Ontogenetic changes in the flipper-beating behavior in free-range versus tank-housed green turtle (*Chelonia mydas*) juveniles

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Abstract — Recently, acceleration data loggers have been used to quantify the flipper (or wing) beating behavior of free-ranging aquatic animals, and this has contributed to our understanding of the swimming activity of marine life. By using acceleration data loggers, we quantitatively evaluated the difference in flipper beat frequency of juvenile green turtles at sea and in tanks for four different stages of growth. The results indicated that juveniles about two weeks old after emergence exhibited significantly higher swimming activity at sea than in the tank; this may help them to reach the oceanic gyre habitat. Juveniles gradually decreased their activity enhancement at sea after their peak, at two weeks old, through the next two months before finally leveling-off. This may reflect their adaptation of passive drifting using the ocean currents. This is the first intensive study that shows the flipper beating behavior of juveniles at sea, and it reveals that ontogenetic changes in this activity are more pronounced at sea, indicating the importance of field observations for understanding the dispersal of sea turtle juveniles.

Key words: acceleration data logger, flipper beat frequency, field observation, ontogeny

Introduction

Until recently, quantitative investigations aimed at understanding the natural history and feeding strategies of animals have been difficult to obtain. This is especially true for free-ranging swimming animals (Boyd et al. 2004) that are expected to exhibit both natural and adaptive behaviors. Recently, however, various approaches using data loggers have been developed to quantify the behavior of free-ranging animals. In particular, acceleration data loggers have been used in recent years to record the flipper or wing beating behavior of various free-swimming animals (e.g. Watanuki et al. 2003, Sato et al. 2003, 2004, 2007, Ropert-Coudert et al. 2006), and these instructions have greatly increased our understanding of the swimming effort of marine life (Hays 2008). While the flipper beating behavior of adult sea turtles has been investigated at sea with acceleration data loggers (Sato et al. 2007), research on hatchling and juvenile sea turtles has been conducted mostly in tanks and evaluated visually (e.g., Davenport and Clough 1986, Wyneken 1997), which may be misleading when trying to understand their swimming efforts. The only previous study referring to the flipper beat frequency of hatchlings in the field (Salmon and Wyneken 1987) presented the values for frenzy hatchlings only, but the

data are not definitive because of the short observation time (10 powerstroke bouts per hatchling). To better understand sea turtle flipper-beating behavior, it is important to measure this behavior quantitatively at sea using acceleration data loggers to monitor the turtles for longer periods of time.

Wyneken (1997) showed that the flipper beat frequency of green turtle hatchlings in tanks decreased significantly between the frenzy period, where hatchlings swim continuously for about 24 h after the emerging from their nests (Salmon and Wyneken 1987, Wyneken and Salmon 1992), and the postfrenzy period. Because it has been used as an index of activity (Hays et al. 2007, Jones et al. 2007), this seems to suggest that turtles decrease their activity level after the frenzy period, even though hatchlings are thought to continue swimming until they reach the oceanic current systems (Salmon and Wyneken 1987, Wyneken and Salmon 1992). Some cues from the sea may play essential roles during dispersal migrations (e.g., wave motion for orientation; Lohmann and Lohmann 1992, Wang et al. 1998), so juvenile may swim more actively at sea. Therefore, evaluating the ontogenetic change in sea turtle flipper beat frequency as swimming activity at sea could improve our knowledge about their dispersal migration. We focused on the difference between the frequency of flipper beats between turtles at-sea and in-tank as an indicator of increased swimming activity while the

turtles are at sea.

This is the first comprehensive study that examines the flipper beating behavior of juvenile green turtles at sea. We employed juveniles as young as hatchlings and as old as two to three months. First, we measured the flipper beat frequency of juvenile green turtles quantitatively by using acceleration data loggers. Second, we examined the differences between at-sea and in-tank flipper activity at four stages of turtle development. These differences offer new insight into the changes in behavior during the initial dispersal migration.

Materials and Methods

Animals

Green turtles (*Chelonia mydas*) eggs were collected at beaches in Ibaruma, East Hirakubo, and Osaki, Ishigaki Island, Okinawa Prefecture, Japan. About 20 eggs (in the middle or late stages of incubation) were collected from each of 15 clutches and transported to the Ishigaki Tropical Station (24.272°N, 124.125°E), part of Seikai National Fisheries Research Institute (permission of Okinawa Prefecture government no. 18–45). Each set of eggs was buried at a depth of about 50 cm at an outdoor artificial beach on the station. The temperature and humidity of the beaches were not controlled. Hatchlings were captured just after their emergence or just

prior to the emergence when their heads were protruding from the sand in the evening. The average hatching rate of the eggs was 88%. Hatchlings were reared in containers (3 different sizes, length×width×height, in cm; 48×34×15; 40×30×15; or 55×27×12) located in a shaded area until the experiments were finished. A maximum of 4 juveniles were reared in a container until they were 1 month old. Every juvenile over 1 month old was housed in a separate container. Juveniles were fed once a day starting on the third day after the emergence (Wyneken and Salmon 1992). Their diet was a mixtures of anchovies, mysids, and clams supplemented with vitamins and calcium. The containers and carapaces of the juveniles were cleaned almost every night. The water temperature of the containers varied from 23.3 to 29.8°C. Twenty juveniles (1–3 juveniles from each clutch) that were not noticeably inactive or injured in attacks from their siblings were selected and used for both at-sea and in-tank experiments (Table 1). They were divided into 4 groups as follows: the 'emergence' group, which consisted of hatchlings who seemed to be in the frenzy period, was 1 day (the field experiment) or 2 days (the tank experiment) old after the emergence (weight, 23.1 ± 1.1 g; ID1–6); the '2 weeks' group was 11–19 days old (weight, 31.6 ± 1.5 g; ID7–11); the '1 month' group was 32–37 days old (weight, 44.0 ± 1.9 g; ID12–15); and the '2–3 months' group was 63–99 days old (74.0 ± 15.9 g; ID16–20). After one experiment, juveniles were

Table 1. Summary of ID of juveniles, beaches where eggs were collected, the dates when they emerged from the nests, ages of the juveniles after the emergence when field experiments and tank experiments were conducted, straight carapace length (SCL), and body weight (BW). Juveniles were divided into 4 groups, which were 'emergence' (ID1–6), '2 weeks' (ID7–11), '1 month' (ID12–15), and '2–3 months' (ID16–20).

Group	ID	Egg collection beach	Dates of emergence	Age in days		SCL (cm)	BW (g)
				Field	Tank		
'emergence'	1	Ibaruma	25 Oct. 2006	1	2	4.46	22
	2	Ibaruma	25 Oct. 2006	1	2	4.52	22
	3	Ibaruma	4 Nov. 2006	1	2	4.60	22
	4	Ibaruma	4 Nov. 2006	1	2	4.60	24
	5	Ibaruma	4 Nov. 2006	1	2	4.77	24
	6	Ibaruma	25 Oct. 2006	1	2	4.81	24
'2 weeks'	7	Ibaruma	10 Oct. 2006	15	19	5.24	30
	8	Ibaruma	10 Oct. 2006	15	19	5.36	31
	9	Ibaruma	14 Oct. 2006	11	14	5.56	31
	10	Ibaruma	9 Oct. 2006	16	19	5.41	32
	11	Ibaruma	20 Oct. 2006	14	13	5.50	34
'1 month'	12	East Hirakubo	21 Sep. 2006	35	37	6.60	41
	13	East Hirakubo	21 Sep. 2006	34	37	6.50	44
	14	Ibaruma	1 Oct. 2006	33	32	6.10	45
	15	Ibaruma	5 Oct. 2006	35	32	6.30	45
'2–3 months'	16	Ibaruma	21 Aug. 2006	66	68	7.11	56
	17	Ibaruma	21 Aug. 2006	80	77	7.40	65
	18	Ibaruma	14 Aug. 2006	87	80	7.43	69
	19	Osaki	4 Sep. 2006	66	63	8.13	82
	20	East Hirakubo	2 Aug. 2006	99	92	8.61	97
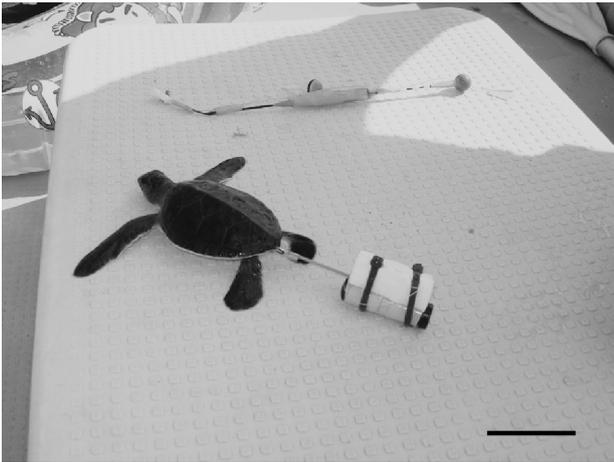
Fig. 1. A juvenile attached to the acceleration data logger. The scale bar indicates 5 cm.

stored in the containers for at least one night to allow them to recover from fatigue. They were subjected to the other experiment within 1 week. Both experiments were conducted between 9 am and 5 pm on sunny days with patchy clouds. After both experiments were finished, the juvenile turtles were released at the beach where their eggs were collected.

Acceleration data loggers

An acceleration data logger (UME190-D2GT; Little Leonardo Co. Ltd.; diameter 15 mm, length 53 mm, mass in air 15 g) attached to a wooden rod was towed behind a juvenile turtle (diameter 0.8 mm, length 5 cm) (Fig. 1). A hook attached to the end of the rod was inserted into a marginal scute at the posterior edge of the carapace (Witherington 1991). The wooden rod was as long as the juvenile's hind limbs, to prevent them from kicking the data logger. Foam polystyrene was attached to the data logger so that it maintained a nearly neutral buoyancy at the sea surface, which reduced the influence of the weight of the data logger on the juveniles. The device weighted 21.15 g on land and -0.36 g in water. A float was attached to the data logger through a fishing line (length 80 cm) to increase visibility during tracking. The acceleration data logger recorded longitudinal acceleration at 32 Hz in order to measure the flipper strokes while the logger was being towed by a juvenile.

Field experiment

Each juvenile was released at a beach near Ishigaki Tropical Station and allowed to swim towing the acceleration data logger. Five of the juveniles (ID3–5, 11, 14) were followed by a snorkeling observer for 30 min, while the other 15 juveniles were followed first by a snorkeling observer and then by a boat for a total of 1 h. The snorkeling observer followed no closer than 3 m behind the turtles and the boat stayed at least 10 m behind the turtles. Turtles swimming behavior was observed during the tracking. At the end of the

experiment, the acceleration data loggers and the juveniles were retrieved by the observers. Water temperature during the experiment was $26.0\pm0.6°C$.

Tank experiment

Each juvenile swam freely in a large tank (10×12 m, average depth 1.2 m) while towing an acceleration data logger and its attached float for about 25 min. There were few or no waves in the tank, which differed from the conditions at sea. While the turtles swam, their swimming behavior was recorded by a camcorder. Ten of these juveniles (ID1, 2, 6–10, 12, 13, 16; representing every group) also swam for about 10 min without towing a data logger, and their swimming behavior was recorded by a camcorder. Average flipper beat frequency of the juveniles was measured by video observation and the difference between them was investigated using a paired t-test to evaluate the effect of the data logger on flipper beat frequency. Water temperature during the experiment was $25.5\pm1.2°C$.

Data analysis

Data recorded in the data logger was downloaded to a computer and analyzed using Igor Pro Version 5.03 software (WaveMatrics Inc.). The power spectral density (PSD) was calculated from the acceleration data set of each juvenile to determine the predominant flipper beat frequency for each experiment (Sato et al. 2007). In the tank experiment, the periods when juveniles were touching the walls or resting were excluded. The predominant value in PSD was compared to the average stroke rate per powerstroking bout, as measured from the video analysis, using a paired t-test to confirm the validity of the dominant value in PSD as the flipper beat frequency. To evaluate the difference in activity between at sea and in the tank, the flipper beat frequency of each turtle in the tank was subtracted from its frequency at sea. The differences, excluding the effect of the body size, were compared among the 4 groups using one-way ANOVA and post hoc Scheffe's tests. Unless otherwise noted, values are presented as means$\pm$SD (n=sample number).

Results

Both at sea and in the tank, all juveniles swam by powerstroking (sweeping the foreflippers roughly up and down as a pair) interrupted by dogpaddling (moving the diagonally-opposite limbs together) while breathing (Wyneken 1997). Some juveniles occasionally stopped swimming in the tank, but all juveniles swam continuously at sea. All but two juveniles in the tank experiment (ID7, 9) and one juvenile in the field experiment (ID1) showed clear peaks of longitudinal acceleration while powerstroking (Fig. 2) and two peaks in PSD without the low frequency variations that were expected to be
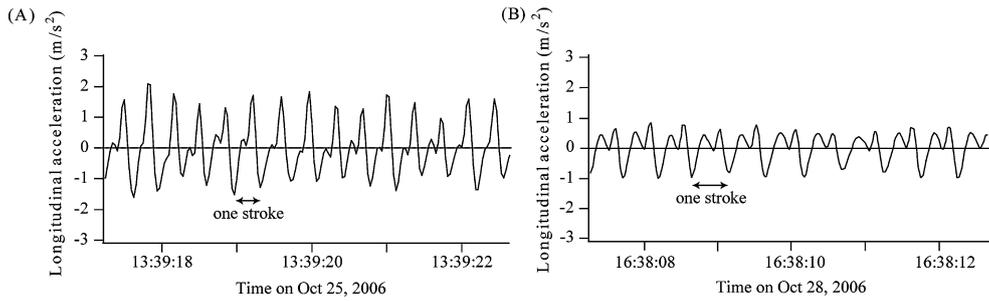
Fig. 2. Examples of longitudinal accelerations estimated to represent flipper beating of ID10 at sea (a) and in the tank (b). Arrows indicate examples of longitudinal acceleration representing one stroke cycles during powerstroking.
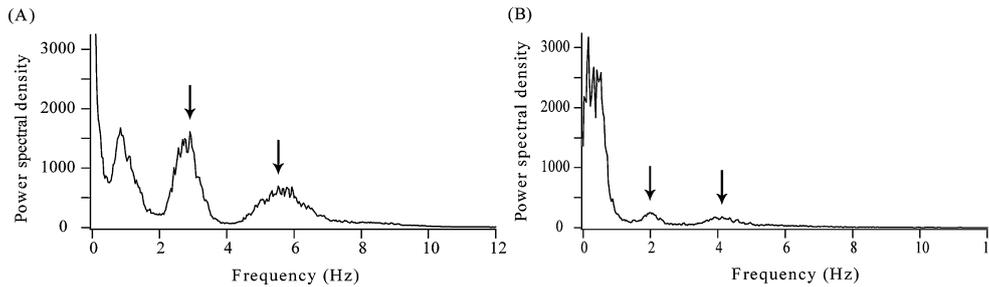
Fig. 3. Examples of PSD calculated from longitudinal accelerations of ID10 at sea (a) and in the tank (b). Arrows indicate peaks derived from flipper beating.

gravitational components (Tanaka et al. 2001, Sato et al. 2003, 2004) (Fig. 3). Analysis of the video in the tank experiment revealed that a single stroke cycle while powerstroking had one or two positive peaks of longitudinal acceleration (Fig. 2). Thus, the lower of two peaks in the PSD analyses was adopted as the flipper beat frequency because it was expected to represent the dominant flipper stroke cycle.

In the tank experiment, the dominant flipper beat frequency calculated by PSD (1.79 ± 0.47 Hz) was not significantly different from the average stroke cycle measured by video analyses (1.75 ± 0.39 Hz) (paired t-test; n=17, p=0.25). Therefore, we adopted the average stroke cycle measured by the video observation as the flipper beat frequency in the tank of the juveniles with unclear peaks in PSD (ID7 and ID9). We excluded the juvenile ID1 from subsequent analyses because we could not estimate the flipper beat frequency for it at sea. In the tank, the juveniles towing acceleration data loggers (1.84 ± 0.41 Hz) exhibited a significantly higher flipper beat frequency than the juveniles swimming with no acceleration data loggers (1.67 ± 0.33 Hz) (paired t-test; n=10, p<0.01).

The flipper beat frequency of juveniles at sea and in the tank is shown in Fig. 4. The one-way ANOVA showed significant differences in the activity induced by the sea among the 4 groups (p=0.004) (Fig. 4). The Scheffe's tests revealed significant differences between the 'emergence' and '2 weeks' (p=0.015) groups as well as between the '2 weeks' and '2-3 months' (p=0.009) groups, but no significant differences were found between other pairs (p=0.15–0.99) (Fig. 4). The
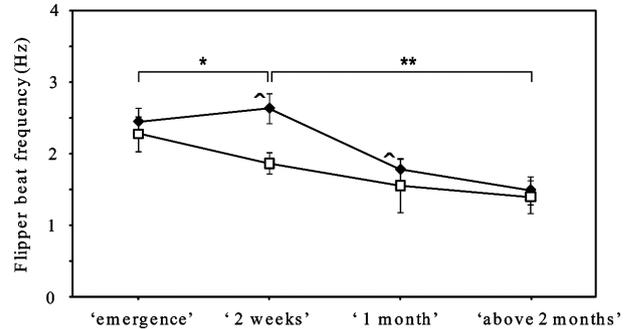
Fig. 4. Flipper beat frequency of juveniles at sea (solid diamond) and in the tank (open square). The flipper beat frequency of the juveniles at sea was 2.45 ± 0.20 Hz ('emergence'; n=5), 2.64 ± 0.21 Hz ('2 weeks'; n=5), 1.78 ± 0.16 Hz ('1 month'; n=4), and 1.49 ± 0.20 Hz ('2–3 months'; n=5). In contrast, that of the juveniles in the tank was 2.32 ± 0.25 Hz ('emergence'; n=5), 1.89 ± 0.16 Hz ('2 weeks'; n=5), 1.45 ± 0.27 Hz ('1 month'; n=4), and 1.41 ± 0.28 Hz ('2-3 months'; n=5). The significant differences in the mean difference in flipper beat frequency between at sea and in the tank among the 4 groups are noted by asterisks (*: p<0.05, **: p<0.01). The symbols (^) denote a mean difference significantly higher than zero (see text), indicating that flipper beat frequency was significantly higher at sea than in the tank.

95% confidence intervals of the mean difference in each group were from −0.11 to 0.37 ('emergence'), 0.51 to 0.99 ('2 weeks'), 0.06 to 0.60 ('1 month'), and −0.15 to 0.33 ('2–3 months'), indicating that flipper beat frequency in the '2 weeks' and '1 month' groups was significantly higher at sea than in the tank.

Discussion

Powerstroking interrupted by dogpaddling during breathing was observed during the early stages of sea turtle development (Frick 1976, Salmon and Wyneken 1987, Wyneken 1997, Salmon et al. 2004). Longitudinal acceleration had two positive peaks during most stroke cycles (Fig. 2). This may indicate that a single flipper stroke cycle for turtles includes an upstroke and a downstroke, both of which produce thrust during routine swimming (Davenport et al. 1984). On the other hand, some single stroke cycles had only one positive peak (Fig. 2). These stroke cycles would indicate that the blade of the flipper during an upstroke or a downstroke is held nearly parallel relative to the water flow, generating little or no lift or drag. This was previously observed during the upstroke of vigorous swimming in green turtle juveniles (Davenport et al. 1984), and the stroke cycles with one positive peak might simply represent vigorous swimming.

In this study, there were two peaks of longitudinal acceleration in the PSD, excluding low frequency variations that were expected to be gravitational components (Tanaka et al. 2001, Sato et al. 2003, 2004) (Fig. 3). The higher frequency peak corresponded to each flipper stroke, while the lower frequency peak corresponded to the dominant stroke cycle frequency (Sato et al. 2007). In the tank experiment, the dominant stroke cycle frequency calculated by PSD was not significantly different from the average stroke rate per powerstroking bout measured by video analyses. Thus, the dominant flipper beat frequency calculated by PSD represented the real flipper beat frequency per powerstroking bout. This indicates that an acceleration data logger towed by a juvenile turtle can record its flipper beating behavior. In the field experiment, the flipper beat frequency of the juveniles that seemed to be during the frenzy period, known as a highly energetic phase relocating hatchlings from shallow near-shore waters to deeper offshore waters (Salmon and Wyneken 1987, Wyneken and Salmon 1992), was 2.45 ± 0.20 Hz (n=5) (Fig. 4). This frequency was similar to that of hatchling green turtles during the frenzy period at sea (2.59 ± 0.20 Hz) (Salmon and Wyneken 1987). On the other hand, in the tank experiment, the flipper beat frequency of the juveniles in 'emergence' was 2.32 ± 0.25 Hz (n=6), which was similar to that of hatchling green turtles in the tank during the frenzy (2.2 ± 0.4 Hz; mean$\pm$SE) (Wyneken 1997). However, it is important to remember that the juveniles towing acceleration data loggers showed higher flipper beat frequency in the tank, probably due to the increment of the drag. There is a possibility that tethering the hatchlings or attaching the floats to them also exerted an influence on their flipper beat frequency in previous studies (Salmon and Wyneken 1987, Burgess et al. 2006, Jones et al. 2007). In this study, however, we focused on the difference in flipper beat frequency between at sea and in the tank swimming conditions, which was expected to be less influenced by the data logger assuming that data loggers affected juveniles both at sea and in the tank in the same manner.

The 95% confidence interval of the mean difference in flipper beat frequency showed that the flipper beat frequency of 'emergence' juveniles at sea was not significantly higher than in the tank (Fig. 4). Therefore, 'emergence' juveniles may have similar swimming activity at sea and in the tank. This may reflect the fact that juveniles in the frenzy period have high swimming activities both at sea and in the tank (Salmon and Wyneken 1987, Wyneken and Salmon 1992). On the other hand, flipper beat frequencies for '2 weeks' and '1 month' juveniles were significantly higher at sea than in the tank (Fig. 4), indicating higher swimming activity of these juveniles at sea at least for a short period of time. For example, wave motion is not only an orientation cue (Lohmann and Lohmann 1992, Wang et al. 1998), but it may also cue the turtles to swim. This higher flipper beat frequency may help them to reach the oceanic gyre habitat, suggesting that it would be important for hatchlings to accomplish offshore migration by about 1 month after emergence. However, Scheffe's tests indicated that while the response was significantly larger in the '2 weeks' group than in the 'emergence' or '2–3 months' groups, it was not significantly different between the '1 month' and 'emergence' or '2–3 months' groups (Fig. 4). Therefore, juveniles about 2 weeks old demonstrated higher activity at sea. No significant difference in flipper beat frequency between at sea and in the tank was shown in the '2–3 months' groups (Fig. 4), indicating that juveniles over 2 months may fail to display higher activity at sea. The results indicate that juveniles gradually decrease their activity at sea over the period of time from 2 weeks to 2 months of age. Although differences in how long turtles were held in captivity might affect their performance at different ages (Salmon et al. 2004), this trend may reflect their programmed adaptation to passive drifting in the ocean currents (Musick and Limpus 1997, Witherington 2002).

In conclusion, this is the first intensive study that shows the flipper beat frequency of juveniles at sea, revealing the differences in flipper beat frequency between juvenile green turtles at sea and in the tank. Our results show that simple tank observations may estimate juvenile activity erroneously. Also, the significant difference in two-week-old juveniles indicates that this increased swimming activity may help them to reach the oceanic gyre. The results raise concerns about determining the purpose of animal behaviors using only laboratory observations, and they indicate the importance of field observations. Although efforts to reduce the influence of data loggers are necessary, the loggers are useful to quantify the behavior of sea turtle juveniles at sea. In this way, evaluating the differences in the ontogenetic change in flipper

beat frequency of green turtle juveniles at sea and in the tank would enhance our knowledge about the changes in behavior that occur during dispersal migration.

Acknowledgements

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