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What makes marine turtles go: A review of metabolic rates and their consequences

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Abstract

Quantification of metabolic rates (MR) is fundamental to understanding an individual organism's physiology and life history, as well as overall population dynamics. Applications of MR measurements have increased both in quantity and quality across animal ecology over the past 50 years. Included in this trend, research on MRs of marine turtles and its consequences for these unique ectothermic vertebrates has matured significantly. We reviewed existing literature on marine turtle MRs in the context of the physiology, ecology, and life history of these animals. Metabolic rates have been obtained and published for 4 of 7 marine turtle species, but not for all life stages for all of these species. Studies of marine turtle metabolism have ranged from straightforward MR measurements of a few individuals to use of innovative techniques to estimate energy expenditure of natural activities and for applications to marine turtle energetics and diving physiology. Comparisons of allometric relationships between resting MR (RMR) and body mass for leatherbacks (*Dermochelys coriacea*), green turtles (*Chelonia mydas*), other reptiles, and mammals revealed no differences between leatherbacks and green turtles, nor between those species and other reptiles, but significant differences with mammals. In addition, we synthesized research on the thermal biology of the leatherback turtle, which ranges from temperate to tropical waters, and concluded that leatherbacks achieve and maintain substantial differentials between body and ambient temperatures in varied thermal environments through an integrated balance of adaptations for heat production (e.g., adjustments of MR) and retention. Finally, we recommend that future research should 1) address remaining data gaps in current knowledge of MRs of some species, 2) apply MR measurements to important physiological, ecological, and conservation topics, 3) investigate cellular metabolism of marine turtles, and 4) focus on quantification of at-sea energy expenditure incurred by marine turtles during natural activities.

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1. Understanding *The Fire of Life*

Animal metabolism has long been considered *The Fire of Life* (Kleiber, 1961), a suite of processes unequivocally fundamental to an organism's individual physiology, life history, and survival, and thus to overall population-level

processes. During the past half-century, developments in metabolism research have dramatically improved understanding of animal physiology and ecology. These developments have included novel and enhanced metabolic rate measurements, elucidation of the factors that influence metabolic rates, and the ecological and evolutionary implications of metabolism. Further, the importance of characterizing metabolism's essential role at various ecological scales has resulted in abundant theoretical and empirical research of interspecific allometries relating organism body size and metabolism to various physiological, population, and ecosystem processes (Schmidt-Nielsen, 1984; Brown et al., 2004).

Oxidative metabolism of food resources is the principal process that supplies an animal with the chemical energy to perform various basic and vital functions (Schmidt-Nielsen, 1997). The overall use of chemical energy is referred to as

Abbreviations: MR, metabolic rate; RMR, resting metabolic rate; BMR, basal metabolic rate; SMR, standard metabolic rate; AMR, active metabolic rate; MMR, maximum metabolic rate; FMR, field metabolic rate; DMR, diving metabolic rate; cADL, calculated aerobic dive limit; T_a , ambient temperature; T_b , body temperature; T_w , water temperature.

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energy metabolism, and the rate at which that energy is used is termed metabolic rate (MR). Thus, metabolism is a permanent component of an animal's energy budget because it is central to many physiological regulation processes (i.e., homeostasis) and to resource acquisition and allocation in animals (Congdon et al., 1982; Spotila and Standora, 1985a; Congdon, 1989). The most basic MR is the basal or standard MR (BMR or SMR, respectively), which refer to MRs of inactive and fasting organisms under no physiological stress (Willmer et al., 2000). Specifically, BMR is associated with thermoneutral endotherms (i.e., animals that maintain constant body temperatures in varying thermal environments), whereas SMR is associated with ectotherms (i.e., animals whose body temperatures are dependent upon the thermal conditions of their environment) at a specified temperature. Routine or resting metabolic rate (RMR) includes BMR or SMR and loosely refers to the MR associated with minimal (but unrestrained and normal) activity (Willmer et al., 2000), and can comprise as much as 30–80% of an organism's energy budget (Speakman, 1997). Active and maximum metabolic rates (AMR and MMR, respectively) also affect animal energetics and include metabolic costs in addition to RMR costs incurred during activities such as locomotion, foraging and feeding, courtship and mating.

Important phylogenetic differences with respect to metabolism manifest in different patterns of energy acquisition and allocation, and thus in life-history strategies, between endotherms (e.g., almost all birds and mammals, some fish) and ectotherms (e.g., all other animals). In general, ectotherms differ from their endothermic counterparts regarding their relatively lower mitochondrial density and their dependence on heat exchange with their environment to maintain body temperatures and thus physiological functions (Bennett, 1978; Spotila and Standora, 1985a). While most metabolism research has focused on endotherms, studies of ectotherm metabolism also have yielded important insights for organismal ecophysiology and life-history theory (Dunham et al., 1989).

Among ectothermic vertebrates, marine turtles exhibit unique physiological adaptations to biotic and abiotic conditions of their marine environments, but also to reproduction tied to nesting beaches. Marine turtle physiology – including metabolism – reflects tradeoffs between phylogenetic constraints (i.e., ectotherms with relatively low MRs), abiotic challenges of their aqueous environment (e.g., high salinity, high heat transfer via convection), and considerable energetic demands of their life histories (e.g., reproductive migrations, iteroparity, high fecundity). As with animal metabolism research in general, research on marine turtle metabolism has progressed from early, basic MR measurements of a few individuals to multi-faceted, innovative studies involving several animals, activities, and life stages with important applications to physiology and conservation.

In this review, we summarize current knowledge of metabolism and its consequences for marine turtles in the context of their ecology, physiology, and life history, with a focus on leatherback turtles (*Dermochelys coriacea*). Specifically, we provide 1) an overview of methods used to measure, infer, or model marine turtle MRs, 2) a comparison of marine turtle MRs among life stages and species, 3) a discussion of

applications of MR measurements to marine turtle ecology and physiology, and finally 4) a focused review of research on leatherback metabolism and thermoregulation. We conclude with recommendations for future research directions.

2. Overview of methods to obtain metabolic rates

Several methods have been used to obtain MRs in studies of animal physiology in general and marine turtles in particular. In this section, we present descriptions of these methods, their associated advantages and disadvantages, and studies that have employed them to measure or estimate marine turtle MRs (see Table 1 for summary).

2.1. Direct and indirect calorimetry

As the title of Kleiber's (1961) book infers, direct calorimetric measurements of MRs require quantification of total heat production by an organism because heat is produced as a byproduct of chemical reactions in energy metabolism (Schmidt-Nielsen, 1997). However, this method is technically very difficult to perform due to the challenges inherent in accurately measuring heat produced in all metabolic reactions and in external work that an organism performs. Thus, indirect methods are typically employed to obtain animal MRs.

Indirect calorimetric techniques that quantify an animal's oxygen consumption rate (\dot{V}_{O_2}), namely respirometry (closed-circuit and open-flow), are more feasible technically and thus have been employed widely to measure MRs (Schmidt-Nielsen, 1997). Oxygen consumption as measured by respirometry is based on the principles of adenosine triphosphate (ATP) production through the oxidation of food stuffs (carbohydrates, protein, fat). ATP yield or chemical energy production (heat) is fairly constant per unit volume of oxygen consumed regardless of the food source being oxidized. For example, there is only a 10% difference in energy yield (20.9 to 18.8 kJ) per liter of oxygen consumed from the highest to lowest energy source (carbohydrates and proteins, respectively). Furthermore, \dot{V}_{O_2} is technically straightforward to measure and respirometry is so readily used in physiological studies for MR determinations that the two terms (MR and \dot{V}_{O_2}) are often used interchangeably (Schmidt-Nielsen, 1997). In fact, respirometry recently has been coined the 'Gold Standard' technique for animal MR measurements (Frappell, 2006).

The majority of marine turtle metabolism studies have employed respirometry to obtain MR measurements (Table 2). Respirometry measurements on marine turtles have been performed in either closed-circuit systems (Davenport et al., 1982; Lutz and Bentley, 1985; Clusella Trullas et al., 2006; Jones et al., 2007) or in open-flow systems (Prange and Ackerman, 1974; Prange, 1976; Butler et al., 1984; Lutcavage and Lutz, 1986; Lutz et al., 1989; Lutcavage and Lutz, 1991; Wyneken, 1997; Southwood et al., 2003; Hochscheid et al., 2004; Jones et al., 2006). Both methods typically involve metabolic chambers, but modifications of open-flow systems, such as the use of masks around a turtle's head, nostrils or mouth (Prange and Jackson, 1976; Jackson and Prange, 1979; Paladino et al., 1990, 1996;

Table 1
Methods used to obtain marine turtle metabolic rates (MRs) and related references

Method	How it works	Advantages	Disadvantages	Marine turtle studies
Indirect calorimetry (respirometry)	Measures changes in concentrations of respiratory gases (O ₂ and CO ₂)	Accurate, technically easy, activity-specific	Difficult, if not impossible, to use for natural, in-water activities	Butler et al. (1984), Davenport et al. (1982), Davenport and Oxford (1984), Davenport and Scott (1993), Hochscheid et al. (2004), Jackson and Prange (1979), Jones et al. (2006), Lutcavage and Lutz (1986), Lutcavage et al. (1987, 1990, 1992), Lutz et al. (1989), Paladino et al. (1990, 1996), Prange (1976), Prange and Ackerman (1974), Prange and Jackson (1976), Southwood et al. (2003)
Doubly labeled water	Estimates CO ₂ production from divergence of hydrogen and oxygen isotope washout curves	Energy expenditure estimates (and water turnover rates) for natural, in-water activities	Expensive, logistically and technically difficult, not activity-specific, validation experiments crucial	Clusella Trullas et al. (2006), Jones et al. (2006), Southwood et al. (2006), Wallace et al. (2005)
Behavioral inference	Statistically infers aerobic dive limits from dive data and estimates MR	Analytically straightforward	Numerous physiological assumptions, not activity-specific	Bradshaw et al. (2007)
Biophysical model	Use biophysical equations to model heat transfer (including heat production or MR)	Input parameters mostly from literature, allows for testing several 'what if' scenarios	Numerous physiological and anatomical assumptions	Bostrom and Jones (2007), Paladino et al. (1990)

Lutcavage et al., 1990, 1992), have also been used extensively to facilitate MR measurements of large-bodied adult marine turtles. Durations of most respirometry experiments on marine turtles have been ≤ 90 min, but some studies lasted for nearly 5 h (Lutz et al., 1989; Southwood et al., 2003), for a 24 h period (Hochscheid et al., 2004), or for several days (Jones et al., 2006).

Closed-circuit systems typically have been used for ectotherms (low MRs) or for cellular and isolated tissue preparations (McDonald, 1976). With respect to marine turtles, researchers have used closed-circuit systems for 12 to 100 g hatchlings and post-hatchlings (Wyneken, 1997; Clusella Trullas et al., 2006; Jones et al., 2007), for 0.5 to 1.5 kg juveniles (Davenport et al., 1982; Davenport and Oxford, 1984; Davenport and Scott, 1993; Lutz and Bentley, 1985), as well as for 10 kg to > 100 kg sub-adult to adult turtles (Jones et al., 2005). In closed-circuit systems, metabolism is measured by monitoring the changing composition of gases within a respirometer of known volume (McDonald, 1976). Closed-circuit respirometers tend to have less error in baseline O₂ measurements than open-flow respirometers because the drop in partial pressure of O₂ (P_{O_2}) measured in a closed-circuit system directly represents the O₂ consumed by the study animal, such that baseline error contributes little to the perceived overall depletion of O₂ as the experiment progresses (Kaufmann et al., 1989). Minor changes in pressure in closed-circuit systems can be compensated for with a flexible window in the metabolic chamber (McDonald, 1976) or by allowing water level flux to dampen pressure change by using lids that do not cover the entire surface of respirometer dome, thereby sealing the air chamber but keeping tank water exposed to ambient pressure (Jones et al., 2007).

Open-flow systems offer the advantage of exposing the study animal to constantly refreshed atmospheric air or to a predetermined mixture of gases, thus allowing for a stable

dynamic condition throughout the study (McDonald, 1976; Kaufmann et al., 1989). This facilitates experiments of longer durations than are feasible with closed-circuit respirometers due to the drop in P_{O_2} or accumulation of CO₂ in closed systems. Oxygen consumption is determined in open-flow systems by multiplying the flow rate of air through the chamber throughout the study period by the difference between the P_{O_2} s of the inflow air and the outflow air (McDonald, 1976). Major challenges of open-flow systems include the error inherent in flow control devices, complications of scrubbing CO₂ before or after the flow control device, and problems with humidity and total flow (Withers, 1977). In addition, any errors in baseline O₂ determinations are accumulated over the trial length, whereas closed-circuit respirometers are less affected by baseline O₂ measurements during an experimental trial. Open-flow respirometers are easily calibrated using the one-step N₂ dilution technique developed by Fedak et al. (1981). A derivation of the Fedak et al. (1981) N₂ dilution technique can be used for closed-circuit respirometers as well by injecting a N₂ bolus of known volume into the respirometer and calculating the consequent displacement of O₂ by the N₂ bolus (T.T. Jones and M. Hastings unpublished data). This technique works best if equivalent volumes of air and N₂ are drawn simultaneously from or injected into the respirometer, respectively.

Despite being considered the 'Gold Standard' in MR determinations (Frappell, 2006), respirometry has important disadvantages. For example, researchers must bring study animals into the lab or construct make-shift field laboratories to hold animals for extended experimental periods. While this is beneficial for controlling experimental variables and for determining metabolic costs of specific activities, respirometry techniques do not allow for MR measurements of free-ranging

marine turtles. Nonetheless, respirometry continues to hold primary importance in obtaining MRs for specific physiological conditions. Additionally, as use of alternative techniques to determine at-sea MRs increases, respirometry will have an enhanced role as a validation tool (see below).

2.2. Doubly labeled water

While conventional respirometry is technically straightforward and can provide measures of RMRs and AMRs, using these techniques to measure MRs of free-ranging marine animals is logistically infeasible in most cases (but see Castellini et al., 1992). Alternatively, the doubly labeled water (DLW) method has proven to be a useful tool for studying field energetics and activity of marine animals (Costa, 1988). Briefly, the DLW method estimates CO_2 production (rCO_2) from the divergence between washout curves (i.e., the elimination rates) of heavy hydrogen (deuterium or tritium) and oxygen (^{18}O -oxygen) stable isotopes introduced into an animal's total body water (TBW) (Lifson et al., 1955). Specifically, the divergence in isotopic washout curves occurs because hydrogen isotopes are lost via various routes of water turnover (e.g., respiration, defecation, urination, etc.), whereas oxygen isotopes are lost via water turnover but also via rCO_2 . The resulting difference in the two washout curves approximates total rCO_2 by the organism (see Lifson et al., 1955; Speakman, 1997 for reviews). Thus, results of DLW experiments provide valuable information about water turnover as well as energy expenditure of animals associated with natural activities during the study period (field metabolic rate, FMR). However, it is important to note that DLW-derived FMRs are integrations of energy expenditures during the entire study period, not for particular activities.

Despite the potential utility of DLW, there are considerable disadvantages of the method that generally preclude its use to obtain FMRs for a substantial sample size of large animals. First, the high cost of the isotopes ($\sim \$250 \text{ ml}^{-1}$ for highly concentrated DLW) is often prohibitive by itself. Second, the method relies on significant divergence of the isotope washout curves that is created by a relatively higher rCO_2 than water turnover rate (rH_2O). The accuracy of the DLW method decreases as the ratio of rCO_2 to rH_2O decreases (Speakman, 1997; Butler et al., 2004). This issue typically is not problematic for endothermic animals, but can represent risk of failure of the method for ectotherms, particularly those with high rH_2O , such as marine turtles.

Despite these formidable technical challenges, marine turtle FMRs have been obtained successfully in a few recent studies (Table 1). Clusella Trullas et al. (2006) obtained DLW-derived FMRs for hatchling olive ridley turtles (*Lepidochelys olivacea*) during nest emergence, crawling on sand, and swimming to quantify the energetics of hatchling dispersal behavior. In this experiment, sequential blood samples of hatchlings in each treatment allowed for calculation of isotopic washout and demonstrated wide variation among FMRs associated with different activities (Clusella Trullas et al., 2006) (Table 2).

In another DLW study, Southwood et al. (2006) reported FMRs along with thermal sensitivities of muscle enzyme

activities and diving behavior between seasons to identify temporal patterns in energy expenditure and activity in free-ranging juvenile green turtles (*Chelonia mydas*). Juvenile green turtle FMRs were slightly but not significantly different (given associated measurement errors) between summer and winter, and water flux rates varied little across individuals and between seasons (Southwood et al., 2006) (Table 2).

With respect to application of DLW to adult marine turtles, Wallace et al. (2005) combined FMRs with information on diving activity to quantify energy expenditure of female leatherbacks during the internesting period (i.e., time between consecutive nesting events). High water turnover rates (and likely low FMRs) resulted in complete isotopic washout in two turtles, thus preventing calculation of FMRs for these animals (Wallace et al., 2005). However, FMRs of three other free-ranging adult female leatherbacks were similar to MRs of nesting leatherbacks (Paladino et al., 1996), thus suggesting energy conservation by leatherbacks during the internesting period while in warm tropical water (Table 2).

Considering the numerous potential sources of error inherent to the DLW method, relating DLW-derived MR measurements to simultaneous MR measurements obtained by respirometry is crucial to interpretation of the data acquired via DLW (Speakman, 1997). However, performing simultaneous metabolic measurements on adult marine turtles is extremely difficult, due to factors such as their marine lifestyle, large size, endangered status, and the high cost of the large volume of enriched DLW required. In general, DLW validation experiments indicate that although individual variation might account for serious discrepancies between DLW measurements and those acquired by reference methods, the DLW method tends to overestimate rCO_2 by less than 5% among different animal taxa (Butler et al., 2004).

In the only truly simultaneous validation study that has been performed for marine turtles, Jones et al. (2006) compared DLW-derived MRs with simultaneous MR measurements using open-circuit respirometry for 6 green turtles ($22.3 \pm 3.2 \text{ kg}$) that were either fed or fasted during the experiment. For the 'fed' group, TBW remained relatively constant and the average intra-individual difference between MRs obtained by the two methods was $<15\%$. In contrast, fasted animals exhibited changing TBW pool size and greater reductions in MR than in water turnover, thus violating several assumptions of the DLW method (Speakman, 1997). Considering these results, researchers should use caution when using the DLW method for marine turtles, especially when the physiological state of the study animals is unknown. The DLW method may be more informative when comparing seasons or habitats within species rather than as an absolute measure of FMR.

Thus, the DLW method can provide extremely valuable MR data associated with natural activities and energy expenditures, but must be applied carefully and strategically with its disadvantages in mind. Due to the high cost of conducting a DLW experiment on large animals such as marine turtles, researchers interested in using this technique should thoughtfully design their experiments to test specific hypotheses about natural patterns of energy expenditure to ensure maximizing

Table 2
Summary of reported metabolic rates (MRs) for marine turtles

Species	Activity	<i>n</i>	Mass (kg)	\dot{V}_{O_2} (ml min ⁻¹)	Mass-specific MR (W kg ⁻¹)	Temperature (°C)	Method	Reference
Cc ^a	Resting	4	0.820	0.85	0.34	22 (air)	Respirometry	Lutz and Bentley (1985)
Cc	Routine	5	0.022±0.001	0.08	1.15	24	Respirometry	Lutcavage and Lutz (1986)
Cc	Resting	8	9.5±1.5	13.3	0.47	25 (air)	Respirometry	Lutcavage et al. (1987)
Cc ^b	Resting (fasted)	8	13.0	0.85	0.002	10	Respirometry	Lutz et al. (1989)
Cc ^b	Active (fasted)	8	13.0	2.63	0.068	10	Respirometry	Lutz et al. (1989)
Cc ^b	Resting (fasted)	8	13.0	1.32	0.03	15	Respirometry	Lutz et al. (1989)
Cc ^b	Active (fasted)	8	13.0	4.07	0.10	15	Respirometry	Lutz et al. (1989)
Cc ^b	Resting (fasted)	8	13.0	2.04	0.05	20	Respirometry	Lutz et al. (1989)
Cc ^b	Active (fasted)	8	13.0	6.31	0.16	20	Respirometry	Lutz et al. (1989)
Cc ^b	Resting (fasted)	8	13.0	3.16	0.08	25	Respirometry	Lutz et al. (1989)
Cc ^b	Active (fasted)	8	13.0	9.77	0.25	25	Respirometry	Lutz et al. (1989)
Cc ^b	Resting (fasted)	8	13.0	4.90	0.13	30	Respirometry	Lutz et al. (1989)
Cc ^b	Active (fasted)	8	13.0	15.13	0.39	30	Respirometry	Lutz et al. (1989)
Cc ^c	Resting	10	0.018±0.002	0.16	2.97	24 (air)	Respirometry	Wyneken (1997)
Cc ^c	Active	10	0.019±0.002	0.33	5.81	24	Respirometry	Wyneken (1997)
Cc ^c	Maximum	10	0.02±0.001	0.32	5.35	24	Respirometry	Wyneken (1997)
Cc	Routine	9	24.7±22.2	3.97	0.05	25	Respirometry	Hochscheid et al. (2004)
Cc	Routine	9	25.8±21.9	2.88	0.04	22	Respirometry	Hochscheid et al. (2004)
Cc	Routine	9	26.0±21.8	1.56	0.02	19	Respirometry	Hochscheid et al. (2004)
Cc	Routine	9	25.8±21.7	0.76	0.01	16	Respirometry	Hochscheid et al. (2004)
Cm ^d	Resting	9	0.031	0.05	0.55	25 (air)	Respirometry	Prange and Ackerman (1974)
Cm ^d	Active	7	0.031	0.17	1.87	25	Respirometry	Prange and Ackerman (1974)
Cm ^e	Resting	5	0.735	0.86	0.39	25 (air)	Respirometry	Prange (1976)
Cm ^e	Active	5	0.735	1.35	0.61	25	Respirometry	Prange (1976)
Cm ^e	Maximum	5	0.735	2.82	1.28	25	Respirometry	Prange (1976)
Cm ^f	Resting	1	142	56.8	0.13	23–27 (air)	Respirometry	Prange and Jackson (1976)
Cm ^f	Active	1	142	488	1.15	23–27 (air)	Respirometry	Prange and Jackson (1976)
Cm ^g	Resting	5	128	128	0.33	26–30 (air)	Respirometry	Jackson and Prange (1979)
Cm ^g	Active	5	128	493	1.29	26–30 (air)	Respirometry	Jackson and Prange (1979)
Cm	Resting	6	1.14±0.22	2.24	0.66	25 (air)	Respirometry	Davenport et al. (1982)
Cm	Resting (fasted)	3	1.50±0.65	1.86	0.42	25 (air)	Respirometry	Davenport et al. (1982)
Cm	Resting	5	1.15±0.07	2.28	0.65	29	Respirometry	Butler et al. (1984)
Cm ^h	Active	5	1.15±0.07	4.34	1.26	28	Respirometry	Butler et al. (1984)
Cm ^h	Active	5	1.15±0.07	5.26	1.53	29	Respirometry	Butler et al. (1984)
Cm ^h	Active	5	1.15±0.07	6.44	1.87	30	Respirometry	Butler et al. (1984)
Cm	Resting	6	0.047±0.01	0.09	0.64	25 (air)	Respirometry	Davenport and Oxford (1984)
Cm ⁱ	Resting	8	0.785	1.11	0.47	22 (air)	Respirometry	Lutz and Bentley (1985)
Cm ^j	Resting	12	0.350	1.07	1.02	25 (air)	Respirometry	Davenport and Scott (1993)
Cm ^c	Resting	10	0.025±0.002	0.12	1.61	24	Respirometry	Wyneken (1997)
Cm ^c	Active	10	0.026±0.001	0.34	4.37	24	Respirometry	Wyneken (1997)
Cm ^c	Maximum	10	0.025±0.002	0.52	6.96	24	Respirometry	Wyneken (1997)
Cm ^k	Routine	5	24.1±1.9	11.1	0.15	26	Respirometry	Southwood et al. (2003)
Cm ^k	Routine	5	32.5±2.8	16.0	0.16	26	Respirometry	Southwood et al. (2003)
Cm ^k	Routine	5	28.3±4.9	9.30	0.11	17	Respirometry	Southwood et al. (2003)
Cm ^k	Routine	5	27.9±1.8	9.51	0.11	17	Respirometry	Southwood et al. (2003)
Cm	Field	5	15.3±1.9	77.6	1.70	26	DLW	Southwood et al. (2006)
Cm	Field	4	16.7±2.9	49.8	1.00	21	DLW	Southwood et al. (2006)
Cm	Routine	6	22.3±3.24	17.7	0.27	24–26	Respirometry	Jones et al. (2006)
Cm	Routine	6	22.3±3.24	21.7	0.33	24–26	DLW	Jones et al. (2006)
Cm	Routine (fasted)	6	22.0±3.18	12.5	0.19	24–26	Respirometry	Jones et al. (2006)
Lo ^l	Resting	8	0.017±0.002	0.07	1.38	27 (air)	Respirometry	Clusella Trullas et al. (2006)
Lo ^l	Swimming	10	0.018±0.002	0.50	9.29	25	DLW	Clusella Trullas et al. (2006)
Lo ^l	Crawling	7	0.017±0.002	0.28	5.51	27 (air)	DLW	Clusella Trullas et al. (2006)
Lo ^l	Digging	5	0.019±0.001	0.34	5.98	28 (sand)	DLW	Clusella Trullas et al. (2006)
Lo	Resting	8	0.013±0.0001	0.04	1.03	29 (air)	Respirometry	Jones et al. (2007)
Lo	Maximum	8	0.013±0.0001	0.09	2.32	26	Respirometry	Jones et al. (2007)
Lo	Resting	8	0.015±0.0001	0.04	0.90	29 (air)	Respirometry	Jones et al. (2007)
Lo	Maximum	8	0.015±0.0001	0.09	2.04	26	Respirometry	Jones et al. (2007)
Lo	Resting	8	0.019±0.0003	0.04	0.70	29 (air)	Respirometry	Jones et al. (2007)
Lo	Maximum	8	0.019±0.0003	0.16	2.75	26	Respirometry	Jones et al. (2007)
Dc	Active	8	0.053±0.002	0.25	1.58	24	Respirometry	Lutcavage and Lutz (1986)
Dc ^m	Laying	3	305±24	76.3	0.08	21–24 (air)	Respirometry	Lutcavage et al. (1990)
Dc ⁿ	Resting	6	340	443	0.39	No data	Respirometry	Paladino et al. (1990)
Dc ⁿ	Active	6	340	1398	1.23	No data	Respirometry	Paladino et al. (1990)
Dc ⁿ	Maximum	5	340	1715	1.51	No data	Respirometry	Paladino et al. (1990)
Dc ^o	Resting	3	358±10	390	0.36	22–27 (air)	Respirometry	Lutcavage et al. (1992)
Dc ^p	Laying	3	300±5	261	0.33	23 (air)	Respirometry	Paladino et al. (1996)
Dc ^p	Resting	10	354±5	425	0.40	23 (air)	Respirometry	Paladino et al. (1996)
Dc ^p	Active	10	366±5	1050	1.12	23 (air)	Respirometry	Paladino et al. (1996)
Dc ^c	Resting	10	0.045±0.003	0.18	1.34	24	Respirometry	Wyneken (1997)

Table 2 (continued)

Species	Activity	<i>n</i>	Mass (kg)	\dot{V}_{O_2} (ml min ⁻¹)	Mass-specific MR (W kg ⁻¹)	Temperature (°C)	Method	Reference
Dc ^c	Active	10	0.047±0.005	0.37	2.63	24	Respirometry	Wyneken (1997)
Dc ^c	Maximum	10	0.044±0.003	0.44	3.34	24	Respirometry	Wyneken (1997)
Dc ^d	Field	4	278.5±19.7	329	0.40	14–28	DLW	Wallace et al. (2005)
Dc	Resting	8	0.040±0.001	0.23	1.92	29 (air)	Respirometry	Jones et al. (2007)
Dc	Maximum	8	0.040±0.001	0.30	2.50	26	Respirometry	Jones et al. (2007)
Dc	Resting	8	0.048±0.001	0.12	0.86	29 (air)	Respirometry	Jones et al. (2007)
Dc	Maximum	8	0.048±0.001	0.26	1.81	26	Respirometry	Jones et al. (2007)
Dc	Resting	8	0.078±0.001	0.21	0.90	29 (air)	Respirometry	Jones et al., 2007
Dc	Maximum	8	0.078±0.001	0.33	1.43	26	Respirometry	Jones et al. (2007)
Dc ^f	Calculated	NA	300	576	0.65	NA	Biophysical Model	Bostrom and Jones (2007)
Dc ^s	Calculated	9	312±18	230	0.24	No data	Behavioral Inference	Bradshaw et al. (2007)

Species codes: Cc = *Caretta caretta*, loggerhead; Cm = *Chelonia mydas*, green turtle; Lo = *Lepidochelys olivacea*, olive ridley; Dc = *Dermochelys coriacea*, leatherback. Activity levels: Resting = fed (unless noted as fasted), quiescent turtles; Routine = periods of quiescence and activity; Active = continuous non-maximal activity (i.e., swimming, crawling, etc.); Maximum = sustained maximal metabolic rate; Field = at-sea field metabolic rates (FMR, including all activities of daily existence); Laying = during oviposition; Calculated = MRs derived from models based on activity, behavior and environmental factors. Mass values are mean±S.D., unless otherwise noted. See detailed footnotes for description of data presented relative to each reference.

^a Lutz and Bentley (1985) — Mass was reported as range (520–1120 g), so we present the midpoint of that range. We calculated the oxygen consumption in ml O₂ min⁻¹ from the ends of the range (520 and 1120 g) using the value reported for resting (62.0 ml O₂ kg⁻¹ h⁻¹) and reported the mean of these values. Temperature reported is of water in the holding tank that the turtles were in before placement in the respirometer in air.

^b Lutz et al. (1989) — Mass was reported as average (13.02 kg) and a range (4.3–22.7 kg) (no S.D. reported). The regression equations reported appeared to be reversed as the equation for resting gives rates ~3 times higher than the respective equation for activity. Metabolic rate at 25 degrees C was not reported in paper but calculated for this table. The active measurement is of swimming turtles.

^c Wyneken (1997) — Resting is in air and maximum measurements are during 'frenzy swimming', the active measurements are of 'post-frenzy' swimming (i.e., sustained activity, but not at maximum, 'frenzy' rates). Mass data were obtained from J. Wyneken via personal communication. Note that maximum measurement for loggerheads is less than active however the measurements were not reported as significantly different.

^d Prange and Ackerman (1974) — Mass was reported as average (30.9 g) and range (29.5–33.5 g) (no S.D. reported). Active animals were either crawling inside respirometer or swimming in respirometer chamber partially filled with water. No mass data is given for the active animals (*n*=7); thus, we used the average (30.9 g) from resting turtles (*n*=9).

^e Prange (1976) — Mass data was reported as average (735 g) and range (250–900 g) (no S.D. reported). Active and maximum oxygen consumption rates were determined using the reported equation ($1 \text{ O}_2 \text{ kg}^{-1} \text{ h}^{-1} = 0.07 + 0.978(m \text{ s}^{-1})^{1.662}$) and the listed swim speeds of 0.14 m s⁻¹ (active) and 0.34 m s⁻¹ (maximum).

^f Prange and Jackson (1976) — Oxygen consumption rates were measured for two turtles (127 and 142 kg), however only data for the 142 kg turtle were reported. Oxygen consumption data given in the paper (Table 2 on page 376) does not correspond with data reported in text. We used the reported data in text to determine resting and active (crawling on sand) oxygen consumption rates. The active measurement is an average of oxygen consumption rates at 7–9 and 21 min into crawling activity.

^g Jackson and Prange (1979) — Mass was reported as average (128 kg) (no range or S.D. reported). Oxygen consumption data is from 5 captive turtles and the activity measurement is from turtles crawling on a flat, grassy patch of land. An oxygen consumption rate for nesting turtles (*n*=6) was reported but mass and phase of nesting are omitted; thus, we did not include this datum (0.27 l O₂ kg⁻¹ h⁻¹).

^h Butler et al. (1984) — The active oxygen consumption rates are of swimming turtles at 0.4, 0.5 and 0.6 m s⁻¹, respectively.

ⁱ Lutz and Bentley (1985) — Mass was reported as range (650–920 g). We calculated the oxygen consumption in ml O₂ min⁻¹ from the ends of the range (650 and 900 g) using the value reported for resting (84.7 ml O₂ kg⁻¹ h⁻¹) and present the midpoint of these values. Temperature reported is of the water in the holding tank in which turtles were kept before placement in the respirometer in air.

^j Davenport and Scott (1993) — Oxygen consumption data reported refers to another publication for mass data (Davenport and Scott, 1993, Herp. Journ. 3:19–25). Days of mass measurements were reported, however the mass values themselves were not provided. Thus, we approximated the mass values from a figure in the paper with no equation (200–500 g). We calculated the oxygen consumption rates (ml O₂ min⁻¹) from the endpoints of the mass range (200–500 g) using the value reported for resting (0.184 ml O₂ g⁻¹ h⁻¹); we present the midpoint of these values.

^k Southwood et al. (2003) — Mass data for turtles at 17 °C were obtained from A. Southwood via personal communication. Because reported oxygen consumption rates were mass-corrected and reported as kg^{0.83}, we recalculated using whole animal (ml min⁻¹) and mass-specific (W kg⁻¹).

^l Clusella Trullas et al. (2006) — The reported metabolic rates were given as kJ day⁻¹; we recalculated using 20.3 kJ per l O₂ metabolized (based on mixture of carbohydrate and fat catabolism).

^m Lutcavage et al. (1990) — Mass was not measured directly but inferred from curved-carapace length to mass relationships.

ⁿ Paladino et al. (1990) — Mass was reported as range (250–430 kg, *n*=6). We used the midpoint of this range to include a single mass value in the allometric analysis (Fig. 1, this study). Resting oxygen consumption rate is from turtles restrained in a cargo net, active oxygen consumption rate is from turtles covering nests and crawling on the beach, and maximum oxygen consumption rate is from the highest oxygen consumption peaks during crawling and nest covering.

^o Lutcavage et al. (1992) — Mass presented is the mean of turtles for which metabolic rate data were acquired in the study. The resting oxygen consumption data refer to turtles restrained in a cargo net.

^p Paladino et al. (1996) — Resting oxygen consumption rate data were from turtles restrained in a cargo net and the active measurements were during vigorous exercise while turtles were pulling 100 kg sleds or actively covering their nest.

^q Wallace et al. (2005) — We recalculated mass based on turtles for which FMRs were obtained. The temperature range presented is the range of water temperatures presented in Fig. 6 (p 3882). The oxygen consumption rate value (ml min⁻¹) was calculated from W kg⁻¹ using 20.3 kJ per l O₂ metabolized.

^r Bostrom and Jones (2007) — Metabolic rate estimates were based on a 300 kg turtle maintaining 0.7 m s⁻¹ swim speed. The oxygen consumption rate value (ml min⁻¹) was calculated from W kg⁻¹ using 20.3 kJ per l O₂ metabolized.

^s Bradshaw et al. (2007) — Mass data were not measured directly but inferred from curved-carapace length to mass relationships. No temperature data were provided.

return on their significant research investment. In addition, we suggest that additional DLW-respirometry validation studies are imperative and should be species-specific, and we recommend that future field-based DLW studies include validation experiments, when possible, to augment the interpretive power of the DLW data.

2.3. Other field-based methods

In addition to the DLW method, other field-based methods for estimating FMRs include deploying data loggers to measure heart rates (Butler et al., 2004) or changes in acceleration (Wilson et al., 2006). In contrast to the DLW method, these techniques provide far greater temporal resolution of activity patterns, and thus facilitate improved activity-specific estimates of energy expenditure. On the other hand, like the DLW method, these methods depend on calibration of either heart rate or acceleration measurements with simultaneous MR measurements recorded under controlled conditions to enable estimation of FMRs from these field-based proxy data. Some studies have reported heart rates for marine turtles (Berkson, 1966; Southwood et al., 1999; Myers and Hays, 2007), and a few have reported both heart rates and MRs (although not necessarily in direct relation to each other) (Davenport et al., 1982; Butler et al., 1984; Lutcavage et al., 1992; Southwood et al., 2003). However, we are not aware of any study that has used heart rate or acceleration measurements specifically to estimate marine turtle FMRs. If accompanied by appropriate validation experiments, these methods hold promise for field studies of marine turtle metabolism, diving physiology, and activity-specific energy expenditure.

Other field-based methods can be used to estimate or infer patterns of energy expenditure by marine turtles. For example, Hays et al. (1992) recorded body mass losses of nesting female green turtles to estimate energy spent during fasting periods associated with reproductive cycles. While this method is limited in its ability to explain specific patterns of energy expenditure and mechanisms of body mass loss in relation to physiological demands of reproduction (e.g., migration, egg production, etc.), it is helpful to provide estimates of reproductive energy budgets of marine turtles (see below).

2.4. Inferred or modeled metabolic rates

Due to logistical, interpretive, and financial limitations of the available methods to measure marine turtle MRs outlined above, alternative methods to estimate MRs of free-ranging marine turtles would be useful to develop our understanding of natural variations in energy expenditure and behavior. Two recent studies have presented alternative analytical approaches to obtain marine turtle MRs by using behavioral inferences from diving data (Bradshaw et al., 2007) and biophysical models (Bostrom and Jones, 2007).

The use of electronic archival and satellite linked instruments to acquire information on diving behavior and movements of free-ranging marine turtles in relation to their marine environments has increased remarkably in the past two decades. Thus,

because such information has been collected for various marine turtle populations worldwide, analysis of copious dive depth and duration data over long periods could allow broad inferences into the physiological limitations of marine turtle diving activity. Specifically, aerobic dive limits (ADLs) are commonly calculated to provide estimates of oxygen-limited physiological boundaries to activity patterns of air-breathing, diving animals (see Costa et al., 2001 for review; also, see below for further discussion of ADLs).

Using dive data from adult female leatherbacks (Hays et al., 2004a), Bradshaw et al. (2007) developed an analytical technique that enabled statistical estimation of ADLs from an asymptotic relationship between dive duration and maximum dive depth. After determining putative ADLs for individual turtles, the authors then used published values for leatherback total body oxygen stores (Lutcavage et al., 1992) to calculate 'maximum diving MRs (DMRs),' which only include activities associated with diving, and not surfacing, and thus are typically lower than FMRs (Bradshaw et al., 2007). Because FMR-derived ADLs typically underestimate true ADLs due to the inclusion of surface activity in FMR measurements, using DMRs to estimate ADLs theoretically eliminates this bias (Costa et al., 2001). DMRs were lower than FMRs measured for free-swimming, adult female leatherbacks (Wallace et al., 2005) and higher than predictions from allometric relationships of reptile FMRs (Bradshaw et al., 2007). Thus, this technique should be useful and accessible to a large number of marine turtle researchers interested in obtaining reasonable estimates of FMRs from available dive data.

Obviously, several assumptions are necessary to employ this technique, which are discussed in detail by Bradshaw et al. (2007). Briefly, this method likely underestimates the actual MRs associated with at-sea activities because marine turtles rarely approach, let alone exceed ADLs (Lutcavage and Lutz, 1991, 1997; Southwood et al., 1999; Wallace et al., 2005). In addition, this technique does not take into account the influence of thermoregulatory requirements on metabolism during different behavioral phases and at different latitudes (James et al., 2005; Southwood et al., 2005; Wallace et al., 2005; Bostrom and Jones, 2007). Nonetheless, where dive data and relevant physiological information are available, Bradshaw et al. (2007) have demonstrated that behavioral inference of FMR can provide valuable insights to energy expenditure patterns associated with natural activities of marine turtles.

In addition to behaviorally inferred estimates of FMRs, applications of biophysical models can be extremely valuable for generating realistic expectations of physiological responses of animals to their physical environments. In particular, these models can be used to compute heat production rates (i.e., MRs) necessary to achieve and maintain differentials between internal body (T_b) and ambient temperatures (T_a). Input parameters for relevant heat transfer processes (i.e., convection, conduction) and biological variables (i.e., MRs, body sizes) for these models can include empirical data as well as assumptions for terms for which no data exist. This approach has been used widely for reptiles, including crocodylians (Grigg et al., 1979) marine turtles (Paladino et al., 1990), and even dinosaurs (Spotila et al., 1991).

Along these lines, [Bostrom and Jones \(2007\)](#) created a detailed, highly informative biophysical model to accentuate the crucial role of behavioral adjustments in swimming activity that affect metabolic heat production to achieve high $T_b - T_a$ differentials for leatherbacks. Comparisons with empirical studies ([Southwood et al., 2005](#); [Wallace et al., 2005](#)) appeared to confirm several of the model's predictions of necessary adjustments in swimming behavior to achieve certain MRs and T_b ([Bostrom and Jones, 2007](#)). Because behavioral modification of MR was underemphasized in previous models ([Paladino et al., 1990](#)), this new generation model represents a valuable improvement to understand leatherback thermal biology (see below).

Heuristic models (e.g., [Bostrom and Jones, 2007](#)) are intended to provide ranges of reasonable response values for predictive purposes, and are dependent upon the accuracy of input parameter values and the strength of the assumptions used in model construction. Thus, model outputs will more closely predict empirical values as inputs and assumptions are refined to reflect actual values and conditions. In the case of the [Bostrom and Jones \(2007\)](#) model, improved assumptions of insulation thickness and blood flow adjustments probably would have substantially altered predicted MRs. Also, while this model provided compelling results to highlight the importance of behavioral adjustments in achieving $T_b - T_w$ differentials, [Bostrom and Jones \(2007\)](#) appeared to de-emphasize the importance of leatherbacks' large body size (and other adaptations) in maintaining those differentials. Nonetheless, [Bostrom and Jones \(2007\)](#) clearly demonstrated the merit in creating well-designed biophysical models to compute marine turtle MRs.

Selecting the appropriate method to obtain marine turtle MRs obviously depends on the particular research question(s), logistical constraints (e.g., field conditions, accessibility of animals), and available resources (e.g., equipment, funding) ([Table 1](#)). Regardless of the method used, careful planning and sound experimental design will dramatically increase the chances of successful measurement of marine turtle MRs.

3. Comparison of MRs among species and life stages

Measurements of marine turtle MRs obtained by various methods have been reported for several species and for different life stages ([Table 2](#)). Metabolic studies have been conducted and published on four species of hatchlings (loggerhead *Caretta caretta*, green, olive ridley, and leatherback turtles), two species of juveniles (loggerheads, greens), and two species of adults (greens, leatherbacks). To our knowledge, no published MRs exist whatsoever for flatback turtles (*Natator depressus*), hawksbill turtles (*Eretmochelys imbricata*), or Kemp's ridley turtles (*Lepidochelys kempii*). Here, we synthesize all published MR data in the context of ontogeny, allometry, and general marine turtle physiology.

3.1. Hatchlings and post-hatchling juveniles

During the post-hatching dispersal (often termed 'frenzy'; [Wyneken and Salmon, 1992](#)) period, marine turtle hatchlings

incur significant costs while performing various activities, including digging out of the nest, crawling to the sea, and sustained swimming, all of which is fueled by residual yolk not consumed during embryonic development ([Wyneken, 1997](#)). During the past 30 years, several studies have addressed various aspects of the influence of metabolism on energetics during the distinct phases of hatchling dispersal. In the first study of marine turtle hatchling MRs, [Prange and Ackerman \(1974\)](#) measured similar \dot{V}_{O_2} values for late-term green turtle embryos and hatchlings, and reported that AMR was 3 to 4 times greater than RMR in emergence hatchlings. Subsequently, [Lutcavage and Lutz \(1986\)](#) expanded on the terrestrial focus of the [Prange and Ackerman \(1974\)](#) study by combining \dot{V}_{O_2} measurements of 3 to 5 day-old loggerhead and leatherback hatchlings during routine, undisturbed swimming with energy content of a local jellyfish (*Cassiopeia xamachana*, i.e., a tropical, largely estuarine, shallow water species not likely ever consumed by typically open-ocean leatherbacks) to estimate swimming costs and required energy intake rates of marine turtle hatchlings. Assuming that the AMR measurements represented energy expenditure of a typical 24 h period, the authors determined that a post-hatchling leatherback would have to consume its entire body mass in jellyfish daily to meet maintenance and growth costs.

Because hatchling performance and thus metabolic demands during the frenzy and post-frenzy periods are crucial to their survival, understanding the differential energetic costs of activities and how they change over time is critical. In a seminal work on hatchling metabolism, [Wyneken \(1997\)](#) measured 'frenzy' swimming \dot{V}_{O_2} rates (i.e., maximum metabolic rates or MMRs) of loggerhead, green, and leatherback hatchlings in the first 24 h post-emergence, and then measured post-frenzy (>24 h post-emergence) AMRs (routine swimming) and RMRs (in air). Green turtles had the largest factorial aerobic scope (i.e., the ratio between MMR and RMR; [Schmidt-Nielsen, 1984](#); [Willmer et al., 2000](#)) and highest MMR measured of the 3 species, while leatherbacks were intermediate both in factorial aerobic scope as well as RMR, and loggerheads had the narrowest factorial aerobic scope and the highest RMRs ([Wyneken, 1997](#)). In addition, loggerhead post-frenzy AMR was roughly equivalent to frenzy (MMR) swimming. [Wyneken \(1997\)](#) concluded that these differences reflected divergent modes of locomotion and behavior that related to species-specific life-history demands, specifically the 'sprinting' strategy of the loggerheads and greens that use burst swimming characterized by high MRs punctuated by periods of relative inactivity, in contrast to the 'marathon' strategy of the leatherbacks, characterized by sustained AMRs that are relatively lower than those of loggerhead and green hatchlings.

In the decade since [Wyneken's \(1997\)](#) hatchling MR review, only two additional papers on hatchling MRs have been published ([Clusella Trullas et al., 2006](#); [Jones et al., 2007](#)). [Clusella Trullas et al. \(2006\)](#) published the first MR measurements for olive ridley hatchlings, and also the first marine turtle hatchling MRs obtained by the DLW method. Additionally, [Clusella Trullas et al. \(2006\)](#) successfully separated the energetic costs of the three distinct phases of hatchling

dispersal: digging out of the nest, crawling down the beach to the sea, and sustained swimming. The highest MR measurement was associated with swimming, which was as much as 1.5 and 1.8 times the MRs associated with digging and crawling, respectively (Clusella Trullas et al., 2006). However, all three phases were associated with high MRs, as digging, crawling, and swimming AMRs were 4.1, 5.0, and 7.5 times olive ridley RMRs, respectively.

While the Clusella Trullas et al. (2006) study reported energetic costs of nest emergence and frenzy swimming, it did not address how marine turtle hatchling activity and MRs might change in the subsequent post-frenzy period. In the first study to examine the ontogeny of MRs and factorial aerobic scope as hatchlings shift from frenzy to post-frenzy and to a steady-state where energetic expenditure is sustained by food intake, Jones et al. (2007) measured RMRs, AMRs, and MMRs of olive ridley and leatherback hatchlings from emergence to 4-weeks post-emergence. Jones et al. (2007) found that while factorial aerobic scope increased with age for both species, factorial aerobic scope of olive ridley hatchlings was greater than that of leatherback hatchlings. Furthermore, olive ridley MMRs and AMRs during routine swimming were similar, whereas leatherback AMRs during routine swimming were only 10% greater than their RMRs. Based on these results, Jones et al. (2007) concluded that these interspecific differences in relationships between MMRs, AMRs, and RMRs reflected divergent early life-history stratagems; the float-and-wait, superficial foraging of the olive ridley versus the active, oceanic, vertical, water column foraging of the leatherback.

Hatchling frenzy and post-frenzy MRs have been applied in separate analyses of energetic costs and physiological consequences of hatchling frenzy behavior (Kraemer and Bennett, 1981; Jones et al., 2007) and in determination of total yolk energy reserves available upon emergence (Kraemer and Bennett 1981; Silas et al., 1984; Hewavisenthi and Parmenter, 2002; Jones et al., 2007). Kraemer and Bennett (1981) measured the quantity and calorific value of loggerhead hatchling post-emergence residual yolk and used published values for swimming green turtle hatchlings (Prange and Ackerman, 1974) to estimate that loggerheads should have sufficient energy reserves for <72 h of sustained frenzy swimming. According to these calculations, Kraemer and Bennett (1981) determined that loggerhead hatchlings would not be able to reach major off-shore currents. Similarly, Clusella Trullas et al. (2006) combined their MR measurements during hatchling dispersal and residual yolk energy content values from Silas et al. (1984) to conclude that olive ridleys had adequate yolk reserves for 72 h of sustained frenzy swimming. Using a more sophisticated approach, Jones et al. (2007) applied their RMR, AMR and MMR measurements to modeled diel energy expenditure based on time-activity budgets during frenzy and post-frenzy swimming (Wyneken and Salmon, 1992) to determine that activity of olive ridley and leatherback hatchlings could be sustained for up to three weeks post-emergence on residual yolk reserves alone.

Considering the above, RMRs, AMRs and MMRs of marine turtle hatchlings vary greatly among and within species (Table 2).

Interesting questions remain regarding the evolutionary and ecological implications of intra- and interspecific differences in factorial aerobic scopes and MRs of marine turtle hatchlings. Specifically, MR differences among species might reflect divergent selection pressures of ecology and early life histories (i.e., diet, habitat, diel activities), or phylogenetic constraints (Wyneken, 1997; Jones et al., 2007). Furthermore, Jones et al. (2007) pointed out that reported interspecific MR differences probably are not due to species-specific physiological adaptations if the slight discrepancies in MRs disappear after taking into account differences in body mass, acclimation conditions, and experimental protocols. Therefore, due to the high variability in marine turtle hatchling RMR and AMR measurements, it is imperative that more measurements are made and experimental methods (e.g., definition of AMR, DLW versus respirometry) are reasonably comparable to improve the available data and enhance our understanding of the selective pressures involved in shaping hatchling MRs.

3.2. Juveniles and sub-adults

Studies of juvenile marine turtle metabolism have explored various biological and physiological issues. For example, much research on juvenile marine turtles has focused on physiological performance during swimming and under varying environmental conditions. Prange (1976) measured AMRs of juvenile green turtles at various swimming speeds and used these values to calculate aerobic swimming efficiencies of juvenile and adult turtles. Likewise, numerous other studies have investigated the physiological responses (e.g., MRs, heart rates, blood biochemistry) of immature marine turtles to swimming activities (Davenport et al., 1982; Butler et al., 1984; Lutcavage et al., 1987; Lutz et al., 1989). Juvenile marine turtles typically show elevated MRs during active swimming, and accompanying adaptations of their respiratory physiology allow them to remain aerobic during vigorous exercise (Lutz and Bentley, 1985).

The responses of juvenile marine turtles to changes in environmental conditions can have serious energetic and possible survival consequences (Musick and Limpus, 1997). Juvenile marine turtle MRs have been measured with respect to simulated (Lutz et al., 1989; Southwood et al., 2003; Hochscheid et al., 2004) and natural (Southwood et al., 2006) environmental temperature changes, as well as under different scenarios of resource availability (Jones et al., 2006). For juvenile green turtles that reside in sub-tropical areas year-round, Southwood et al. (2003) reported only minor seasonal differences in MRs, cardiovascular performance, and enzymatic activity in captive green turtles, indicating relatively low thermal dependence of physiological adjustments to T_a changes in a laboratory setting. Likewise, in the only study of at-sea metabolism of juvenile marine turtles, seasonal differences in FMRs of free-ranging juvenile green turtles were not statistically significant (Southwood et al., 2006). In contrast, MRs, activity, and food intake of juvenile loggerheads declined significantly with decreasing T_a s in a laboratory setting that imitated natural conditions in the wild (Hochscheid et al., 2004). Similarly, mass-specific MRs of fasting juvenile green turtles

declined 55% over 10–15 days, while turtles that were fed consistently showed no decline in MR (Jones et al., 2006).

Despite these developments, many issues remain unexplored with respect to juvenile marine turtle physiology and ecology. First, metabolic studies for only juvenile greens and loggerheads exist in the literature (Table 2). Second, the studies discussed above also demonstrate the importance of clarifying the effects of T_w and acclimation time on juvenile marine turtle MRs. Both juvenile green and loggerhead turtles exhibited decreased MRs in response to acute T_w changes (Davenport et al., 1982; Lutz et al., 1989), but green turtles demonstrated a much lower degree of MR depression in response to long-term acclimation to cold T_w (Southwood et al., 2003) than did loggerhead turtles (Hochscheid et al., 2004). It is important to note that both of these studies measured changes in MRs via open-flow respirometry in controlled laboratory settings over similar temperature ranges (26 to 17 °C in the Southwood et al. (2003) study; 25 to 16 °C in the Hochscheid et al. (2004) study). Third, further research could improve characterization of natural variation in species-specific metabolic and other physiological responses of juvenile marine turtles (e.g., time and energy allocations to foraging and growth) to fluctuations in environmental conditions.

3.3. Adults

Nearly all studies of adult marine turtle metabolism have taken place on land, largely due to the accessibility of nesting females. MRs for adult marine turtles have been measured only for leatherbacks and greens (Table 2). In general, MRs associated with vigorous activities (e.g., walking on land and sand-throwing during nesting) are 2–4 times higher than MRs associated with 'resting' activities (e.g., quiescent nest construction and oviposition) (Prange and Jackson, 1976; Jackson and Prange, 1979; Lutcavage et al., 1990, 1992; Paladino et al., 1990, 1996). Factorial aerobic scope appears to increase with turtle body size (Jackson and Prange, 1979), thus probably enabling adults to make long-distance migrations due to enhanced energy storage and utilization and lower resting metabolic costs than juvenile and sub-adult turtles (Jackson and Prange, 1979). Combined measurements of MRs and several respiratory parameters have thoroughly characterized physiological responses of adult marine turtles to various levels of activity while on land (see Lutcavage and Lutz, 1997 for review).

Metabolic costs of terrestrial activities in adult marine turtles are relatively well-studied compared with metabolic costs of natural at-sea activities. In the only study to date of free-ranging adult marine turtle metabolism, Wallace et al. (2005) measured FMRs for gravid leatherbacks during their approximately 10 day interesting periods off North Pacific Costa Rica. The FMRs were similar to leatherback MRs measured during oviposition, nest chamber construction, or restraint on the beach, and lower than MRs during vigorous nest covering and walking on land for leatherbacks (Paladino et al., 1990, 1996) and greens (Prange and Jackson, 1976; Jackson and Prange, 1979). However, given the low sample size, the errors associated with the DLW technique (see above), and the lack of activity-specific energy expenditure values in the Wallace

et al. (2005) study, further measurements of at-sea FMRs for all species are critical to ascertain energy expenditure of natural, in-water activity patterns and to improve understanding of adult marine turtle physiology.

3.4. Allometric relationships between marine turtle MRs and body sizes

Allometric scaling of various biological traits with animal body size has provided a valuable conceptual framework for understanding relationships between physiological processes and life history traits and animal body sizes within and among taxonomic groups (Schmidt-Nielsen, 1984; Brown et al., 2004). Body size allometries of endotherms and ectotherms can differ due to the fundamental differences between these groups with respect to metabolism and thus energy acquisition and allocation patterns (Bennett, 1982; Schmidt-Nielsen, 1984). Among ectotherms generally and reptiles specifically, marine turtles are unique because within individual species, body size encompasses between 3 and 4 orders of magnitude (Table 2). Therefore, description of the intra- and interspecific allometric relationships between body sizes and MRs in marine turtles and comparison of these relationships with those of other reptiles and of mammals are warranted.

In addition, leatherbacks specifically have been subjects of several metabolism studies (Table 2) primarily due to their unique thermoregulatory capabilities (see below). While leatherback MRs are clearly not endothermic (i.e., mammalian), questions remain about the relationship between leatherback MRs and MRs of other marine turtles and of reptiles in general. For example, measurements of nesting leatherback RMRs were intermediate to allometric predictions of reptilian and green turtle RMRs and mammalian RMRs (Paladino et al., 1990), but so were FMRs for interesting leatherbacks during consistent diving activity (Wallace et al., 2005). In contrast, other RMR values of nesting leatherbacks (Lutcavage et al., 1990) conformed more closely to reptilian RMRs. Thus, there is no consensus about whether leatherbacks, and possibly other marine turtle species, differ fundamentally in their metabolic physiology from other reptiles, or whether their MRs are 'typical' for a reptile of their size.

To resolve this ambiguity, we compared allometric relationships between body size (mass) and RMRs for leatherbacks and green turtles to each other and then to similar equations for other reptiles and for mammals. We restricted our analyses to leatherbacks and greens because they were the only two marine turtle species with RMR data that encompassed full intraspecific ranges of body size (Table 2). Specifically, we compared the slopes (b) and intercepts or elevations (a) of the power equations ($RMR = aM^b$) that described the relationships between RMRs and body size (mass, M) for both leatherbacks and greens to those parameters in similar allometric equations of reptile and mammal RMRs and body size (from Bennett, 1982). In these allometric power functions, b is the allometric scaling exponent, representing the quantitative patterns in variations in MR across body sizes, while a is the allometric coefficient, is taxon-specific and mass independent, and thus can illustrate fundamental MR differences among taxa.

It is important to point out some caveats of these allometric comparison analyses. First, the reptile RMR allometric equation (Bennett, 1982) was not created including data points within the body mass range of adult marine turtles, which limits the true explanatory power of this equation to the size range of the marine turtle data. Second, the lack of intermediate data points for leatherbacks (i.e., RMRs of juveniles) represents problems for regression analyses. However, because we were making straightforward comparisons between slopes and intercepts of allometric equations for marine turtles with those of generalized allometric equations for reptiles and mammals, traditional probability threshold statistics were sufficient to allow meaningful interpretation of results. To enhance these interpretations, we report the slope and intercept values for the leatherback and green turtle equations along with their associated 95% confidence intervals (CIs). Thus, despite the inherently arbitrary nature of significance thresholds (i.e., typically $P \leq 0.05$), if CIs of best-fit slope and intercept values for leatherbacks and greens include the null values (i.e., the slope and intercept values from the generalized reptile and mammal equations), the interpretation that the parameters from the leatherback and green turtles equations were not significantly different from those from the reptile and mammal equations can be considered robust.

There were no significant differences between slopes ($b_{\text{leatherback}} = -0.169$, 95% CI: -0.30 to 0.03 ; $b_{\text{green}} = -0.207$, 95% CI: -0.35 to -0.06 ; $F_{1,18} = 1.77$, $P = 0.679$) or intercepts ($a_{\text{leatherback}} = 0.768$, 95% CI: 0.50 to 1.19 ; $a_{\text{green}} = 0.494$, 95% CI: 0.35 to 0.75 ; $F_{1,18} = 1.92$, $P = 0.183$) of allometric equations describing the relationships between RMR and body mass in leatherbacks and green turtles. Furthermore, there were no significant differences between slopes (leatherbacks: $F_{1,7} < 0.001$, $P = 0.990$; greens: $F_{1,11} = 0.360$, $P = 0.561$) and intercepts (leatherbacks: $F_{1,7} = 2.58$, $P = 0.153$; greens: $F_{1,11} = 1.41$, $P = 0.260$) of the leatherback and green turtle allometric equations and those parameters from the general reptile equation ($\text{RMR}_{\text{reptiles}} = 0.378 \text{ M}^{-0.17}$; Bennett, 1982) (Fig. 1). Moreover, the slopes of the leatherback and green turtle equations did not differ significantly (leatherbacks: $F_{1,7} = 0.948$, $P = 0.363$; greens: $F_{1,11} = 0.400$, $P = 0.540$) from the slope of the mammal equation ($\text{RMR}_{\text{mammals}} = 3.35 \text{ M}^{-0.25}$; Bennett, 1982). However, mammalian RMRs were significantly elevated relative to RMRs of leatherbacks ($F_{1,7} = 516.3$, $P < 0.0001$) and green turtles ($F_{1,11} = 1250$, $P < 0.0001$) (Fig. 1) across the range of body masses. In addition, leatherback and green turtle AMRs and MMRs generally were higher than RMRs for these species and for reptiles, but less than or roughly equivalent to mammalian RMRs (Fig. 2). AMRs and MMRs were highly variable, probably due to the diversity of methods used to obtain these measurements, to differences in 'activity,' and to the difficulty in controlling experimental conditions (see above).

Allometric exponents describing relationships between MRs and body sizes have been reported for green turtles (~ -0.18 for mass-specific MRs; Prange and Jackson, 1976) and for juvenile loggerheads (0.353 for absolute MRs; Hochscheid et al., 2004). With the inclusion of more data points, the green turtle allometric equation we report here is similar to that of Prange and Jackson (1976). The difference between the allometric

exponent reported by Hochscheid et al. (2004) and those we report here could be due to differences in body size ranges (only juveniles 2–60 kg in Hochscheid et al. (2004); hatchling to adult masses in the present study), and/or interspecific differences. Acquisition of more MR data across body size ranges and for all species of marine turtles is necessary to characterize intra- and interspecific allometric relationships.

Our analyses of allometric relationships of RMR and body mass revealed two important conclusions: 1) the relationship between body mass and RMR in leatherbacks is similar to that of green turtles and presumably other marine turtles and 2) the relationship between body mass and RMR in marine turtles appears to be similar to that of other reptiles, but fundamentally different from that of mammals. Therefore, while metabolism plays a central role of heat generation in the thermoregulation of leatherbacks (and other marine turtles), apparent phylogenetic constraints on metabolic physiology underscores the enormous importance of heat retention mechanisms to leatherback (and other marine turtle) thermal biology (see below). In addition, the inclusion of RMR data for large body sizes of adult marine turtles (> 100 kg) into existing reptile RMR datasets would greatly improve the current status of reptile RMR-body size allometry and thus enhance our understanding of reptilian metabolism and physiology.

4. Applications of MR measurements to marine turtle ecology

While MR data are valuable by themselves, applications of MRs to broader, multi-faceted questions increase the relevance and importance of MR data to the study of marine turtle ecology and conservation. Metabolic rates – particularly at-sea MRs – for marine turtles are the most critical components in calculating individual and population energy requirements, improving our understanding of physiological limitations on diving and thermoregulation, and for refinement of demographic

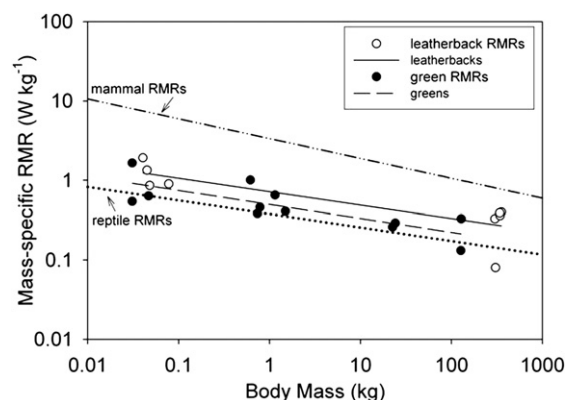


Fig. 1. Mass-specific resting metabolic rates (RMRs, W kg^{-1}) versus body mass (kg) (plotted on log–log scales) of leatherbacks (open circles) and green turtles (filled circles) compared to allometric equations for reptiles (dotted line: $\text{RMR}_{\text{reptile}} = 0.378 \text{ M}^{-0.17}$) and mammals (dash-dot-dash line: $\text{RMR}_{\text{mammal}} = 3.35 \text{ M}^{-0.25}$). Data points represent RMRs measured for fasted animals (where indicated in each study) by respirometry at 'normal' temperatures (generally 22–27 °C). Regression lines representing the power equations for leatherbacks (solid line; $\text{RMR}_{\text{leatherback}} = 0.768 \text{ M}^{-0.169}$) and green turtles (dashed line; $\text{RMR}_{\text{green}} = 0.494 \text{ M}^{-0.207}$) are also shown.

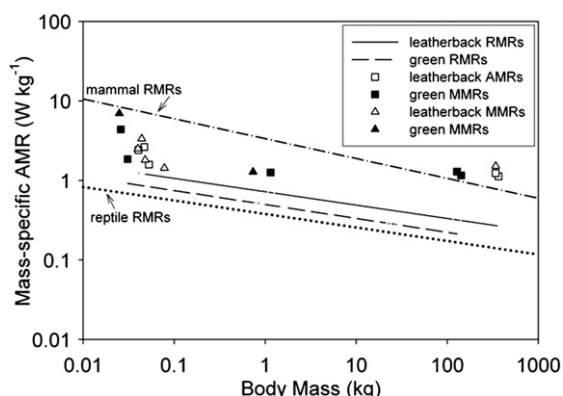


Fig. 2. Mass-specific active metabolic rates (AMRs: squares) and maximum metabolic rates (MMRs: triangles) (W kg^{-1}) versus body mass (kg) (plotted on log–log scales) of leatherbacks (open symbols) and green turtles (filled symbols) compared to the allometric equations shown in Fig. 1 (solid line: leatherbacks, dashed line: green turtles, dotted line: reptiles, dash–dot–dash line: mammals). Data points represent AMRs and MMRs measured by respirometry at ‘normal’ temperatures (generally 22–27 °C).

parameters necessary to estimate population trends (Jones et al., 2004). Here we discuss applications of marine turtle MRs under one of three, non-mutually exclusive categories: energetics and energy budgets, diving physiology, and thermoregulation.

4.1. Energetics and energy budgets

Physiology, environment, and resource limitation are the dominant influences on an organism’s bioenergetics and thus its life history (Dunham et al., 1989). Tradeoffs with and constraints of an organism’s physiological state and limitations, biophysical environment (Spotila and Standora, 1985a), and resource availability, acquisition and assimilation (Congdon et al., 1982) affect both time and energy allocation to different functions (Congdon, 1989). Depending on resource availability, metabolic requirements influence reproductive outputs and schedules, as well as growth and morphometrics, which in turn affect overall population demography (Dunham et al., 1989; Brown et al., 2004). Therefore, MR measurements are critical for answering fundamental questions about animal ecology and life history, particularly that of marine turtles.

Costs of swimming are central to marine turtle energetics. For example, Bostrom and Jones (2007) computed the metabolic costs of various swimming speeds for adult leatherback turtles under feeding and non-feeding conditions to estimate required energy intake rates. Further, Prange (1976) used MR measurements from small juvenile green turtles obtained over a range of swim speeds to demonstrate that the cost of transport for marine turtles was lower than that of a flying bird but greater than that of a swimming fish. In addition, these MRs allowed for calculations of aerobic efficiency of juvenile and adult green turtles and estimations of energetic costs of reproductive migrations by adults (Prange, 1976). An important extension of this work that has great potential for informing numerous research protocols is the quantification of hydrodynamic effects (e.g., increased drag and decreased swimming efficiency) of electronic archival or satellite linked

data loggers attached to marine turtles (Watson and Granger, 1998).

In addition to cost of transport, marine turtle energy budgets include costs of migration, foraging, growth, reproductive investments, and nesting, as well as to basic maintenance requirements (e.g., thermoregulation, osmoregulation) (Wallace et al., 2006). Combining measurements of energy expenditure of free-ranging adult marine turtles during migration and interesting periods with values for other components of reproduction, such as nest construction and egg production, would allow for calculation of energetic costs of reproduction, and thus individual and population reproductive energy budgets (Jones et al., 2004). Along these lines, Hays et al. (1992) combined measurements of body mass loss during presumed fasting periods with estimates of duration of reproductive seasons (i.e., time required to migrate to and from nesting grounds, mate, and nest repeatedly) of adult female green turtles to infer total energy expenditure during a reproductive cycle. In addition, morphometric and reproductive traits are influenced by resource quality and availability in marine turtles (Bjorndal, 1982; Limpus and Nicholls, 1988; Hays, 2000; Solow et al., 2002) and other reptiles (Congdon et al., 1982). Therefore, estimating costs of all components of marine turtle energy budgets, especially metabolic costs, is crucial to characterizing individual and population responses to variation in resource availability.

In this vein, Wallace et al. (2006) combined FMRs measured for gravid leatherbacks during the interesting period (Wallace et al., 2005) with metabolic costs of nesting and estimated costs of egg clutches and migration to calculate reproductive energy budgets and required energy intake rates for leatherback populations in the Eastern Pacific and North Atlantic Oceans. Based on these energetic calculations, the authors speculated that relative differences in resource availability could render Eastern Pacific leatherback populations unable to match the size, reproductive output, and resilience to anthropogenic perturbations exhibited by North Atlantic populations. This application of measured FMRs and MRs to calculation of marine turtle energy budgets provides a valuable framework for further research on effects of resource availability and environmental fluctuations on marine turtle populations (e.g., Saba et al., 2007). Clearly, marine turtle energy budget estimations would benefit from refinement of input parameters, such as energy content of prey items (Doyle et al., 2007), energetic costs of specific components (e.g., osmoregulation, thermoregulation, egg production), and activity/stage-dependent MRs.

4.2. Diving physiology

For air-breathing, diving animals, acquisition of the two most vital resources – oxygen and food – cannot occur simultaneously due to spatial separation of atmospheric air and submerged prey. Thus, these animals possess physiological adaptations for diving that represent tradeoffs between predominantly oxygen-fueled activity underwater (which often include foraging and feeding), and temporary fasting

events at the surface to replenish on-board oxygen stores. In addition to specialized cardiovascular and respiratory traits, such as blood flow adjustments, bradycardia, and large blood and muscle oxygen stores, metabolic demands significantly influence time-activity tradeoffs for air-breathing marine animals (Costa et al., 2001).

One physiological parameter that can provide useful estimates of physiological and energetic constraints on activity is the aerobic dive limit (ADL), which refers to the dive duration beyond which blood lactate levels increase above resting levels (Kooyman et al., 1980). However, because direct measurements of post-dive blood lactate concentrations are difficult to obtain from free-swimming animals, many reports combine data on individual total oxygen stores and at-sea MRs to obtain calculated aerobic dive limits (cADL) (Costa et al., 2001). However, FMR-derived cADLs typically underestimate true cADLs, because FMRs include all at-sea activities – not just those associated with diving (Costa et al., 2001) – and do not compensate for the effects of hypometabolism during diving in calculation of ADL (Butler, 2004). Due to their relatively low MRs, marine turtles generally have much longer cADLs than marine mammals (Lutcavage and Lutz, 1997; Costa et al., 2001; Hochscheid et al., 2007a). Aerobic dive limits based on total body oxygen stores have been calculated for loggerheads (Lutz and Bentley, 1985) and leatherbacks (Lutcavage et al., 1990), and have been estimated for loggerheads and other marine turtle species based on allometric scaling of lung volume with body size (Hochscheid et al., 2007a). Generally, marine turtles tend to dive within their aerobic limits and probably only utilize anaerobic metabolism under duress (Lutz and Bentley, 1985; Lutcavage and Lutz, 1991, 1997; Hochscheid et al., 2007b).

Given their capacity for deep (>1,200 m; Hays et al., 2004b) and prolonged (>60 min; Southwood et al., 1999) dives, leatherback ADLs have been calculated in several studies using various types of physiological and behavioral information. The first estimate of leatherback ADL was 44 min (Kooyman, 1999), and was derived from green turtle MRs (Prange and Jackson, 1976; Jackson and Prange, 1979) and total oxygen stores of loggerheads (Lutz and Bentley, 1985). Based on measurements of total oxygen stores and MRs of nesting turtles, Lutcavage et al. (1990, 1992) estimated that leatherback ADL was between 5 and 70 min. Subsequently, Southwood et al. (1999) recorded the longest dive duration for a leatherback (67.3 min) and refined the ADL estimate to between 33 and 67 min based on heart rates and dive patterns of free-swimming adult female leatherbacks during the internesting period. Recently, using a novel approach intended to estimate diving MRs, Bradshaw et al. (2007) statistically inferred (from dive duration and depth data) leatherback cADLs (mean: 38 min, range: 19–48 min) that were similar to previous results. Ultimately, however, actual measurements of MRs of free-swimming leatherbacks are necessary to accurately calculate ADLs. Using DLW-derived FMRs, Wallace et al. (2005) reported cADLs for internesting female leatherbacks to be between 11.7 and 44.3 min.

Thompson and Fedak (2001) proposed that an air-breathing, diving animal should regularly approach and often exceed its

ADL when foraging conditions are advantageous and doing so would allow it to better exploit such conditions. This hypothesis is corroborated by the fact that many marine mammals and birds routinely exceed calculated cADLs while actively foraging (Costa et al., 2001). Conversely, an animal should limit its energy expenditure and dive well within its ADL if potential foraging success is low. Internesting leatherbacks rarely approach the FMR-derived maximum cADL (44 min) (Eckert, 2002a; Southwood et al., 1999; Wallace et al., 2005), suggesting that prey availability off nesting beaches is low and turtles are not actively foraging (Thompson and Fedak, 2001; Hays et al., 2004a). Likewise, post-nesting leatherbacks also routinely dive within the cADL range of Wallace et al. (2005) during long-distance migrations and while on foraging grounds (Hays et al., 2004a; James et al., 2005; Bradshaw et al., 2007). These analyses further support the conclusion that marine turtles dive well-within physiological limits, and are seldom anaerobic (Lutz and Bentley, 1985; Lutcavage and Lutz, 1991, 1997; Hochscheid et al., 2007b). However, further research on at-sea MRs is necessary to identify physiological constraints on diving activity and relationships between dive patterns and energetic tradeoffs in marine turtles.

4.3. Thermoregulation

Similar to all ectothermic vertebrates, marine turtle energy budgets are influenced heavily by metabolism and thermoregulation (Spotila and Standora, 1985a). Therefore, combined heat and energy budgets can provide a unified approach to elucidate how physiology and resource availability affect marine turtle bioenergetics and life history (Dunham et al., 1989). Sea turtle thermal biology depends on heat exchange properties and processes of a turtle's body in relation to its air or aqueous environment (Spotila and Standora, 1985b). Thus, understanding marine turtle thermoregulation requires the integration of thermal properties of water, specifically its high convection coefficient and specific heat compared to air, and physiological traits (e.g., low MRs, strong influence of T_a on T_b) and life history demands of marine turtles.

In water, heat loss is greater than heat gain for marine turtles, but the reverse is true on land. In addition, large thermal inertia conferred by the large body sizes of marine turtles dampens the response of T_b to changes in T_a (Spotila and Standora, 1985b; Spotila et al., 1997). This combination of factors has contributed to selection for highly active, metabolically costly nesting activity to occur nocturnally in most marine turtle species (with the exception of diurnal nesting by the small-bodied species, e.g., *L. kempii*) (Spotila and Standora, 1985b; Spotila et al., 1997). Therefore, the dependence of T_b maintenance on large body size has important ontogenetic and phylogenetic implications for thermoregulatory abilities of marine turtles, thus affecting life stage-specific habitat selection and life history (Spotila et al., 1997).

While large body size is undeniably important in marine turtle thermoregulation, other physiological mechanisms of metabolic heat production and retention also contribute to maintenance of T_b . Standora et al. (1982) reported substantial

differences between T_b s of vigorously swimming green turtles and T_w , and concluded that green turtles utilized the combination of internal heat generated during swimming, insulation from peripheral tissues, and thermal inertia to achieve regional endothermy (i.e., sustained, elevated temperatures in certain parts of the body). Similarly, Sato et al. (1995) concluded that large differences between T_b and T_w in loggerheads were not due to absorption of solar radiation, but rather to metabolic heat produced by swimming. Moreover, like T_b s of other reptiles (Grigg et al., 1979), marine turtle T_b s tend to heat faster than they cool, demonstrating an effective combination of heat generation and retention mechanisms (Frair et al., 1972; Standora et al., 1982; Smith et al., 1986; Hochscheid et al., 2002).

In general, marine turtles, like other reptiles, possess effective physiological, anatomical, and behavioral mechanisms by which they regulate their T_b s. However, the geographic and thermal ranges of nearly all species are constrained to tropical and sub-tropical latitudes because of an inability to withstand consistently low T_w (Hawkes et al., 2007). The exception to this rule is the leatherback, whose unique thermoregulatory abilities have been studied with great interest for decades.

4.4. Leatherback thermoregulation

Reports of leatherback turtles swimming actively around ice floes at sub-arctic latitudes (Bleakney, 1965; Goff and Lien, 1988) – habitat normally associated with blubber-covered, endothermic marine mammals – have long held the interest of comparative biologists, physiologists, and the public in general. Sparked by this interest, several generations of researchers have studied leatherbacks' special physiological adaptations for thermoregulation and the role of metabolism in particular. However, the current status of leatherback thermoregulation research is somewhat reminiscent of the 'blind man and the elephant' anecdote, in which a blind man's characterization of an elephant is limited to the portion of the elephant's body (i.e., its trunk, its leg, etc.) that he can immediately examine, and thus his myopic perspective renders him unable to 'see' the elephant in its entirety. In this sense, a cohesive, integrated characterization of leatherback thermoregulation appears lacking. Here, we synthesize this body of research to provide a holistic perspective of leatherback thermal biology.

Because of the vast geographic range and depth leatherbacks inhabit, they face two major thermoregulatory challenges: 1) maintaining a high core temperature while in cold (down to 5 °C) waters of higher latitudes and great depths (Mrosovsky and Pritchard, 1971; Frair et al., 1972; Standora et al., 1984; James and Mrosovsky, 2004; James et al., 2006), and 2) avoiding overheating while in tropical waters, especially while on land during nesting (Paladino et al., 1990; Southwood et al., 2005; Wallace et al., 2005). To meet these distinct thermoregulatory demands, leatherbacks possess several unique anatomical and physiological adaptations, including counter-current heat exchangers in their flippers that conserve heat while in cold T_w and likely dissipate heat in tropical T_w (Greer et al., 1973), thick peripheral insulation (6–7 cm; Goff and Lien,

1988; Davenport et al., 1990) containing brown adipose tissue (Goff and Stenson, 1988), and thermal independence of muscle tissue metabolism (Penick et al., 1998). In addition to these traits, leatherback body size and metabolism are crucial components of their thermal biology. Wallace et al. (2005) proposed that the unique thermoregulatory capabilities of leatherbacks probably allowed them to exploit an ecological niche unavailable to other marine turtle species (Davenport, 1997), similar to the 'thermal niche expansion theory' developed by Block et al. (1993) to explain the multiple and diverse origins of endothermy in the Family Scombroidei (tunas, billfish).

Large body size (i.e., large thermal inertia) has been recognized as essential to thermoregulation of ectotherms for many decades (Colbert et al., 1946), including leatherbacks (Mrosovsky and Pritchard, 1971; Frair et al., 1972; Paladino et al., 1990). For example, leatherbacks <100 cm in carapace length appear to be restricted to $T_w \geq 26$ °C (Eckert, 2002b), suggesting that the thermal advantage of large body size conferred upon adult leatherbacks is a prerequisite for exploiting colder water habitats. Building on this concept, Paladino et al. (1990) incorporated nesting adult leatherback MRs into a biophysical model to demonstrate that leatherbacks can thermoregulate in varied environments by combining large body size with low MRs, blood flow adjustments, and peripheral insulation. The authors termed this suite of thermoregulatory adaptations 'gigantothermy,' to highlight its uniqueness from strict ectothermy and endothermy. Moreover, the gigantothermy model, partly based on MR measurements of leatherbacks, supported previous predictions from purely mathematical models of low (i.e., ectothermic) MRs of extremely massive dinosaurs (Spotila et al., 1973).

While acknowledging the importance of body size and metabolism, recent work has focused more attention on behavioral thermoregulation by leatherbacks, which is a well-established thermoregulatory strategy for other reptiles (O'Connor, 1999; Seebacher et al., 1999). For example, Southwood et al. (2005) measured T_b of free-ranging leatherbacks in tropical waters, and observed that T_b responded to swimming activity patterns (i.e., AMRs) and to different T_w s. The observed differences between T_b measurements and T_w corresponded well to the gigantothermy model's predictions for leatherbacks in tropical seas (Paladino et al., 1990). Additionally, Wallace et al. (2005) surmised that the interaction between FMR, T_b , and available T_w might result in leatherbacks shuttling either to cooler T_w in order to dump excess heat produced during active swimming in the tropics, or to warmer T_w to minimize heat loss while in cooler temperate waters (James et al., 2005). Furthermore, biophysical modeling of leatherback MRs clearly demonstrated the pivotal role of adjustments in swimming activity (a proxy for metabolic heat production) in achieving substantial $T_b - T_w$ differentials (Bostrom and Jones, 2007). Taken together, these studies clearly articulate the importance of behavioral thermoregulation for leatherbacks.

Each of the studies discussed above emphasized one or a few particular factors relevant to leatherback thermoregulation (e.g., Paladino et al., 1990: body size, MRs, blood flow, insulation, $T_b -$

T_w ; Southwood et al., 2005: $T_b - T_w$, swim speed, diving activity in the tropics; Wallace et al., 2005: FMR, T_w , diving activity in the tropics; Bostrom and Jones, 2007: swim speed, MR, $T_b - T_w$). However, no single study took a synthetic approach to the available information on all factors. For example, the gigantothermy model emphasized a primary role of large thermal inertia in leatherback thermoregulation, but did not similarly highlight the critical role of behavioral adjustments of metabolic heat production (Paladino et al., 1990). On the other hand, the Bostrom and Jones (2007) model provided robust results to underscore the importance of behavioral adjustments in achieving $T_b - T_w$ differentials, but did not emphasize the role of leatherbacks' large body size, blood flow adjustments, and peripheral insulation in maintaining those differentials. (Interestingly, despite the apparent incongruities between the models, both predict similar $T_b - T_w$ differentials for similar MRs.) Also, while adjustments in leatherback MRs are pivotal, the results of our allometric comparisons indicate that such MR adjustments are phylogenetically constrained (Fig. 1), and that mechanisms for retaining internally generated heat are essential for thermoregulation. Thus, considering all of these factors collectively, we conclude that leatherback thermoregulation depends on an integrated balance between their unique suite of adaptations for heat production (e.g., metabolic and behavioral modifications) and retention (e.g., large thermal inertia, blood flow adjustments, insulation, and behavioral modifications) to achieve and maintain preferred differentials between T_b and T_w in varied thermal environments. Therefore, a more accurate approach would be to combine the role of swim speed (exercise, MR) in heat production (Bostrom and Jones, 2007) with the mechanisms of heat retention through insulation and large body mass (Paladino et al., 1990) to generate a more dynamic model of leatherback thermoregulation.

5. Future directions

While obtaining MR data for marine turtles is not always straightforward, the data themselves have great potential for important applications to physiology and conservation of these animals. Thus, despite the impressive body of research on marine turtle metabolism, there are several areas that still deserve attention. First, we propose that measuring MRs for species for which no MR data exist (Table 2) should be a priority. Second, where MR data exist, we recommend maximizing their potential interpretive power through application to several topics, including resolution of physiological parameters, calculation of energy budgets, and characterization of population trends. Third, extremely little research has been conducted with respect to cellular metabolism of marine turtles (e.g., mitochondrial density, thermal sensitivity of enzymatic activity, but see Penick et al., 1996, 1998; Southwood et al., 2003) and how it compares to that of other reptiles and other animals. Fourth, and most importantly, we strongly encourage efforts to obtain more information on at-sea MRs of marine turtles during natural behaviors. Most aspects of physiology, ecology, life history, and conservation of nesting females (and their eggs and hatchlings) already have received significant attention. However, focused efforts to elucidate at-sea energy

expenditure and activity patterns of marine turtles would dramatically advance our understanding of marine turtle energetics and population dynamics, and would provide critical insights for prioritization of conservation efforts.

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