



Monitoring beak movements with an acceleration datalogger: a useful technique for assessing the feeding and breathing behaviors of sea turtles

Junichi Okuyama^{1,*}, Yuuki Kawabata¹, Yasuhiko Naito^{2,3}, Nobuaki Arai¹,
Masato Kobayashi⁴

¹Graduate School of Informatics, Kyoto University, Yoshida Honmachi, Sakyo, Kyoto 606-8501, Japan

²National Institute of Polar Research, Itabashi, Tokyo 173-8515, Japan

³Bio-logging Institute, 2-3-10 Rex Yushima 301, Bunkyo, Tokyo 113-0034, Japan

⁴Yaeyama Station of the Stock Enhancement Technology Development Center, Seikai National Fisheries Research Institute, Fisheries Research Agency, Fukaiohta 148, Ishigaki, Okinawa 907-0451, Japan

ABSTRACT: This study was performed to determine whether the attachment of acceleration dataloggers to the lower beaks of loggerhead turtles *Caretta caretta* could be a useful technique for monitoring their feeding and breathing behaviors. Attaching acceleration dataloggers to the lower beak of turtles allows determination of the pitch of the head from the low frequency component of the acceleration data, and of dynamic movements (e.g. biting) from the high frequency component. In addition, to determine whether the acceleration datalogger could distinguish between different food sources and feeding locations based on acceleration characteristics, we fed the turtles with different types of food (squid rings, fins, and heads that include arms and tentacles) across different locations. Our results demonstrate that the acceleration datalogger was able to detect the lower beak movements of loggerhead turtles, which enabled detection of 99.6 ± 1.1 (SD) % of feeding and 100% of breathing behaviors, with respective false detection rates of 24.8 ± 12.4 % and 2.4 %. Furthermore, our results demonstrate that it is possible to (1) determine whether feeding on prey requires a strong biting force, and (2) differentiate between feeding at the sea floor and in the water column. Attaching an acceleration datalogger is thus established as a useful technique for monitoring the feeding and breathing behaviors of sea turtles. Future studies employing acceleration dataloggers should provide new insights into the biology of sea turtles and their feeding and diving strategies.

KEY WORDS: Biologging · *Caretta caretta* · Feeding ecology · Respiratory physiology

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Advances in microelectronics in recent years have allowed researchers to develop small, lightweight dataloggers to minimize their physiological and hydrodynamic impacts on animals (Hawkins 2004, Naito 2004). Consequently, researchers can now attach dataloggers to wild animals to study the behavior, physiology and ecology of species that are difficult to observe (Ropert-Coudert & Wilson 2005). Animal-borne biologgers are increasingly being applied to the study of animal biology and conservation (Cooke et

al. 2004, Ropert-Coudert & Wilson 2005, Wilson et al. 2008).

The miniaturization of dataloggers with a variety of sensing abilities has enabled researchers to monitor the movements of isolated body parts of animals such as the beak or mandible (Wilson et al. 2002) and flipper (Hays et al. 2004). One of the most recent techniques is the recording of the beak-opening events of an animal by using an Inter-Mandibular Angle Sensor (IMASEN; Wilson et al. 2002) with a magnet/Hall sensor combination connected to a datalogger that records changes in the intermandible angle. This tech-

*Email: okuyama@bre.soc.i.kyoto-u.ac.jp

nique is a useful tool for detecting essential behaviors of animals (e.g. feeding, breathing, drinking, vocalization, and sensing) of various species (e.g. penguins: Wilson et al. 2002, Takahashi et al. 2004; pinnipeds: Liebsch et al. 2007; and sea turtles: Hochscheid et al. 2005, Myers & Hays 2006, Fossette et al. 2008, Houghton et al. 2008).

Dataloggers with accelerometer sensors have also provided novel insights into the biology of animals (e.g. Yoda et al. 1999, Tanaka et al. 2001, Sato et al. 2003, Wilson et al. 2006). For example, acceleration dataloggers have provided information on the angle and dynamic movements of appendages (Tanaka et al. 2001), and allowed determination of the classification of behavioral patterns and the temporal characteristics of these patterns (Yoda et al. 2001, Shepard et al. 2008, Wilson et al. 2008). Acceleration dataloggers allow researchers to monitor the movements of isolated body parts of animals, as the IMASEN does. For example, its attachment to the head or lower mandible has enabled researchers to monitor the feeding events of seals (Naito 2007, Suzuki et al. 2009). Previous studies have been conducted on the feeding and breathing behaviors of sea turtles using IMASENs (e.g. Hochscheid et al. 2005, Myers & Hays 2006, Fossette et al. 2008). However, compared to the IMASEN, one of the benefits of using the acceleration datalogger for determining feeding and breathing behaviors is that it can record head pitch as well as lower beak movements. The head pitch during feeding may provide additional information on feeding behavior, such as the situation or feeding location. In addition, based on the beak opening-closing motion detection by an IMASEN (Fossette et al. 2008), it is difficult to distinguish between feeding and breathing events, during which sea turtles open their mouths at the sea surface. When turtles breathe at the surface, they extend their necks upward (Reina et al. 2005). Therefore, if breathing events could be distinguished from surface feeding events based on an analysis of the head pitch, this technique could be useful for studying the breathing behavior of sea turtles.

In the present study, we attached acceleration dataloggers to the lower beaks of loggerhead turtles *Caretta caretta* in a captive setting to assess the applicability of this monitoring technique for determining feeding and breathing behaviors in the wild. In addition, to examine beak movements associated with feeding, we provided different types of food to test whether the consumption of different kinds of food might result in different patterns of beak acceleration. The relationship between the head pitch of turtles and their feeding location in the water column was also examined.

MATERIALS AND METHODS

Experimental protocol and instruments. Our experiments were conducted in a 200 kiloliter tank ($H \times L \times W = 10 \times 10 \times 2.2$ m) at the Yaeyama Station in the Stock Enhancement Technology Development Center, Seikai National Fisheries Research Institute, Fisheries Research Agency, Japan. Six captive juvenile loggerhead turtles were used to study feeding behavior, and one of these (Turtle B) was also used to study breathing movements (Table 1).

An acceleration datalogger (M190L-D2GT: 15 mm diameter, 53 mm length, 17 g in air, memory capacity of 8 million data points; Little Leonardo) was affixed to the lower beak of each loggerhead using epoxy putty (Konishi) and a 2-component epoxy resin (ITW Industry) (Fig. 1). Acceleration dataloggers can record depth and temperature at 1 s intervals, and 2-axis accelerations (surging and heaving) at 1/32 s intervals. Using these intervals, we can theoretically record data for ~70 h. The maximum range of the depth sensor is down to 190 m, with a resolution of 0.046 m. The measurement range of the accelerometers is ± 39.2 m s⁻², with a resolution of 0.019 m s⁻².

Each turtle affixed with a datalogger was released into the tank and allowed to acclimate for >1 h to recover from handling stress. The turtles were then fed with squid rings (main bodies), fins, and heads (includ-

Table 1. Physical characteristics of experimental turtles *Caretta caretta* and summary of experiments. SCL: straight carapace length; BW: body weight

Turtle ID	SCL (cm)	BW (kg)	Monitored behavior	Total observation period (min.)	Date of experiment dd/mm/yy
A	57.2	34.2	Feeding	66	19–20/04/08
B	63.3	35.4	Feeding and respiration	72	22–23/04/08
C	60.5	36.0	Feeding	95	10–12/05/08
D	62.0	38.9	Feeding	67	12–13/05/08
E	64.7	36.0	Feeding	88	13–15/05/08
F	61.6	36.0	Feeding	74	15–16/05/08

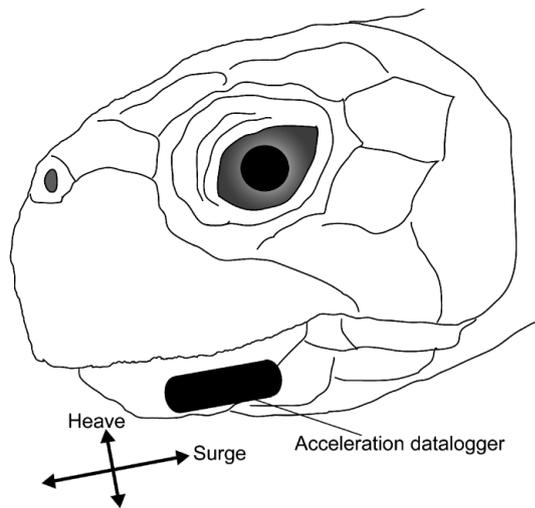


Fig. 1. *Caretta caretta*. Schematic drawing of attachment site of acceleration datalogger on the lower beak. Attachment was accomplished using epoxy putty (see 'Materials and methods' for details)

ing arms and tentacles), and the times when the turtles bit prey were recorded by visual observation from above. The masses and lengths of the prey items are given in Table 2. For Turtle B, we also recorded the times when breaths were taken. After the experiments, the 2-axis accelerations and depth data were downloaded from the recovered dataloggers. The temperature during the experiments ranged from 23 to 26°C.

Extraction of breathing and feeding behaviors from acceleration data. High frequency acceleration signals represent animal movements such as flipper strokes and tail beats, which can be expressed by the component that remains after filtering out the low frequency signal from the original acceleration data (Tanaka et al. 2001, Yoda et al. 2001, Sato et al. 2003). Thus, we extracted the opening and closing motion of the lower beak from the surging and heaving acceleration data using IGOR, IGOR Filtering Design Laboratory, IFDL, (WaveMetrics) and Ethographer (S. Q. Sakamoto, Hokkaido University; see Sakamoto et al. 2009 for details) software. In the present study, we defined a feeding signal as an acceleration $>+0.3$ or <-0.3 m s^{-2} in both the surging and heaving axes of lower beak motion, which was the most appropriate definition for

a high detection rate and a low false detection rate, based on data analysis. When 2 feeding signals were within 5 s of each other, they were regarded as 1 feeding event. To eliminate the noise pulse caused by contact with the tank wall and breathing behavior, we removed the feeding signals that occurred within 1 s of breathing or contact from the analysis. To determine whether the pitch of the head differed when turtles were feeding on prey at the bottom of tank versus prey in the water column, we calculated the low frequency signals of the acceleration data, which are indicative of the pitch of the head during feeding (see following paragraph).

Sea turtles complete a single exhalation and inhalation with each respiration (Lutz & Bentley 1985, Kontos & Eckert 1988). When turtles breathe at the surface, they extend their necks upward (Reina et al. 2005). Therefore, the time spent breathing can be measured if the pitch of the head can be measured. The low frequency signals of the longitudinal accelerations allow estimation of the pitch of animal body parts tagged with a datalogger (Tanaka et al. 2001). In the present study, we regarded the pitch of the lower beak as the pitch of the head, because the pitch of the lower beak is nearly equal to that of the head when turtles close their beaks. In addition, the opening-closing movements of the lower beak were represented by the high frequency signals. The pitch of the lower beak was extracted by filtering out the high frequency signals from the surging acceleration data using IGOR, IFDL (WaveMetrics) and Ethographer (S. Q. Sakamoto, Hokkaido University; see Sakamoto et al. 2009 for details) software. Upward and downward orientations were represented by positive and negative pitch values, respectively. We defined breathing behavior as occurring when the pitch was $>30^\circ$ and the water depth was <0.15 m, which was the most appropriate definition to allow high detection rate and low false detection rate, as demonstrated by the data analysis below.

Comparing the timing of feeding and breathing behaviors extracted from the acceleration data with those from visual observation, we calculated the detection and false detection rates of breathing and feeding behaviors. The detection rate was defined as the ratio of the number of behaviors that were detected by both

Table 2. Lengths and masses of food items provided during the experiments and corresponding biting force and feeding durations. All values are means \pm SD. (*) Significant differences between marked groups

Squid body parts	n	Length (cm)	Mass (g)	Biting force (m s^{-2})	Feeding duration (s)
Rings of main body	142	2.8 ± 0.8	19.4 ± 5.4	$8.7 \pm 4.1^*$	10.6 ± 9.2
Fins	39	5.1 ± 1.8	11.5 ± 4.6	10.4 ± 5.2	10.4 ± 5.1
Heads	24	–	30.3 ± 5.7	$11.5 \pm 3.7^*$	11.3 ± 5.5

the acceleration data and visual observation to the number of the behaviors that were detected by visual observation alone. The false detection rate was defined as the ratio of the number of false detections of behaviors detected by acceleration data to the number of total behaviors detected by acceleration data. Breathing and feeding behaviors extracted from acceleration data were considered to be identical to those from visual observation if the time difference between them was ≤ 3 s.

Data analysis of feeding behavior. To relate acceleration data characteristics during feeding behavior to specific prey items, we looked at the relationships between the prey item mass and feeding duration as well as the biting force. Biting force was calculated from the maximum value of the squared sum of the high frequency components of the surging and heaving accelerations during feeding. Furthermore, for Turtles C through F, we investigated the relationship between the pitch of the head and the feeding location (bottom of tank versus water column), since after observing Turtles A and B, we hypothesized that the turtles changed their head pitch depending on the feeding location.

RESULTS

During the experiments, we fed 6 turtles with a total of 249 prey items, all of which were consumed. A feeding event was always initiated by a turtle holding a prey item while craning its neck forward and opening

its beak widely. After this, the turtle would open and close its beak several times while holding on to the prey item, and then finally swallow it. During consumption, the lower beak wiggled not only up and down but also back and forth. This series of lower beak movements associated with feeding behavior was manifested as continuous feeding pulses in the acceleration data of both the surging and heaving axes (Fig. 2). The detection rates (\pm SD) of feeding behaviors were nearly perfect ($99.6 \pm 1.1\%$) for all 6 turtles, indicating that the feeding behavior of loggerhead turtles was successfully detected by the acceleration datalogger (Table 3). However, the mean false detection rate (\pm SD) was $24.8 \pm 12.4\%$, indicating that the acceleration datalogger detected other movements of the lower beak or head that resembled feeding behavior based on the acceleration data but did not actually represent feeding.

There was no correlation between the biting force and feeding duration (Spearman rank correlation test, $r_s = 0.18$, number of feeding events [N] = 205, $p > 0.05$), although the biting force during feeding was significantly different among prey types (Kruskal-Wallis test, $H = 15.3$, $df = 2$, $p < 0.01$). The biting force associated with feeding on the rings of the main squid body differed significantly from that involved in feeding on the head (posthoc Scheffe test, $p < 0.01$; Table 2). The length and mass of the prey items did not correlate with the biting force (Spearman rank correlation test, $r_s = 0.03$, $N = 181$, $p > 0.05$ for length; $r_s = 0.09$, $N = 205$, $p > 0.05$ for mass). There was no difference in feeding duration among the prey types (Kruskal-Wallis test, H

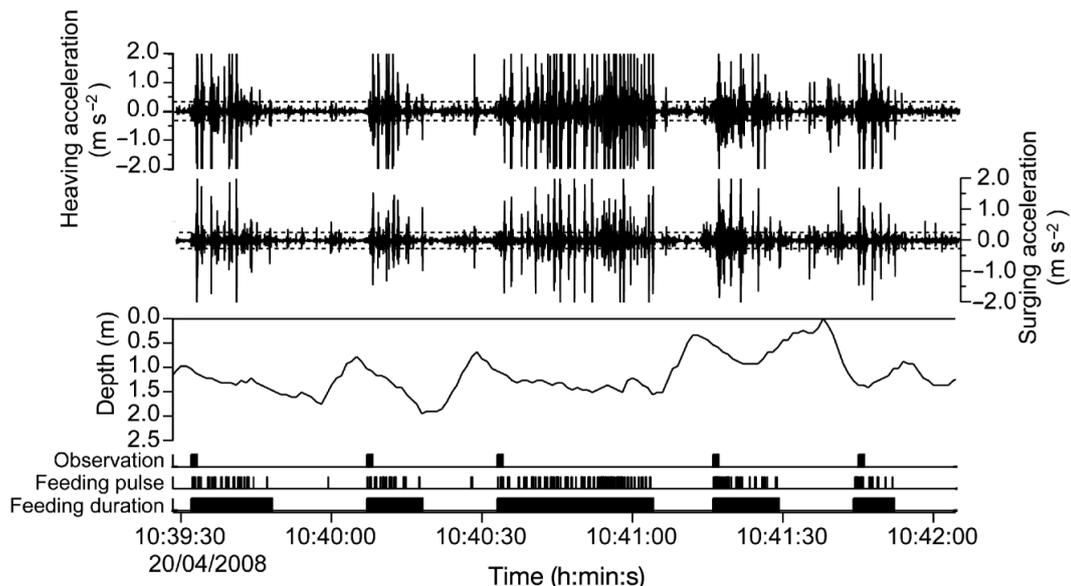


Fig. 2. *Caretta caretta*. A typical profile of feeding behavior, showing heaving and surging accelerations of the lower beak, and depth. Horizontal broken lines in heaving and surging acceleration profiles represent the thresholds for identifying feeding pulses (see 'Materials and methods' for details). Horizontal bars at the bottom represent the time the turtles hold food items into their mouth (identified by visual observation), the time the feeding pulses occur, and feeding duration

Table 3. *Caretta caretta*. Detection and false detection rates (%) of feeding behavior by the acceleration datalogger. Values in parentheses for detection rate are the ratios of the number of behaviors that were detected by both the acceleration data and a visual observation to the number of the behaviors that were detected by visual observation alone. Values in parentheses for false detection rate are the ratios of the number of false detections of behaviors by acceleration data to the number of total behaviors detected by acceleration data

Turtle ID	Detection rate of feeding (%)	False detection rate of feeding (%)
A	97.4 (38/39)	13.6 (6/44)
B	100.0 (29/29)	9.4 (3/32)
C	100.0 (72/72)	16.3 (14/86)
D	100.0 (24/24)	35.1 (13/37)
E	100.0 (47/47)	32.9 (23/70)
F	100.0 (38/38)	37.7 (23/61)
Mean \pm SD	99.6 \pm 1.1 (248/249)	24.8 \pm 12.4 (82/330)

= 4.21, $df = 2$, $p > 0.05$), nor was there a correlation between feeding duration and length or mass of the prey (Spearman rank correlation test, $r_s = 0.05$, $N = 181$, $p > 0.05$ for length; $r_s = 0.01$, $N = 205$, $p > 0.05$ for mass). The turtles positioned their necks slightly downward (mean \pm SD: $-16 \pm 17^\circ$) when feeding at the bottom of the tank, whereas they approached the prey with their heads in a nearly horizontal position ($2 \pm 11^\circ$) when feeding in the water column. These positions were significantly different (Mann-Whitney test, $Z = 6.30$, $p < 0.0001$).

Forty breathing events were observed for Turtle B during the experiment. Our observations reveal that respiration always occurred with the neck arched upward. From the pitch and depth data, we inferred

that the turtle swam up to the surface to breathe and then extended its neck upward (Fig. 3). All breathing events ($n = 40$) were detected by the datalogger, and the false detection rate was only 2.4% (1/41). The mean duration of the detected breathing events was 1.99 ± 0.56 s.

Specific movements of the lower beak were not observed except during feeding and breathing, although we observed that the turtles bit and held onto the polyvinyl chloride (PVC) pipes and protrusions in the tank. The buccal oscillations reported by previous studies (Hochscheid et al. 2005, Myers & Hays 2006, Houghton et al. 2008) were not detectable using analysis of the acceleration data profiles of the lower beak.

DISCUSSION

Our results demonstrate that the acceleration dataloggers were able to detect the lower beak movements of loggerhead turtles. The acceleration data enabled us to identify both feeding and breathing behaviors. Because the acceleration datalogger used in this study is a single-packaged device with a sensor and logger, it does not need sensor cables. It is thus easy to attach to the lower beak of turtles and is free from the device problems and influences on the behavior of animals that are caused by sensor cables (e.g. Wilson et al. 2002). Therefore, the acceleration datalogger could be an alternative tool for studying feeding ecology and diving physiology in sea turtles.

The near-perfect detection rate of feeding behavior attained in our study indicates that this method of detection is highly sensitive. The false detection rate was

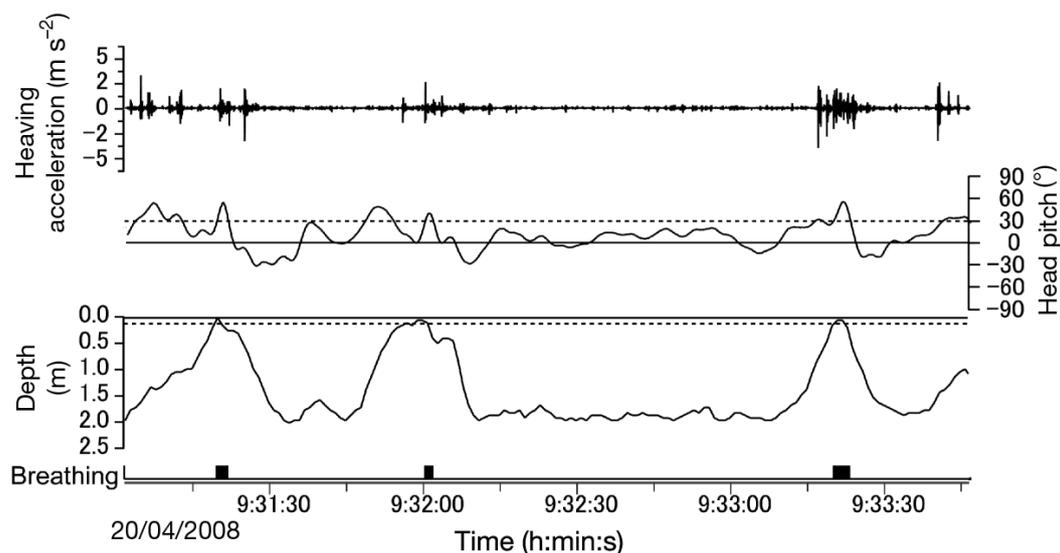


Fig. 3. *Caretta caretta*. A typical profile of breathing behavior, showing heaving acceleration of the lower beak, head pitch, and depth. Horizontal broken lines in head pitch and depth profiles represent the thresholds for identifying breathing behavior (see 'Materials and methods' for details). Horizontal bars at the bottom represent breathing duration

~25%, although this value would likely change under field conditions. We observed that the turtles sometimes bit and held the PVC pipes and protrusions in the tank. Therefore, a possible reason for false detection is the detection of the movements of the head or lower beak similar to those in feeding. This result suggests that the detection of feeding behavior by the acceleration datalogger might also be indicative of other similar behaviors. However, this technique for the detection of feeding behavior could provide an index of feeding effort similar to that obtained using the IMASEN technology (Fossette et al. 2008), which could offer new insights into the feeding ecology of sea turtles.

From the acceleration datalogger, we were able to infer the feeding duration, biting force and head pitch. The biting force was greater when turtles were eating the intricately shaped heads of squid, including the arms and tentacles, than when they were feeding on the ring of the main body (Table 2). When the IMASEN is used in field studies, the intermandibular distance is not investigated because the Hall signal is highly affected by water pressure in relation to depth (Fossette et al. 2008). Such mechanical problems in relation to water pressure have not been reported for the acceleration datalogger. Thus, the acceleration datalogger has the advantage of being able to detect the biting force of sea turtles during feeding. Additionally, the pitch of the head was slightly downward when feeding at the bottom of the tank, but it was close to horizontal when feeding in the water column. These results indicate that data from an acceleration datalogger may accurately represent the movements and posture of turtle heads. However, the kinds of prey preferred by sea turtles differ between species, populations and life stages (Mortimer 1995, Bjorndal 1997). In the present study, we could not simulate feeding on all of the possible prey items of loggerhead turtles in the wild to evaluate the possibility of detection by the acceleration datalogger in the field. However, the opening-closing movements of the lower beak are considered to be common during feeding on all of the different prey items of loggerheads. Therefore, our results demonstrate that it is possible to (1) determine whether feeding on the prey requires a strong biting force, and (2) differentiate between feeding at the sea floor and in the water column.

We also detected the breathing behavior of a loggerhead turtle from its head pitch, which suggests that acceleration dataloggers may be useful for measuring the respiratory frequency of loggerheads. The breathing behavior of Turtle B was comprehensively detected, and we were able to distinguish it completely from feeding behavior at the surface, which is a concern when using the IMASEN (Fossette et al. 2008). The false detection rate was very low. False detection occurred when the turtle swam up to the surface just before breathing. Usually, before arriving at the surface, the pitch of the turtle's

neck was $<30^\circ$, and then increased to $>30^\circ$ during breathing (Fig. 3). The false detection was due to the steep ascent to the surface at an angle $>30^\circ$. The breathing duration was also calculated in the present study. The ~2 s breathing duration observed is very similar to that recorded for juvenile loggerhead turtles using the IMASEN (2–3 s; Hochscheid et al. 2005), and adult female leatherback turtles *Dermochelys coriacea* (~3 s; Reina et al. 2005). The breathing duration calculated in the present study may represent the period in which turtles complete a single respiration. However, further study is needed to investigate the relationship between the breathing duration calculated using acceleration and depth data, and tidal volume.

Buccal oscillations of sea turtles, which might represent their state of consciousness (Houghton et al. 2008) and their sensing of the immediate environment (Hochscheid et al. 2005, Myers & Hays 2006), were not detectable using the acceleration dataloggers. This represents a disadvantage compared to the IMASEN. Therefore, this detection technique for the lower beak movements may be an inadequate tool for studies on the buccal oscillations of sea turtles.

In conclusion, the attachment of acceleration dataloggers to the lower beaks of loggerheads allows the monitoring of their feeding and breathing behaviors. Future field studies using this device may provide additional information on the biology of sea turtles, including more precise classifications of their behavioral patterns, such as feeding and breathing, and the temporal distribution of these behaviors. This will be possible because acceleration dataloggers provide information on an animal's posture, dynamic movements and activity level (e.g. Wilson et al. 2006, Halsey et al. 2008). By attaching acceleration dataloggers to the lower beak and body of diving animals, novel insights could be gained into their diving physiology, such as the relationships among dive duration, respiratory behavior, and the amount of activity.

Acknowledgements. We thank K. Okuzawa (Ishigaki Tropical Station, Seikai National Fisheries Research Institute) and N. Naito for assistance with experiments. We also thank the staffs of the Ishigaki Tropical Station and Yaeyama Station, Seikai National Fisheries Research Institute for research help and constructive comments. This study was supported by the GCOE program 'Informatics Education and Research Center for Knowledge-Circulating Society'. All experiments were conducted in accordance with the Japan Ethological Society guidelines for the experimental use of animals (<http://www.soc.nii.ac.jp/jes2/guideline.html>).

LITERATURE CITED

- Bjorndal KA (1997) Feeding ecology and nutrition of sea turtles. In: Lutz PL, Musick JA (eds) *The biology of sea turtles*. CRC Press, Boca Raton, FL, p 199–231

- Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Wolcott TG, Butler PJ (2004) Biotelemetry: a mechanistic approach to ecology. *Trends Ecol Evol* 19:334–343
- Fossette S, Gasper P, Handrich Y, Maho YL, Georges JY (2008) Dive and beak movement patterns in leatherback turtles *Dermochelys coriacea* during interesting intervals in French Guiana. *J Anim Ecol* 77:236–246
- Halsey LG, Shepard ELC, Hulston CJ, Venables MC, White CR, Jeukendrup AE, Wilson RP (2008) Acceleration versus heart rate for estimating energy expenditure and speed during locomotion in animals: tests with an easy model species, *Homo sapiens*. *Zoology* 111:231–241
- Hawkins P (2004) Bio-logging and animal welfare: practical refinements. *Mem Natl Inst Polar Res Spec Iss* 58:58–68
- Hays GC, Metcalfe JD, Walne AW, Wilson RP (2004) First records of flipper beat frequency during sea turtle diving. *J Exp Mar Biol Ecol* 303:243–260
- Hochscheid S, Maffuccia F, Bentivegna F, Wilson RP (2005) Gulps, wheezes, and sniffs: how measurement of beak movement in sea turtles can elucidate their behaviour and ecology. *J Exp Mar Biol Ecol* 316:45–53
- Houghton JDR, Cedras A, Myers AE, Liebsch N, Metcalfe JD, Mortimer JA, Hays GC (2008) Measuring the state of consciousness in a free-living diving sea turtle. *J Exp Mar Biol Ecol* 356:115–120
- Kontos A, Eckert SA (1988) The relationship between the number of breaths, surface time and dive time of the hawksbill turtle (*Eretmochelys imbricata*) in the wild. *Am Zool* 28:180A
- Liebsch N, Wilson RP, Bornemann H, Adelung D, Plotz J (2007) Mouthing off about fish capture: Jaw movement in pinnipeds reveals the real secrets of ingestion. *Deep-Sea Res II* 54:256–269
- Lutz PL, Bentley PJ (1985) Respiratory physiology of diving in the sea turtle. *Copeia* 1985:671–679
- Mortimer JA (1995) Feeding ecology of sea turtles. In: Bjornndal KA (ed) *Biology and conservation of sea turtles*. Smithsonian Institution Press, Washington, DC, p 103–109
- Myers AE, Hays GC (2006) Do leatherback turtles *Dermochelys coriacea* forage during the breeding season? A combination of data logging devices provide new insights. *Mar Ecol Prog Ser* 322:259–267
- Naito Y (2004) Bio-logging science. *Mem Natl Inst Polar Res Spec Issue* 58:118–132
- Naito Y (2007) How can we observe the underwater feeding behavior of endotherms. *Polar Sci* 1:101–111
- Reina RD, Abernathy LJ, Marshall GJ, Spotila JR (2005) Respiratory frequency, dive behaviour and social interactions of leatherback turtles, *Dermochelys coriacea* during the inter-nesting interval. *J Exp Mar Biol Ecol* 316:1–16
- Ropert-Coudert Y, Wilson RP (2005) Trends and perspectives in animal-attached remote sensing. *Front Ecol Environ* 3:437–444
- Sakamoto SQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S (2009) Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE* 4(4):e5379 doi:10.1371/journal.pone.0005379
- Sato K, Mitani Y, Cameron F, Siniff BD, Naito Y (2003) Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *J Exp Biol* 206:1461–1470
- Shepard ELC, Wilson RP, Liebsch N, Quintana F, Gómez Laich A, Lucke K (2008) Flexible paddle sheds new light on speed: a novel method for the remote measurement of speed in aquatic animals. *Endang Species Res* 4:157–164
- Suzuki I, Naito Y, Folkow LP, Miyazaki N, Blix AS (2009) Validation of a device for accurate timing of feeding events in marine animals. *Polar Biol* 32:667–671
- Takahashi A, Dunn MJ, Trathan PN, Croxall JP, Wilson RP, Sato K, Naito Y (2004) Krill-feeding behavior in a chinstrap penguin *Pygoscelis antarctica* compared with fish-eating in magellanic penguins *Spheniscus magellanicus*: a pilot study. *Mar Ornithol* 32:47–54
- Tanaka H, Takagi Y, Naito Y (2001) Swimming speeds and buoyancy compensation of migrating adult chum salmon *Oncorhynchus keta* revealed by speed/depth/acceleration data logger. *J Exp Biol* 204:3895–3904
- Wilson RP, Steinfurth A, Ropert-Coudert Y, Kato A, Kurita M (2002) Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Mar Biol* 140:17–27
- Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J Anim Ecol* 75:1081–1090
- Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endang Species Res* 4:123–137
- Yoda K, Sato K, Niizuma Y, Kurita M, Bost CA, Le Maho Y, Naito Y (1999) Precise monitoring of porpoising behaviour of Adelie penguins determined using acceleration data loggers. *J Exp Biol* 202:3121–3126
- Yoda K, Naito Y, Sato K, Takahashi A and others (2001) A new technique for monitoring the behavior of free-ranging Adélie penguins. *J Exp Biol* 204:685–690

Editorial responsibility: Jeffrey Seminoff,
La Jolla, California, USA

Submitted: March 16, 2009; Accepted: June 17, 2009
Proofs received from author(s): August 22, 2009