A COMPARISON OF THE ONTOGENY OF ENERGY CONSUMPTION IN LEATHERBACK, DERMOCHELYS CORIACEA AND OLIVE RIDLEY, LEPIDOCHELYS OLIVACEA SEA TURTLE HATCHLINGS

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A Comparison of the Ontogeny of Energy Consumption in Leatherback, *Dermochelys coriacea* and Olive Ridley, *Lepidochelys olivacea* Sea Turtle Hatchlings

by

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This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Peter L. Lutz, Department of Biological Sciences, and has been approved by the members of his supervisory committee. It was submitted to the faculty of The Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

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Title:	A Comparison of the Ontogeny of Energy Consumption in Leatherback, *Dermochelys coriacea* and Olive Ridley, *Lepidochelys olivacea* Sea Turtle Hatchlings
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Changes in activity related oxygen consumption and energy partitioning were measured in leatherback and olive ridley sea turtle hatchlings over their first month after nest emergence. Leatherbacks emerge with about 75–90 KJ of energy in the residual yolk at their disposal for growth and movement. In comparison, the residual yolk energy reserves for the olive ridley are estimated to be much less (45 KJ). In leatherbacks resting specific oxygen consumption rates decreased by 53% over the first post–hatching month (0.0065 ml O_2 min^{-1} g^{-1} – 0.0031 ml O_2 min^{-1} g^{-1}), while for ridleys the fall was 32% (0.0038 ml O_2 min^{-1} g^{-1} – 0.0026 ml O_2 min^{-1} g^{-1}). Greater differences were seen in aerobic scope. For olive ridleys the factorial aerobic scope doubled over the first month but there was no significant increase in the leatherback's factorial aerobic scope. Leatherback hatchlings gained on average 33% body mass (10 g) over the first week however 70 to 80% of this increase was due to water accumulation. The differences in aerobic scope and energy reserves are related to differences in early life ecological stratagems of these species.

"To Mom, Dad, and Mike"

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INTRODUCTION

Natural History

Some 235 million years before present, the first animals recognized as turtles, order Testudinata, appeared and were believed to be terrestrial (Gaffney 1990; Pritchard 1997). During the Jurassic period two families (Pleurosternidae and Thalassemyidae; now both extinct) invaded the marine world, then 150 million years ago in the Cretaceous period four more families of turtle (Toxochelyidae, Protostegidae, Cheloniidae, and Dermochelyidae) entered the sea of which two are extant making up the modern sea turtle, the Dermochelyidea (100 mya) and the Cheloniidae (40 – 60 mya; Pritchard 1997). All sea turtles, although aquatic, are tied to the land as their early predecessors for oviposition.

Life History

As all seven species of extant sea turtles are tied to the land they share similar life history stages. Males and females can be found off nesting beaches during breeding seasons. Females will then clamber up the beach to lay ~ 7 clutches of eggs at ~ 10 to 14 day intervals. The breeding season usually lasts 2 to 5 months. Both the males and females will then return to foraging areas where the female will wait from 2 to 8 years before making another breeding migration though males may make the breeding migration yearly (Miller 1997). The only exceptions from this breeding regime are the olive and kemp's ridley sea turtle. Both of these species are known to have mass nesting

"arribadas" where thousands of gravid females will nest over a few days time (Miller 1997).

Once the female leaves the clutch of eggs her parental investment is over. The eggs incubate in the sand for ~ 8 to 10 weeks before the hatchlings pip from the eggshell, emerge in unison at night, and scurry down the beach into the water (Miller 1997). The remaining part of parental investment (Hewavisenthi & Parmenter 2002) is the residual yolk sac the hatchlings retain for up to a week or more (Jones et al. 2000). Once the hatchlings emerge from the nest they enter a 'frenzy period' consisting of crawling down the beach dunes into the sea and then powerstroke swimming for up to 24 hours (Wyneken and Salmon 1992).

Evidence suggests that after leaving the beach hatchlings of most species of sea turtle swim to major offshore oceanic currents where they passively drift for up to a decade while feeding on organisms within large seaweed drifts (Bolten 1995; Carr 1986). Sea turtles can then either remain in the oceanic environment or return to neritic zones. These divergent developmental life history patterns are described by Bolten (2003) as 'Type 2: oceanic – neritic developmental pattern' and 'Type 3: the oceanic developmental pattern'. Leatherbacks are the only sea turtle believed to be completely oceanic from hatching through adult life history stages (Type 3). Whereas the olive ridley has an ontogenetic shift from oceanic to neritic habitat upon reaching juvenile size (Type 2). Studies have suggested that the East Pacific populations of olive ridleys might share the Type 3 developmental pattern of leatherbacks (Bolten 2003; Pittman 1990).

However, these olive ridley sea turtles were still described as float and wait foragers (Bolten 2003) whereas leatherbacks can be considered to be active pelagic foragers (Salmon et al. 2004).

After this initial life stage the sub-adults migrate to coastal habitats where they grow to maturity (Carr 1962). In the Western Atlantic, for example, hatchlings are entrained in the Gulf Stream current, circling the North Atlantic by way of the Azorean and Canary currents and eventually finding themselves back in the Western Atlantic Ocean (Carr 1962 & 1986). Frick (1976), as well as Carr and Meylan (1980), found direct evidence of hatchling green turtles associating themselves with the sargassum flats. Frick (1976) also noted that hatchling green turtles fed on comb jellies, a finding corroborated by Salmon et al. (2004) who found that both green turtle and leatherback hatchlings feed upon gelatinous zooplankton at depths < 18 m. Loggerheads have also been found to entrain in sargassum rafts (Carr 1986; Witherington 2002). Witherington (2002) found that small loggerheads are inactive in the sargassum rafts only showing signs of active oriented swimming when the sargassum becomes fragmented or there is a risk of being swept ashore or being swept in cold waters.

Oceanic gyres are the nursery for sea turtle hatchlings as they mature into juveniles. The leatherback hatchling however possibly swims directly to tropical upwelling and downwelling zones where they assume a completely pelagic active lifestyle for the rest of their lives. Eckert (2002) showed that leatherbacks are not found above ~30^{o} latitude until they are > 80 cm (ccl) or that they are not found in water < 26^{o}

C until larger than 100 cm (ccl). This finding removes leatherbacks from Carr's (1986) theory that hatchlings are entrained in the North Atlantic gyre as this cycle would take leatherback hatchlings well above the 30° latitude. Leatherbacks instead may actively pursue a preferred habitat rather than being passengers in oceanic currents. Wyneken and Salmon (1992) studied the diel activity model of swimming in loggerheads, greens, and leatherback hatchling and post-hatchlings. Their findings showed that leatherbacks swam proportionally longer than the other species during post-hatchling night hours and were thus maintaining high levels of activity.

Salmon et al. (2004) looked at early foraging and diving behavior in leatherbacks showing that leatherbacks actively feed on gelatinous zooplankton by diving within 20 m of the surface. Whereas green turtles fed upon floating bits of *Thallasia spp.* (turtle grass) and *Sargassum spp.* at the surface (as well as gelatinous zooplankton at shallow depth; Salmon et al. 2004) and loggerheads fed upon *Sargassum spp.* and *Sargassum spp.* commensals at the surface (Witherington 2002).

Although both Dermochelidae and Chelonidae hatchlings share grossly similar life-history patterns the way they go about their early life is quite divergent. Cheloniid turtles passively migrate and can be considered sedentary sit and wait foragers while leatherbacks (only extant Dermocheliid) actively move to and through equatorial convergence zones feeding throughout the water column.

Background

When first emerging from the nest, sea turtles are in a highly energetic phase termed the 'frenzy' (Carr 1961). The elevated activity levels during this frenzy period allow the hatchlings to swim to nearshore gyres and currents where they passively drift and forage for up to a decade (Carr 1986; Bolten 1995; Witherington 2002).

All chelonid sea turtles, such as the olive ridley (*Lepidochelys olivacea*), return to neritic or near shore habitats for further development, from juvenile to adult. Leatherbacks (*Dermochelys coriacea*), on the contrary, are the only sea turtles that have a completely oceanic life, from hatching to adult (Bolten 2003). The hatchlings of these species have contrasting life styles. Olive ridley sea turtles are described as float and wait foragers (Davenport and Pearson 1994; Bolten 2003) whereas leatherback hatchlings can be considered active oceanic-pelagic foragers. Leatherback hatchlings feed throughout the water column making vertical migrations to feed upon the variety of gelatinous zooplankton (Salmon et al. 2004). Olive ridley hatchlings probably feed opportunistically like loggerhead (*Caretta caretta*) hatchlings upon available animal and plant matter such as ocean surface and near surface hydroids, copepods, fishes, crabs, shrimp and algae at the surface in convergence zones (Witherington 2002).

A further distinction in the energetics and ecology of leatherback and olive ridley hatchlings can be seen in their modes of locomotion. Davenport et al. (1984) pointed out that hatchling chelonid sea turtles, such as olive ridleys, loggerheads and Kemp's ridley hatchlings, had similar modes of locomotion (synchronized hindlimb propulsion) while

leatherbacks are quite distinct (synchronous forelimb propulsion). Davenport & Pearson (1994) concluded that loggerhead and olive ridley hatchlings appeared to have a low-energy lifestyle, compatible with inactive drifting for long periods of time at the sea surface while leatherbacks are geared towards a continuously energy consuming slow constant movement relevant to a oceanic-pelagic lifestyle (Davenport 1987).

In essence the two species have divergent early-life strategies. The olive ridley is a sit and wait, sedentary, forager while the leatherback is an active, oceanic, water column forager.

There have been previous studies on the metabolic rates of frenzy and post-frenzy hatchlings (Prange & Ackerman 1974; Davenport & Oxford 1984; Lutcavage & Lutz 1986; Wyneken 1997; See Table 3 this study), measurements of the yolk energy reserves on emergence (Kraemer & Bennett 1981; Silas et al. 1984; Hewavisenthi & Parmenter 2002) and the anaerobic component of the hatchling frenzy (Dial 1987; Baldwin et al. 1989). However, little is known of the early physiology of sea turtle hatchlings during the critical period when they leave the beach and enter the ocean and the corresponding shift from frenzy to post-frenzy. In particular there is no information on the changes in energetics over this first month when the animal has to have sufficient capacity and reserves to reach the oceanic upwelling or gyre habitat. All previous studies examined one component or one moment in time of hatchling energetics during the frenzy or post-frenzy state. This study offers the first inclusive and quantitative determination of hatchling energetics (i) between metabolic states (resting, swimming,

maximal exercise), (ii) as hatchlings shift from frenzy to post–frenzy and (iii) as hatchlings enter a steady-state equilibrium (1-month post-hatching), where energetic expenditure is sustained by food items (Peterson et al. 1990). This study also provides the first measurements of metabolic rates in olive ridley sea turtles.

Aerobic scopes were determined from resting metabolic rate (RMR) and maximal metabolic rates (MMR) as per Fry (1947). The current definitions of aerobic scope use basal or standard metabolic rate instead of RMR (Hochachka and Somero 2002). However these metabolic states require the animal to be post-absorptive (thus animals are not expending energy for digestion and/or growth), a condition which is not possible in hatchlings due to their yolk reserves and is deleterious (leatherback hatchlings are notoriously fragile and difficult to maintain thus when animals are feeding it is best to maintain them in the feeding state) for raising post-hatchlings (Lutcavage and Lutz 1986; Jones et al. 2000). Scopes are given as both absolute scopes (difference between MMR and RMR; Willmer et al. 2000) and factorial scopes (ratio between MMR and RMR; Willmer et al. 2000). I measured flipper stroke rate and breath rate as an index of activity as did Lutcavage and Lutz (1986). As growth rates and body size (Nagy 2000; Darveau et al. 2002) can influence an ectotherm's metabolism, scope, and activity state these factors were included in the analysis.

The purpose of this study was to compare the changes in oxygen consumption, aerobic scope, and energetic reserves over the period from frenzy to post-frenzy to a quasi steady-state; in these two species of sea turtle with divergent developmental life

history patterns and ecologies. I studied the development of aerobic scope as it changed both temporally (age) and with mass. I measured the consumption of oxygen, as an indirect measurement of metabolism (Kleiber 1961), in both leatherback and olive ridley hatchlings (from emergence to 1-month) and the energy reserves in yolk of leatherbacks during their initial emergence (frenzy period), at one week of age (post-frenzy), and at 1 month of age (steady-state equilibrium).

My objectives were to (I) determine if and how metabolism changes during early development of hatchling sea turtles? and (II) determine where routine swimming lies within the scope of activity?

Objective (I)

I hypothesize that the metabolism will change during post-hatchling development in leatherback and olive ridleys. Furthermore that the scope will increase with age as maximal metabolic rates should scale at a higher exponent than resting rates thus leading to greater differences in scope as the animals increase mass (Schmidt-Nielsen 1984). I hypothesize that the scope of the leatherbacks will increase at a greater rate than olive ridleys as leatherbacks are believed to reach adult size or sexual maturation in ~ 4 - 11 years (Rhodin 1985) faster than any other sea turtle.

Objective II)

I hypothesize that routine swimming metabolism for leatherbacks will be moderate to low within their scope. Leatherbacks are a constantly moving animal foraging throughout the water column. Thus they would benefit from low routine swimming costs. I hypothesize swimming for olive ridleys will be at the higher end of their scope as swimming is not routine activity for ridleys and their swimming style is that of the 'sprinter' whereas leatherbacks maintain a constant economical stroke like that of the 'marathoner' (Wyneken 1997).

MATERIAL AND METHODS

This work was approved by IACUC at FAU and carried out under MINAE permit (358-2000-OFAU) and Florida Sea Turtle Permit #073.

Animals

Forty leatherback hatchlings *Dermochelys coriacea* (from two nests) and 12 olive ridley hatchlings *Lepidochelys olivacea* (from one nest) were collected as they emerged from the nest during January and February (2001) from the hatchery at Playa Grande, Parque Nacional Marino Las Baulas, Costa Rica. Hatchlings were allowed to orient and crawl down the dry sand to the water's edge before collection and relocation to the lab. Eight animals from each group were randomly chosen to perform in the following experiments.

Olive ridley hatchlings were maintained in a 120 L pool. I did daily water changes to prevent high levels of ammonia from accumulating in the tank. One UVA/UVB incandescent lamp (150 W) was mounted at the edge of the pool. Turtles were fed ad libitum on a pelleted turtle chow (ZooMed Aquatic Turtle Food^{TM}). Nutritional analysis of olive ridley diet is given in Table 1. At the conclusion of the study hatchlings were released in waters in front of Playa Grande.

Leatherback hatchlings were maintained in the lab as described by Jones et al. (2000). In brief: Animals were tethered in a large 800 L pool. Small (1 cm^2) velcro^{TM}

Species	Protein	Fat	Kj/Kg DM	WM/DM ratio
Leatherback	44.30%	30.20%	22,330	7.0
Olive ridleys	35.00%	5.00%	17,058	1.2

Table 1. Nutritional Analysis of Leatherback and Olive Ridley Diet. Energy and nutritional analysis of the diets fed to leatherback and olive ridley sea turtles. Protein and fat analysis is from manufacturer's label. Protein and fat is given as percent weight of dry mass (DM) of food. Energy content and wet mass (WM) to DM ratio is from drying oven and bomb calorimeter analysis. Energy content and WM/DM ratios are from two samples only.

patches were attached to the carapace with cyanoacrylate cement. Monofilament line ran from the patch to a swivel attached to wooden dowels running in quadrants across the top of the pool. Each hatchling was restricted to its respective quadrant thus preventing bumping and rubbing into sidewalls, bottom, and other hatchlings. As leatherback turtles are oceanic-pelagic animals this tethering system prevents them from damaging themselves against tank walls and bottom (Jones et al. 2000). Water quality for the pool was maintained by two filter systems: an ultraviolet filter (Startronics^{TM}), with a 25 W UV element and a "Skilter" (Supreme 400^{TM}) filter containing a protein skimmer, ground carbon and fiberglass mat. UVA/UVB incandescent lamps (150 W) mounted in four positions at the edge of the pool provided UV radiation. Water pH, salinity, and ammonia were monitored daily and water quality was maintained at a pH of 8 to 8.3, a

salinity of 28 – 35 ppt, and daily water changes prevented high levels of ammonia. Hatchlings were hand-fed strips of formulated food (nutritional analysis; see Table 1) to satiation daily, as per Jones et al. (2000). Leatherback food was blended and mixed with flavorless gelatin and water as leatherbacks are gelativores and will not accept food of a hard consistency (unlike olive ridleys). At the conclusion of the study hatchlings were released in waters in front of Playa Grande.

Oxygen Consumption

Animals were placed inside a closed system respirometer for experimental trials with an average air volume of 2,164.81 $\pm$ 350.84 cc. Closed systems tend to have less error due to baseline O_2 measurements (Kaufmann et al. 1989) and metabolism can be measured by monitoring the changing composition of gases within a respirometer of known volume (McDonald 1976). Minor changes in pressure can be compensated for with a flexible window (McDonald 1976) or, in our case, water level flux as water made up the bottom seal or confinement of our respirometer dome and was open to ambient pressure outside of dome (Figure 1). Air was pumped from the respirometer through Drierite® (water absorbant) and soda lime (CO_2 absorbant) to an oxygen analyzer (Qubit Systems™ S102 Oxygen Sensor) at 200 – 300 ml min^{-1}. The oxygen analyzer measured partial pressure of oxygen to 0.01 percent. Volume of air inside the respirometer was recorded; ambient oxygen percentage minus post -trial oxygen percentage gave total volume of oxygen consumed, thus $VO_2 = (\{[(\%O_2^I - \%O_2^F)/100]*VR\}/ t_1 - t_0)$. Where $\%O_2^I$ = percentage of oxygen in respirometer pre-trial, $\%O_2^F$ = percentage of oxygen in respirometer post-trial, VR = volume of air inside the respirometer as well as extra air

space in tubing and drierite/soda lime holders, and t_0 = initial or start time and t_1 = time at end of trial.

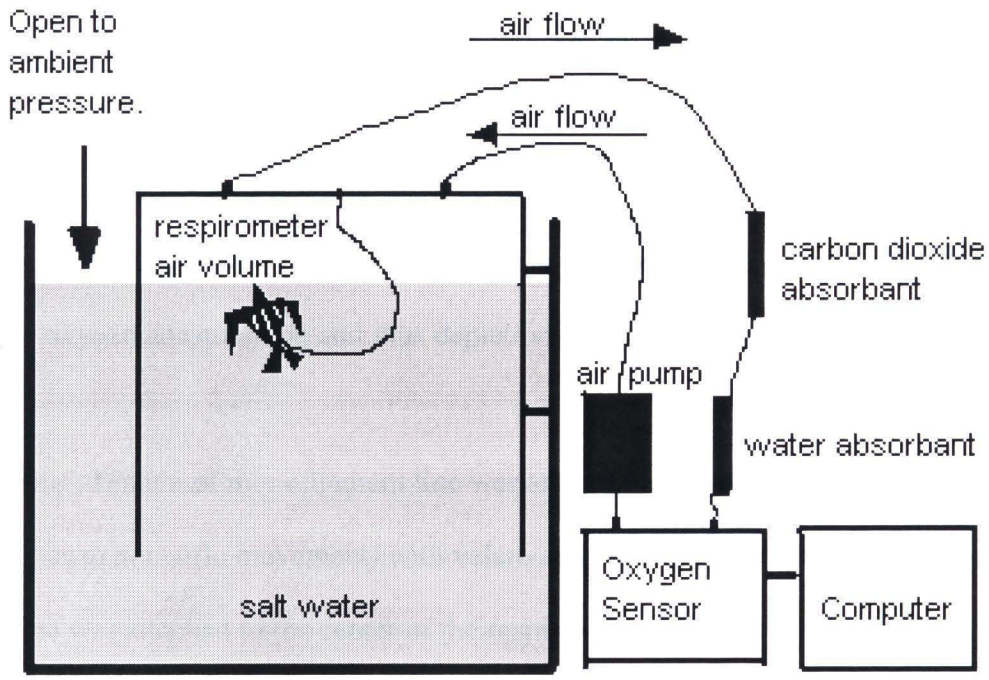


Figure 1. Closed system respirometer. Diagrammatic of the metabolic chamber used to measure oxygen consumption during swimming and maximal exercise.

Leatherbacks and olive ridleys were run through experimental trials at emergence, 1 week, and 4 weeks of age. Experimental trials consisted of a 30 min acclimation in the chamber followed by a 30 min trial (maximum exercise 30 min acclimation followed by 15 min trial). Trials consisted of three different treatments: 1) resting, 2) swimming, and 3) maximal exercise, as follows:

Rest. Animals were placed in an opaque jar (900 cc for leatherbacks and 412 cc for olive ridleys) moistened on the inside with wet paper towels. Movement was impeded due to the small size of the jar. Additionally, olive ridley hatchlings were restrained by use of velcro straps holding the fore flippers together. The olive ridleys initially struggled against the restraints however within 5 min they typically became quiescent. I periodically (every 5 – 10 minutes) listened for struggling and watched for sudden declinations in oxygen to assure that the hatchlings were resting, as activity would increase oxygen consumption and thus depletion of oxygen in chamber.

Swimming. Ten cm of monofilament line was attached to the carapace (at their center of rotation; as to not stifle movement) with velcro and cyanoacrylate cement, the other end of the line was attached to the center of the respirometer chamber. Animals could dive or swim in any direction without hitting the sidewalls or bottom of the tank, and as hatchlings surfaced to breath the tether kept them inside the respirometer dome (Wyneken 1991, 1997).

Maximal Exercise. Animals were tethered in the respirometer as in the swimming trial. Animals were then agitated from behind with a probe to induce maximal exercise or flight response. For the purposes of this study, I describe this state as maximal exercise as I cannot be confident I reached V_{max}. The probe was entered into dome from underneath allowing agitation of the subject without disrupting respirometer air volume.

Breath and Stroke Rate

Breath and stroke rates were recorded during swimming and maximal exercise. Upon onset of the experimental trials breaths and fore flipper stroke rates were recorded for one minute in the first, second, and third 10 min portion of each trial or during the first, second, and third 5 min portion of each 15 min trial (maximal exercise). When animals were breathing, dog paddling (synchronous movement of fore and rear flippers; olive ridleys; Wyneken 1997) was not counted as fore flipper strokes. Breath and stroke rates were averaged for each animal and calculated as breaths per minute (bpm) and strokes per minute (spm).

Whole Hatchling and Yolk Energetics

Hatchlings that died from natural causes at emergence, 1 week, and $\geq$ 4 weeks were immediately frozen for analysis of energy content (calories) of yolk and whole hatchling. Hatchlings were later thawed and the residual yolk sacs removed. Hatchlings and yolk were dried at 60^{o} C for 3 days to constant weight. The dry mass was then ground to a fine powder then placed in a bomb calorimeter to determine energy content. All determinations of body water were made from initial whole animal wet mass (WM) minus the dry mass (DM). All energy analyses were run on a Parr Instrument Company bomb calorimeter. All calculations and corrections were performed as described by Paine (1971). Energy content was determined as heat and then converted to calories and then to joules. The WM, DM, and energy values for hatchlings and yolk were then compared at the different age groups (emergence, 1-week, 1-month).

Data Analysis

All statistical analyses were carried out with JMP® Statistical Package version 4 2001. I followed the suggestions of Packard and Boardman (1999), as well as, Hayes (2001) and avoided the use of mass-specific analysis to compare animals of different mass. I corrected for differences in body mass using a mass-metabolism exponent of 0.83. Prange and Jackson (1976) derived this exponent from green sea turtles spanning 0.3 to 141.5 kg in body mass. Other studies involving reptiles have derived similar exponents (0.82, Aldabra giant tortoise, Hughes et al. 1971; 0.83, 26 species of lizard, Bennett and Dawson 1976). I used the Kruskal-Wallis non-parametric test for differences between means of 2 or more treatments for comparisons of the 2 species (leatherback and olive ridley), 3 activity states (RMR, AMR, and MMR), and 3 age groups (Frenzy, 1-week, and 1-month; N = 6 or 8 in all cases). I used the student's test to determine if differences existed between the slope and y-intercept of oxygen consumption regressed against mass for the different species at RMR and MMR (N = 16 in all cases). Aerobic scopes were determined from resting metabolic rate (RMR) and maximal metabolic rates (MMR) data as per Fry (1947). I compared both the absolute scopes (difference between MMR and RMR; Willmer et al. 2000) and factorial scopes (ratio between MMR and RMR; Willmer et al. 2000) of leatherbacks and olive ridleys at emergence, 1-week, and 1-month. I used Simple Linear Regression to determine if relationships existed between the volume of oxygen consumed and breath rate and volume of oxygen consumed and fore-flipper stroke rate for both species (N is variable).

RESULTS

Frenzy Metabolism

Figure 2 shows the differences in MMR and RMR for leatherback and olive ridley hatchlings during the frenzy period (first 24-hours after emergence). MMR and RMR were 0.60 $\pm$ 0.12 ml O_2 hr^{-1} $g^{-0.83}$ and 0.39 $\pm$ 0.09 ml O_2 hr^{-1} $g^{-0.83}$ for leatherbacks, respectively (all oxygen consumption values are given as means $\pm$ 1 standard deviation). While MMR and RMR were 0.50 $\pm$ 0.08 ml O_2 hr^{-1} $g^{-0.83}$ and 0.28 $\pm$ 0.11 ml O_2 hr^{-1} $g^{-0.83}$ for olive ridleys, respectively. A Kruskal-Wallis test showed significant differences existed between metabolic states (ChiSquare 21.92, $p < 0.0001$) with MMR having higher oxygen consumption than RMR. However there was no significant difference between species ($Z = -0.61$, $p > 0.5268$). Leatherback hatchlings ranged in mass from 35.70 to 45.40 g while olive ridleys ranged in mass from 12.70 to 13.60 g.

Post-Frenzy Metabolism

Figure 3 shows the trends for MMR and RMR in leatherbacks and olive ridleys at 1-week of age. Leatherback post-frenzy (1-week of age) metabolism was 0.42 $\pm$ 0.08 ml O_2 $g^{-0.83}$ and 0.21 $\pm$ 0.08 ml O_2 hr^{-1} $g^{-0.83}$ for MMR and RMR, respectively. Olive ridley post-frenzy metabolism was 0.49 $\pm$ 0.03 ml O_2 hr^{-1} $g^{-0.83}$ and 0.23 $\pm$ 0.07 ml O_2 hr^{-1} $g^{-0.83}$ for MMR and RMR, respectively. Leatherback hatchlings ranged in mass from 43.40 to 54.70 g while olive ridleys ranged in mass from 14.40 to 15.90 g. A Kruskal-Wallis test comparing states across species showed significant differences between metabolic states (ChiSquare 22.11, $p < 0.0001$) with MMR having higher oxygen consumption values

than RMR for both species. There was no significant differences between species' when the same rates were compared ($Z=0.60$, $p > 0.5328$).

Figure 2. Frenzy Metabolism

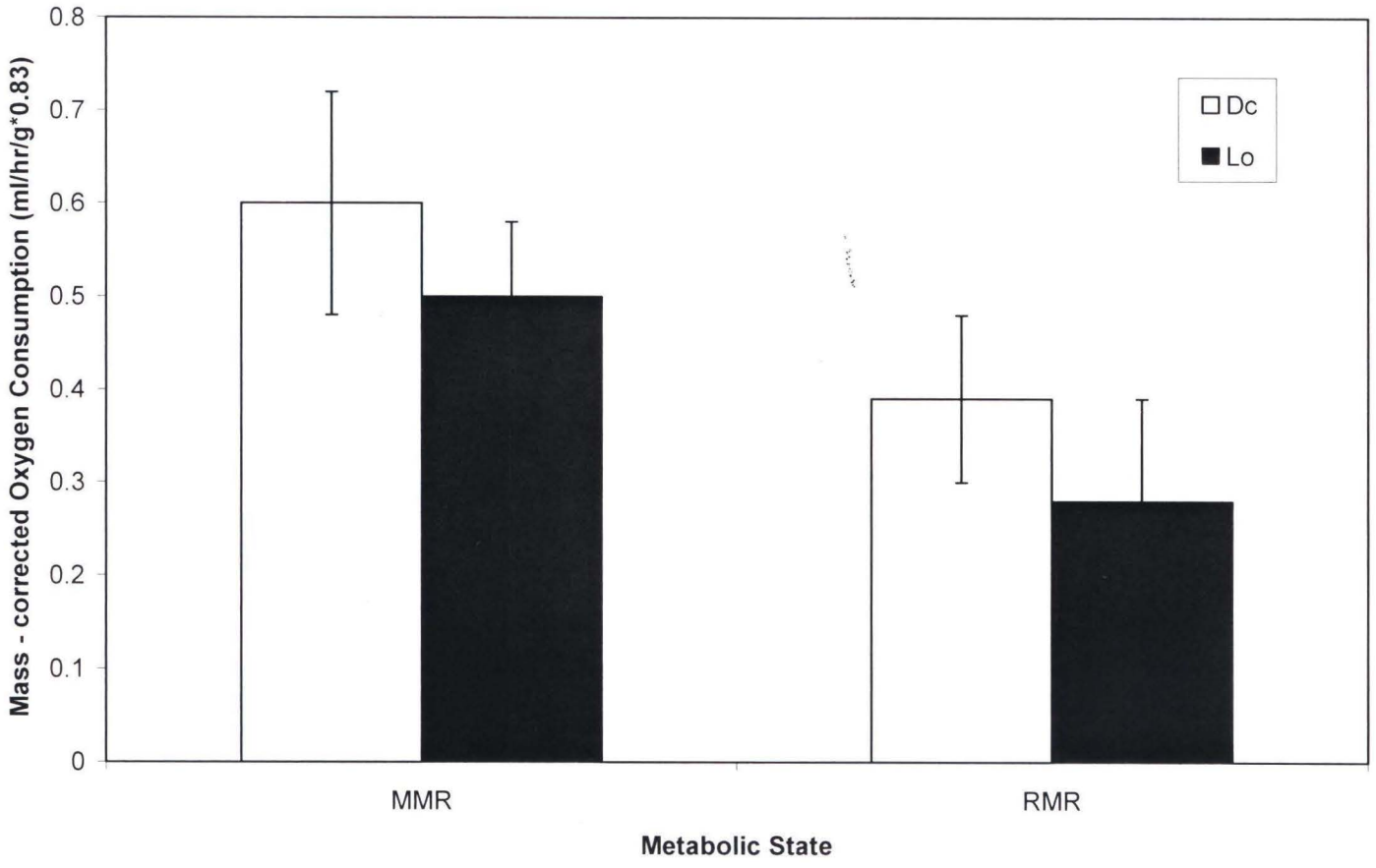
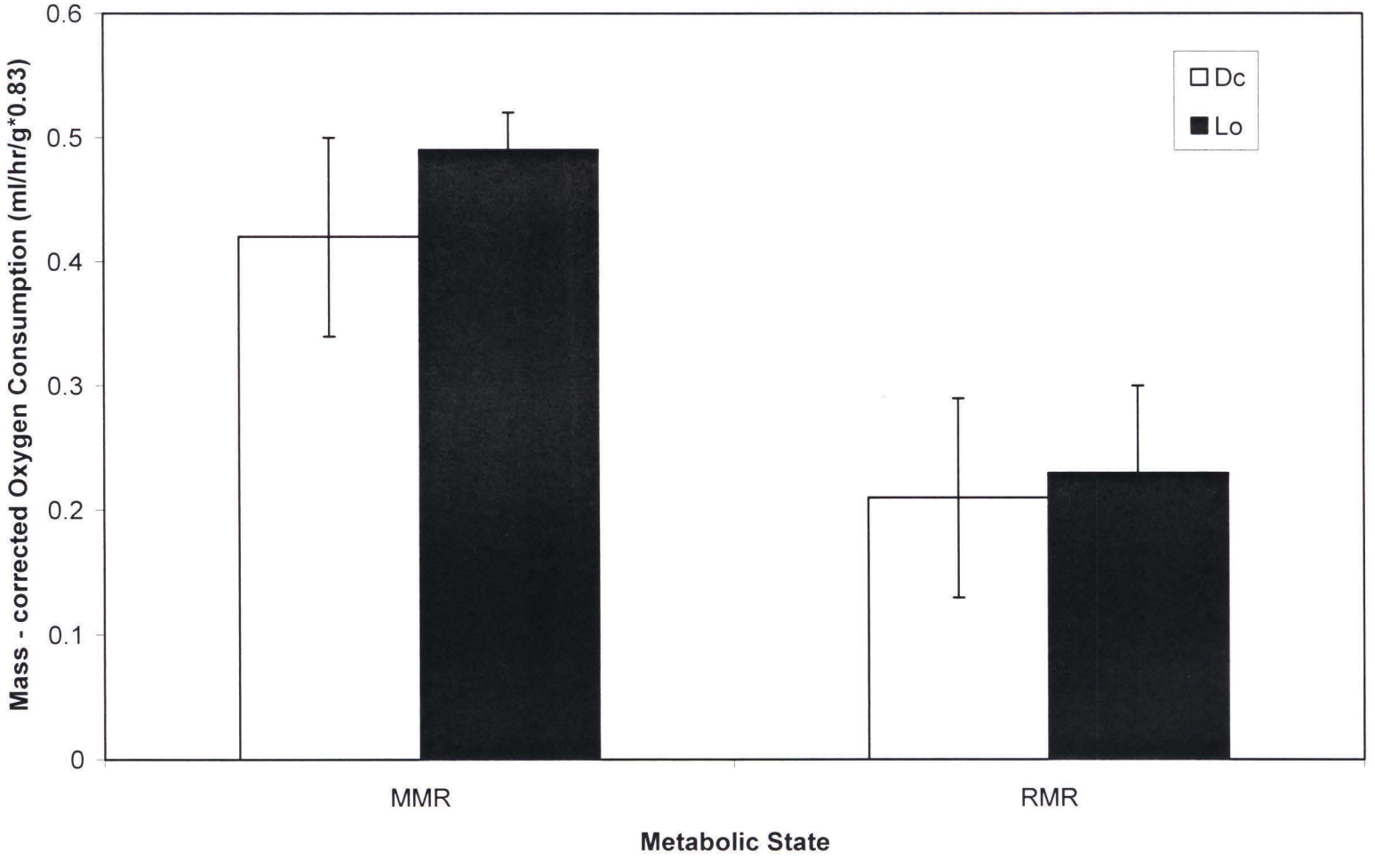


Figure 3. Week-1 Metabolism



Both leatherback and olive ridley sea turtles showed Frenzy metabolism; it was significantly higher than post-frenzy metabolism ($Z = -2.38$, $p = 0.0169$).

At 1-month of age significant differences developed between species ($Z = 2.90$, $p = 0.003$) with olive ridleys having higher MMR than leatherbacks. Along with the continued trend of elevated MMR over RMR for both species (ChiSquare = 18.44, $p = 0.0004$). These trends are shown in Figure 4. Leatherback MMR and RMR were 0.35 ± 0.06 ml O_2 hr^{-1} $g^{-0.83}$ and 0.22 ± 0.03 ml O_2 hr^{-1} $g^{-0.83}$, respectively. While olive ridley MMR and RMR were 0.67 ± 0.19 ml O_2 hr^{-1} $g^{-0.83}$ and 0.18 ± 0.03 ml O_2 hr^{-1} $g^{-0.83}$, respectively. Leatherbacks ranged in mass from 72.90 to 84.10 g at 1-month while olive ridley turtles ranged in mass from 18.90 to 21.30 g.

In figure 5 whole-animal MMR and RMR are regressed against mass for both species individually. Intraspecific MMR scaled to mass to the power of 1.65 for olive ridleys ($y = -1.13 + 1.65$ [x]; $R^2 = 0.66$, $F = 34.46$, $p < 0.0001$). While intraspecific MMR scaled with mass to 0.61 for leatherbacks ($y = 0.19 + 0.61$ [x]; $R^2 = 0.43$, $F = 10.60$, $p = 0.0057$). For leatherbacks RMR scaled proportionally with mass, 1.01 ($y = -0.74 + 1.01$ [x]; $R^2 = 0.64$, $F = 23.14$, $p = 0.0003$). However for olive ridley RMR there was not a significant relationship with mass. Although the data show a regression to the power of 0.44 this line is not significantly different than a slope of zero ($y = -0.07 + 0.44$ [x]; $R^2 = 0.09$, $F = 1.83$, $p = 0.1931$). The slope of leatherback RMR (1.01) is significantly higher than that of olive ridley (0.44; t test: 8.10, $p < 0.0001$).

Figure 4. Month-1 Metabolism

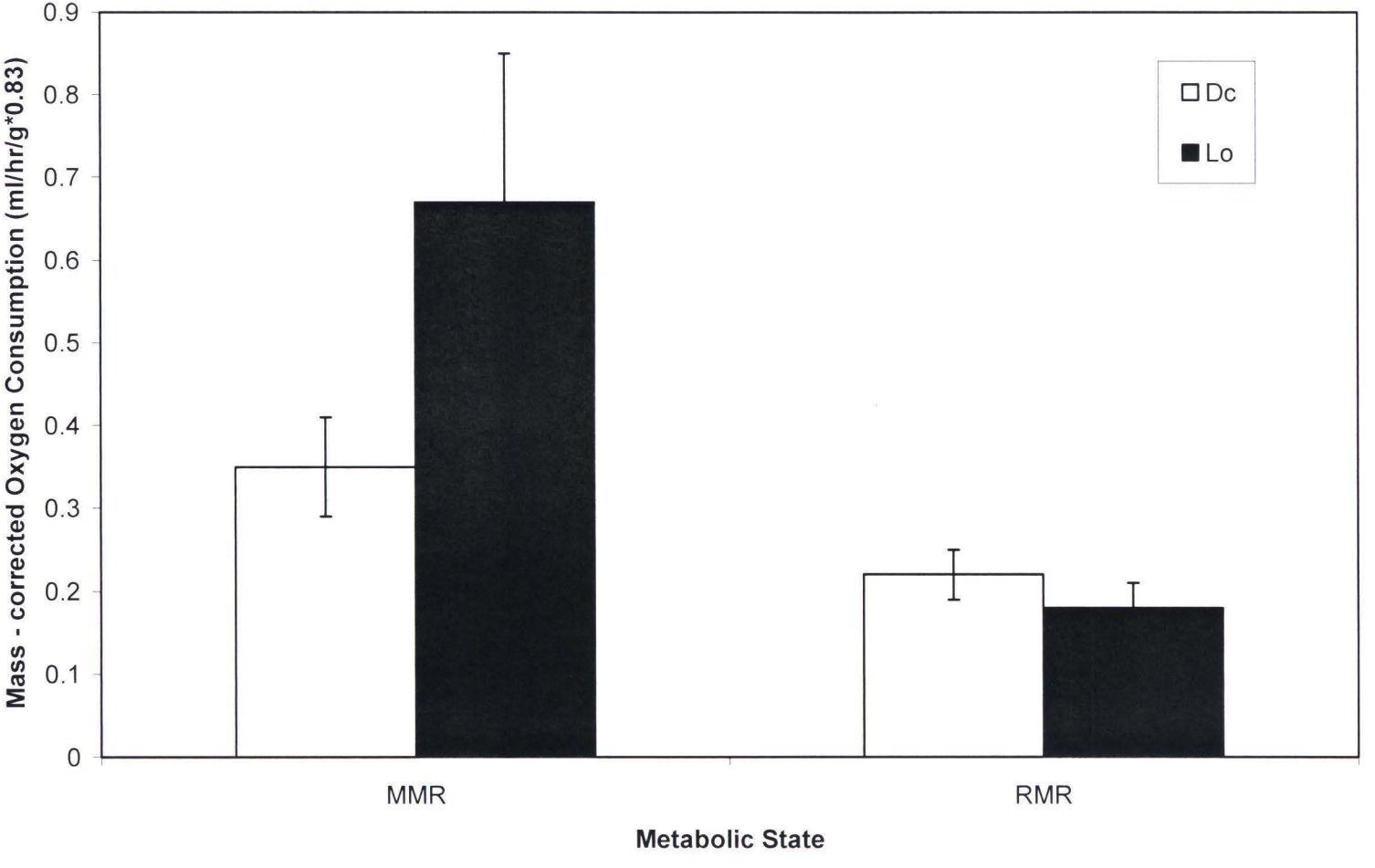
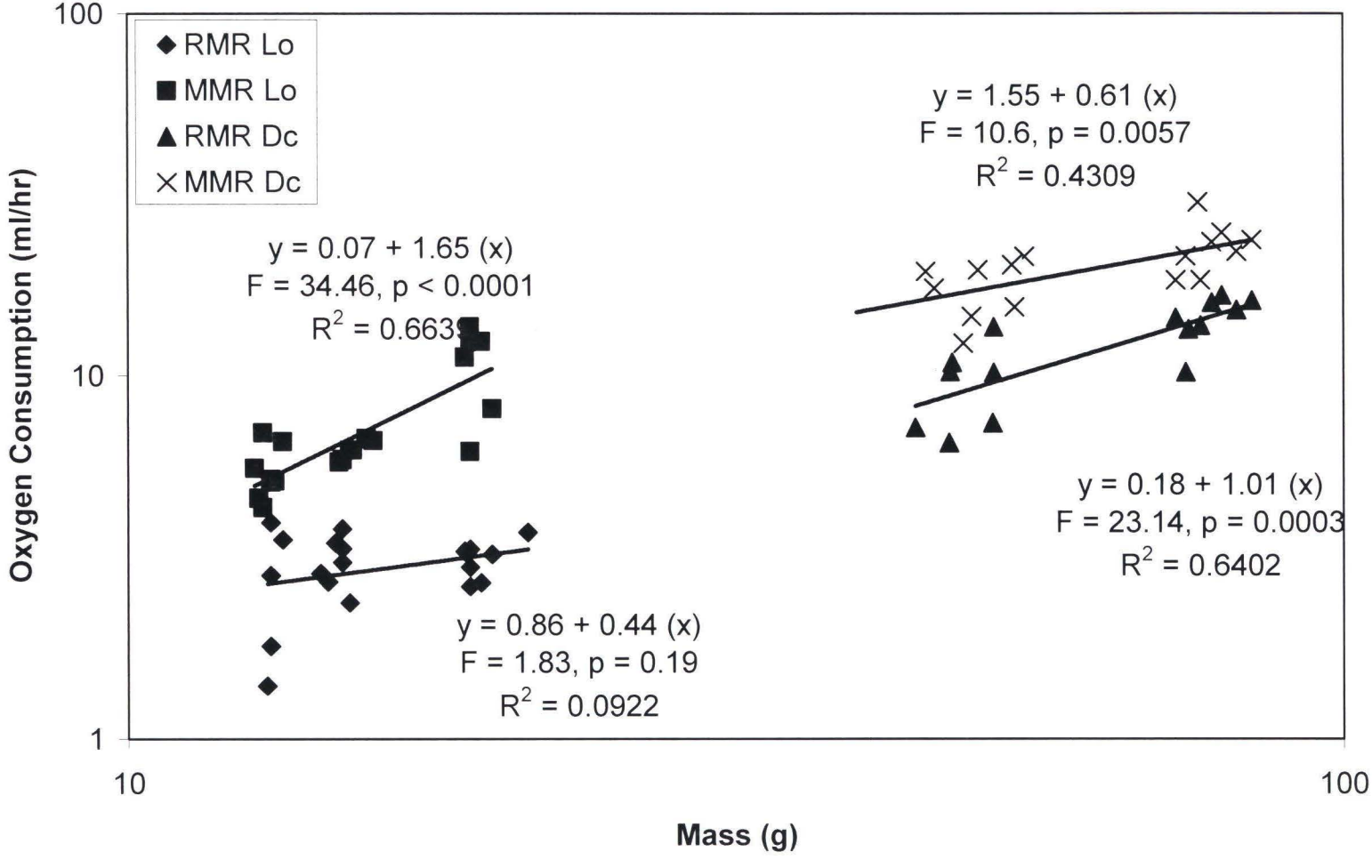


Figure 5. RMR vs MMR (Dc vs Lo)



While the slope (0.61) of leatherback MMR is significantly lower (t test 3.80, p = 0.0008) than that of the olive ridley (1.65). The aerobic scopes obtained from the scaling relationships in Figure 5 are summarized in Table 2.

	Dc		Lo	
	Absolute	Factorial	Absolute	Factorial
Emergence	4.61 ± 6.17	1.39 ± 0.60	2.42 ± 1.20	1.93 ± 0.84
1 – Week	9.02 ± 4.82	2.88 ± 2.77	3.32 ± .02	2.50 ± 1.45
1 – Month	8.44 ± 4.38	1.60 ± 0.36	7.87 ± 3.18	3.97 ± 1.43

Table 2. Absolute and factorial aerobic scope for leatherback (Dc) and olive ridley (Lo) sea turtle hatchlings. Values are given with ± 1 Standard Deviation. Absolute scopes are in ml O_2 hr^{-1}.

Swimming Metabolism (Post-Frenzy)

Swimming metabolism (AMR, active metabolic rate) decreased from 0.34 ± 0.25 ml O_2 hr^{-1} $g^{-0.83}$ to 0.23 ± 0.04 ml O_2 hr^{-1} $g^{-0.83}$ in leatherbacks from one week of age to 1-month. AMR in olive ridleys decreased from 0.45 ± 0.19 ml O_2 hr^{-1} $g^{-0.83}$ to 0.40 ± 0.02 ml O_2 hr^{-1} $g^{-0.83}$ from 1-week to 1-month of age (Figure 6). Leatherbacks ranged in mass from 43.20 to 84.10 g during this period while olive ridleys ranged from 14.90 – 19.27 g.

A Kruskal-Wallis test showed that significant differences existed between levels of AMR (ChiSquare 15.67, p = 0.0013). Olive ridley AMR was significantly higher than leatherback AMR (Z = 3.78, p = 0.0002) however there was no significant difference between AMR at 1-week to 1-month for either species (Z = 0.39, p = 0.6960).

Figure 7 shows swimming or AMR as a percentage of absolute aerobic scope at 1-week and 1-month of age for both leatherbacks and olive ridleys. RMR was subtracted from AMR and MMR values. Thus 0 % represents RMR and 100 % represents MMR for their respective categories of specie and age in Figure 7. I ran a Kruskal-Wallis test to determine statistical differences between the 4 levels (ChiSquare 10.39, $p = 0.0155$).

The trend for both species was for AMR to decrease within scope as turtles aged. Leatherbacks AMR went from 22.57 ± 5.57 to 10.63 ± 13.71 as % of scope while olive ridleys AMR as % scope decreased from 87.67 ± 32.03 to 56.83 ± 13.10. However, only Leatherback AMR at 1-month was significantly different from that of olive ridleys at 1-month ($Z = 2.19$, $p = 0.028$).

Figure 6. Swimming Metabolism

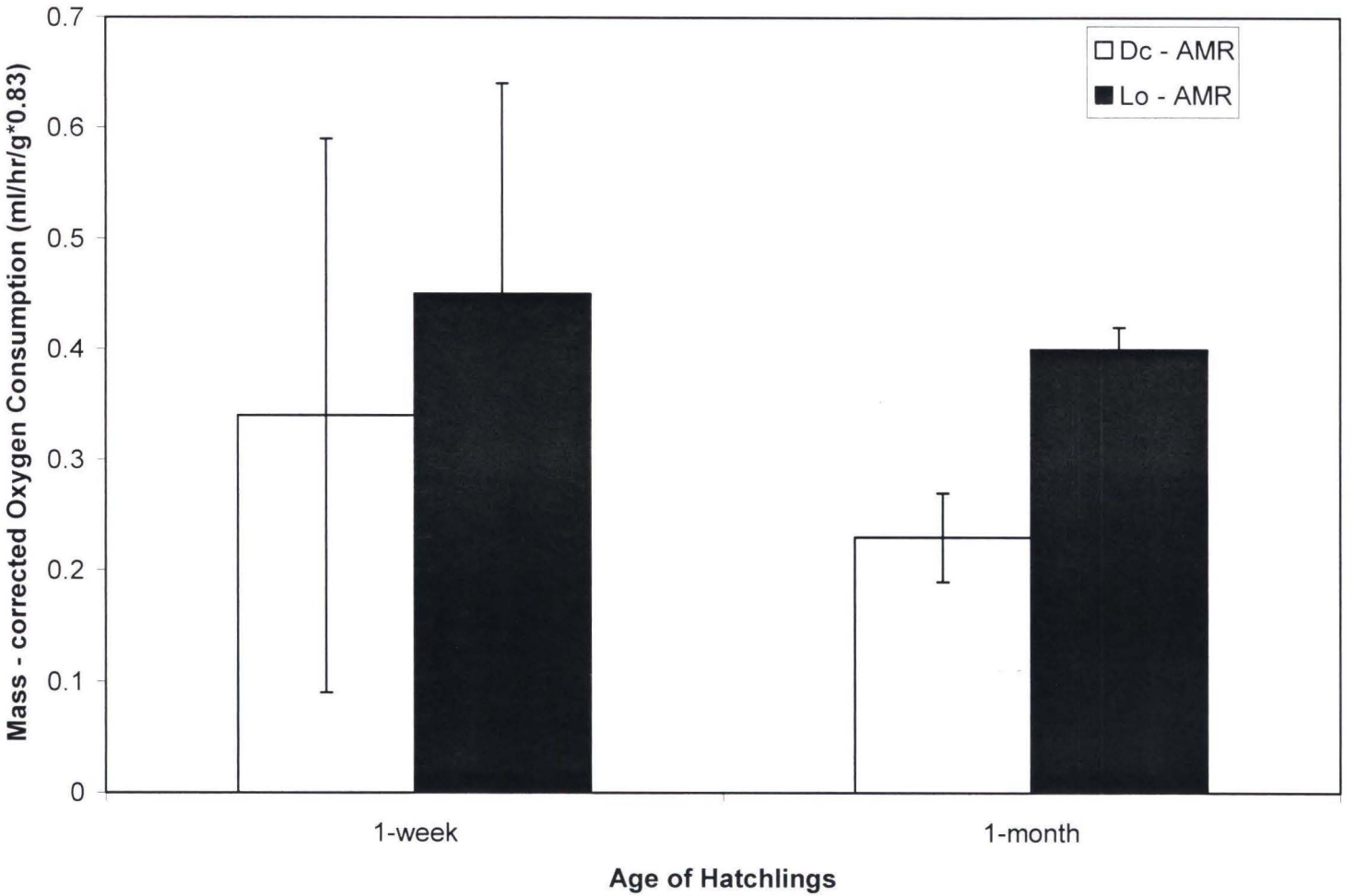
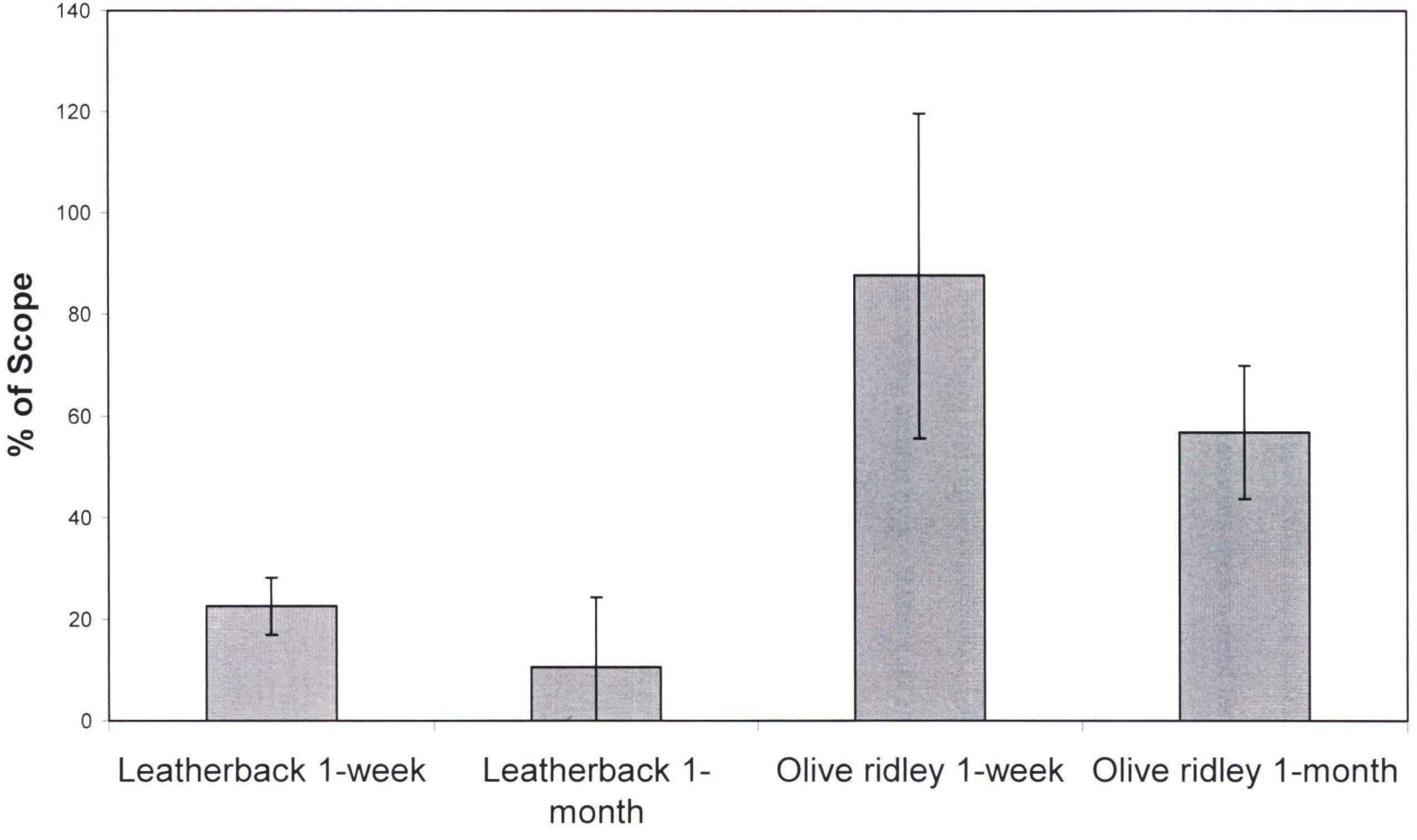


Figure 7. AMR (swimming) as percentage of Aerobic Scope



Breath and Fore Flipper Stroke Frequency

Figures 8a – 8d show a regression of oxygen consumption in ml O_2 hr^{-1} g^{-1} against breath rate or breaths per minute (bpm) and fore flipper stroke rate or strokes per minute (spm) in both leatherbacks and olive ridleys. Both animals show a trend for increasing oxygen consumption with both activity (spm) and with increased breaths (bpm). For both (bpm) and (spm) in leatherbacks and olive ridleys the lines were significantly different then a line drawn through the median with a slope of zero. Leatherbacks had a tighter relationship and higher R^2 values for both (bpm) and (spm) regressions. Leatherback oxygen consumption increased with increasing breaths by $y = 0.06x + 0.11$ ($R^2 = 0.68$, $F = 78.23$, $p < 0.0001$; Fig. 8a) while olive ridley oxygen consumption increased by $y = 0.05x + 0.24$ ($R^2 = 0.38$, $F = 11.13$, $p = 0.004$; Fig. 8c). The trend for increasing oxygen consumption with increasing fore flipper stroke rate was $y = 0.005x - 0.12$ ($R^2 = 0.52$, $F = 33.49$, $p < 0.0001$; Fig. 8b) and $y = 0.006x - 0.12$ ($R^2 = 0.34$, $F = 9.08$, $p = 0.008$; Fig. 8c) for leatherbacks and olive ridleys, respectively.

Figure 8a. Dc Oxygen Consumption as a function of Breath Rate

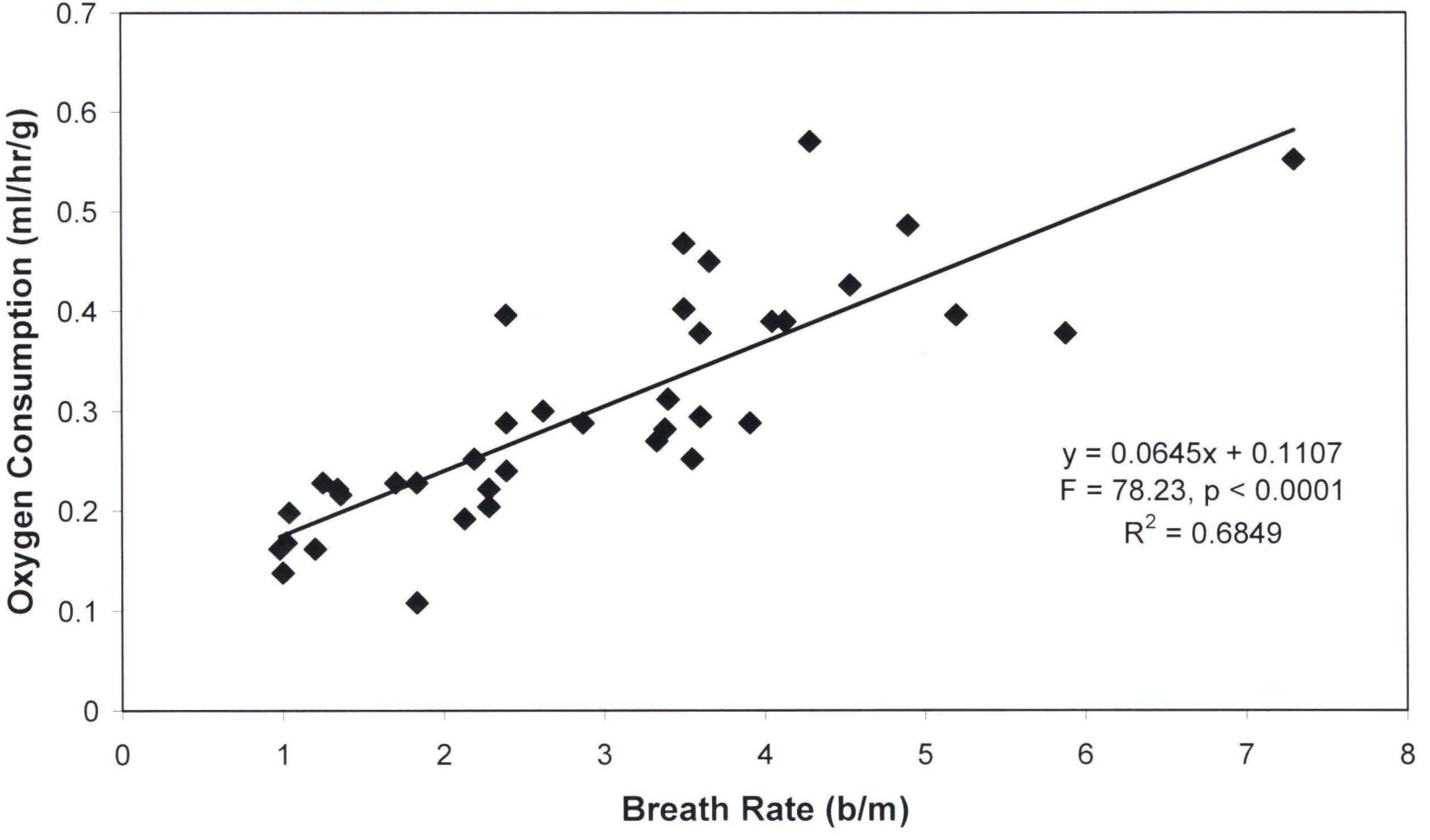


Figure 8b. Dc oxygen consumption as a function of stroke rate

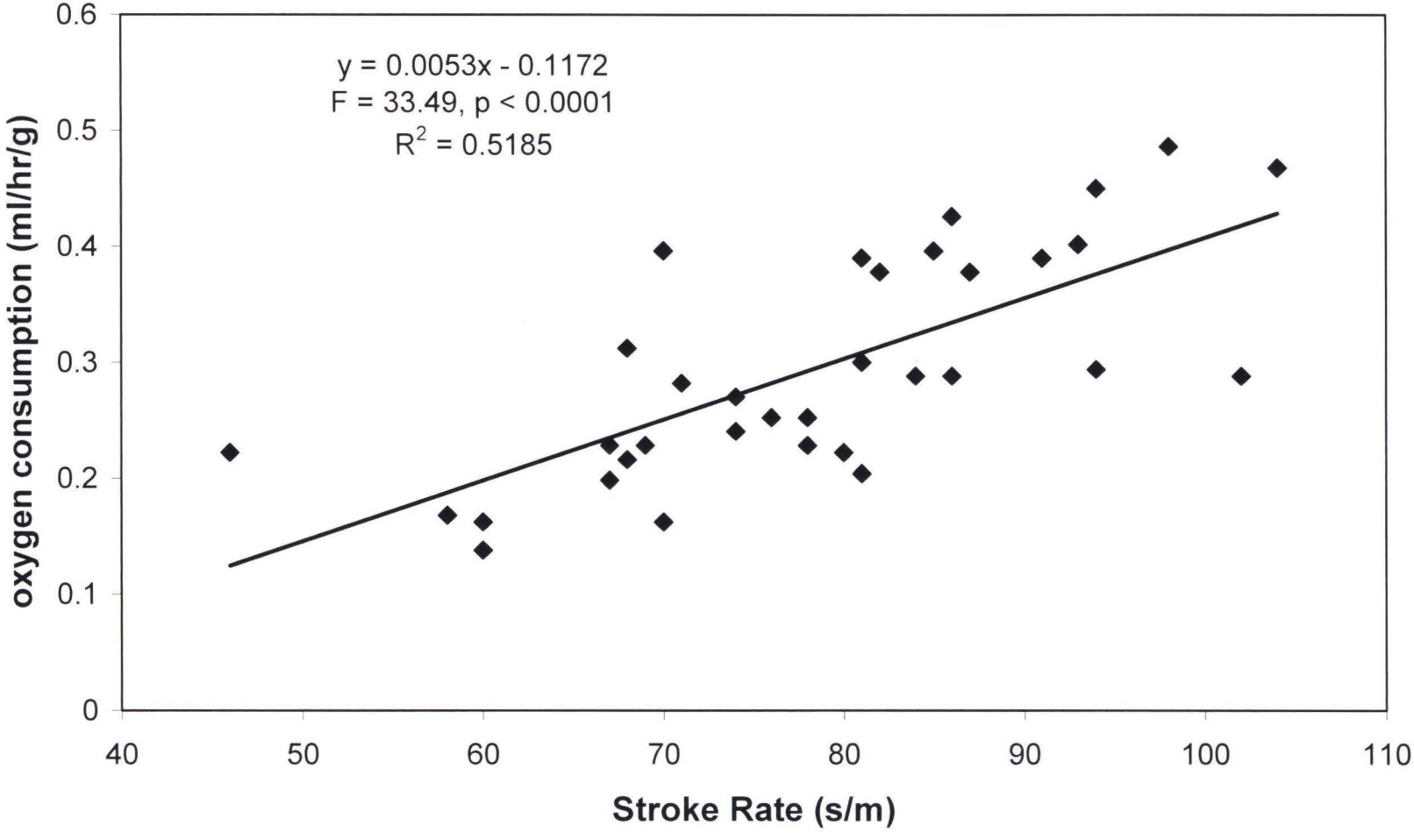


Figure 8c. Lo Oxygen Consumption as a function of breath rate

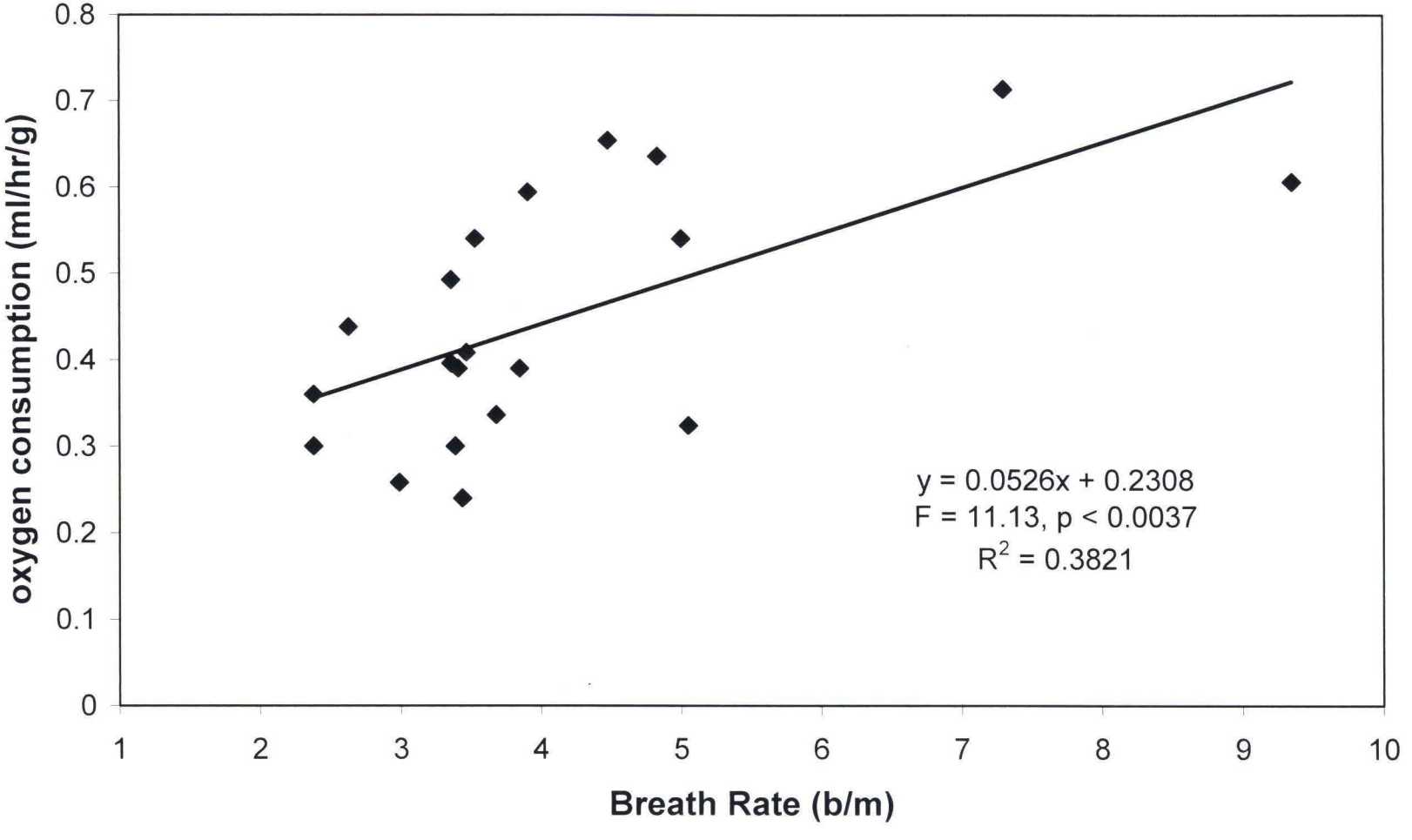
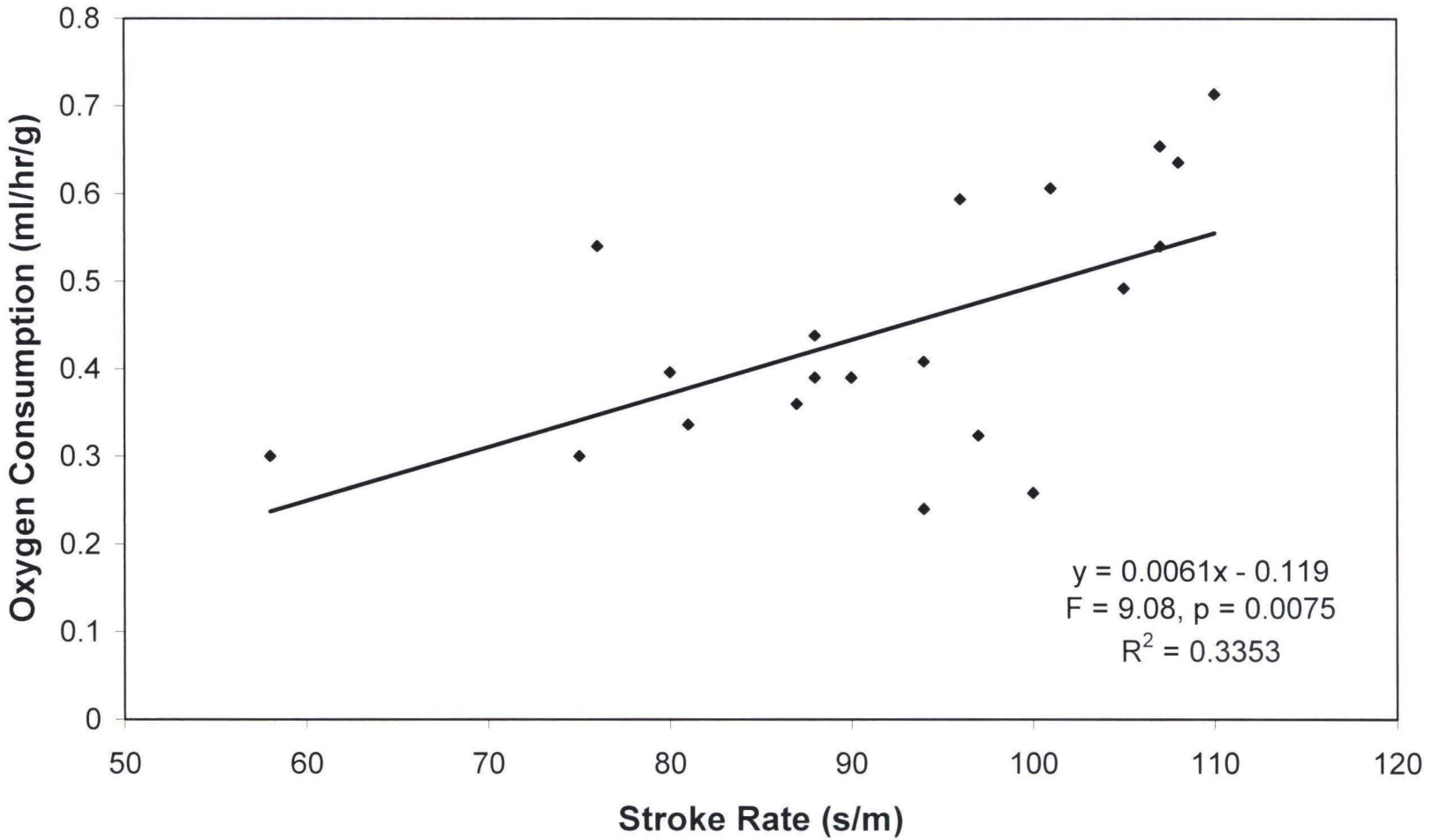


Figure 8d. Lo Oxygen Consumption as a function of Stroke Rate



Hatchling and Yolk Energetics

Leatherback hatchlings increased their % body water as they aged 59.77 $\pm$ 3.17 % water at emergence to over 80% water at 4 to 6 weeks of age. The yolk also became more diluted, ~ 48% water at emergence to roughly 70% water at 4 to 6 weeks. Leatherbacks maintained a dry mass of 10.36 $\pm$ 0.07 to ~ 10.00 g of Dry Mass (DM) from emergence to 4 to 6 weeks, while the yolk dropped over 4 g DM to less than 0.17 g DM. Hatchlings maintained roughly 20 to 23 KJ/g DM from emergence to 4 – 6 weeks of age, while yolk had a higher energy value at 30.71 KJ/g DM. Due to small sample size (1 to 3 samples) I was unable to run statistics. These data are summarized in Table 3.

Sample	Sampling Time	WM (g)	DM (g)	%Water	KJ/g DM
Hatchling	Emergence	28.09	10.52	62.55	23.42
		29.22	10.33	64.64	22.51
		21.34	10.22	52.11	25.48
mean		26.21	10.36	59.77	23.80
S.E.		2.01	0.07	3.17	0.23
Hatchling	1 Week	35.30	9.43	73.29	22.76
		35.65	8.74	75.48	22.49
		33.77	9.74	71.16	23.22
mean		34.91	9.30	73.21	22.82
S.E.		0.47	0.24	1.02	0.21
Hatchling	4 – 6 Weeks	57.87	9.48	83.62	21.10
		53.76	10.12	81.18	19.80
Yolk	Emergence	7.32	3.74	48.91	29.64
		4.50	2.31	48.67	28.46
Yolk	1 Week	2.13	0.96	54.93	30.71*
		1.18	0.40	66.10	
		1.59	0.62	61.01	
mean		1.63	0.66	60.68	
S.E.		0.22	0.15	2.59	
Yolk	4 – 6 Weeks	0.48	0.17	64.58	
		0.22	0.06	72.73	

Table 3. Energetic analysis of leatherback hatchlings and yolk. Wet mass in grams (WM), dry mass in grams (DM), % water content and energetic values (KJ g^{-1} DM^{-1}) of whole hatchling and dissected yolk sacs of leatherback hatchlings during emergence, 1-week, and 4-6 weeks of age. All animals died of natural causes and emergence turtles were of second or third emergence and did not make it to the surf or died while digging out of nest. Yolk energetic value at 1-week, 30.71*, represents the value of three yolk sacs pooled together. The bomb calorimeter used required sample size of 1 g. Sample size of yolk at 4 – 6 weeks was too small for analysis. All calculations after Paine (1971).

DISCUSSION

I hypothesized that because of their more active lifestyle, large size, and fast growth rates that leatherbacks would have higher aerobic metabolic rates and develop larger scopes than olive ridley hatchlings. As animals grow in mass, the empirical data suggests that aerobic scope should increase as MMR typically scales at a higher mass exponent than RMR (Schmidt-Nielsen 1984). I failed to reject my null hypothesis as leatherback aerobic scope is not significantly different than olive ridley scope during the Frenzy ($Z = -0.613$, $p = 0.539$), Post-Frenzy ($Z = 0.602$, $p = 0.546$), and olive ridley scope is larger than leatherbacks at 1-Month ($Z = 2.90$, $p = 0.0037$) the trend can be seen in Figure 5 and is summarized in Table 2.

I hypothesized that AMR or routine swimming would be less costly in leatherbacks than olive ridleys and that AMR would be at the lower end of leatherback's aerobic scope. I reject my null hypothesis as the trend shows AMR to be less in leatherbacks than olive ridleys at 1-week and significantly less than olive ridley AMR at 1-month ($Z = 3.78$, $p = 0.0002$). AMR is significantly more efficient, only 10 – 20% of aerobic scope, in leatherbacks while olive ridley AMR is 57 to 88% of their aerobic scope (ChiSquare 10.39, $p = 0.015$). These trends can be seen in Figures 6 and 7.

The energy content of the diet for leatherbacks and olive ridleys was slightly different with leatherbacks having ~ 20% more energy available per g DM (Table 1).

However leatherback food was more diluted with a WM/DM ratio of 7 to only 1.2 for olive ridleys. Although leatherback food has slightly more energy per g DM it is possible that leatherbacks were limited due to gut size and the necessity of a higher turnover rate of food (Ricklefs 2003) to obtain the same energy that olive ridleys could obtain in a smaller amount of food. I do not however, know how much food each animal ate per day and thus cannot make a quantitative statement or analysis on energy limitation to activity for one species or the other. All animals were either fed ad libitum (olive ridleys) or to satiation (leatherbacks) and as these diets are more energy dense than the turtle's natural diets I do not see this as a limitation.

As can be seen in Figures 2 and 3, leatherback and olive ridley MMR and RMR once corrected for mass are not significantly different from one another. Thus, with regard to the initial dispersal stage there is no species specific adaptation or metabolic niche that allows one to gain or obtain separation from the other species. Physiologically speaking the two species are simply hatchlings of different mass leaving the beach and nearshore areas. However within their physiological capabilities the animals may be experiencing niche separation through their initial behavior and ecology (Wyneken and Salmon 1992; Salmon et al. 2004).

By 1-month olive ridleys had a significantly higher MMR than leatherbacks (Figure 4). This finding is perplexing however as leatherbacks are seen as the more aerobic active turtle. The animals however did not have to sustain MMR for periods longer than 15 minutes in this study and it is possible that olive ridleys, although capable

of initial high outputs of energy would have a lower Sustained Metabolic Rate (SusMR) (Peterson et al. 1990). Leatherbacks could possibly maintain levels of MMR for much longer periods than olive ridleys. Leatherbacks may be constrained by their lifestyle and mode of transportation. Their body shape and fore flipper morphology as well as their swimming gait are designed for slow continuous movement (Davenport 1987; Wyneken 1997) thus leatherbacks possibly have not developed the metabolic machinery (energy transportation, supply) for high energy output.

Leatherback scope becomes less than olive ridleys by 1-month (Table 2). Factorial scope is larger at 1-week for leatherbacks but at 1-month olive ridley factorial scope is nearly 2 times that of leatherbacks. This trend is seen in Figure 5. Leatherback scope narrows with size while ridley scope increases. The general trend for increasing mass across species is for aerobic scope to increase with size (Schmidt-Nielsen 1984). In figure 5 leatherback RMR scales to mass proportionately (b = 1). This high exponent is most likely due to growth as leatherbacks are the largest (Buskirk and Crowder 1994) and fastest growing (Rhodin 1985) of all sea turtles, thus leading to narrowing of aerobic scope rather than increasing with size (as RMR is increasing with mass at a greater rate than MMR). However as leatherbacks transition into different life history stages (where *growth may not be as high) this increase in RMR with mass may tail off.*

Olive ridley turtles do not show a strong relationship with RMR and increasing mass (Figure 5). Ridleys only added around 5 g body mass (33%) while leatherbacks

more than doubled their mass in the same period. Growth is the driving force behind differences in intraspecific RMR between leatherback and olive ridley turtles (Figure 5).

The turtles in my study were obtaining energy from yolk (emergence to 1-week) and yolk and food items (1-week to 1-month) thus all of my measurements of RMR include maintenance metabolism (SMR) plus the cost of digestion (SDA, specific dynamic action) and biosynthesis (Hochachka and Somero 2002). As leatherbacks have higher growth rates than ridleys over the first month and as I measured RMR which includes the cost of growth, I can infer that the increase in RMR with mass in leatherbacks versus olive ridleys (Figure 5) is due to high growth rates (Nagy 2000; Steyermark 2002).

Thompson and Withers (1997) found that the intraspecific allometry for SMR scaled from 0.43 to 1.2 while MMR scaled from 0.44 to 1.3 for nine species of goanna against mass. My measurements ranged from 0.44 to 1.01 (RMR) and from 0.61 to 1.65 (MMR). Maxwell et al. (2003) found green iguana SMR to scale with mass to 0.73 however the intra-individual (ontogenetic) scaling relationship ranged from 0.61 to 0.89 for SMR regressed against mass. Prange and Jackson (1976) found that green turtle oxygen consumption regressed with mass to 0.83 for RMR (not clear what state animals were in, RMR or SMR) and to 0.94 for MMR. However, the high end of the scale was based on only two animals. I use RMR for our regression while both Thompson and Withers (1997) and Maxwell et al. (2003) use SMR. Thus, my regression exponents could be elevated due to growth costs.

Thompson and Withers (1997) found factorial aerobic scope to narrow with increasing size. They attributed the decrease in factorial scope with size due to increased SMR. Indeed this is the case with our animals as leatherback RMR scaled proportionately with mass while olive ridleys did not significantly increase RMR with mass. However RMR does not solely explain the decrease in factorial scope with size in leatherbacks as their MMR scaled with mass much lower 0.61 than did ridleys 1.65. Thompson and Withers (1997) inferred that increase in SMR or decreased factorial scopes were related to their ecology. More specifically, that active widely foraging goannas have higher SMRs and narrower factorial scopes than do sedentary goannas. Actively foraging animals may maintain high SMR, have increased food intake, and have high SusMRs to pursue and obtain food but comparably lower MMRs than sedentary animals thus leading to narrow aerobic scopes. Whereas sedentary animals have lower SMRs than active animals and are perhaps capable of high but short maximal aerobic bursts leading to larger aerobic scopes. Thus, it is possible that leatherback RMR not only scales to 1 due to high growth rates but also due to their active oceanic-pelagic lifestyle versus the sedentary, sit-and-wait lifestyle of the olive ridley.

In the leatherback post-hatchlings there was a clear relationship between oxygen consumption and activity, with increased stroke rate or swimming activity resulting in increased oxygen consumption (Figure 8b). The accompanying increase in breath rate indicates that this was achieved, at least in part, by increased ventilation (Figure 8a) and suggests that the leatherback hatchling relies mainly on aerobic metabolic pathways to

meet the increased energy demands. By contrast, the activity related increase in oxygen consumption in olive ridleys, although significant, had much more scatter and the trend is not as evident (Figure 8d). Nor is any relationship between breath rate and oxygen consumption (Figure 8c). Thus, olive ridleys are not likely to have high energetic demand and possibly might meet demand anaerobically.

The tight coupling between O_2 consumption and activity in the leatherback may be related to its continuously active lifestyle. Salmon et al. (2004) found that leatherback juveniles are water column feeders. Leatherbacks ranging in age from 2 – 10 weeks post hatching dived from 0.5 to 17.5 m in depth. The hatchlings utilized the water column to locate gelatinous prey that they would eat at depth or bring to the surface. If leatherbacks did not stay within their aerobic dive limits (ADL) this could deleteriously affect their foraging budget and thus prey capture as accruing an oxygen debt would force the turtles to stay at the surface. Air-breathing marine predators need to remain submerged (maximize dive time) in order to forage efficiently (Hindell et al. 2000). Thus, by meeting increased demand aerobically (Figures 8a and 8c) leatherbacks are able to increase foraging time. Lutcavage and Lutz (1986) found that leatherback post-hatchlings and possibly 250 kg adults need to eat their weight in gelatinous zooplankton daily in order to meet resting metabolic demands. This coupled with the extreme growth rate in leatherbacks 4 – 11 years (Rhodin 1985) for a 6,000 fold mass increase while consuming an energy poor diet (jellyfish) make it an imperative for leatherbacks to maximize foraging time.

The looser association in the olive ridley and the possible reliance on anaerobic pathways may be associated with its drift, sit and wait strategy (Carr 1986; Witherington 2002), where meeting demand anaerobically would not deleteriously affect foraging opportunity. Olive ridleys are presumably like loggerheads that feed opportunistically on their surrounding biota (in floating algae mats) thus meeting energetic demand anaerobically would not stunt foraging opportunity.

The energy in residual yolk sac that can be retained for up to a week is of essential value to the hatchling (Hewavisenthi & Parmenter 2002). Leatherbacks do not begin feeding until 5 – 8 days after emergence (Jones et al. 2000; this study) and therefore must have a large enough energy store to reach their foraging habitat within 8 days. If leatherbacks are foregoing the gyre system, to actively forage in equatorial convergence zones (Jones et al. in press) then they would need large energy reserves to get them to their post-hatchling habitat. Leatherback hatchlings also spend relatively more time actively swimming than chelonid hatchlings (Wyneken & Salmon 1992). Therefore leatherbacks require large energy reserves. Leatherback turtles produce the largest eggs and thus the largest hatchlings of any other sea turtle (Buskirk and Crowder 1994). They also emerge from the nest with on average 90 KJ of energy in their yolk sac (Table 3) almost three times that of the loggerhead (34 KJ of energy; Kraemer and Bennett 1981) and double that of olive ridleys (45 KJ of energy; Silas et al. 1984). Leatherbacks are thus large out of necessity. Size gives leatherbacks larger initial energy reserves and possibly confers more efficient swimming (stroke frequency, distance traveled per stroke; Blake 1991).

Leatherback hatchlings gained 10 g in wet mass during their first week of age but this was mainly water since they maintained the same dry mass over this period (Table 3). Hatchlings (2 emergence and three 1-week old turtles) did consume on average 2.35 g in yolk DM however this loss in DM was replaced by tissue. Hatchling sea turtles have been shown to drink sea water to hydrate then subsequently remove ions and osmoregulate through lachrymal salt glands (Reina et al. 2002).

The 2.35 g DM of yolk consumed during their first week equates to nearly 68.59 KJ of energy spent on growth and swimming. By comparison, using my oxygen consumption data for frenzy turtles (Figure 2), post-frenzy swimming turtles (Figure 6) and resting turtles (Figure 3) along with Wyneken and Salmon's (1992) leatherback diel activity model I calculated that a 40 g leatherback turtle would only consume 47.18 KJ of energy. This discrepancy probably lies in the small sample size for yolk consumptions and the caveats of modeling. Using Wyneken's (1997) velocity of 0.93 Km h^{-1} (frenzy leatherbacks) and 0.43 Km h^{-1} (post-frenzy hatchlings; Salmon et al. 2004) this animal could swim nearly 76 Km (both measurements were from field conditions in local currents) during its first week consuming only 50 to 76% of its yolk reserves. By 4 – 6 weeks leatherback turtles had consumed nearly 92.5% of their yolk reserves (Table 3). From 1-week to 1-month post-emergence leatherbacks utilized an additional 15 to 38 KJ in yolk reserves. After their first week post-emergence hatchlings probably utilize both forage items and yolk reserves to fuel growth and movements.

Kraemer and Bennett (1981) determined that loggerhead turtles leaving the shore would not have sufficient energy reserves to reach the major ocean currents. I have found, however, that leatherback turtles have sufficient energy reserves to reach the prevailing offshore currents and beyond. From my measurements of oxygen consumption in leatherbacks for routine swimming (Figure 4) I determined that their yolk reserves (Table 3) could fuel nearly three weeks of straight swimming. Kraemer and Bennett found that loggerhead hatchlings would not have enough energy reserves for more than 70 h of swimming post-emergence. However Dial (1987) found that loggerhead turtles rely heavily on anaerobic pathways. Loggerhead hatchling metabolism was 77% anaerobic for the hatchling and frenzy and up to 20% anaerobic derived energy for the initial swimming frenzy. Baldwin et al. (1989) found that during frenzy swimming hatchling lactate levels were nearly 10 times resting values. Thus loggerheads might possibly have more than 70 h of swimming fuel if they were to maintain swimming aerobically.

My ranges for oxygen consumption fit within the scattered reports of hatchling oxygen consumption in the literature (Table 4). My leatherback mass-specific RMR is slightly higher than that found by Wyneken (1997) and higher than that found for green turtles (Prange and Ackerman 1974; Wyneken 1997). However, it is lower than what Wyneken found for loggerheads. Olive ridley emergence RMR was the lowest found for any turtles except that of green hatchlings measured by Prange and Ackerman (1974). This measurement of green turtle RMR by Prange and Ackerman is 2.3 to 4.8 times lower than any other study of mass-specific RMR during emergence. RMR in emergence

turtles went from highest consumption to lowest as follows, loggerhead > leatherback > green > olive ridley (compiled from Wyneken [1997] and this study).

My measurement of mass-specific MMR during emergence is only slightly less than that found by Wyneken (1997). Again the value of Prange and Ackerman (1974) for MMR during emergence in green turtles is the lowest of any hatchling study. The order of highest to lowest MMR during emergence is green > loggerhead > leatherback > olive ridley (compiled from Wyneken [1997] and this study).

My measurements for mass-specific MMR post-frenzy more closely match those of Lutcavage and Lutz (1986). Both my measurements and those of Lutcavage and Lutz for post-frenzy leatherback MMR are lower than Wyneken (1997). The species trend for post-frenzy MMR is loggerhead > green > olive ridley > leatherback (compiled from Lutcavage and Lutz [1986], Wyneken [1997] and this study). Wyneken's measurement for post-emergence leatherbacks would put them as energetically more demanding than olive ridleys. Lutacavage and Lutz's (1986) measurements of active post-frenzy loggerheads are substantially lower than any other study of active post-frenzy hatchlings. Measurements of breath rates were similar between studies regardless of activity state or species. The small physiological differences found amongst these species are not necessarily adaptive. Behavioral adjustments may supplement or substitute physiological adjustments. When considering mass differences, acclimation, and methodological protocols it is possible that the slight differences found in these species will disappear. And, thus the differences do not imply species specific physiological adaptation.

CONCLUSIONS

My results show that the divergent energetic strategies reflect differences in the early life history stages of leatherback and olive ridley hatchlings. Ridleys use a combination of swimming and drifting to reach oceanic gyres whereupon they passively feed and migrate. In contrast, leatherbacks utilize continued high performance aerobic swimming to possibly reach convergent zones, not feeding during this extended journey. Leatherbacks carry the fuel for this journey in a large "fuel tank" yolk sac. This unique strategy could be considered "energetic neoteny".

species	Emergence (frenzy) Resting	Active	b/m	Post – Frenzy Resting	Active	b/m	Study
Leatherback	0.39 ± 0.09	0.51 ± 0.10	4.62 ± 1.26	0.17 ± 0.07	0.35 ± 0.06	3.97 ± 1.0	(this study)
	0.24	0.60			0.54		Wyneken 1997
					0.286 ± 0.02	4.3 ± 1.60	Lutcavage and Lutz 1986
Olive ridley	0.23 ± 0.09	0.42 ± 0.07	3.25 ± 0.51	0.19 ± 0.05	0.41 ± 0.02	4.43 ± 2.56	(this study)
Green	0.30	1.26			0.78		Wyneken 1997
				0.12			Davenport and Oxford 1994
	0.10 ± 0.01	0.34 ± 0.03					Prange and Ackerman 1974
Loggerhead	0.48	0.9			1.02		Wyneken 1997
					0.21 ± 0.84		Lutcavage and Lutz 1986

Table 4. Mass Specific Oxygen Consumption for Leatherbacks, Olive Ridleys, Greens, and Loggerheads all Studies. Specific VO_2 given as ml O_2 hr^{-1} g^{-1}, with ± 1 Standard Deviations this study and ± 1 Standard Error all other studies. For active specific metabolism breath rate as breaths per minute (b/m) is shown where applicable. Emergence column is during the frenzy period or first 24 – hours after emerging from nest. Post – frenzy is from > 24 – hours to 1-week of age. Values from other studies were converted to ml O_2 hr^{-1} g^{-1} to match this study.

BIBLIOGRAPHY

Bennett, A. F. and W. R. Dawson. 1976. Metabolism. In *The Biology of Reptilia*, vol. 5 (ed. C. Gans and W. R. Dawson), pp. 127-223. New York: Academic Press

Baldwin J., E. Gyuris, K. Mortimer and A. Patak. 1989. Anaerobic metabolism during dispersal of green and loggerhead turtles hatchlings. Comparative Biochemistry and Physiology A 94: 663 – 665

Bolten A. B. 1995. Biology of the early pelagic stage the 'lost year'. Biology and Conservation of Sea Turtles (Revised Edition). Smithsonian Institution Press. Washington, D.C. 579 – 581

Bolten A. B. 2003. Variation in sea turtle life history patterns: neritic vs. oceanic development stages. In (Lutz P. L., J. A. Musick and J. Wyneken eds.) The Biology of Sea Turtles. CRC Press, Boca Raton 2: 243 – 258

Blake R. W. 1991. On the efficiency of energy transformations in cells and animals. In (Blake R. W. ed.) Efficiency and economy in animal physiology. Cambridge University Press, Cambridge 13 – 32

Buskirk J. V. and L. B. Crowder 1994. Life-history variation in marine turtles. Copeia 1994(1): 66 – 81

Carr A. and H. Hirth. 1961 Social facilitation in green turtle hatchlings. Animal Behavior 9: 68 – 70

Carr A. 1962. The ecology and migrations of sea turtles. 6. Comparative features of isolated green turtle colonies. American Museum Natatives. 2091: 1 - 42

Carr A. and A. B. Meylan. 1980. Evidence of passive migration of green hatchlings in sargassum. Copeia 1980: 366

Carr A. 1986. Rips, fads and little loggerheads. Bioscience 36(2): 92 – 110

Davenport J. 1984. Feeding, gut dynamics, digestion and oxygen consumption in hatchling green turtles (*Chelonia mydas)*. British Journal of Herpetology 6: 351 – 358

Davenport J., S. A. Munks and P. J. Oxford. 1984. A comparison of the swimming of marine and fresh-water turtles. Proceedings of the Royal Society of London B 220: 447 – 475

Davenport J. 1987. Locomotion in hatchling leatherback turtles *Dermochelys coriacea*. Journal of Zoology London 212: 85 – 101

Davenport J. and G. A. Pearson. 1994. Observations on the swimming of the pacific ridley, *Lepidochelys olivacea* (Eschscholtz 1829): Comparisons with other sea turtles. Herpetological Journal 4: 60 – 63

Darveau C., R. K. Suarez, R. D. Andrews and P. W. Hochachka. 2002. Allometric cascade as a unyfing principle of body mass effects on metabolism. Nature 417: 166 – 170

Dial B. E. 1987. Energetics and performance during nest emergence and the hatchling frenzy loggerhead sea turtles (*Caretta caretta*). Herpetelogica 43: 307 - 315

Eckert S. A. 2002. Distribution of juvenile leatherback sea turtle *Dermochelys coriacea* sightings. Marine Ecology Progress Series 230: 289-293

Frick J. 1976. Orientation and behaviour of hatchling green sea turtles (*Chelonia mydas*) in the sea. Animal Behavior 24: 849

Fry F. E. J. 1947. Effects of environment on animal activity. Publications of the Ontario Fisheries Research Laboratory 55: 1 -62

Gaffney E. S. 1990. The comparative osteology of the Triassic turtle *Proganochelys.* Bulletin American Museum of Natural History 194: 1 – 263

Hayes J. P. 2001. Mass-specific and whole-animal metabolism are not the same concept. Physiological and Biochemical Zoology 74(1): 147 – 150

Hewavisenthi S. and C. J. Parmenter. 2002. Egg components and utilization of yolk lipids during development of the flatback turtle *Natator depressus*. Journal of Herpetology 36: 43 -50

Hindell M. A., M. Lea, M. G. Morrice and C. R. MacMahon. 2000. Metabolic limits on dive duration and swimming speed in the southern elephant seal *Mirounga leonine*. Physiological and Biochemical Zoology 73(6): 790 – 798

Hochachka P. W. and G. N. Somero. 2002. Biochemical Adaptation. Mechanism and Process in Physiological Evolution. Oxford University Press, New York

Hughes G. M., R. Gaymer, M. Moore and A. J. Woakes. 1971. Respiratory exchange and body size in the aldabra giant tortoise. Journal of Experimental Biology. 55: 651 - 665

Jones T. T., R. Reina, and P. L. Lutz. *In press*. The ontogeny of oxygen consumption in leatherback (*Dermochelys coriacea*) and olive ridley (*Lepidochelys olivacea*) sea

turtle hatchlings. Proceedings from the twenty-second annual symposium on sea turtle biology and conservation.

Jones T. T., M. Salmon, J. Wyneken and C. Johnson 2000. Rearing leatherback hatchlings: protocols, growth and survival. Marine Turtle Newsletter 2000(90): 3 – 6

Kaufmann R., H. Forstner and W. Wieser. 1989. Respirometry – methods and approaches. In (Bridges C. R. and P. J. Butler eds.) Techniques in Comparative Respiratory Physiology. Cambridge University Press, Cambridge 51 – 76

Kleiber M. 1961. The Fire of Life. John Wiley & Sons, Inc., New York

Kraemer J. E. and S. H. Bennett. 1981. Utilization of posthatching yolk in loggerhead sea turtles, *Caretta caretta*. Copeia 1981(2): 406 – 411

Lutcavage M. and P. L. Lutz. 1986. Metabolic rate and food energy requirements of the leatherback sea turtle, *Dermochelys coriaceia*. Copeia 1986(3): 796 – 798

Maxwell L. K., E. R. Jacobson and B. K. McNab. 2003. Intraspecific allometry of standard metabolic rate in green iguanas, *Iguana iguana*. Comparative Biochemistry and Physiology A 136: 301 – 310

McDonald H. S. 1976. Methods for the physiological study of reptiles. In (Gans C. and W. R. Dawson eds.) Biology of the Reptilia. Academic Press, London 5: 70 – 83

Miller J. D. 1997. Reproduction in sea turtles. In (Lutz P. and J. Musick eds.) The Biology of Sea Turtles. CRC Press, Boca Raton 51 – 81

Nagy K. A. 2000. Energy costs of growth in neonate reptiles. Herpetological Monographs 14: 378 – 387

Packard G. C. and T. J. Boardman. 1999. The use of percentages and size-specific indices to normalize physiological data for variation in body size: wasted time, wasted effort? Comparative Biochemistry and Physiology A 122: 37 – 44

Paine R. T. 1971. The measurement and applications of the calorie to ecological problems. Annual Revue Ecological Systems 2:145 – 164

Peterson C. C., K. A. Nagy and V. H. Shoemaker. 1984. Field energetics and food consumption of the Galapagos marine iguana, *Amblyrhynchus cristatus*. Physiological Zoology 57: 281 – 290

Peterson C. C., K. A. Nagy and J. Diamond. 1990. Sustained metabolic scope. Proc. Natl. Acad. Sci. 87: 2324 – 2328

Pitman. 1990. Pelagic distribution and biology of sea turtles in the eastern tropical pacific. Proceedings of the tenth annual workshop on sea turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFC-278: 143 - 148

Prange H. D. and R. A Ackerman. 1974. Oxygen consumption and mechanisms of gas exchange of green turtle (*Chelonia mydas*) eggs and hatchlings. Copeia 1974(3): 758 – 763

Prange H. D. and D. C. Jackson. 1976. Ventilation, gas exchange and metabolic scaling of a sea turtle. Respiration Physiology 27: 369 – 377

Pritchard P. C. H. 1997. Evolution, phylogeny, and current status. In (Lutz P. and J. Musick eds.) The Biology of Sea Turtles. CRC Press, Boca Raton 1 – 28

Reina R. D., T. T. Jones and J. R. Spotila. 2002. Salt and water regulation by the leatherback sea turtle *Dermochelys coriacea*. The Journal of Experimental Biology 205: 1853 – 1860

Rhodin A. G. J. 1985. Comparative chondro-osseous development and growth of marine turtles. Copeia 1985: 752 – 771

Ricklefs R. E. 2003. Is rate of ontogenetic growth constrained by resource supply or tissue growth potential? A comment on West et al.'s model. Functional Ecology. 17: 384 - 393

Salmon M., T. T. Jones and K. Horch. 2004. Ontogeny of diving and feeding behavior in juvenile sea turtles: A comparison study of green turtles (*Chelonia mydas L.*) and leatherbacks (*Dermochelys coriacea L.*) in the Florida current. Journal of Herpetology 38: 36-43

Schmidt-Nielsen K. 1984. Scaling: Why is Animal Size so Important?. Cambridge University Press, Cambridge

Silas E. G., M. Vijayakumaran and M. Rajagopalan. 1984. Yolk utilization in the egg of the olive ridley *Lepidochelys olivacea*. CMFRI BULLETIN 35(3):22 – 35

Steyermark A. C. 2002. A high standard metabolic rate constrains juvenile growth. Zoology 105: 147 – 151

Thompson G. G. and P. C. Withers. 1997. Standard and maximal metabolic rates of goannas (Squamata: varanidae). Physiological Zoology 70(3): 307 – 323

Willmer P., G. Stone and I. Johnston. 2000. Environmental Physiology of Animals. Blacwell Science Ltd., Malden

Witherington B. E. 2002. Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a gulf stream front. Marine Biology 140:843-853

Wyneken J. 1991. Comparisons of oxygen utilization by hatchling loggerheads, greens, and leatherbacks during the swimming frenzy: sprinting vs. marathon strategies revisited. Proceedings 11th Annual Workshop on Sea Turtle Biology and Conservation. NOAA Technical Memorandum NMFS-SEFC-232: 131 – 132

Wyneken J. 1997. Sea turtle locomotion: mechanisms, behavior, and energetics. In (Lutz P. and J. Musick eds.) The Biology of Sea Turtles. CRC Press, Boca Raton 165-198

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

Figure Legends

Figure 2. MMR and RMR shown for leatherbacks and olive ridleys during the frenzy period. Oxygen consumption is given as ml O_2 hr^{-1} $g^{-0.83}$. Error bars represent $\pm$ 1 Standard Deviation.

Figure 3. MMR and RMR shown for leatherbacks and olive ridleys during the post-frenzy (1 week of age) period. Oxygen consumption is given as ml O_2 hr^{-1} $g^{-0.83}$. Error bars represent $\pm$ 1 Standard Deviation.

Figure 4. MMR and RMR shown for leatherbacks and olive ridleys 1-month of age. Oxygen consumption is given as ml O_2 hr^{-1} $g^{-0.83}$. Error bars represent $\pm$ 1 Standard Deviation.

Figure 5. Leatherback and olive ridley oxygen consumption expressed intraspecifically as MMR and RMR regressed against mass. Oxygen consumption is given as ml O_2 hr^{-1} $g^{-0.83}$ and mass in grams (g). Regression equations are significant for leatherback MMR ($F = 10.60$, $p = 0.0057$), leatherback RMR ($F = 23.14$, $p = 0.0003$), and olive ridley MMR ($F = 34.46$, $p < 0.0001$). Olive ridley RMR is not significant from zero ($F = 1.83$, $p = 0.1931$).

Figure 6. Swimming metabolic rate (AMR) in leatherback and olive ridley sea turtles at 1-week and 1-month. Oxygen consumption is given as ml O_2 hr^{-1} $g^{-0.83}$. Error bars represent $\pm$ 1 Standard Deviation.

Figure 7. Swimming metabolic rate (AMR) as percentage of scope. Subtracted RMR from AMR and MMR, then took AMR as percentage of MMR. Zero % represents RMR and 100 % represents MMR. Error bars stand for $\pm$ 1 Standard Deviation.

Figure 8a. Oxygen consumption in ml O_2 hr^{-1} g^{-1} of leatherbacks during AMR and MMR from emergence through 1-month of age regressed against Breath Rate in breaths per minute (b/m). $R^2 = 0.68$, $F = 78.23$, $p < 0.0001$.

Figure 8b. Oxygen consumption in ml O_2 hr^{-1} g^{-1} of leatherbacks during AMR and MMR from emergence through 1-month of age regressed against Stroke Rate in fore flipper strokes per minute (s/m). $R^2 = 0.52$, $F = 33.49$, $p < 0.0001$.

Figure 8c. Oxygen consumption in ml O_2 hr^{-1} g^{-1} of olive ridleys during AMR and MMR from emergence through 1-month of age regressed against Breath Rate in breaths per minute (b/m). $R^2 = 0.38$, $F = 11.13$, $p = 0.0037$.

Figure 8d. Oxygen consumption in ml O_2 hr^{-1} g^{-1} of olive ridleys during AMR and MMR from emergence through 1-month of age regressed against Stroke Rate in fore flipper strokes per minute (s/m). $R^2 = 0.34$, $F = 9.08$, $p = 0.0075$.