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REPORT

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Swimming performance of hatchling green turtles is affected by incubation temperature

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Abstract In an experiment repeated for two separate years, incubation temperature was found to affect the body size and swimming performance of hatchling green turtles (*Chelonia mydas*). In the first year, hatchlings from eggs incubated at 26°C were larger in size than hatchlings from 28 and 30°C, whilst in the second year hatchlings from 25.5°C were similar in size to hatchings from 30°C. Clutch of origin influenced the size of hatchlings at all incubation temperatures even when differences in egg size were taken into account. In laboratory measurements of swimming performance, in seawater at 28°C, hatchlings from eggs incubated at 25.5 and 26°C had a lower stroke rate frequency and lower force output than hatchlings from 28 and 30°C. These differences appeared to be caused by the muscles of hatchlings from cooler temperatures fatiguing at a faster rate. Clutch of origin did not influence swimming performance. This finding that hatchling males incubated at lower temperature had reduced swimming ability may affect their survival whilst running the gauntlet of predators in shallow near-shore waters, prior to reaching the relative safety of the open sea.

Keywords Marine turtle · Coral cay · Development · TSD · Locomotor performance

Introduction

Sea turtles are large marine reptiles that have high fecundity (Hendrickson 1980). A typical nesting green turtle (*Chelonia mydas*) from the Heron Island rookery in the southern Great Barrier Reef will lay four clutches, each containing 115 eggs, in a nesting season and return to nest once every 4 years (Limpus et al. 1984). Hatching success in this rookery is usually high (between 85 and 95%, Bustard 1972; Limpus et al. 1983), so that in a single nesting season a female produces in excess of 400 hatchlings. High fecundity in sea turtles is hypothesised to have evolved in response to high predation rates on hatchlings (Gyuris 1994). It is likely that less than 50% of green turtle hatchlings survive longer than 24 h after leaving the safety of the nest in the Heron Island rookery because hatchlings are eaten by crabs and occasionally by birds as they leave the nest and scramble down the beach to the water's edge (Bustard 1972), and further predation occurs by fish as the hatchlings swim across the fringing reef (Gyuris 1994). Immediately upon entry into the water, hatchlings swim using rapid "power strokes" of their front flippers to move them offshore (Wyneken and Salmon 1992; Gyuris 1994). These power strokes are interrupted by brief periods of "dog paddling" when a breath of air is taken (Wyneken and Salmon 1992). The rapid swimming phase (known as the "frenzy phase" sensu Wyneken and Salmon 1992) may last up to 24 h and rapidly moves the hatchling from shallow to deeper offshore waters (Gyuris 1994). During the swimming frenzy, hatchlings swim in a straight line perpendicular to waves and do not take evasive action if approached by predators (Gyuris 1994). On coral cays such as Heron Island, predation of hatchlings within the first few minutes of entering the water and whilst they are crossing the fringing reef platform surrounding the cay is extremely high, with only 18–55% of hatchlings expected to survive. The variation in survival rate depends on the time of day and tide level (Gyuris 1994). Given that hatchlings do not take evasive action when approached by predators, and that the probability of being eaten by a predator is directly proportional to the time spent swimming over the fringing reef (Gyuris 1994), one would expect swimming performance during the early part of the frenzy phase to be crucial to the overall sea turtle life history.

In many reptiles, incubation temperature can influence hatchling attributes such as size, morphology,

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behaviour, post-hatch growth and locomotor performance (see Deeming 2004; Rhen and Lang 2004 for recent reviews). These attributes clearly have the potential to influence the life-history characters and survival of individuals within a species. For example, it is well established that the nest temperature during the middle third of embryonic development determines the sex of sea turtles; cooler incubation temperatures produce males and warmer temperatures produce females (Standora and Spotila 1985; Spotila et al. 1987; Yntema and Mrosovsky 1992). In green turtles, incubation temperature also influences hatchling mass, the amount of yolk converted to hatchling tissue during incubation (Booth and Astill 2001a) and the stroke rate of front flippers during swimming (Booth et al. 2004). Hatchling size can directly affect locomotor performance. For instance, in lizards, larger hatchlings are generally faster runners than smaller hatchlings (Sinervo and Huey 1990), so it is possible that incubation temperature induced differences in hatchling size may account for differences in hatchling locomotor performance. In green turtle hatchlings it is possible that the larger front flipper size of hatchlings from eggs incubated at a cool temperature compensates for their slower stroke rate so that their overall swimming performance is similar to hatchlings incubated at higher temperatures. Because swimming ability of hatchlings is likely to be a major determinant of the survival of green turtles nesting on coral cays, this study empirically tested the hypothesis that incubation temperature influences the post-hatch swimming performance of green turtles. A range of experimental incubation temperatures was chosen to span the range that produces all males (25.5, 26.0°C) to all females (30°C). This range of temperatures is found in natural nests at Heron Island (Bustard 1972; Booth and Astill 2001b), although natural nests do not experience constant temperature. Because the clutch of origin is known to influence the phenotype of hatchling turtles (Janzen 1993; Packard and Packard 1993), the relative importance of clutch identity and incubation temperatures in influencing hatchling size and swimming performance was also examined.

Materials and methods

Egg collection and incubation

Eggs were collected at oviposition from female green turtles, *Chelonia mydas*, nesting on Heron Island, Great Barrier Reef (23°26′S, 151°55′E) in November 2000 (60 eggs from each of four females) and November 2002 (30 eggs from each of four females). The Heron Island rookery is typical of other nesting islands in the Capricorn-Bunker group that make up the southern Great Barrier Reef nesting population of green turtles (Bustard 1972; Limpus et al. 1984). Eggs were chilled to 10–15°C and transported to the laboratory within 48 h of collection as recommended by Harry and Limpus (1989). In the laboratory, eggs were weighed, marked with a number and placed on moist perlite (hydrated to a water potential of approximately ~ -100 kPa throughout incubation) in plastic containers, eight per container. Two eggs from each clutch were placed in each container and containers assigned to a constant incubation temperature so that an equal number of eggs from each clutch were incubated at 26, 28 and 30°C in 2000 and 25.5 and 30°C in 2002.

Two different experimental protocols to explore swimming performance were used over two nesting seasons (2000 and 2002). Preliminary analysis of the results from the year 2000 indicated that hatchlings from the cool incubation temperature had a lower front flipper stroke rate, but were larger in size. It was possible that any decrease in swim performance due to a slower stroke rate could have been compensated for by an increase in hatchling size. To test this possibility, in the year 2002 experiments, the force generated by swimming hatchlings (which would take into account both stroke rate and hatchling size) was used as a measure of swimming ability.

Morphological measurements of hatchlings and sex determination

Incubation containers were inspected four times daily at the time of expected hatching to record the day of hatch. Newly hatched turtles were marked on the carapace with their assigned egg number and then placed in a darkened container with other hatchlings at the appropriate incubation temperature for 48 h after hatching to simulate the time hatchlings usually spend digging out of natural nests. At the end of this period, hatchlings were weighed and their carapace length and width, front flipper length and width and head width measured with calipers. After morphological measurement, hatchlings underwent swimming trials and when these trials finished they were killed. In the 2000 experiments most hatchlings had their sex determined by histological examination of their gonads. In these hatchlings the right kidney with gonad attached was dissected free, and sex determined following the methods of Miller and Limpus (1981).

Swimming trials

Forty-eight hours after hatching, hatchlings were swum individually in a glass aquarium ($41 \times 32 \times 25$ cm^3 high) filled with 20 cm of seawater at 28°C (the average sea water temperature at Heron Island during the hatching season). A Velcro patch (1×1 cm^2) was glued to the carapace and a monofilament nylon line attached to the Velcro. A low intensity light was placed at one end of the tank, and the other sides of the tank covered with black plastic to encourage unidirectional swimming.

In the year 2000 swim trials, the nylon line was attached to a bracket suspended above the middle of the tank. The length of the tether was adjusted so that hatchlings could swim freely below the water or on the surface but could not touch the bottom or sides of the tank. This restraint allowed resistance for the hatchling to swim against and did not interrupt the swimming activity (Salmon and Wyneken 1987). Hatchlings were videotaped for 10 min at time intervals of 0.5, 2, 6, 12, 18 and 23 h after being introduced to the tank. Power stroke rate was later calculated for each time interval from the videotapes by manual counting with a stopwatch and hand-held counter. This was done by counting all power strokes in a 1 min interval at the first, fifth and ninth minutes of a 10 min recording period and these three values averaged to give a single value for each individual for each recording period. During the 1 min counting period, hatchlings typically underwent one or more periods of dog paddling or non-swimming, so this measure of power stroking rate represents the average power stroke rate per minute, and not the power stroke rate per power stroking bout.

In the year 2002 swim trials the nylon tether was threaded through a hole in the bracket and attached to a force transducer (Power Lab MLT050). The nylon tether was attached in a plane perpendicular to the force transducer at all times (Fig. 1), so measured force was in the vertical plane no matter in which direction the turtle was swimming. The force transducer was calibrated before each 10 min recording period by suspending a known mass from it in the vertical plane. The force transducer was connected to a computer data acquisition system (Power Lab 2/20 connected with a ML110 Bridge amplifier) that sampled force 100 times per second. The force traces for each 10 min period were later analysed (Fig. 2) to determine the stroke rate per power stroking bout (by counting the number of force peaks per second within a power stroking bout at the beginning, middle and end of a 10 min measurement period and taking an average of these three counts), mean time spent power stroking, mean time spent dog paddling, mean time spent not swimming and mean force generated for each 10 min period by averaging the force recorded across the 60,000 data points collected during the period.

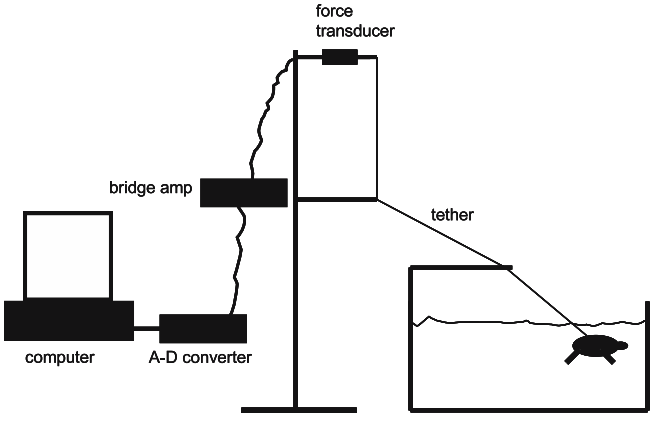

Fig. 1 Schematic diagram of the setup used to measure swimming performance in *Chelonia mydas* hatchlings

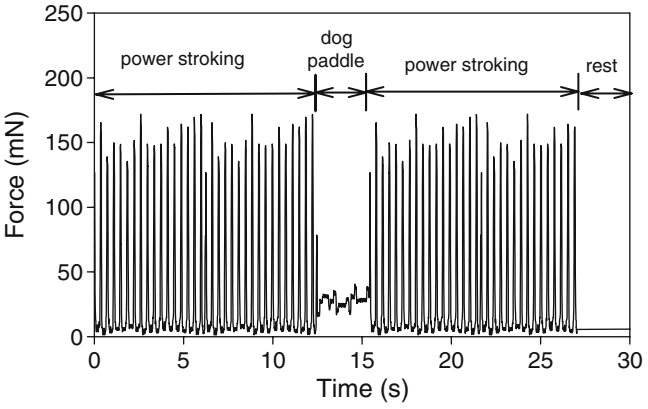

Fig. 2 Thirty seconds sample of a typical force trace during a swimming trial. Power stroking bouts (typically 5–20 s in duration) were separated by periods of dog paddling (typically 2–8 s in duration) when breaths of air were taken. Rest periods were highly variable in length (2–3,600 s) and occurred after either power stroking or dog paddling bouts

Statistical analysis

Data were tested for the assumption of homogeneity of variances using Bartlett's test (ANOVA) or Box M test (ANCOVA) and the assumption of normal distribution of data using the Kolmogorov–Smirnov test before proceeding with ANOVA/ANCOVA. If data did not conform to these assumptions, non-parametric Kruskal–Wallis ANOVA of ranks tests were performed. Because of the different experimental protocols used, data from experiments in 2000 and 2002 were analysed separately. For the year 2000 experiments that involved three test temperatures, post hoc comparisons were made using Tukey HSD for unequal sample size. Egg mass and incubation period were analysed using mixed model ANOVA modelling incubation temperature as a fixed factor and clutch as a random factor. All data are presented as means ± SE.

Hatchling size

The covariance of the six hatchling size variables measured (mass, carapace length and width, head width and front flipper length and width) hampers the simple interpretation of any one variable. To avoid this problem a single hatchling size index was generated using principle component analysis (Lindeman et al. 1980). Briefly, the six size variables from all hatchlings in 2000 and 2002 were used to generate a correlation matrix and the first principle component (which explained 54% of the total variance) was extracted and used as a hatchling

size index. This index was then used to examine the influence of incubation temperature and clutch on hatchling size. Clutch effects were explored statistically by stipulating clutch as a random factor in ANOVA/ANCOVA. A significant clutch effect on hatchling size could be the result of differences in egg size between clutches, and/or other factors such as differences in genetic background and differences in nutrient composition of eggs. Hatchling size differences due to differences in initial egg size were removed using ANCOVA, with initial egg mass as the covariate. Size index data are represented as ANCOVA-adjusted least square means ± SE.

Hatchling swimming performance

Repeated measures ANOVA was used to analyse the swimming ability over a 23 h period between temperature treatments (Temperature, fixed factor; Clutch, random factor). Percentage data were arcsin transformed before statistical analysis. The influence of hatchling size on swimming performance was investigated by assuming that mean force output for the swimming period 30 min after swimming commenced was representative of overall swimming performance (see Results). The relationship between the PCA-generated size index and mean force was investigated in hatchlings from eggs at each incubation temperature using regression analysis, and ANCOVA (hatchling size index as the covariate) used to test whether the relationships differed between temperature treatments.

The software STATISTICA® release 7.0 was used for all statistical calculations. Statistical significance was assumed at $P < 0.05$ except for swimming variables where the Bonferroni correction for five comparisons of non-independent data was applied and statistical significance was assumed if $P < 0.01$.

Results

Hatchling morphology

The 2000 experiments. Of the 80 eggs set at each incubation temperature, 60, 62 and 64 eggs produced hatchlings from 26, 28 and 30°C, respectively, but several hatchlings died during the 72 h post-hatch period and data from these animals were excluded from analysis giving final sample sizes of 55, 54 and 60. There was a minimum of four hatchlings in each treatment by clutch experimental unit. All hatchlings whose gonads were histologically examined from 26°C ($N = 20$) were male, all hatchlings examined from 30°C ($N = 20$) were female and from 28°C, 20 hatchlings were female and 34 male. Preliminary analysis indicated that there were no differences in egg mass, incubation period or size in males and females incubated at 28°C, so male and female data at this temperature were pooled in further analysis. Mean egg size did not differ between incubation temperatures, but egg size varied between clutches ($P < 0.001$, Fig. 3a). Lower incubation temperature resulted in longer incubation periods ($P < 0.001$, Fig. 3b). Eggs from all clutches had similar incubation periods at temperatures of 28 and 30°C, but incubation period varied between clutches at 26°C ($P < 0.001$, Fig. 3b) resulting in a significant ($P < 0.001$) temperature by clutch interaction. Incubation temperature ($P = 0.013$) and clutch ($P = 0.030$) influenced hatchling size (Fig. 3c). In all clutches hatchlings from 26°C were larger than hatchlings from 28°C ($P < 0.03$, Fig. 3c). In three clutches hatchlings from 28°C were larger than hatchlings from 30°C ($P < 0.04$), while in one clutch females from 30°C were similar in size to males from 26°C (Fig. 3c), which explains a significant ($P = 0.001$) treatment by clutch interaction. With the exception of hatchlings from clutch D incubated at 30°C, hatchlings from clutch B were larger than hatchlings from the other clutches ($P < 0.01$), even after hatchling size had been adjusted for differences in initial egg mass by the ANCOVA procedure (Fig. 3c).

The 2002 experiments. Of the 60 eggs set at 25.5 and 30°C, respectively, 52 and 35 eggs hatched successfully,

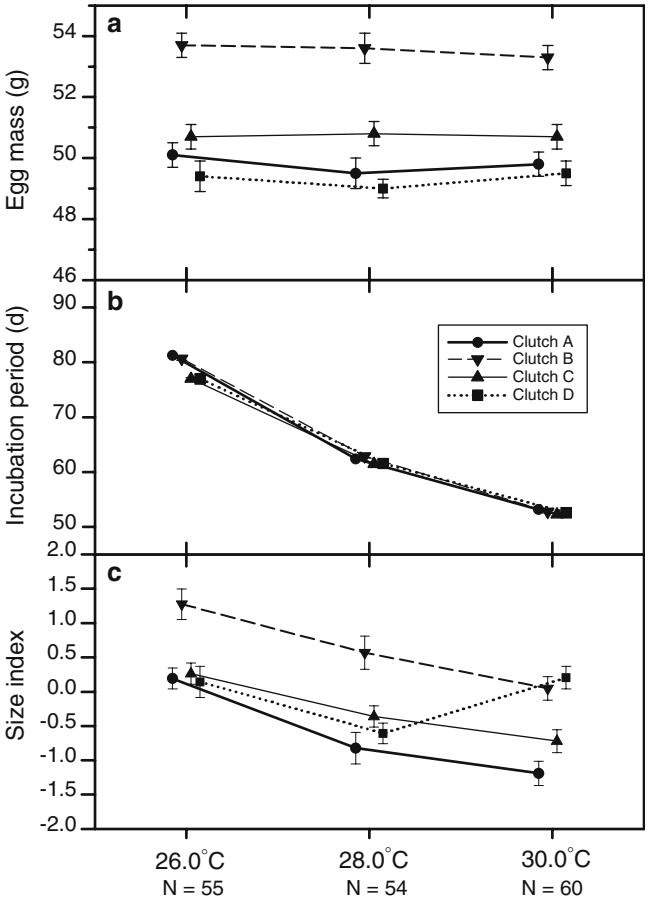

Fig. 3 Relationship between incubation temperature and initial egg mass (**a**), incubation period (**b**) and hatchling size index (**c**) for *Chelonia mydas* eggs and hatchlings from the year 2000 experiments

but several hatchlings died during the 72 h post-hatch period and data from these animals have been excluded from analysis giving final sample sizes of 46 and 31. There was a minimum of five hatchlings in each temperature by clutch experimental unit. Initial egg mass varied between clutches ($P < 0.001$), but was similar across incubation temperatures (Fig. 4a). Incubation period was longer at 25.5°C than at 30°C ($P < 0.001$, Fig. 4b), and clutch influenced incubation period at 30°C, but not at 25.5°C ($P < 0.001$, Fig. 4b) which explains a significant temperature by clutch interaction ($P = 0.001$). Heterogeneity in variance precluded ANCOVA analysis of the hatchling size index. However, a Kruskal–Wallis ANOVA of ranks test indicated no effect of incubation temperature on hatchling size index. Clutch significantly influenced the magnitude of the hatchling size index ($P = 0.009$, Fig. 4c) and this persisted even when the hatchling size index was standardized for differences in initial egg mass by dividing it by the initial egg mass (Kruskal–Wallis ANOVA of ranks test $P = 0.009$). The Kruskal–Wallis ANOVA of ranks test does not allow statistical examination of temperature by clutch interaction.

Swimming performance

Swimming performance was qualitatively similar in both nesting seasons with all hatchlings fatiguing as hours of swimming increased (Fig. 5). Hatchlings from 26 and 25.5°C were consistently weaker swimmers than hatchlings from higher temperatures. In the year 2000 experiments, stroke rate decreased as hours of swimming increased (repeated measures ANOVA $P < 0.001$) and was also influenced by incubation temperature ($P < 0.001$), but was unaffected by clutch of origin. Male hatchlings from 26°C had slower stroke rates compared to all other treatment groups ($P < 0.001$), but males and females from 28°C and females from 30°C had similar stroke rates.

In the year 2002 experiments the more sophisticated method of measuring swim performance allowed the measurement of five variables: power stroke rate within a power stroking bout, time spent power stroking, time spent dog paddling, time spent resting and average force output. Stroke rate decreased as hours of swimming increased ($P < 0.001$), was greater at 30°C than at 25.5°C ($P = 0.008$), but was unaffected by clutch of origin.

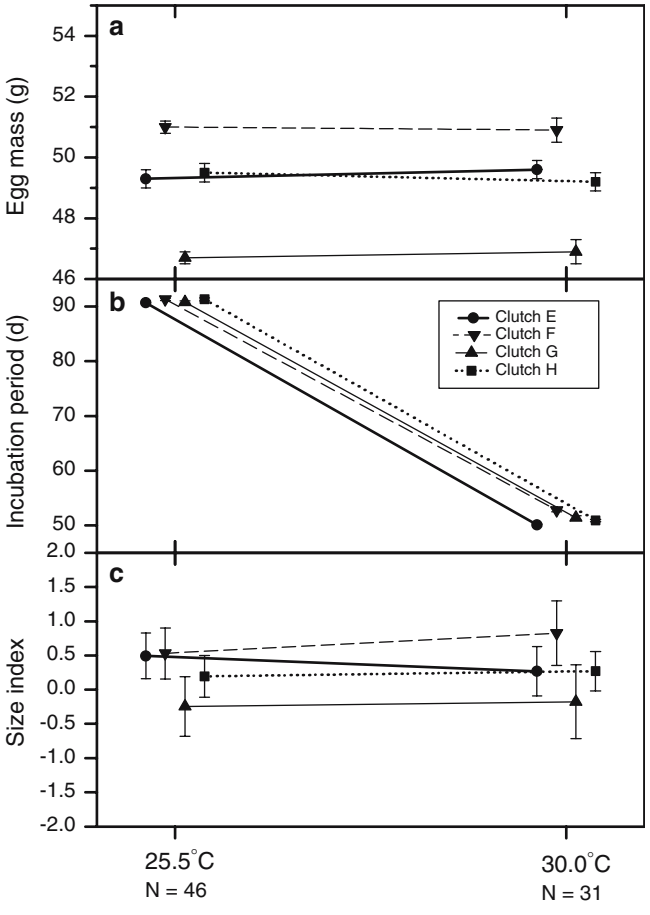

Fig. 4 Relationship between incubation temperature and initial egg mass (**a**), incubation period (**b**) and hatchling size index (**c**) for *Chelonia mydas* eggs and hatchlings from the year 2002 experiments

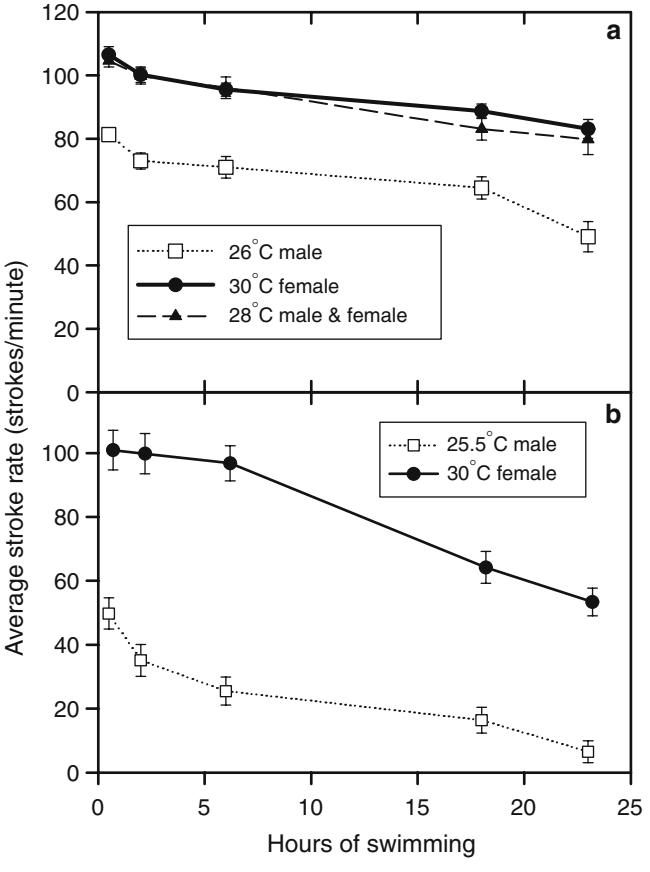

Fig. 5 Relationship between mean power stroke rate of *Chelonia mydas* hatchlings and hours of swimming. Means ± SE. **a** 2000 nesting season. Stroke rate calculated by reviewing video footage and counting with a stopwatch (modified from Booth et al. 2004). **b** 2002 nesting season. Stroke rate calculated as the product of power stroke rate during a power stroking rate and the proportion of time spent power stroking

The power stroke rate of hatchlings from 30°C in both 2000 and 2002 was similar for the entire 23 h swimming period (multiple student's t test with Bonferroni correction), but the hatchlings from 25.5°C in 2002 had significantly slower stroke rates than the hatchlings from 26°C in 2000 (multiple student's t test with Bonferroni correction, critical $P < 0.01$, all experimental $P < 0.001$).

In 2002, hatchlings from 30°C spent more time power stroking and less time dog paddling and not swimming than hatchlings from 25.5°C across all time periods (Figs. 6, 7a). Time spent dog paddling was unaffected by hours of swimming, clutch of origin or incubation temperature. Time spent not swimming increased with hours of swimming ($P < 0.001$), was greater in hatchlings from 25.5°C ($P = 0.007$), but was not influenced by clutch of origin. Time spent power stroking decreased with hours of swimming ($P < 0.001$), was greater in hatchlings from 30°C than 25.5°C ($P = 0.010$) and was not influenced by clutch of origin. The proportion of hatchlings exhibiting power stroking behaviour was also greater in hatchlings from eggs incubated at 30°C (Fig. 7b). Stroke rate within a power stroking bout decreased as hours of swimming increased ($P < 0.001$), but was unaffected by incubation temperature or clutch of origin (Fig. 8a). However, because power stroking bouts occurred more frequently in hatchlings from eggs incubated at 30°C, the average number of power strokes taken per minute was greater in this group (Fig. 5b). Mean force decreased as hours of swimming increased ($P < 0.001$), was greater in hatchlings that were incubated at 30°C ($P = 0.009$) but was not influenced by clutch of origin (Fig. 8b). The greater mean force generated by hatchlings from eggs incubated at 30°C was the result of them spending more time power stroking than hatchlings from 25.5°C. Mean force generated by swimming hatchlings 30 min after swimming began was weakly correlated with hatchling size, but hatchlings of similar size generated greater force if they came from eggs incubated at 30°C (ANCOVA $P < 0.001$, Fig. 9).

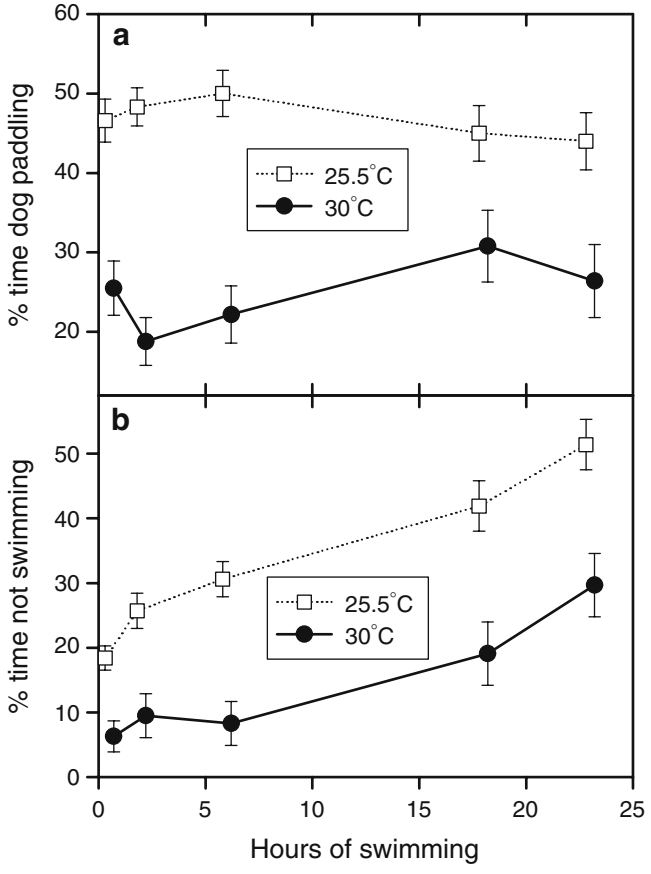

Fig. 6 Percent of time spent dog paddling (**a**) or not swimming (**b**) for *Chelonia mydas* hatchlings from eggs collected from four clutches in November 2002 and incubated at 25.5 or 30°C over the 23 h swimming period. Means ± SE

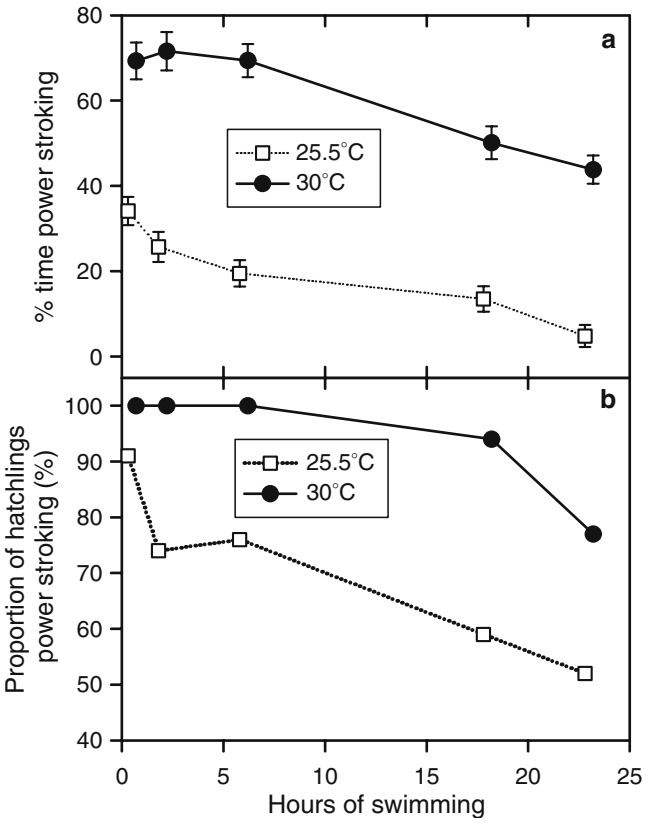

Fig. 7 Percent of time *Chelonia mydas* hatchlings spent power stroking (**a**) and the proportion of hatchlings that showed at least one power stroking bout during the 10 min monitoring period (means ± SE) (**b**). Eggs were collected from four clutches laid in November 2002 and incubated at either 25.5 or 30°C (means only)

Discussion

Hatchling size

In this study both clutch of origin and incubation temperature influenced hatchling size. Egg mass, which influences hatchling mass and size attributes (Booth and Astill 2001a), is relatively uniform within a clutch, but

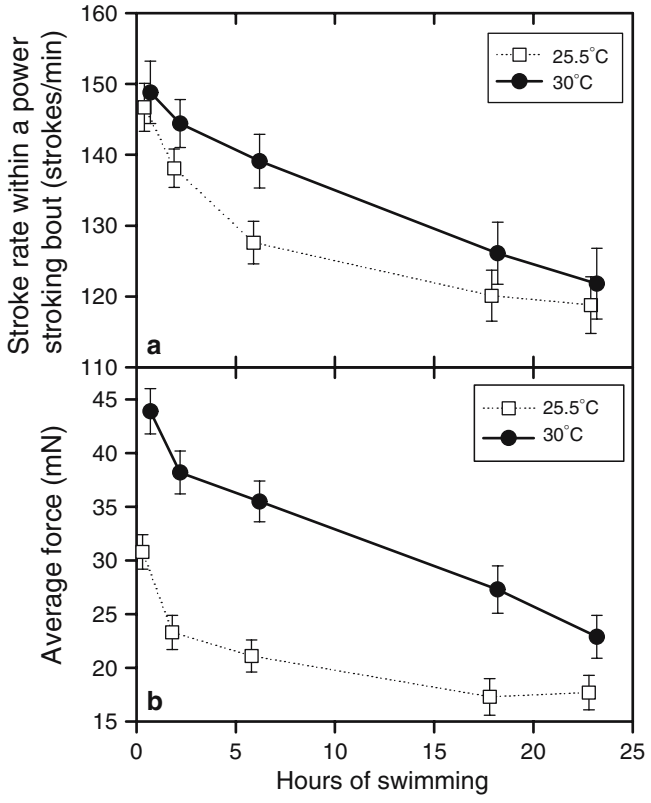

Fig. 8 **a** Power stroke rate within a power stroking bout and **b** average force production during the 10 min monitoring period of *Chelonia mydas* hatchlings from eggs collected from four clutches in November 2002 and incubated at 25.5 or 30°C over the 23 h swimming period. Means ± SE

can vary substantially between clutches. However, even when differences due to egg mass variation were accounted for, significant clutch effects on hatchling size

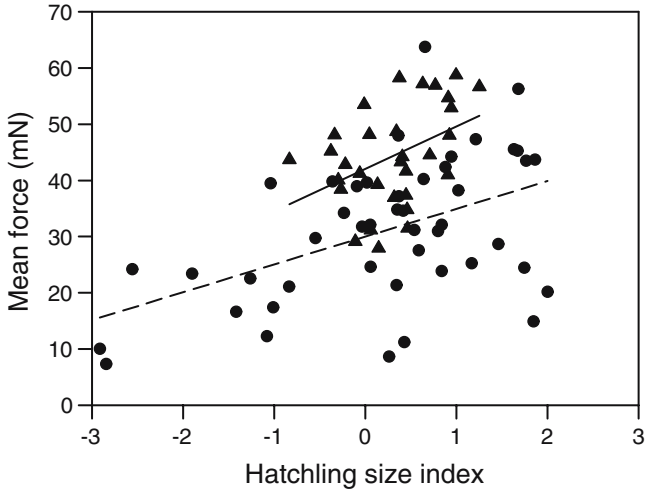

Fig. 9 Relationship between mean force generated 30 min after swimming began and *Chelonia mydas* hatchling size for 2002 experiments. *Triangles* and *solid line* represent data from hatchlings incubated at 30°C ($y = 42.05 + 7.54x$, $r^2 = 0.17$, $P = 0.019$, $N = 31$). *Circles* and *dashed line* represent data from hatchlings incubated at 26°C ($y = 29.99 + 4.95x$, $r^2 = 0.23$, $P < 0.001$, $N = 46$)

persisted. The influence of clutch may be the result of differences in genetic makeup and/or differences in provisioning of nutrients (i.e. relative proportions of lipid, protein and water in the egg) laid by different females. Sea turtles also lay several clutches within a season but no studies have explored possible variation in hatchling quality from different clutches laid by the same female. Most studies examining the influence of incubation temperature on hatchling morphology in reptiles have ignored the influence of clutch; however, these findings suggest that future studies should be designed to take this into account, as it is likely to be a key factor determining hatchling attributes.

Incubation temperature, as well as sex, influenced the size of hatchlings in three clutches in the year 2000 experiments. Hatchlings from eggs incubated at 26°C were larger than hatchlings from eggs incubated at 30°C, as previously reported for green turtles (Booth and Astill 2001a). However, in one clutch from the 2000 experiments and in all clutches from the 2002 experiments, hatchlings from 26 or 25.5°C were similar in size to hatchlings from 30°C. Clearly there is inter-clutch variation in the influence of incubation temperature on hatchling size. In clutches where lower incubation temperature results in larger hatchlings, size difference is caused by more yolk being converted to hatchling tissue during incubation because these hatchlings have heavier yolk-free mass and lighter residual yolk mass compared to hatchlings from higher temperatures (Booth and Astill 2001a). Hatchling size may affect hatchling survival as larger size may preclude predation by gape limited predators (Bustard 1972) and larger hatchlings are generally better swimmers (see below), but the ecological relevance of these relatively small incubation temperature induced differences in hatchling size remains to be investigated.

Swimming performance

In these experiments hatchlings were left in darkened containers for 48 h after hatching in order to mimic the time they spend in natural nests before emerging. In natural nests 4–7 days are spent in the nest before emergence occurs (Godfrey and Mrosovsky 1997). During this time, hatchlings dig their way to the surface, but this digging activity occurs in bouts which are separated by rest periods when hatchlings are quiescent (Bustard 1972). In the laboratory incubators, hatchlings tended to be active most of the time, so it was decided to shorten the "in nest period" to 2 days because continual activity is known to decrease green turtle hatchling swimming performance (Pilcher and Enderby 2001). Because the post-hatch to pre-swim period was the same across all incubation treatments it was assumed that the "energy depletion" that occurs in hatchlings during this period would also be the same.

Hatchlings were swum in water at 28°C which is the mean water temperature during the hatching season, but water temperature can vary between 26 and 32°C over

the season (Heron Island Research Station water temperature records). Because water temperature determines the body temperature of hatchlings and body temperature influences locomotor performance in reptiles, measurement of swimming performance at a different water temperature is expected to result in quantitatively different, but qualitatively similar results. In other words, it would be expected that the incubation temperature induced difference in swimming performance would persist independently of hatchling body temperature during the swimming trials. This expectation has previously been demonstrated in studies on hatchling lizards (Downes and Shine 1999; Braña and Ji 2000).

Clutch of origin had no influence on hatchling swimming performance. This was a somewhat surprising result because clutch of origin influenced hatchling size and has been found to influence running and swimming performances in freshwater turtle hatchlings (Janzen 1993). Within an incubation temperature, hatchling size was also positively related to swimming performance in the present study. This apparent anomaly is explained by the low power of the test for clutch in the current study and suggests that ideally more clutches should be included in subsequent studies to clarify the importance of clutch effects on performance.

Incubation temperature had a large influence on swimming performance with hatchlings from 25.5 and 26°C being consistently poorer swimmers than hatchlings from 28 and 30°C in terms of both power stroke rate and force generation. This difference can be attributed to an incubation temperature effect as males from 28°C had a similar swim performance to females from 28 and 30°C. Incubation temperature has previously been shown to affect post-hatching locomotor performance in freshwater turtles (Janzen 1993; Doody 1999; Du and Ji 2003), lizards (Van Damme et al. 1992; Shine et al. 1995; Downes and Shine 1999) and snakes (Burger 1990, 1991; Webb et al. 2001) and therefore probably plays an important role in determining hatchling fitness in these species.

Power stroke rate was poorer in hatchlings from eggs incubated at 25.5°C compared to eggs incubated at 26°C. Both temperatures are at the lower end of the viable range of incubation temperatures for green turtles and this indicates that hatchling swimming performance decreases markedly as temperature approaches the bottom end of the viable incubation temperature range. On Heron Island, only nests that are laid at the very beginning of the incubation season when the general sand temperatures are still low (Booth and Astill 2001b) are likely to experience such low temperatures. When these early nests are laid, nest temperatures are typically 23–24°C, but these increase as incubation proceeds as a result of the general rise in sand temperature and the production of metabolic heat from the developing embryos (Booth and Astill 2001b). In most years these early nests are probably the only ones to produce large numbers of male hatchlings and are thus important for population structure.

As expected, the greatest force was generated during power stroking bouts, the mean force during these bouts typically being twice as great as during dog paddling periods. No force was generated during rest periods. Average force production is probably the best overall indicator of swimming performance as it indicates forward thrust power and takes into account differences in flipper size, stroke rate, force generated per power stroke and time spent power stroking, dog paddling and not swimming. If differences in average force generation are directly related to swim speed, hatchlings from 30°C would swim on average 60% faster than hatchlings from 25.5°C. Interestingly, the lower average force generated at 25.5°C was caused by a smaller portion of time spent power stroking rather than a slower stroke rate during a power stroking bout. The proportion of individuals that were observed to undergo power stroking bouts within an observation period was also lower in hatchlings from eggs incubated at 25.5°C. These observations suggest that incubation temperature does not influence the ability of the swimming muscle to generate force per se, but strongly influences its fatigue resistance.

Ecological implications

Many sea turtle populations are facing rapid declines and concerted conservation efforts are needed to prevent their extinction (Spotila et al. 2000). One high priority aspect to the conservation of endangered populations is to ensure adequate recruitment of both sexes into the population (Richardson 1999). This conservation aim is complicated by the fact that nest temperature determines the sex of sea turtles, and measurements of nest temperatures from sea turtle rookeries around the world predict a predominance of female hatchlings (e.g. Godfrey et al. 1996; Broderick et al. 2001), and this trend may increase with global warming (Formia 1996; Miller 1997). The experimental results from this study further reinforce the crucial role that incubation temperature plays in sea turtle life history by potentially affecting the swimming performance of the hatchling turtle, a trait that is likely to influence the survival of hatchlings in a predator-dense environment. Significant mortality of sea turtles hatching on Heron Island occurs as a result of fish predation when the hatchlings first enter the water and traverse the shallows (Gyuris 1994, 2000). Males produced at low incubation temperatures with a poor swimming performance are likely, therefore, to suffer greater predation than males and females emerging from nests at higher temperatures. On Heron Island the production of male hatchlings is likely to be highest at the beginning of the nesting season when sand temperatures are still cool (Booth and Astill 2001b). These results suggest that a large number of these male hatchlings will not reach the open ocean because of their poor swimming performance while crossing the predator-rich reef flat.

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