The Journal of Experimental Biology 214, 3972-3976
© 2011. Published by The Company of Biologists Ltd
doi:10.1242/jeb.061747

RESEARCH ARTICLE

Locomotor activity during the frenzy swim: analysing early swimming behaviour in hatchling sea turtles

Carla M. Pereira[1,*], David T. Booth[1] and Colin J. Limpus[2]

[1]The University of Queensland, Physiological Ecology Group, School of Biological Sciences, Queensland 4072, Australia and
[2]Department of Environment and Resource Management, PO Box 2454, Brisbane, Queensland 4001, Australia

*Author for correspondence (carla.limapereira@uqconnect.edu.au)

Accepted 3 September 2011

SUMMARY

Swimming effort of hatchling sea turtles varies across species. In this study we analysed how swim thrust is produced in terms of power stroke rate, mean maximum thrust per power stroke and percentage of time spent power stroking throughout the first 18 h of swimming after entering the water, in both loggerhead and flatback turtle hatchlings and compared this with previous data from green turtle hatchlings. Loggerhead and green turtle hatchlings had similar power stroke rates and percentage of time spent power stroking throughout the trial, although mean maximum thrust was always significantly higher in green hatchlings, making them the most vigorous swimmers in our three-species comparison. Flatback hatchlings, however, were different from the other two species, with overall lower values in all three swimming variables. Their swimming effort dropped significantly during the first 2 h and kept decreasing significantly until the end of the trial at 18 h. These results support the hypothesis that ecological factors mould the swimming behaviour of hatchling sea turtles, with predator pressure being important in determining the strategy used to swim offshore. Loggerhead and green turtle hatchlings seem to adopt an intensely vigorous and energetically costly frenzy swim that would quickly take them offshore into the open ocean in order to reduce their exposure to near-shore aquatic predators. Flatback hatchlings, however, are restricted in geographic distribution and remain within the continental shelf region where predator pressure is probably relatively constant. For this reason, flatback hatchlings might use only part of their energy reserves during a less vigorous frenzy phase, with lower overall energy expenditure during the first day compared with loggerhead and green turtle hatchlings.

Key words: frenzy, swimming behaviour, power stroke rate, thrust, energy, hatchling sea turtle, predator.

INTRODUCTION

The highest rate of mortality in sea turtles is thought to occur in embryos in the nest and/or in newly emerged hatchlings as they crawl down the beach and swim offshore (Crouse et al., 1987). Once the newly emerged hatchlings reach the ocean, they engage in a frantic swim, commonly known as the 'swim frenzy' (Lohmann et al., 1997). This continuous energetically demanding swim usually lasts about 24 h after emergence and quickly transports hatchlings to offshore oceanic currents (Salmon and Wyneken, 1987; Hays et al., 2010; Putman et al., 2010), while relying solely on their yolk reserves (Wyneken and Salmon, 1992; Wyneken, 1997). It has been suggested that these dispersion patterns could persist throughout adulthood, with post-breeding adults using similar routes when migrating from breeding areas to their distant foraging grounds (Hays et al., 2010). During the swim frenzy, hatchlings usually alternate between bouts of a high thrust production, lift-based movement of the fore-flippers, the 'power stroking' gait, and bouts of a lower thrust production 'dog paddling' gait in which alternate movement of all four flippers in a paddle-like motion produces drag-based thrust (Salmon and Wyneken, 1987; Wyneken and Salmon, 1992). Power stroking bouts typically last between 2 and 20 s and are interspersed with short periods of dog paddling (1–5 s), when hatchlings surface to breathe (Salmon and Wyneken, 1987; Burgess et al., 2006; Booth, 2009) (Fig. 1). Power stroke rates and oxygen consumption are highest immediately after the hatchlings enter the water and decline as the swim frenzy progresses (Salmon and Wyneken, 1987; Wyneken and Salmon, 1992; Burgess et al., 2006; Booth, 2009; Ischer et al., 2009). As power stroking bouts become less intense, dog paddling bouts become longer and resting periods may increase over time (Burgess et al., 2006). Booth showed that swimming effort in green turtle *Chelonia mydas* (Linnaeus 1758) hatchlings can be divided into three phases: (a) rapid fatigue, from 0 to 2 h; (b) slow fatigue, from 2 to 12 h; and (c) sustainable swimming effort, from 12 to 18 h (Booth, 2009). The decrease in swimming effort is the result of a decrease in power stroke rate during power stroking bouts, a decrease in the proportion of time spent power stroking and a decrease in thrust produced per power stroke (Booth, 2009). Other studies have shown that there are intra-specific (Wyneken et al., 2008) and inter-specific (Wyneken and Salmon, 1992; Jones et al., 2002; Jones et al., 2007) differences in sea turtle hatchling swimming behaviour. Green turtle hatchlings have the largest aerobic scope (ratio between oxygen consumption at rest and oxygen consumption during maximal swimming) and both green turtle and leatherback turtle *Dermochelys coriacea* (Vandelli 1761) hatchlings consume oxygen at a higher rate than loggerhead turtle *Caretta caretta* (Linnaeus 1758) hatchlings during the swim frenzy (Wyneken, 1997). Flatback turtle *Natator depressus* (Garman 1880) hatchling oxygen consumption rate during the first hours of the frenzy swim is lower than that of green turtle but higher than that of loggerhead turtle hatchlings (C.M.P., D.T.B. and C.J.L.,

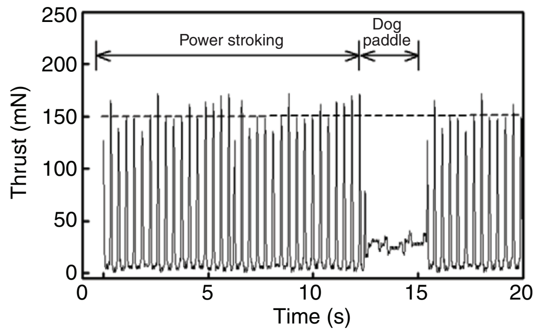

Fig. 1. Sample of thrust produced by green turtle hatchlings during swimming (modified from Booth and Evans, 2011), showing the power stroking and dog paddling behaviours. The dashed line represents the mean maximum thrust per power stroke.

unpublished). Swimming speed and power stroking rates also vary among species, with green turtle hatchlings having the highest values, followed by loggerhead turtle hatchlings, with lowest values in leatherback turtle hatchlings (Wyneken, 1997). Although seemingly less active, when motivated, flatback hatchlings can be faster swimmers than green turtles (Salmon et al., 2010), as they seem to be able to detect predators and take avoidance action (Salmon et al., 2009), unlike green turtle hatchlings, which keep swimming straight ahead when approached by predators (Gyuris, 1994). Each species appears to have developed a different swimming strategy in response to predator pressure in shallow near-shore waters (Chung et al., 2009a; Chung et al., 2009b; Salmon et al., 2009). Hatchings of green turtles, loggerhead turtles and leatherback turtles engage in a frenzy swim as they enter the sea in order to minimize the time spent in shallow water and thus decrease the chance of encountering predators (Gyuris, 1994; Gyuris, 2000; Booth et al., 2004; Whelan and Wyneken, 2007; Salmon et al., 2009). Hawksbill *Eretmochelys imbricata* (Linnaeus 1766) hatchlings, however, appear to use a different strategy in which they may hide in flotsam or remain inactive to minimize detection by predators during the first few days of off-shore dispersion (Chung et al., 2009a). Flatback turtle hatchlings, on the other hand, appear to have a less intensive (C.M.P., D.T.B. and C.J.L., unpublished) but more prolonged frenzy swim period of up to 4 days (Salmon et al., 2009), although this species' swimming behaviour is still poorly understood (Wyneken, 1997; Salmon et al., 2009).

In this study we analysed differences in swimming behaviour in terms of thrust production, power stroke rate during a power stroking bout, mean maximum thrust per power stroke and the proportion of time spent power stroking in loggerhead turtle and flatback turtle hatchlings and compared it with previous data from green turtle hatchlings. We hypothesized that flatback hatchlings would have a less vigorous frenzy swim characterized by lower power stroke rates and longer dog paddling periods because they do not swim long distances to reach oceanic currents but instead remain in inshore water inside the continental shelf (Limpus, 2008b).

MATERIALS AND METHODS

Study site

This research conforms with Australian Animal Welfare laws and was approved by a University of Queensland Animal Ethics Committee (approval no. SBS/481/09).

We conducted this study at Mon Repos Conservation Park (24°48′S, 152°27′E), the largest and best monitored turtle rookery on the east coast of the Australian mainland (Pfaller et al., 2008). This rookery typically has 200–300 loggerhead turtle (*C. caretta*) females and 5–10 flatback turtle (*N. depressus*) females nesting each nesting season (Limpus et al., 1984; Limpus and Limpus, 2003; Limpus, 2008a; Limpus, 2008b).

Evaluation of swimming behaviour

Newly emerged loggerhead and flatback turtle hatchlings were collected between 5 January and 11 February 2010. We monitored nests for emergence throughout the night, and when an emergence event occurred, a single hatchling from a nest was captured and transported dry in a bucket to the laboratory. This process took between 10 and 15 min and during transport hatchlings crawled around inside the bucket, a behaviour similar to a wild hatchling crawling down the beach towards the sea.

Swimming behaviour was measured during the first 18 h of swimming by a previously published method (Booth, 2009). Briefly, hatchlings were placed in a tank (34 cm long × 28 cm wide × 19 cm high) filled with 16 cm of 28°C seawater, the average offshore water temperature at Mon Repos (28±1°C) (Bennett, 1986). The tank was painted black except on one side, where a low intensity light was placed to induce directional swimming. The hatchling was fitted with a lycra harness with an attached monofilament tether, connected to a force transducer to measure thrust produced during swimming (MLT050 ADInstruments, Colorado Springs, CO, USA). The force transducer was connected to a bridge amplifier (ML112 ADInstruments) and the output of the bridge amplifier recorded via a data acquisition system (Power Lab 8/20 using LabChart v6.0 software, ADInstruments). Thrust was sampled at 40 Hz. The length of the tether was adjusted so that the hatchling could swim freely without touching the walls or bottom of the tank. The force transducer was calibrated before and after each swimming trial by suspending a known mass from the force transducer. Water temperature in the tank was monitored by a thermocouple converter (SMCJ-T Omega.com, Omega Engineering Inc., Stamford, CT, USA). Mean thrust, mean stroke rate per power stroking bout and proportion of time spent power stroking were calculated for each individual hatchling turtle, using LabChart v6.0, at 10 min intervals throughout the entire 18 h period of swimming. All results were confirmed manually and corrected if necessary. In addition, the mean maximum thrust produced in each power stroking bout was also determined for each hatchling by scanning the raw data and calculating the mean between peaks of overall thrust (Fig. 1) at 10 min intervals. Change points were calculated in R (www.r-project.org) with the methods of CUSUM and Segmented Linear Models to estimate when there was a significant change in swimming behaviour.

Statistical analysis

Data of green turtle hatchlings from a previous study (Booth, 2009) were included to enable comparisons across three species. Repeated measures ANOVA were used to assess the effect of time and species on mean thrust production, stroke rate during a power stroking bout, mean maximum thrust per power stroking bout and repeated measures ANOVA after an arcsin transformation used to compare the proportion of time spent power stroking. For all four variables, a Tukey *post hoc* test for uneven sample sizes was used for cross-species comparisons at four different times: the first 10 min (0–10 min), at 2 h (1 h 50 min to 2 h), at 12 h (11 h 50 min to 12 h) and the last 10 min (17 h 50 min to 18 h) of the swimming trial. Statistical significance was assumed if $P<0.05$.

RESULTS

A total of 28 hatchlings were swum: 15 loggerhead turtles and 13 flatback turtles; data from 5 green turtle hatchlings collected by Booth (Booth, 2009) were also included for comparison. Hatchlings swam no more than a centimetre below the surface, a behaviour that has been described as typical during the off-shore swimming of hatchling sea turtles, probably to reduce surface drag (Hays et al., 2001) and minimize their visibility to aerial predators (Witherington and Salmon, 1992; Hays, 2001). The change point analysis did not accurately distinguish the exact 10 min period when the rate of change of a variable occurred because of individual variation, so we report such changes in terms of a range of time periods when these transitions were made.

Mean thrust production

Mean thrust production decreased with swimming time in all three species (P<0.001) and was significantly different between species (P<0.001). The pattern of change of mean thrust production was similar in green turtle and loggerhead turtle hatchlings: a relatively rapid decline in mean thrust during the first 2 h, followed by a more gradual decline with significant changes between 5 and 8 h and between 10 and 12 h, after which mean thrust remained relatively constant (Fig. 2A). In flatback turtle hatchlings, mean thrust declined relatively rapidly during the first 2 h, and then continued to decrease at a moderate rate until the trial ended at 18 h (Fig. 2A). Mean thrust production was similar in green and flatback turtle hatchlings but greater than that in loggerhead turtle hatchlings during the first 10 min of swimming. At 2 h, mean thrust was greatest in green turtles, intermediate in flatback turtles and lowest in loggerhead turtles. At 12 h, green turtles still maintained the greatest mean thrust, while the thrust of flatback turtles had fallen to a level similar to that of loggerhead turtles, and by 18 h green turtles remained the strongest thrust generators, followed by loggerhead turtles, with flatback turtles now producing the lowest thrust (Fig. 2A).

Power stroke rate during a power stroking bout

Power stroke rate during a power stroking bout decreased with swimming time (P<0.001) and was significantly different between species (P<0.001), with loggerhead and green turtles having similar power stroking rates throughout the entire 18 h trial (Fig. 2B). The magnitude and pattern of the decrease in power stroke rate was almost identical in green and loggerhead turtle hatchlings: a rapid decrease in the first 2 h, followed by a slower decrease until 8–12 h, with stroke rate then remaining relatively constant until the end of the trial (Fig. 2B). Power stroke rate of flatback turtle hatchlings was lower than that of green and loggerhead turtle hatchlings throughout the swimming trial, and decreased at a relatively rapid rate during the first 4 h of swimming, before remaining relatively constant for the last 14 h of the 18 h swimming trial (Fig. 2B).

Mean maximum thrust per power stroke

Mean maximum thrust per power stroke decreased with swimming time (P<0.001) and was significantly different between species (P<0.001). The pattern of change in mean maximum thrust with time was similar in green and loggerhead hatchlings, with a gradual decrease for the first 10–12 h, after which it remained relatively constant (Fig. 2C). However, maximum thrust for green turtles was approximately twice that of loggerhead turtles (Fig. 2C). Mean maximum thrust of flatback turtle hatchlings decreased rapidly during the first 2 h of swimming, continued to decrease gradually until 10–12 h and then remained relatively constant (Fig. 2C). Mean maximum thrust was significantly lower for flatback turtle hatchlings than for both green and loggerhead turtle hatchlings from 4 to 18 h.

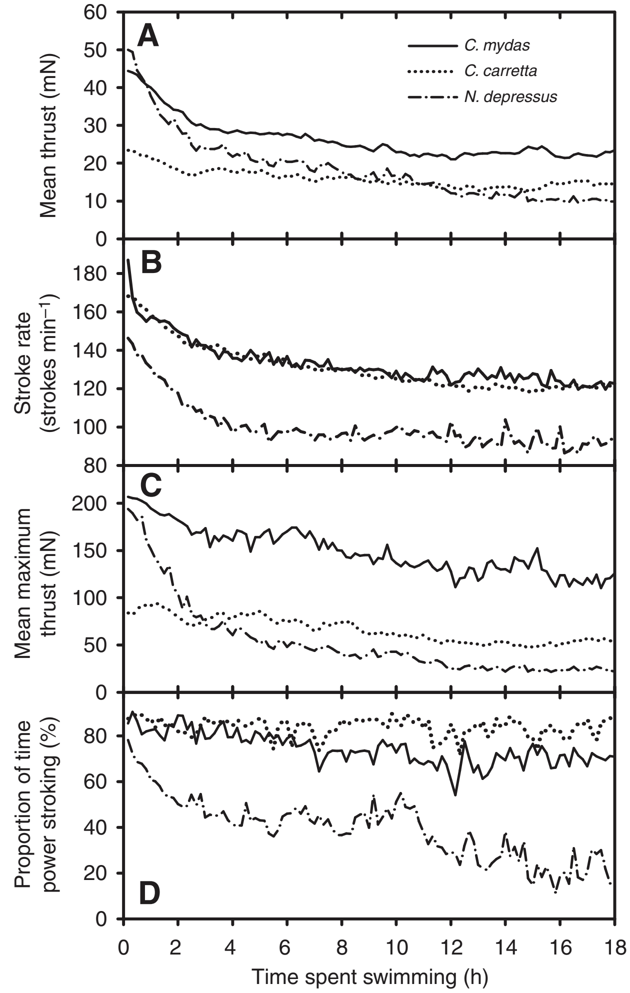

Fig. 2. Change in swimming variables with swimming time during the first 18 h of the frenzy swim of green (*Chelonia mydas*), loggerhead (*Caretta caretta*) and flatback (*Natator depressus*) turtle hatchlings swum in seawater at 28°C. (A) Mean thrust. (B) Power stroke rate during a power stroking bout. (C) Mean maximum thrust per power stroke. (D) Proportion of time spent power stroking.

Proportion of time spent power stroking

The proportion of time spent power stroking remained relatively constant throughout the 18 h swimming trial in loggerhead turtle hatchlings (mean 85%, range 72–89%) and decreased slightly from 85% to 70% over the 18 h swimming trial in green turtle hatchlings, but there was no significant difference between loggerhead and green turtle hatchlings (Fig. 2D). In green turtle hatchlings, the decrease from 85% to 70% occurred between 10 and 12 h (Fig. 2D). The proportion of time spent power stroking by flatback hatchlings decreased from 80% to 50% in the first 2 h of swimming, with another significant change around 10–12 h (decrease from 50% to 30%), from which it continued to decrease slowly until it reached just 20% by the end of the swimming trial (Fig. 2D).

DISCUSSION

The method used to assess the swimming effort in this study has been used before on hatchling sea turtles and is a good estimate of the free-swimming behaviour (Wyneken, 1997). Despite the generally similar pattern of decrease in mean swim thrust with time in green, loggerhead and flatback turtle hatchlings, there were differences in the swimming behaviour of flatback turtle hatchlings compared with that of loggerhead and green turtle hatchlings.

Loggerhead and green turtle hatchlings

Loggerhead hatchling swimming behaviour during the first 18 h of the swim frenzy is similar to that reported by Booth for green turtle hatchlings (Booth, 2009), in that it can be divided into three, possibly four, distinct phases: rapid fatigue (0–2 h), slow fatigue (2–12 h, possibly divided into a block between 5 and 8 h and another between 10 and 12 h) and sustainable effort (12–18 h). There were no significant differences in either power stroke rate during a power stroking bout or the proportion of time spent power stroking over the entire 18 h swimming trial between green and loggerhead turtle hatchlings (Fig. 2B,D), but there was a difference in mean maximum thrust (Fig. 2C). During the rapid and slow fatigue phases, decreased swimming effort in both species was caused by decreases in both stroke rate and mean thrust per stroke, but the percentage of time spent power stroking remained relatively constant. The pattern of decrease in mean maximum thrust with swimming time was also very similar in green and loggerhead turtle hatchlings, although green turtle hatchlings always had a maximum thrust that was twice that of loggerhead turtles (Fig. 2C) and, consequently, mean thrust of green turtle hatchlings was also twice that of loggerhead turtle hatchlings (Fig. 2A). Wyneken has shown that green and loggerhead turtle hatchlings have the same flipper movement while power stroking and dog paddling (Wyneken, 1997); therefore, the differences in swim thrust cannot be attributed to differences in swimming pattern. We believe these differences are related to fore-flipper size. Green turtle hatchlings from Heron Island are larger in size and have a larger front-flipper total length (FTL) to straight carapace length (SCL) ratio (0.97, D.T.B., unpublished), compared with loggerhead hatchlings from Mon Repos (0.93, C.M.P., D.T.B. and C.J.L., unpublished). The higher swim speed of green turtle hatchlings (Wyneken, 1997) could also be a consequence of these differences in morphology.

Flatback turtle hatchlings

Flatback turtle hatchlings have different swimming attributes from those of green and loggerhead turtle hatchlings. Although also showing the largest decrease in swimming effort within the first 2 h of entering the water, the swimming effort of flatback turtle hatchlings, unlike that of green and loggerhead turtles, continued to decrease throughout the 18 h swimming trial. The decrease in swimming effort during the first 2 h was also much sharper than that of green and loggerhead turtle hatchlings. In flatback turtle hatchlings, the decrease in swimming effort was caused by decreases in all three swimming variables: power stroking rate, mean maximum thrust per stroke and percentage of time spent power stroking; as in green and loggerhead turtle hatchlings, the proportion of time spent power stroking did not change much during the 18 h swimming trial. Compared with that of green and loggerhead turtle hatchlings, flatback turtle hatchling stroke rate during a power stroking bout was much lower (Fig. 2B), less time was spent power stroking (Fig. 2D), and their maximum thrust per power stroke, although starting high, rapidly decreased during the first 2 h of swimming (Fig. 2C). Flatback turtle hatchling mean FTL is 4.76 ± 0.05 cm (C.M.P., D.T.B. and C.J.L., unpublished), with a body ratio FTL/SCL of 0.8, which is lower than that of green and loggerhead turtle hatchlings and may explain why flatback hatchlings have a relative low maximum thrust per power stroke. Salmon and colleagues showed that flatback hatchlings spend their entire first day swimming and that the proportion of time spent swimming only falls slightly during the next 3 days (Salmon et al., 2009), implying that flatback turtle hatchlings might have a greater and more sustained frenzy swim than green or loggerhead turtle hatchlings. However, the older technology used in their study (Salmon et al., 2009) only allowed them to detect whether a hatchling was swimming or not swimming, and could not detect the thrust produced during swimming, or the proportion of time spent power stroking or dog paddling. The current study also found that flatback hatchlings swim close to 100% of the time during the first day, but although the turtles remained continuously active, the swimming effort decreased remarkably, and the proportion of time spent power stroking decreased and the proportion of time spent dog paddling increased dramatically during this time.

Ecological interpretation

These results support the hypothesis posed initially that flatback hatchlings would have a different swimming behaviour from that of green and loggerhead turtles because of their different life-history pattern. Flatback turtles do not have an oceanic phase and this might be the reason for the shorter period of vigorous swimming during their dispersion. A short vigorous spurt might be enough to allow the hatchlings to escape the presumed higher predation pressure of the shallow near-shore waters and, once this is achieved, a more relaxed swimming effort suffices. According to the 'predation risk hypothesis' (Chung et al., 2009a; Chung et al., 2009b), species like the green and loggerhead turtle are expected to have a change in swimming behaviour as they leave shallow near-shore waters and enter deeper off-shore waters, given the predation pressure adjacent to the natal beach is likely to be much higher than the predation pressure off-shore in oceanic currents where hatchlings spend the next few years of their life (Salmon et al., 2009). The dramatic drop-off in swimming effort in the first 2 h (this study), followed by further decreases in swim effort over the next week (Wyneken and Salmon, 1992) by green and loggerhead turtle hatchlings is consistent with this hypothesis. In species like the flatback turtle, where the predation pressure off the natal beach is thought to be similar to that in near-shore waters, the predation hypothesis predicts little change in sea turtle hatchling swimming behaviour (Salmon et al., 2009). The finding that the proportion of time that flatback hatchlings spend swimming changes little over the first 4 days of swimming supports this hypothesis (Salmon et al., 2009). However, in this study we found that, although swimming is continuous during the first 18 h after entering the water, as previously suggested, swimming effort decreases dramatically during the first 2 h and continues to decrease during the following 16 h, which is consistent with the predation hypothesis if the predation pressure on flatback hatchlings is highest immediately adjacent to the nesting beach. Further studies on predation rates of flatback turtle hatchlings during the off-shore dispersion phase are encouraged, in order to confirm the importance of the predation hypothesis in shaping their swimming behaviour.

The lower overall swimming effort of flatback turtle hatchlings, along with the possibility of bigger yolk reserves as a consequence of a bigger body mass (Walker and Parmenter, 1990), suggests that flatback turtles could survive without feeding for a longer period of time than either green or loggerhead hatchlings. Indeed, flatback hatchlings confined to pools do not show any interest in feeding during the first 4 days in the water, unlike loggerhead and green hatchlings, which start feeding after 2–3 days (Salmon et al., 2009). The ability to have a prolonged fasting period may also be advantageous for flatback hatchlings because they live in turbid shallow waters where visibility is generally low (Salmon et al., 2009; Salmon et al., 2010), and the search for food while avoiding predator encounters could be challenging.

In conclusion, loggerhead and green turtle hatchlings have very similar frenzy swim behaviour, one that rapidly takes them away from high predation near-shore waters into off-shore oceanic currents. Although flatback turtle hatchlings have a seemingly similar frenzy swim pattern to that of loggerhead and green turtle hatchlings, their swimming effort decreases more dramatically in the first 2 h and continuously decreases for at least 16 h. This decrease in swimming effort is probably associated with their shorter off-shore dispersion and management of their energy reserves, as finding food may be more difficult in the turbid waters of their post-hatch habitat.

ACKNOWLEDGEMENTS

We thank the Mon Repos Conservation Park staff and volunteers and the DERM Turtle Conservation Volunteers for the help provided during the field work.

FUNDING

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

REFERENCES

Bennett, J. M., Taplin, L. E. and Grigg, G. C. (1986). Sea water drinking as a homeostatic response to dehydration in hatchling loggerhead turtles *Caretta caretta. Comp. Biochem. Physiol.* **83A**, 507-513.

Booth, D. T. (2009). Swimming for your life: locomotor effort and oxygen consumption during the green turtle (*Chelonia mydas*) hatchling frenzy. *J. Exp. Biol.* **212**, 50-55.

Booth, D. T. and Evans, A. (2011). Warm water and cool nests are best. How global warming might influence hatchling green turtle swimming performance. *PloS ONE* **6**, e23162. doi:10.1371/journal.pone.0023162.

Booth, D. T., Burgess, E., McCosker, J. and Lanyon, J. M. (2004). The influence of incubation temperature on post-hatching fitness characteristics of turtles. *Elsevier* **1275**, 226-233.

Burgess, E. A., Both, D. T. and Lanyon, J. M. (2006). Swimming performance of hatchling green turtles is affected by incubation temperature. *Coral Reefs* **25**, 341-349.

Chung, F. C., Pilcher, N. J., Salmon, M. and Wyneken, J. (2009a). Offshore migratory activity of hawksbill turtle (*Eretmochelys imbricata*) hatchlings, I. Quantitative analysis of activity, with comparison to green turtles (*Chelonia mydas*). *Chelonian Conserv. Biol.* **8**, 28-34.

Chung, F. C., Pilcher, N. J., Salmon, M. and Wyneken, J. (2009b). Offshore migratory activity of hawksbill turtle (*Eretmochelys imbricata*) hatchlings, II. Swimming gaits, swimming speed, and morphological comparisons. *Chelonian Conserv. Biol.* **8**, 35-42.

Crouse, D. T., Crowder, L. B. and Caswell, H. (1987). A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology* **68**, 1412-1423.

Gyuris, E. (1994). The rate of predation by fishes on hatchlings of green turtle. *Coral Reefs* **13**, 137-144.

Gyuris, E. (2000). The relationship between body size and predation rates on hatchlings of the green turtle (*Chelonia mydas*): is bigger better? In *Sea Turtles of the Indo-Pacific: Research, Management and Conservation* (ed. N. Pilcher and M. Ismail), pp. 143-147. New York: Academic Press.

Hays, G. C., Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Luschi, P., Martin, C., Metcalfe, J. D. and Papi, F. (2001). The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive duration, dive profiles and depth distribution. *J. Exp. Biol.* **204**, 4093-4098.

Hays, G. C., Fossette, S., Katselidis, K. A., Mariani, P. and Schofield, G. (2010). Ontogenetic development of migration: Lagrangian drift trajectories suggest a new paradigm for sea turtles. *J. R. Soc. Interface* **7**, 1319-1327.

Ischer, T., Ireland, K. and Booth, D. T. (2009). Locomotion performance of green turtle hatchlings from Heron Island Rookery, Great Barrier Reef. *Mar. Biol.* **156**, 1399-1409.

Jones, T., Reina, R. and Lutz, P. (2002). A comparison of the ontogeny of oxygen consumption in leatherbacks, *Dermochelys coriacea*, and olive ridley, *Lepydochelys olivacea*, sea turtle hatchlings – different strokes for different life styles. *NOAA Tech. Memo.* NMFS-SEFSC-503, 191-192.

Jones, T. T., Reina, R., Darveau, C. and Lutz, P. L. (2007). Ontogeny of energetics in leatherback (*Dermochelys coriacea*) and olive ridley (*Lepidochelys olivacea*) sea turtle hatchlings. *Comp. Biochem. Physiol.* **147A**, 313-322.

Limpus, C. J. (2008a). *A Biological Review of Australian Marine Turtles. 1. Loggerhead Turtle Caretta Caretta (Linnaeus).* Freshwater and Marine Sciences Unit, Environmental Sciences Division, ISBN 978-0-9803613-2-2 (online).

Limpus, C. J. (2008b). *A Biological Review of Australian Marine Turtles. 5. Flatback Turtle Natator Depressus (Garman).* Freshwater and Marine Sciences Unit, Environmental Sciences Division, ISBN 978-0-9803613-2-2 (online).

Limpus, C. J. and Limpus, D. J. (2003). Loggerhead turtles in the Equatorial and Southern Pacific Ocean: a species in decline. In *Loggerhead Sea Turtles* (ed. A. B. Bolten and B. E. Witherington), pp. 199-209. Washington DC: Smithsonian Institution.

Limpus, C. J., Fleay, A. and Baker, V. (1984). The flatback turtle, *Chelonia depressa*, in Queensland: reproductive periodicity, philopatry and recruitment. *Aust. Wildlife Res.* **11**, 579-587.

Lohmann, K. J., Witherington, B. E., Lohmann, C. M. F. and Salmon, M. (1997). Orientation, navigation and natal beach homing in sea turtles. In *The Biology Of Sea Turtles* (ed. P. L. Lutz and J. A. Musick), pp. 107-135. Florida: CRC Press.

Pfaller, J. B., Limpus, C. J. and Bjornal, K. A. (2008). Nest-site selection in individual loggerheads turtles and consequences for doomed-egg relocation. *Conserv. Biol.* **23**, 72-80.

Putman, N. F., Bane, J. M. and Lohman, K. J. (2010). Sea turtle nesting distributions and oceanographic constraints on hatchlings migration. *Proc. Biol. Sci.* **277**, 3631-3637.

Salmon, M. and Wyneken, J. (1987). Orientation and swimming behaviour of hatchling loggerhead turtles *Caretta caretta* L. during their offshore migration. *J. Exp. Mar. Biol. Ecol.* **109**, 137-153.

Salmon, M., Hamann, M., Wyneken, J. and Schauble, C. (2009). Early swimming activity of the hatchling flatback sea turtles *Natator depressus*: a test of the predation risk hypothesis. *Endang. Species Res.* **9**, 41-47.

Salmon, M., Hamann, M. and Wyneken, J. (2010). The development of early diving behaviour by juvenile flatback sea turtles (*Natator depressus*). *Chelonian Conserv. Biol.* **9**, 8-17.

Walker, T. A. and Parmenter, C. J. (1990). Absence of a pelagic phase in the life cycle of flatback turtle, *Natator depressa* (Garman). *J. Biogeogr.* **17**, 275-278.

Whelan, C. L. and Wyneken, J. (2007). Estimating predation levels and site-specific survival of hatchling loggerhead sea turtles (*Caretta caretta*) from South Florida beaches. *Copeia* **3**, 745-754.

Witherington, B. E. and Salmon, M. (1992). Predation on loggerhead turtle hatchlings after entering the sea. *J. Herpetol.* **26**, 226-228.

Wyneken, J. (1997). Sea turtle locomotion: mechanisms, behaviour and energetic. In *The Biology Of Sea Turtles* (ed. P. L. Lutz and J. A. Musick), pp. 165-198. Florida: CRC Press.

Wyneken, J. and Salmon, M. (1992). Frenzy and postfrenzy swimming activity in loggerhead, green and leatherback hatchlings sea turtles. *Copeia* **2**, 478-484.

Wyneken, J., Madrak, S. V., Salmon, M. and Foote, J. (2008). Migratory activity by hatchling loggerhead sea turtles (*Caretta caretta* L.): evidence for divergence between nesting groups. *Mar. Biol.* **156**, 171-178.