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Maximum standard metabolic rate corresponds with the salinity of maximum growth in hatchlings of the estuarine northern diamondback terrapin (*Malaclemys terrapin terrapin*): Implications for habitat conservation

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ABSTRACT

I evaluated standard metabolic rates (SMR) of hatchling northern diamondback terrapins (*Malaclemys terrapin terrapin*) across a range of salinities (salinity = 1.5, 4, 8, 12, and 16 psu) that they may encounter in brackish habitats such as those in the Maryland portion of the Chesapeake Bay, U.S.A. Consumption of O_2 and production of CO_2 by resting, unfed animals served as estimates of SMR. A peak in SMR occurred at 8 psu which corresponds closely with the salinity at which hatchling growth was previously shown to be maximized (salinity ~ 9 psu). It appears that SMR is influenced by growth, perhaps reflecting investments in catabolic pathways that fuel anabolism. This ecophysiological information can inform environmental conservation and management activities by identifying portions of the estuary that are bioenergetically optimal for growth of hatchling terrapins. I suggest that conservation and restoration efforts to protect terrapin populations in oligo-to mesohaline habitats should prioritize protection or creation of habitats in regions where average salinity is near 8 psu and energetic investments in growth appear to be maximized.

1. Introduction

The diamondback terrapin (*Malaclemys terrapin*) is a North American estuarine endemic, emydid turtle with a range that extends from the Gulf coast to New England, U.S.A. In Maryland waters of the Chesapeake Bay and tributaries (where salinity is normally less than ~ 50% sea water), the northern diamondback terrapin (*M. terrapin terrapin,* one of seven recognized subspecies) inhabits marshes and shallow subtidal areas along the shoreline (Pfau and Roosenburg, 2010). The diamondback terrapin is an iconic species in Maryland and has the status of State Reptile and the mascot of the University of Maryland. Sea level rise due to climate change is projected to reduce the abundance of required or preferred habitats of *M. t. terrapin* in the Maryland portion of the Chesapeake Bay, suggesting that conservation efforts may be needed if local populations are to be sustained in the future (Woodland et al., 2017).

Dunson (1970) observed diamondback terrapins inhabiting waters of salinity 11–32 psu in several sites on the east and Gulf coasts of the U.S. However their salinity range is likely somewhat broader than that observed in the survey sites used by Dunson (1970). For example, colleagues and I have frequently observed diamondback terrapins in areas of lower salinity in the Chesapeake Bay and tributaries (sometimes in nearly fresh water following high runoff events: Rowe, pers. obs., W. Roosenburg, pers. comm.). The diamondback terrapin's integument is highly impermeable to sodium but quite permeable to water (Robinson and Dunson, 1976), suggesting that incidental ingestion of saline water during feeding as well as water loss across the integument are means by which habitat salinity might present physiological challenges (Robinson and Dunson, 1976; Dunson and Mazzotti, 1989). A lachrymal salt gland provides for osmoregulation at high salinities or under conditions of dehydration (Dunson, 1970; Dunson and Dunson, 1975). However when salinity is low, osmoregulation occurs through the renal pathway (Dunson, 1970); in freshwater exposures the urine was hypo-osmotic to the blood, whereas in 50 and 100% sea water the urine was iso-osmotic to the blood (Gilles-Baillien, 1970). At salinities typically encountered, osmotic pressure of the body fluids is maintained at about 1/3 that of sea water through these osmoregulatory pathways (Dunson, 1970), although variation in blood chemistry in response to salinity does occur. For example, Gilles-Baillien (1970) showed an increase in Na and Cl, as well as blood osmotic pressure, when animals held in fresh water were placed in 50% sea water for 3 days.

The above observations suggest that the optimal salinity for growth appears somewhere intermediate between freshwater and sea water, as would be expected from an obligate estuarine species. Indeed, Dunson (1985) reported the optimum salinity for growth of hatchlings was 25%

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sea water (salinity ~ 9 psu) when tested at salinities of 0, 25, 50, 75, or 100% sea water. Exposure to NaCl solutions revealed maximum growth at 125 mM NaCl, which corresponds with the NaCl concentration in sea water of salinity 8–9 psu (Dunson and Mazzotti, 1989). Furthermore, Dunson's (1985) results showed that above about 60% sea water (salinity ~ 21 psu), positive growth could not be maintained. Supplemental freshwater at high salinities was required in order for positive growth to be achieved (Dunson, 1985).

Growth implies anabolic processes that must be supported by metabolism of assimilated resources. Standard metabolic rate (SMR) is the metabolic rate measured in a resting, post-absorptive individual and, energetically, it represents the base-line costs of survival (maintenance) unaffected by digestion, activity, or growth. However, in a growing animal (e.g. where resources are abundant and assimilated energy exceeds maintenance requirements), SMR measurements may be inflated due to energetic investments in anabolism, even when the animal is in a post-absorptive state (Parry, 1983). Therefore, an actively growing animal may have elevated SMR relative to a non-growing animal (e.g. Parry, 1983; Rosenfeld et al., 2015). On the other hand, if resource abundance is restricted and energy assimilation is relatively low, a high SMR could negatively impact growth by reducing the net (residual) energy available for investment in production of new tissue (see Rowe et al., 1998, 2001; Congdon et al., 2001).

Whether there are metabolic costs associated with exposure to different salinities for diamondback terrapins has been little studied. In the only study of this topic to date, Holliday et al. (2009) reported no influence on CO_2 production of exposures of 8–14 month old juveniles to salinities of 0, 10, 20, or 30 psu. However, it is unknown whether in younger animals (hatchlings) there are metabolic correlates with salinity, or whether finer-scale patterns in response are present that would have eluded Holliday et al. (2009) who evaluated responses at 10 psu increments.

The population of *M. t. terrapin* in Maryland waters of the Chesapeake Bay, where sea level rise is occurring at a much faster pace than in many other regions (Boesch et al., 2013), is at risk of significant habitat loss as sea level rise continues (Woodland et al., 2017). Conservation of local populations of this species may require protection or creation of habitats that are resilient or responsive to sea level rise (Woodland et al., 2017). The choice of specific sites or habitats for conservation efforts should reflect optimal physiological conditions for the target species (Carey, 2005). With respect to the estuarine *M. t. terrapin*, areas where salinity conditions support optimal physiological function should therefore be candidates for habitat protection or creation. Since salinities in the Maryland portion of the Chesapeake Bay range from freshwater to roughly 50% sea water (salinity ~ 17–18 psu), I examined relationships between salinity and SMR in yolk-depleted (actively feeding; Rowe et al., 2017) hatchling terrapins at five levels of salinity (1.5, 4, 8, 12, and 16 psu) representative of Maryland waters of the Chesapeake Bay and tributaries. I evaluate my results in the context of prior research examining the influence of salinity on growth of diamondback terrapins.

2. Material and methods

The hatchling diamondback terrapins used in this study were derived from eggs collected from four females captured while initiating nesting at Naval Air Station Patuxent River, located at the mouth of the Patuxent River on the Chesapeake Bay (Lexington Park, MD, U.S.A.; 38.306, - 76.401). In the laboratory I induced the females to produce the clutch via intraperitoneal injection of oxytocin (30 IU/kg; Ewert and Legler, 1978). Eggs were incubated at 31 °C, a female-producing temperature (Jeyasuria et al., 1994) until hatching (mean = 48 days). I then held the hatchlings in a 25 °C laboratory lit with full spectrum + UV lights on a 12:12 cycle until residual yolk was metabolized and active feeding behavior began (mean = 18 days post-hatching). I used these yolk-independent hatchlings since prior research showed substantial maternal effects on SMR while hatchlings were dependent on yolk, but this effect disappeared after yolk had been metabolized and feeding had begun (Rowe et al., 2017). Hatchlings were held individually in 1 L containers with filtered (0.5 μm) Patuxent River water (average salinity = 16 psu) to a depth of 1 cm and offered chopped, canned clams daily.

From the four clutches of hatchlings I randomly chose 20 individuals to serve as the pool of animals to be used to estimate SMR based on assays of respiration rate (O_2 consumption, CO_2 production) at five different salinities (1.5, 4, 8, 12, or 16 psu). I conducted three respiration assays each consisting of 20 animals (Assay 1: 10 animals each at salinities = 4 and 8 psu; Assay 2: 10 animals each at salinities = 1.5 and 12 psu; and Assay 3: all 20 animals at salinity = 16 psu). Thus half the individuals were assayed at salinity = 4 and 12 psu, the other half were assayed at salinity = 1.5 and 8 psu, and all were assayed at salinity = 16 psu. I assayed 20 rather than 10 animals at salinity = 16 psu since this was the average salinity of the water near the nesting area, so I hoped to gain especially robust estimates for SMR at this salinity which will benefit future work with this population. Representatives (2–4) of each of the four clutches were included at each salinity. Seven to 14 days prior to the start of a respiration assay, I began conditioning ("acclimating") the animals when I replaced the water in holding containers (salinity = 16 psu) with water of target salinity, which was prepared by diluting filtered (0.5 μm) Patuxent River water (salinity = 15.8–16.1 psu) with well water as necessary. Animals were assayed after conditioning for 7 days at target salinity for test salinities = 1.5 and 12 psu (Assay 2), whereas those used in test salinities = 4 and 8 psu (Assay 1) were assayed after 14 days of conditioning. Animals assayed at salinity = 16 psu (= ambient Patuxent River water at the nesting site; Assay 3) had no conditioning period since they had been held at that salinity since hatching. The conditioning period differed among assays due to logistical reasons; the conditioning period used in Assay 2 was decreased to 7 days to facilitate completion of the study and release of the animals before temperatures dropped in autumn. Animals were unfed for 4 days prior to any assay in order to decrease or eliminate any influence digestion might have on respiration (e.g. specific dynamic action, "SDA;" McCue, 2006). After each assay, hatchlings were blotted dry of surface moisture and weighed.

Respiration was measured hourly as O_2 consumption and CO_2 production during 24 h assay periods (at 25 °C) using a 20 channel, computer controlled, closed circuit respirometer (Micro-Oxymax, Columbus Instruments, Columbus, OH). During assays, individuals were held in ~800 ml sealed chambers containing 50 ml of water of target salinity and housed in a dark 25 °C incubator. The respirometer was calibrated prior to each assay using a known gas mixture. After each assay the calibration gases were again analyzed and the instrument was found to have drifted less than 0.02% of the calibration values in any assay.

I used the mean of the lowest quartile of observations for O_2 consumption or CO_2 production as an estimate of SMR (Rowe, 2002). By using only the lowest quartile of observations, I excluded any elevated rates that may have resulted from activity during the assay which would have inflated the estimates of SMR (e.g. Rowe, 2002). I used ANCOVA (covariate = body weight) to statistically analyze the effects of salinity on absolute (per capita) O_2 consumption and CO_2 production. Since much literature on SMR presents data as mass-adjusted values (e.g. rate/weight), I also analyzed mass-adjusted O_2 consumption and CO_2 production using ANOVA. Results are thus presented as both absolute (analyzed by ANCOVA) and mass-adjusted rates (analyzed by ANOVA). For both sets of analyses I first ran full ANCOVA or ANOVA models which included clutch and salinity*clutch as factors, but since neither significantly contributed to the model ($P > .347$ for all; See supplementary material), I removed these terms and conducted the final analyses using salinity as the sole independent variable. I also calculated and compared the respiratory quotient (RQ = CO_2 production/O_2 consumption) as well as animal wet weights among treatments