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Swimming for your life: locomotor effort and oxygen consumption during the green turtle (*Chelonia mydas*) hatchling frenzy

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SUMMARY

Swimming effort and oxygen consumption of newly emerged green turtle *Chelonia mydas* hatchlings was measured simultaneously and continuously for the first 18 h of swimming after hatchlings entered the water. Oxygen consumption was tightly correlated to swimming effort during the first 12 h of swimming indicating that swimming is powered predominantly by aerobic metabolism. The patterns of swimming effort and oxygen consumption could be divided into three distinct phases: (1) the rapid fatigue phase from 0 to 2 h when the mean swim thrust decreased from 45 to 30 mN and oxygen consumption decreased from 33 to 18 ml h^{-1}; (2) the slow fatigue phase from 2 to 12 h when the mean swim thrust decreased from 30 to 22 mN and oxygen consumption decreased from 18 to 10 ml h^{-1}; and (3) the sustained effort phase from 12 to 18 h when mean swim thrust averaged 22 mN and oxygen consumption averaged 10 ml h^{-1}. The decrease in mean swim thrust was caused by a combination of a decrease in front flipper stroke rate during a power stroking bout, a decrease in mean maximum thrust during a power stroking bout and a decrease in the proportion of time spent power stroking. Hence hatchlings maximise their swimming thrust as soon as they enter the water, a time when a fast swimming speed will maximise the chance of surviving the gauntlet of predators inhabiting the shallow fringing reef before reaching the relative safety of deeper water.

Key words: aerobic metabolism, swimming, sea turtle, performance, oxygen consumption.

INTRODUCTION

The first few hours after emerging from the nest are important in determining a sea turtle's chances of recruiting to the oceanic life stage. During this time sea turtles scramble down the beach to the water's edge and then swim to off-shore waters to begin their oceanic life stage. On coral cay rookeries, predation rates average 30% and can be as high as 85% during this vital period, with the majority of deaths occurring in the first few minutes of swimming as hatchlings traverse the relatively shallow near-shore waters (Gyuris, 1994; Gyuris, 2000; Pilcher et al., 2000), but on mainland rookeries predation rates may be much lower averaging about 5% (for a review, see Whelan and Wyneken, 2007). Immediately after entering the water, hatchling sea turtles begin a phase of hyperactivity (frenzy) that is characterised by almost continuous swimming for up to 24 h (Wyneken and Salmon, 1992; Wyneken, 1997). Swimming is achieved by 'power stroking' bouts lasting 2–10 s in which the front flippers are moved in an up and down flying motion to generate lift-drag-lift-based forward thrust (Carr and Ogren, 1960; Davenport et al., 1984; Salmon and Wyneken, 1987; Wyneken, 1997; Burgess et al., 2006). These power stroking bouts are typically separated by brief 1–5 s periods of 'dog paddling'. This occurs when the head is raised to take a breath and the gait switches from front flippers only movement to one in which diagonally opposite flippers move together (Salmon and Wyneken, 1987; Wyneken, 1997; Burgess et al., 2006). As the time since entering the water lengthens, power stroke rates slow, dog paddling bouts become longer, and periods of 'rest' may occur, when there are no flipper movements (Burgess et al., 2006). While swimming out to sea, hatchling green turtles (*Chelonia mydas* Linnaeus) take no evasive action when approached by aquatic predators; their sole anti-predator tactic appears to be swimming as fast as possible across the predator-rich shallow near-shore waters and thus minimising the time they are exposed to heavy fish predation (Gyuris, 1994).

Because the swimming effort of hatchlings is prolonged, it is assumed to be supported almost exclusively by aerobic metabolism (Wyneken, 1997). However, measurement of blood lactate levels suggests that both aerobic and anaerobic metabolism power swimming within the first 10–15 min of hatchlings entering the water (Baldwin et al., 1989). In a study that measured oxygen consumption ($\dot{V}_{O_2}$) of hatchling sea turtles during and after the frenzy, $\dot{V}_{O_2}$ during the frenzy period was found to be considerably greater than in the post-frenzy period (Wyneken, 1991; Wyneken, 1997). However, given the fact that swimming effort during the frenzy period declines considerably as time proceeds (Wyneken, 1997; Booth et al., 2004; Burgess et al., 2006), it is unlikely that $\dot{V}_{O_2}$ would remain constant during the frenzy period. In this study I measured both the swimming effort and the $\dot{V}_{O_2}$ of newly emerged green turtle hatchlings simultaneously and continuously during their first 18 h of swimming in order to test the hypothesis that rates of oxygen consumption should correlate with swimming effort during this vital period.

MATERIALS AND METHODS

This study was conducted on Heron Island (23°26′S, 151°51′E), a vegetated coral cay in the Capricorn-Bunker island group at the southern end of the Great Barrier Reef, Australia. During the week of 4–11 December 2007 the location of green turtle nests was noted. During the week of 28 January–3 February 2008 these nests were relocated and corrals made from plastic mesh (1 m in diameter, 15 cm high) were placed on top of nests from late afternoon until sunrise. Corrals were checked every hour throughout the night and a hatchling from the first cohort to emerge was transported in a bucket

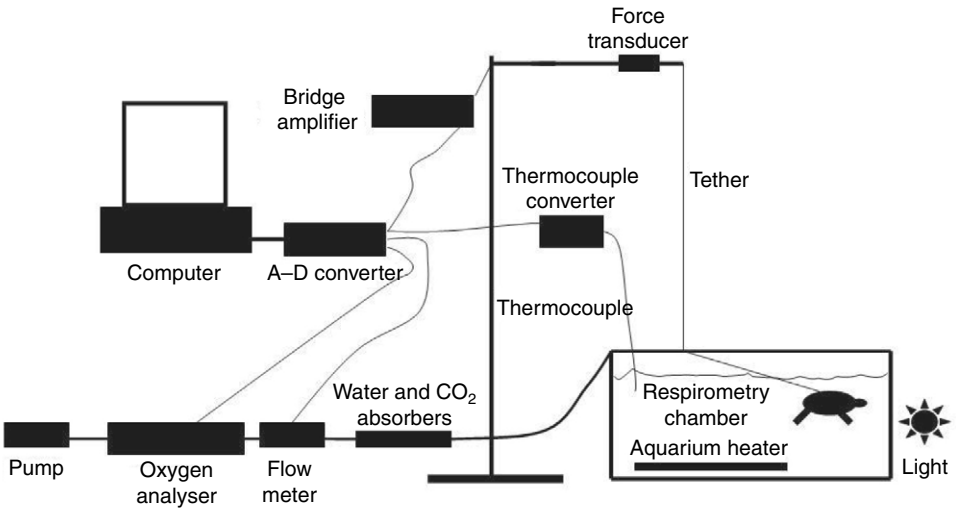

Fig. 1. Schematic diagram of the experimental set up used to simultaneously measure the oxygen consumption and swimming effort of hatchling green turtles.

to the nearby Heron Island research station, a process that took 5–15 min. During this time hatchlings crawled around inside the bucket, a process that mimicked the usual scramble from the nest down the beach to the water's edge.

Once in the laboratory hatchlings were weighed and then fitted with Lycra harnesses which did not inhibit flipper movement. They swam in a Plexiglas chamber (34 cm long×28 cm wide×19 cm high) filled to 13 cm depth with fresh seawater heated to 28°C by an aquarium heater (Fig. 1). The harness was attached *via* a monofilament nylon line, which passed through a small hole in the lid to a force transducer (MLT050 ADInstruments, Colorado Springs, CO, USA) connected to a bridge amplifier (ML112 ADInstruments). The output was recorded *via* a data acquisition system (Power Lab 4/20 ADInstruments) programmed to sample 40 times per second (Fig. 1). Before and after each trial, the force transducer was calibrated by hanging a known mass from it. The swim chamber was painted black on three sides and a dull light was placed at the unpainted end of the container to encourage unidirectional swimming. However, any change in swimming direction was of no consequence as the monofilament line was perpendicular to the force transducer at all times and the tether was of a length which prevented the turtle from touching the sides or bottom of the tank (see Burgess et al., 2006). To test whether the direction and angle of the pull on the tether affected the force recorded by the force transducer, a 98 mN spring balance was attached to a tether and stretched sequentially to 20, 29, 59, 78 and 98 mN in all directions and at various angles. In all cases the direction and angle of the tether did not influence the force recorded by the force transducer. Water temperature was monitored continuously by a thermocouple connected *via* a thermocouple-to-analogue converter (SMCJ-T Omega.com, Omega Engineering Inc., Stamford, CT, USA) to the data acquisition system (Fig. 1). Each hatchling swam continuously for 18 h, after which it was released into the ocean.

Oxygen consumption was measured using open flow respirometry. The lid of the respiratory chamber was sealed with vacuum grease, and air was drawn by a pump at ~80 ml min^{-1} through Tygon® tubing connected to the lid, and sequentially through an indicating soda-lime carbon dioxide absorber, an indicating Dierite® water absorber, a mass flowmeter (GFM17 Aalborg, Orangeburg, NY, USA) and an oxygen analyser (PA-1B Sable Systems, Las Vegas, NV, USA). Room air entered the chamber through the small hole in the lid of the chamber through which the tether connecting the force transducer to the hatchling passed. Outputs of the flowmeter and oxygen analyser were connected to the data acquisition system (Fig. 1). The oxygen analyser was calibrated with high purity nitrogen and dry carbon dioxide-free

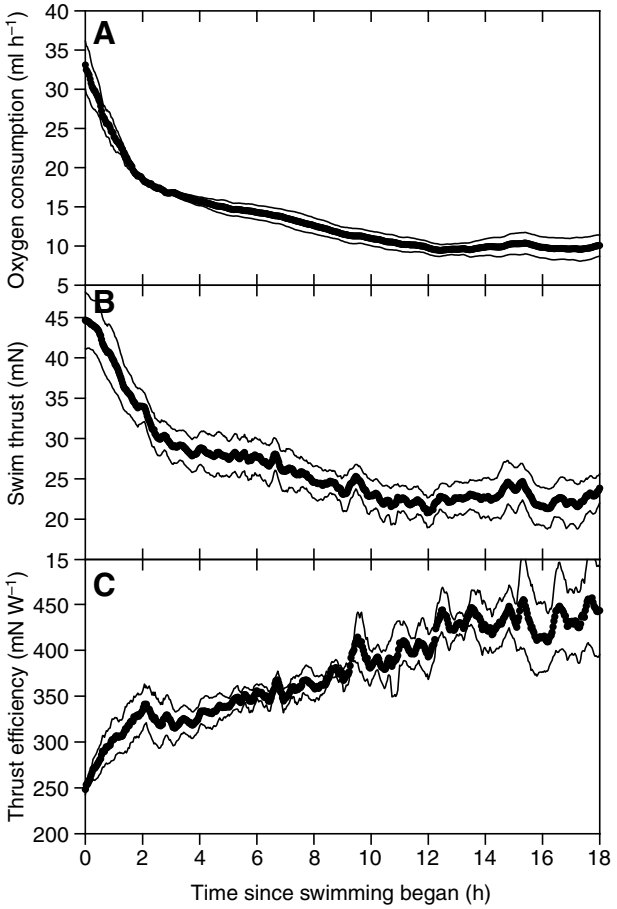

Fig. 2. Oxygen consumption, mean swim thrust and thrust production efficiency during the first 18 h of frenzy swimming of green turtle hatchlings from the Heron Island rookery. To generate each data point, the average oxygen consumption, swim thrust or thrust production efficiency of the five hatchlings was calculated for the previous 2 min, and then the mean of these five averages was taken to give an overall mean. Thin lines represent ±1 s.e.m.

Table 1. Swimming attributes, oxygen consumption and energy consumed during the frenzy swimming period of green turtle hatchlings from the Heron Island rookery

Parameter	Swim phase	Hatchling 1	Hatchling 2	Hatchling 3	Hatchling 4	Hatchling 5	Mean ± s.e.m.
Correlation (R^2)	0–2 h	0.78	0.80	0.65	0.84	0.70	0.75±0.04
between oxygen consumption	2–12 h	0.71	0.60	0.60	0.51	0.85	0.65±0.06
and swim thrust	12–18 h	0.37	0.10	0.42	0.01	0.11	0.20±0.08
Mean oxygen consumption (ml h^{-1})	0–2 h	29.3±0.4	25.5±0.5	21.5±0.3	23.4±0.5	22.7±0.6	24.5±1.4
	2–12 h	14.8±0.1	12.7±0.2	11.4±0.2	13.5±0.2	15.4±0.1	13.6±0.7
	12–18 h	12.7±0.1	6.7±0.1	11.4±0.1	10.3±0.1	7.9±0.1	9.8±1.1
Mean swim thrust (mN)	0–2 h	48.9±0.7	35.7±0.5	33.3±0.4	34.9±0.5	42.9±0.5	39.1±2.9
	2–12 h	30.4±0.2	23.4±0.3	21.5±0.2	23.4±0.3	31.0±0.2	25.9±2.0
	12–18 h	28.1±0.2	15.4±0.4	18.3±0.4	19.7±0.2	21.5±0.4	20.6±2.1
Swim thrust production	0–2 h	318±6	260±3	281±3	285±3	276±3	284±10
efficiency (mN W^{-1})	2–12 h	378±2	361±4	287±2	365±4	320±3	342±17
	12–18 h	433±2	427±10	247±2	393±3	352±4	370±34
Energy consumed (kJ)	0–2 h	1.15±0.02	1.00±0.02	0.85±0.01	0.92±0.02	0.89±0.02	0.96±0.05
	2–12 h	2.92±0.01	2.50±0.01	2.25±0.01	2.66±0.01	3.03±0.01	2.67±0.14
	12–18 h	1.50±0.01	0.79±0.01	1.35±0.01	1.22±0.01	0.93±0.01	1.16±0.13
Energy consumed during 18 h (kJ)		5.57±0.04	4.29±0.04	4.45±0.03	4.80±0.04	4.85±0.04	4.79±0.22
Hatchling mass (g)		25.1	25.2	23.3	26.8	27.7	25.9±0.8
Mean nest temperature (°C)		29.3	29.5	30.3	29.6	29.6	29.7±0.2
Stroke rate during a power stroking	0–2 h	147±6	162±6	161±7	161±5	159±5	158±3
bout (strokes min^{-1})	2–12 h	115±5	132±5	134±3	136±8	148±7	133±5
	12–18 h	110±3	118±2	138±3	124±3	128±5	124±5
Mean maximum thrust per power	0–2 h	202±4	164±13	171±3	207±4	223±4	193±12
stroking bout (mN)	2–12 h	153±7	127±10	139±7	156±10	190±8	153±11
	12–18 h	137±4	80±2	160±8	126±9	114±10	123±14
Proportion of time power stroking (%)	0–2 h	81±1	61±2	77±2	86±1	85±5	78±5
	2–12 h	80±3	52±9	82±4	62±7	80±7	71±6
	12–18 h	81±1	10±6	77±5	63±7	51±5	56±13

The Pearson product-moment correlation procedure was used to generate coefficients of determination (R^2). All correlations except for hatchling 4 during 12–18 h were statistically significant (P<0.05). Data represent means of data collected from individuals for each time interval ±s.e.m.

room air immediately before and after swimming trials. $\dot{V}_{O_2}$ was calculated using equation 4(a) of Withers (Withers, 1977) after a washout correction was applied using the method of Bartholomew and colleagues (Bartholomew et al., 1981). Control runs of the system without a turtle in it indicated that oxygen consumption of organisms in the seawater was so small that it was undetectable, so any detected oxygen consumption could be confidently assigned to the hatchling turtles.

RESULTS

Five hatchlings from five different nests were sampled. Water temperature during swimming trials averaged 27.9±0.1°C (mean ± s.e.m., range 27.4–28.9°C). Swim thrust and $\dot{V}_{O_2}$ data were averaged into 2 min intervals and plotted against time in order to track swimming performance and $\dot{V}_{O_2}$ over time (Fig. 2). Swimming performance (quantified by swim thrust) decreased with time and could be divided into three phases based on the pattern of decline in thrust (Fig. 2B): (1) rapid fatigue (0–2 h), (2) slow fatigue (2–12 h), and (3) sustainable swimming effort (12–18 h). $\dot{V}_{O_2}$ was highly correlated with swim thrust during the rapid and slow fatigue phases, but poorly correlated during the sustainable swimming phase (Table 1; Fig. 3) and, as a consequence, also decreased with swim time (Fig. 2A). Hatchlings having the greatest $\dot{V}_{O_2}$ also produced the greatest swim thrust (Table 1). Thrust production efficiency [swim thrust per watt, calculated assuming lipid was the substrate being metabolised during swimming and that every litre of oxygen consumed corresponded to the expenditure of 19.7 kJ of energy (Schmidt-Nielsen, 1997)] had a tendency to increase as swimming time passed (Fig. 2C), being least efficient during the rapid fatigue phase, of intermediate efficiency during the slow fatigue phase, and of greatest efficiency during the sustainable swimming phase (Fig. 2C; Table 1). To statistically test whether thrust production efficiency changed significantly between the three phases (0–2, 2–12 and 12–18 h), the 2 min values for thrust production efficiency for each of the five hatchlings were averaged across each of the three phases to give a single mean value of thrust production efficiency (Table 2). A repeated measures ANOVA in which mean thrust production efficiency was the dependent variable and swimming phase was the (repeated) independent variable was applied to these data and indicated that thrust production efficiency changed with swimming phase ($F_{2,8}$=6.765, P=0.019).

Stroke rate during a power stroking bout, mean maximum thrust per power stroking bout, and the proportion of time spent power stroking were averaged over 10 min periods (Fig. 4). Stroke rate during a power stroking bout decreased very rapidly within the first 30 min, decreased at a slower rate over the first 4 h and continued to decrease at a slow rate until 12 h, and then did not change significantly between 12 h and 18 h (Fig. 4A). Mean maximum thrust produced during power stroking declined rapidly in the first 2 h, did not consistently increase or decrease from 2 to 6 h, declined steadily from 6 to 12 h and did not change significantly between 12 h and 18 h (Fig. 4B). The proportion of time spent power stroking appeared to remain constant for the first 6 h and then decreased steadily until 12 h, after which it did not consistently increase or decrease (Fig. 4C).

The rate of energy expenditure was greatest during the rapid fatigue phase, but most energy was consumed during the slow fatigue phase because this phase had the longest duration (Table 1). The total energy consumed during the entire 18 h of swimming averaged 4.79 kJ (Table 1).

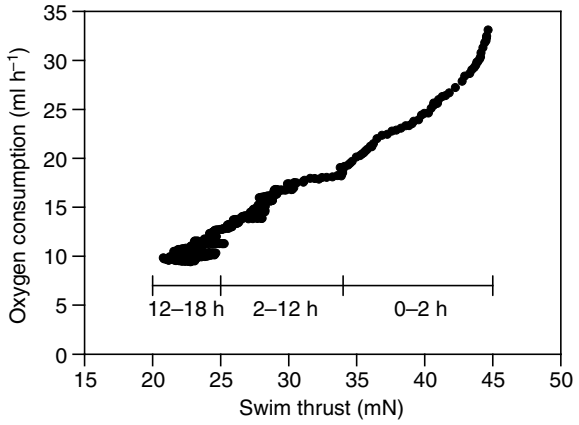

Fig. 3. Mean swim thrust plotted against mean oxygen consumption for swimming green turtle hatchlings. Plotted data are sourced from Fig. 2. Pearson product-moment correlation R^2=0.98, P<0.001. The time intervals when data were collected are indicated at the bottom of the plot.

DISCUSSION

Swimming effort

Swimming effort immediately after entering the water in green turtle hatchlings hatched on coral reef cays is important in determining their chances of surviving to adulthood because large numbers of hatchlings are eaten as they swim through a gauntlet of fish predators inhabiting the shallow fringing reef (Gyuris, 1994; Gyuris, 2000; Pilcher et al., 2000). Once turtles have crossed the fringing reef and entered deeper water it is generally assumed that the density of predators in the surface waters decreases dramatically (otherwise all hatchlings would be predated within the first couple of weeks of entering the sea) so turtles can slow their swimming effort without increasing the chances of predation greatly and join the currents that will ultimately take them into the open ocean for their oceanic life history stage.

Direct measurement of hatchling swimming speed has been made in the field by tethering small floats to hatchlings and following these floats (e.g. Salmon and Wyneken, 1987; Gyruis, 1994; Gyruis, 2000; Pilcher et al., 2000) but this method is logistically intense, requiring individuals to be tracked by surface craft and such resources were not available for this study. Another study (Pilcher and Enderby, 2001) used a swimming flume to assess hatchling swimming performance. However, the drawbacks of this method are that swimming speed is chosen by the experimenter, and that only one hatchling can swim at a time. Using hatchlings tethered in tanks to assess swimming performance as in this study is a good compromise because tethered hatchling swimming behaviour is similar to that of free-swimming hatchlings (Wyneken and Salmon, 1992; Wyneken, 1997), and the only assumption that needs to be made is that the thrust measured from tethered hatchlings is directly related to swimming speed. The added advantage of this method is that swimming effort can be quantified into the different components of power stroke rate during a power stroking bout, the maximum thrust produced per power stroke and the proportion of time spent power stroking, and other energetic measurements such as oxygen consumption can also be made.

The current study indicates that swimming effort as quantified by the mean swim thrust generated has three distinctive phases during the frenzy swimming period: (1) a rapid fatigue phase (0–2 h), (2) a slow fatigue phase (2–12 h), and (3) a sustained effort phase (12–18 h). Changes in the power stroke rate during a power stroking bout, the thrust produced per power stroke and the proportion of time spent power stroking all contributed to this pattern as has been found previously for green turtle hatchlings (Burgess et al., 2006). To generalise, the very rapid decrease in swimming effort observed during the rapid fatigue phase of swimming (0–2 h) was caused by a combination of a dramatic decrease in power stroke rate in the first 30 min which was followed by a less dramatic decrease in power stroke rate between 30 and 120 min, and a continuous decrease in power stroke thrust between 0 and 120 min (Fig. 4A,B). The proportion of time spent power stroking did not change significantly during this period (Fig. 4C). During the slow fatigue phase (2–12 h) decreased swimming thrust was caused by several factors. Firstly, stroke rate during a power stroking bout declined steadily throughout this phase (Fig. 4A). Secondly, towards the end of this phase decreases in both the thrust produced during power stroking and the proportion of time spent power stroking occurred (Fig. 4B,C). During the sustained swimming effort phase (12–18 h) there were no significant changes in power stroke rate, power stroking thrust or proportion of time power stroking.

The rapid decrease in effort during the first 2 h of swimming is likely to be caused by the depletion of muscle cell glycogen stores (Hill et al., 2004) and a decrease in the contribution made by anaerobic metabolism. Anaerobic metabolism is significant during the first 10–15 min of swimming as indicated by an increase in blood lactate concentration at a rate of approximately 1 μmol ml^{-1} of blood per minute in free-swimming green turtle hatchlings (Baldwin et al., 1989). Clearly this accumulation of lactate cannot continue indefinitely and the rapid decrease in stroke rate per power stroking bout during this time (Fig. 4A) probably reflects a shift to predominantly aerobic metabolism. The patterns of change in swim thrust, stroke rate during a power stroking bout and the proportion of time spent power stroking are very similar to those obtained from Heron Island green turtle hatchlings emerging from eggs artificially incubated at 30°C (Burgess et al., 2006) and naturally incubated eggs during the 2006–2007 nesting season (T. Ischer, K. Ireland and D.T.B., unpublished data) indicating that these general patterns are somewhat stereotypic for green turtle hatchlings hatched from the Heron Island rookery.

Table 2. Mean thrust production efficiency (mN W^{-1}) of five hatchling green turtles from the Heron Island rookery over three swimming phrases

Hatchling no.	Rapid fatigue phase (0–2 h)	Slow fatigue phase (2–12 h)	Sustained effort phase (12–18 h)
1	318	378	433
2	260	361	427
3	281	287	247
4	285	365	393
5	276	320	352
Mean ± s.e.m.	284±10	342±17	370±34

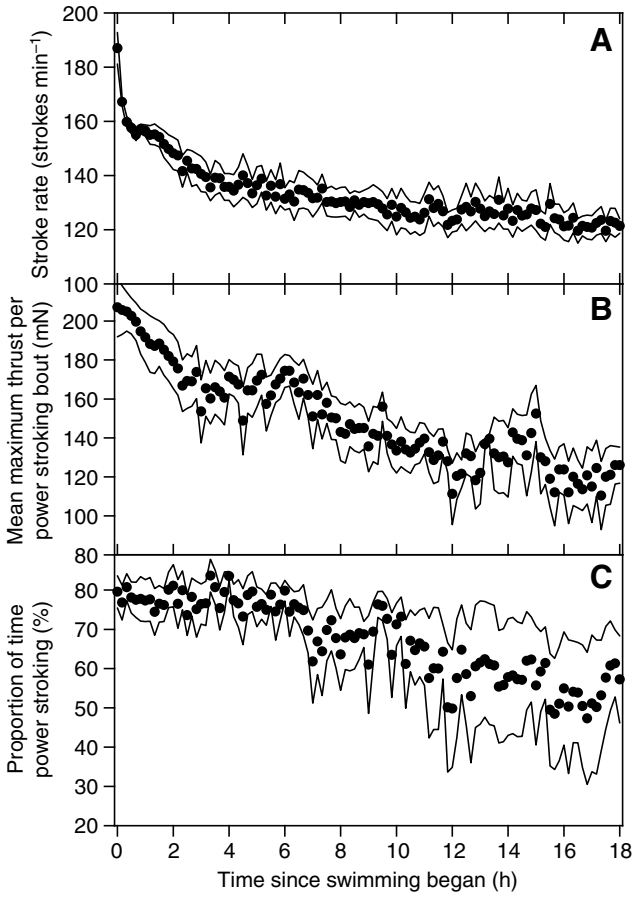

Fig. 4. Plot of stroke rate during a power stroking bout, mean maximum thrust per power stroking bout and the proportion of time spent power stroking during the first 18 h of frenzy swimming of green turtle hatchlings from the Heron Island rookery. To generate each data point, the average stroke rate during a power stroking bout, mean maximum thrust and the proportion of time spent power stroking for each of the five hatchlings were calculated for the previous 10 min, and then the mean of these five averages was calculated to give an overall mean. Thin lines represent ±1 s.e.m.

Energetics of swimming

The method used in the current study allowed measurement of swimming effort and $\dot{V}_{O_2}$ within 2 min of hatchlings being placed in the water. I found that the greatest swimming effort and oxygen consumption occurred within the first 10 min of hatchlings entering the water, and that swimming effort and oxygen consumption decreased rapidly during the first 2 h of swimming (Fig. 2). $\dot{V}_{O_2}$ directly followed the decline in swimming effort during the first 12 h of swimming, an observation consistent with the assumption that hatchling sea turtle swimming is powered predominantly by aerobic metabolism (Butler et al., 1984; Wyneken, 1997). As a consequence, as hypothesised, there was a strong correlation between swimming effort and $\dot{V}_{O_2}$ (Table 1; Fig. 3). Only a few studies have measured $\dot{V}_{O_2}$ in hatchling sea turtles while swimming [leatherback *Dermochelys coriacea* (Lutcavage and Lutz, 1986; Wyneken, 1991; Wyneken, 1997; Jones et al., 2002; Jones et al., 2007); olive ridley *Lepidochelys olivacea* (Jones et al., 2007); loggerhead *Caretta caretta* (Wyneken, 1991; Wyneken, 1997); green (Wyneken, 1991; Wyneken, 1997). Of these studies only Wyneken (Wyneken, 1991; Wyneken, 1997) made measurements in the crucial first few hours of swimming, but even this, the most comprehensive study, confined $\dot{V}_{O_2}$ measurement to just the 0.5–2 h interval after the hatchlings first entered the water, a time when the hatchlings in the current experiment were rapidly decreasing their swimming effort (Fig. 1A). Hatchlings in the present study had generally lower rates of $\dot{V}_{O_2}$ compared with those in Wyneken's study (Wyneken, 1991; Wyneken, 1997) which might be explained by a difference in the swimming effort of different populations of green turtles. Wyneken (Wyneken, 1991; Wyneken, 1997) found $\dot{V}_{O_2}$ for a 26 g green turtle hatchling (the mean mass of hatchlings in the current study) to decrease from 34 to 31 ml h^{-1} (average 33 ml h^{-1}) during the 0.5–2 h interval of the frenzy swimming phase, and I found a maximum value of 34 ml h^{-1} during the first few minutes of swimming but $\dot{V}_{O_2}$ was generally much lower than this for most of the swimming frenzy and decreased from 30 to 18 ml h^{-1} (average 24 ml h^{-1}) for the 0.5–2 h interval. Hatchling $\dot{V}_{O_2}$ in the current study averaged 10 ml h^{-1} from 12 to 18 h of swimming, much lower than the post-frenzy value (20 ml h^{-1}) and only a little above the resting value (8 ml h^{-1}) reported by Wyneken (Wyneken, 1991; Wyneken, 1997), although Prange and Ackerman (Prange and Ackerman, 1974) reported the resting metabolism of newly hatched green turtles to be just 2.6 ml h^{-1}. This suggests that the green turtle hatchlings in the current study were considerably less active swimmers than those studied by Wyneken (Wyneken, 1991; Wyneken, 1997).

The relatively broad range of swimming effort and $\dot{V}_{O_2}$ recorded during the rapid and slow fatigue swimming phases resulted in relatively high correlation coefficients between swimming effort and $\dot{V}_{O_2}$ (Table 1), a result similar to that reported for hatchling leatherback and olive ridley turtles within the first 4 weeks of hatching (Jones et al., 2007). In contrast, the relatively narrow range of swimming effort and $\dot{V}_{O_2}$ experienced during the sustained effort phase resulted in low correlation coefficients (Table 1) and this may also explain why only a weak correlation between swimming effort and $\dot{V}_{O_2}$ was found in hatchling sea turtles previously (Wyneken, 1991).

The tendency for swimming efficiency to increase with time as swim thrust decreased is probably related to the fact that the frequency and speed of muscle contraction decreased with swim time and thus the energy needed to counter the inertial forces of moving limbs through the water decreased (Vogel, 1989), and the fact that faster limb movements create large wakes, and larger wakes dissipate more energy (Prange and Schmidt-Nielsen, 1970). The rate of energy expenditure as indicated by the rate of oxygen consumption clearly tracks the swimming effort of hatchling green turtles (Figs 2 and 3). The rate of energy expenditure decreased precipitously within the first 2 h of entering the water, and declined more slowly between 2 and 12 h before decreasing to a sustainable level after 12 h of swimming.

The dry mass of residual yolk of hatchling green turtles incubated at 28 and 30°C averages 1.5 g (Booth et al., 2004) and has an energy density of 32.5 kJ g^{-1} (D.T.B., unpublished data) so the residual yolk would contain about 49 kJ of energy. Only about 4.8 kJ of energy was expended during the first 18 h of swimming (corresponding to 6.4 kJ day^{-1}, but during the sustained effort phase energy expenditure was 4.7 kJ day^{-1}), so it would appear that a hatchling could survive at least 10 days of continuous swimming without the need to feed. Taking into account the fact that green turtle hatchlings do not swim continuously throughout the day after their first day at sea (Wyneken and Salmon, 1992) this non-feeding period may stretch to 2 weeks. Similar theoretical calculations also indicate that leatherback and olive ridley hatchlings could survive up to 3 weeks without feeding (Jones et al., 2007). Pilcher and Enderby (Pilcher and Enderby, 2001) reported that the swimming ability of green turtle hatchlings was

compromised if hatchlings were contained in beach enclosures for 6 h after emergence from the nest. They suggested that this decrease in swimming performance may be due to depletion of limited energy stores in hatchling turtles during the time that they were trapped within enclosures. However, the calculations above clearly indicate that energy depletion from body stores would not limit the swimming ability of green turtle hatchlings within the first 10 days of hatching. It is far more likely that muscle fatigue is the cause of decreased swimming effort during this time (Burgess et al., 2006).

Ecological implications

Because the chances of a green turtle hatchling surviving the reef flat crossing depends on, among other factors, swimming speed (Gyuris, 1994), it is not surprising to find that hatchlings put their maximum swimming effort into the first few minutes of swimming. Given that fringing reefs surrounding coral cays are typically 100–600 m wide and that swimming speeds of green turtle hatchlings during the frenzy phase are typically 1.0–1.6 km h^{-1} (Pilcher et al., 2000; Wyneken, 2000) it should take a green turtle hatchling between 10 and 40 min to cross the fringing reef. The rapid fatigue phase in which the swimming effort is greatest lasts approximately 2 h, so hatchlings should be well beyond the fringing reef by the time their swimming effort begins to plateau. Once the deeper waters outside the fringe reef are reached, the swimming effort can be eased and the residual yolk can supply enough energy to support continuous swimming for at least 10 days without feeding, and given that green turtle hatchlings do not swim continuously beyond the first 24 h (Wyneken and Salmon, 1992) this theoretical non-feeding period could be as long as 2 weeks.

This research conforms with Australian animal welfare laws and was approved by a University of Queensland Animal Ethics Committee (approval #SIB/135/06/URG/SWRRF) and conducted under Queensland EPA scientific permit #WITK03844706. I thank Nick Holmes and Andrew Evans for assistance in collecting data for this project. This research was made possible by funding from the Sea World Research and Rescue Foundation.

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