD).

Results

Among the 12 turtles equipped with IMASEN, nine individuals returned to the nesting beach. All had lost their magnet and/or Hall sensor and two had also lost their logger. Of the seven returned loggers, three had no recorded data. Consequently, only four turtles provided data for recorded periods varying from 7·3 h (no. 4) to 56·1 h (no. 2) (Table 1).

OVERALL DIVING BEHAVIOUR

The 1009 dives recorded from the four turtles were shallow (11·8 ± 6·3 m) and short (6·6 ± 2·6 min, Table 1), with 50% and 75% of overall dives shallower than 10·7 m and 16·7 m and shorter than 6·2 min and 8·2 min, respectively (Fig. 3). Within a dive, the time spent at the bottom lasted on average 2·6 ± 2·1 min (i.e. 38·9 ± 23·2% of the total dive duration). Wiggles occurred in 65·3% of the dives, with a mean of 2·4 ± 1·0 wiggles per dive. The mean hourly diving effort was 46·0 ± 12·1 min spent diving per hour.

V-, U- and W-shaped dives represented 37·7 ± 15·4%, 54·3 ± 17·3%, and 8·0 ± 4·0% of overall dives, respectively (mean ± SD of the four turtles, Table 2). U-shaped dives were shallower than V- and W-shaped dives (Table 2). W-shaped dives were longer than U- and V-shaped dives (Table 2) due to their longer bottom time.

DIVES ASSOCIATED WITH BEAK MOVEMENT EVENTS

Among the 1009 recorded dives, 342 dives were associated with at least one beak movement event (i.e. 32·7 ± 5·0%, range: 26·2–36·8%, Fig. 2). Those dives associated with beak movements (hereafter called 'b-m' dives) were mainly shallow (14·0 ± 6·6 m) and short (7·5 ± 2·8 min), but were also deeper (*t*-test, $t_{342,667} = 7{\cdot}88$, $P < 0{\cdot}001$) and longer ($t_{342,667} = 7{\cdot}77$, $P < 0{\cdot}001$) than the remaining 667 non-b-m dives (dive depth: 10·7 ± 5·9 m; dive duration: 6·1 ± 2·4 min, Fig. 3). Among the 342 b-m dives, 50% and 75% were shallower than 13·4 and 19·4 m, and shorter than 7·4 min and 9·5 min, respectively (Fig. 3). The turtles performed between 2·3 and 2·6 b-m dives per hour (Table 1). The b-m dives were isolated throughout time rather than distributed in successive bouts (*sensu* Gentry & Kooyman 1986).

The proportion of b-m dives among overall dives increased significantly with dive depth and dive duration when either considering each turtle individually (Spearman's rank correlation, $P < 0{\cdot}05$ in all cases) or when considering all turtles together (Spearman's rank correlation for the grand mean of dive depth: $R^S = 0{\cdot}913$, $n = 4$ turtles, $P = 0{\cdot}011$, Fig. 4a, grand mean of dive duration: $R^S = 0{\cdot}866$, $n = 4$ turtles, $P < 0{\cdot}001$, Fig. 4b).

Regarding dive shapes, b-m dives were mainly U-shaped and V-shaped (44·7 ± 13·9% and 42·2 ± 10·9%, respectively, for the four turtles). W-shaped dives represented only 13·1 ± 3·8% of the b-m dives. However, among all W-shaped dives, 64·7 ± 25·4% were associated with beak movements (i.e. 4·6% of the 1009 recorded dives) compared to 27·8 ± 8·3% of all

Table 1. Summary of diving and beak movement (b-m) occurrence in four leatherback turtles during one internesting interval in French Guiana in 2006. Values are expressed as mean ± standard deviation (SD)

Turtles ID no.	1	2	3	4	All turtles mean ± SD
Departure time	23/05/2006 02 : 30	7/06/2006 23 : 26	9/06/2006 05 : 28	26/06/2006 22 : 50	
Recorded period (h)	35·3	56·1	46·3	7·3	
Total no. of dives recorded	253	407	288	61	1009
Mean dive depth (m)	16·2 ± 6·2	8·8 ± 3·9	13·7 ± 6·3	4·8 ± 1·7	11·8 ± 6·3
Mean dive duration (min)	6·3 ± 2·5	6·1 ± 2·2	8·1 ± 2·8	4·3 ± 1·7	6·6 ± 2·6
Mean hourly diving effort (min/h)	44·1 ± 11·1	47·2 ± 10·2	50·5 ± 6·6	37·4 ± 16·2	46·0 ± 12·1
Total no. of b-m dives	92	128	106	16	342
Mean no. of b-m dives/h	2·6 ± 1·9	2·3 ± 1·8	2·3 ± 1·5	2·3 ± 1·5	2·4 ± 1·7
Mean depth of b-m dives (m)	18·1 ± 6·3	10·4 ± 3·7	16·2 ± 6·4	4·9 ± 1·9	14·0 ± 6·6
Mean duration of b-m dives (min)	6·9 ± 2·9	7·3 ± 2·5	8·8 ± 2·7	4·4 ± 2·0	7·5 ± 2·8
Total no. of b-m events	124	232	229	20	605
Mean no. of b-m events per b-m dives	1·4 ± 0·7	1·8 ± 1·4	2·2 ± 1·9	1·3 ± 0·4	1·8 ± 1·4
% of isolated b-m events	69·4	41·4	49·3	60·0	55·0 ± 12·2
% of groups of b-m events	29·0	50·9	44·1	40·0	41·0 ± 9·1
% of series of b-m events	1·6	7·7	6·6	0	4·0 ± 3·8

Table 2. Summary of dive parameters and beak movement (b-m) occurrence in relation to dive shape (U, V and W) in four leatherback turtles during one internesting interval in French Guiana in 2006. Differences in means and proportions were tested statistically using ^{2}, analysis of variance (ANOVA) followed by a *post-hoc* Tukey test or Kruskal–Wallis test followed by a *post-hoc* Bonferroni test. Different letters (a, b) indicate significant ($P < 0·05$) differences among groups. Values are expressed as mean ± standard deviation

Dive type	All dives	U-shaped	V-shaped	W-shaped	Test, *P*-value
No.	1009	475	444	90	–
Frequency (%)	–	54·3 ± 17·3	37·7 ± 15·4	8·0 ± 4·0	^{2}, $^2_2$ = 180·8, $P < 0·001$
Dive depth (m)	11·8 ± 6·3	11·1 ± 6·6^a	12·5 ± 5·9^b	13·1 ± 5·7^b	ANOVA, $F_{2,1007} = 7·53$, $P < 0·01$
Dive duration (min)	6·6 ± 2·6	6·5 ± 2·5^a	6·3 ± 2·3^a	9·4 ± 2·8^b	ANOVA, $F_{2,1007} = 60·1$, $P < 0·001$
% with b-m events	32·7 ± 5·0	27·8 ± 8·3^a	38·2 ± 7·8$^{a, b}$	64·7 ± 25·4^b	Kruskal–Wallis, $H_{2,12} = 7·54$, $P < 0·05$
No. of b-m events per b-m dives	1·8 ± 1·4	1·9 ± 0·5^a	1·5 ± 0·5^a	1·6 ± 0·4^a	Kruskal–Wallis, $H_{2,12} = 1·76$, $P = 0·415$

U-shaped dives (i.e. 14·1% of the 1009 recorded dives) and 38·3 ± 7·8% of all V-shaped dives (i.e. 15·2% of the 1009 recorded dives, Table 2).

OCCURRENCE OF BEAK MOVEMENT EVENTS DURING THE DIVE

Beak movements were recorded both at the surface and during dives. In both situations, three categories of beak movement events were defined: (a) isolated beak movements (lasting between 1·5 and 4 s); (b) group of two to five successive beak movements (lasting between 3 and 20 s in total); and (c) series of more than five successive beak movements (lasting between 10 s and 5 min in total; Fig. 2). Less than 1% of the events recorded at the surface were isolated beak movements. The category of a beak movement event recorded during a surface time was not linked to the occurrence or the category of beak movement events in the previous or following dive.

Among the b-m dives, beak movement events occurred on average 1·8 ± 1·4 times per dive (range: 1–11, Tables 1 and Fig. 2). The mean number of beak movement events per dive was not significantly different on comparison of the three types of dive profiles (Table 2). Beak movement occurrence was mainly isolated (55·0 ± 12·2% of the events) and grouped (41·0 ± 9·1% of the events), rather than in series (4·0 ± 3·8% of the events; Tables 1 and Fig. 2). Thus, 96·0 ± 4·0% of beak movement events during a dive lasted between 1·5 and 20 s.

There was one single isolated and one single grouped beak movement event in 36·8 ± 9·7%, and in 25·5 ± 8·4% of the b-m dives, respectively. There were several isolated and several grouped beak movements in 12·6 ± 4·5%, and in 11·6 ± 4·9% of the b-m dives, respectively. In 5·1 ± 3·9% of the b-m dives, isolated beak movements preceded groups of beak movements, while it was the contrary for 3·0 ± 2·6% of the b-m dives. This pattern was similar when considering U-shaped and V-shaped b-m dives separately. However, for W-shaped b-m dives, a single group of beak movements occurred in 50·3 ± 33·8% of the cases, and groups of beak movements preceded isolated beak movements in 10·4 ± 10·8%. In addition, W-shaped dives presented significantly more grouped beak movement events than other types of beak movement events, whereas U-shaped and V-shaped dives presented significantly more isolated and grouped beak movement events than series of events (Table 3).

No significant increase was seen in the mean number of beak movement events per b-m dive with dive depth or dive

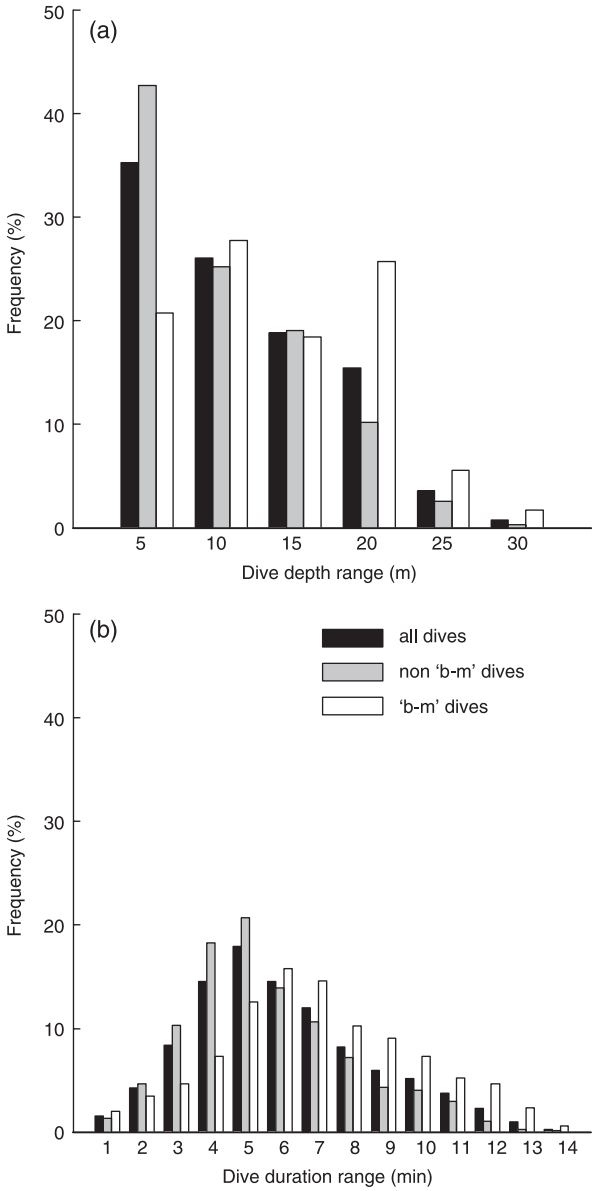


Fig. 3. Frequency distribution of (a) dive depth and (b) dive duration for all recorded dives (n = 1009 dives, in black), dives without beak movement events (n = 667 non-b-m dives, in grey) and dives associated with beak movement (n = 342 b-m dives, in white) in four leatherback turtles during one internesting interval in French Guiana in 2006.

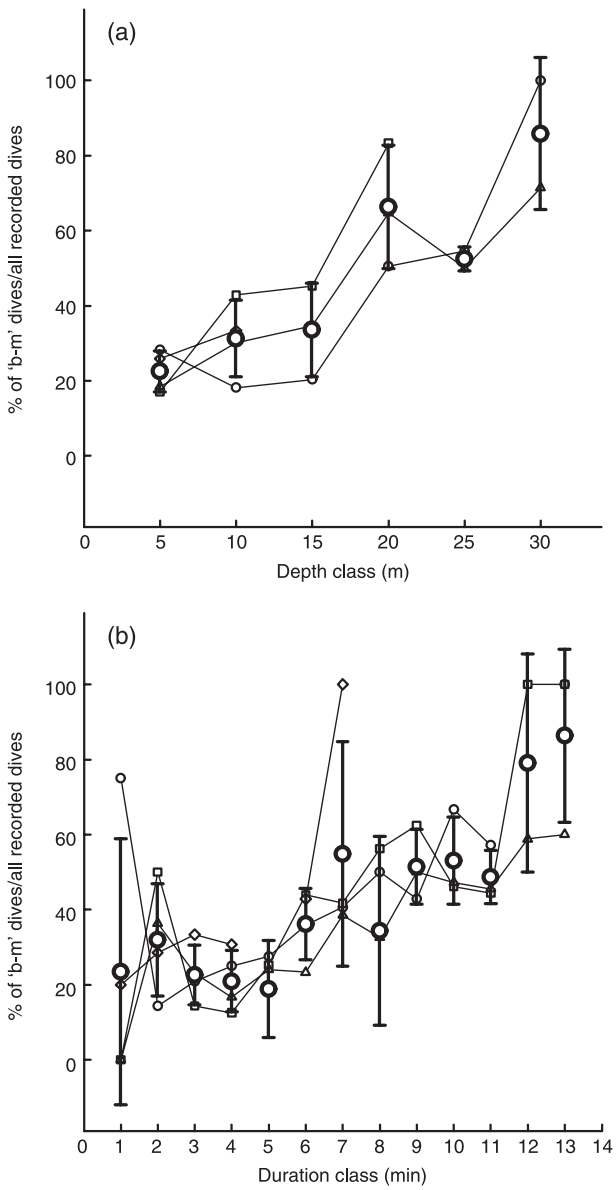


Fig. 4. Proportion of dives associated with beak movement events among all recorded dives in relation to (a) dive depth and (b) dive duration in four leatherback turtles during their internesting interval in French Guiana in 2006. Individual relations were calculated with all recorded dives for each turtle (turtles 1, 2, 3 and 4 in open circles, open squares, open triangles and open diamonds, respectively) and for pooled data (mean ± standard deviation, bold open circles, n = 4 individuals).

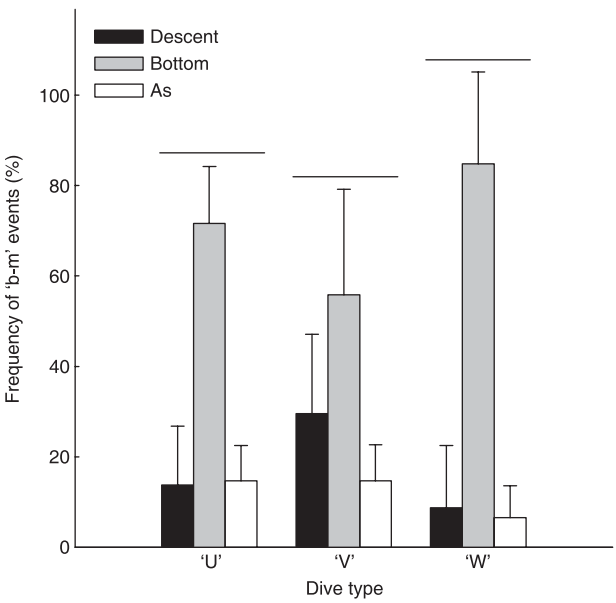
duration, when considering either each turtle individually [analysis of variance (ANOVA), $P > 0{\cdot}05$ in all cases except turtle no. 2, which showed an increase with dive depth, $F_{3,124} = 3{\cdot}14$, $n = 127$ dives, $P = 0{\cdot}03$] or all turtles together (Kruskal–Wallis, dive depth: $H_{5,18} = 4{\cdot}14$, $n = 4$ turtles, $P = 0{\cdot}53$; dive duration: $H_{13,43} = 18{\cdot}3$, $n = 4$ turtles, $P = 0{\cdot}14$).

During U-shaped and W-shaped b-m dives, beak movement events occurred mainly during the bottom phase (71·6 ± 12·6% and 84·8 ± 20·3%, respectively, Table 3, Figs 2 and 5) whatever their category (isolated, group or series). During V-shaped dives, beak movements occurred similarly during the descent (29·6 ± 17·6%), the bottom (55·8 ± 23·4%) or the ascent phase of the dive (14·7 ± 8·0%, Table 3, Figs 2 and 5) except for isolated beak movements, which occurred mainly during both the descent and the bottom phase of the V-shaped dives (38·8 ± 16·6% and 44·4 ± 22·8%, respectively).

There was no significant relationship between the proportion of time spent at the bottom of the dive and the number of beak movement events per dive, whatever their category (Pearson's correlation, $P > 0{\cdot}05$). The majority of beak movement events (62·7%) corresponded to a change in swimming direction, i.e. either a wiggle during the bottom phase (in 28·0 ± 8·0% of the recorded cases, $n = 4$ turtles), or the

Table 3. Proportions of beak movement (b-m) occurrence and types (isolated, grouped, in series) in relation to dive shape (U, V and W) in four leatherback turtles during one internesting interval in French Guiana in 2006. Differences in means and proportions were tested statistically using a Kruskal–Wallis test followed by a *post-hoc* Bonferroni test (n = 4 turtles). Different letters (a, b) indicate significant (P < 0·05) differences among groups

Dive type	% of b-m events in descent phase	% of b-m events in bottom phase	% of b-m events in ascent phase	Test P-value	% isolated b-m events	% grouped b-m events	% series of b-m events	Test P-value
U-shaped	13·7 ± 13·0[a]	71·6 ± 12·6[b]	14·7 ± 7·8[a]	$H_{2,12}$ = 7·4, P < 0·05	57·3 ± 18·4[a]	38·7 ± 15·2[a]	4·0 ± 3·3[b]	$H_{2,12}$ = 8·0, P < 0·05
V-shaped	29·6 ± 17·6[a]	55·8 ± 23·4[a]	14·7 ± 8·0[a]	$H_{2,12}$ = 5·5, P = 0·06	58·9 ± 15·7[a]	37·1 ± 13·8[a]	4·0 ± 4·6[b]	$H_{2,12}$ = 9·0, P < 0·05
W-shaped	8·7 ± 13·8[a]	84·8 ± 20·3[b]	6·5 ± 7·0[a]	$H_{2,12}$ = 7·4, P < 0·05	24·9 ± 18·7[a]	72·1 ± 21·2[b]	3·0 ± 3·5[a]	$H_{2,12}$ = 8·3, P < 0·05



beginning (11·9 ± 8·7%) and the end (7·9 ± 5·1%) of the bottom phase, or the peak of the V-shaped dives (11·4 ± 1·4%), or a 'dive step' (3·5 ± 5·1%) (Fig. 2). The percentage of beak movement events associated with a wiggle was not significantly different among the three categories of beak movement events ($H_{2,11}$ = 3·3, n = 4 turtles, P = 0·19). On average, 39·5 ± 21·4% and 36·1 ± 12·3% of groups and series of beak movements, respectively, were associated with a wiggle and 23·9 ± 2·5% of isolated beak movements.

Discussion

There is considerable interest in assessing the foraging behaviour of marine vertebrates and particularly in establishing the role of different dive types (e.g. Lesage, Hammil & Kovacs 1999; Schreer *et al.* 2001), quantifying foraging effort (e.g. Ropert-Coudert *et al.* 2002; Watwood *et al.* 2006) and foraging success (e.g. Wilson *et al.* 2002; Austin *et al.* 2006) for estimating energy and time budgets of these predators and their trophic role in their ecosystems. Several attempts have been made within this context to study the case of sea turtles (e.g. Hochscheid *et al.* 1999, 2004; Myers & Hays 2006). The present work aims to contribute to this impetus and constitutes the first study where several free-ranging IMASEN-equipped sea turtles are monitored to assess the potential links between diving and mouth-opening patterns.

Among the 12 turtles equipped initially in this study, three were not resighted later in the nesting season. As patrolling occurred every night throughout the study period, this suggests that these turtles initiated their post-nesting migration after deployment. All other turtles were observed renesting normally (S. F. and J. Y. G., personal observation) 7·0–10·9 days after, as reported previously in the area (Georges *et al.* 2007), and did not show any signs of injuries either on the carapace where the loggers were fixed or on the beak where the sensors and the magnets were glued. This suggests that our magnetic devices did not have any welfare or behavioural impacts on the study animals, as reported for other species (Ropert-Coudert *et al.* 2004; Takahashi *et al.* 2004). Consistently, Luschi *et al.* (2007) report that magnets producing fields stronger than Earth's magnetic field may impair sea turtles' navigational performances without, however, preventing the turtles from eventually reaching their goals. Accordingly, the beak-opening events observed in the present study were considered as normal activity rather than as artefacts associated with animal disturbance.

GENERAL DIVING PATTERN

In our study, four leatherbacks were monitored successfully during a maximum of 2 days. In French Guiana, these first days correspond to the period of the internesting interval, when leatherbacks remain in shallow (< 50 m deep) coastal (within 50 km from the coasts) waters before dispersing extensively over the continental shelf (Fossette *et al.* 2007b; Georges *et al.* 2007). Consistently, the four leatherbacks exhibited continuous short and shallow putative benthic