ESTIMATING SURVIVAL TIMES FOR NORTHERN DIAMONDBACK TERRAPINS, *MALACLEMYS TERRAPIN TERRAPIN*, IN SUBMERGED CRAB POTS

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Abstract.—Among air-breathing vertebrates, aquatic turtles exhibit an exceptional capacity for prolonged submergence. Despite this ability, drowning occurs when a turtle entrapped in submerged fishing gear cannot reach the water surface. Mortality in crab pots is the major threat to the Diamondback Terrapin, *Malaclemys terrapin*. Data from laboratory experiments and field observations were integrated to estimate survival time for a terrapin submerged in a crab pot. Voluntary dive time $(8.4 \pm 5.7 \text{ min})$ was compared to a calculated aerobic dive limit (cADL) derived from mass-specific lung volume and metabolic rates. By this estimate, a 200 g terrapin has sufficient oxygen stores to sustain aerobic metabolism for ~19 min at 20° C. These data suggest that voluntary dives are usually less than cADL. Average submergence time for crab pots set in shallow tidal creeks greatly exceeded cADL and were longer for evening tides (310–365 min) than for morning tides (77–156 min) when water temperature was also higher (27–30° C vs. 24–25° C). Terrapins captured in crab pots in the evening had higher plasma lactate concentrations than those caught in the morning. For both groups, lactate concentrations were reduced within 12 h. Without access to air, survival time is dependent on water temperature and activity level. A terrapin forcibly submerged in 27° C water is physiologically stressed within minutes and can reach a lethal lactacidosis in less than 12 h. Conservation efforts should focus on trap designs that prevent entry or facilitate escape while retaining target species.

Key Words.—cADL; conservation; diving physiology; lactate; lung volume; Malaclemys terrapin; turtle

INTRODUCTION

As a group, turtles possess a variety of anatomical, physiological, and behavioral adaptations that allow them to remain submerged for extended periods of time (Jackson 2000). However, forced submergence, especially at high ambient temperatures, reduces the time that turtles can rely on oxygen stores (Gatten 1981; Fuster et al. 1997). For this reason, turtles that are incidentally captured in submerged fishing gear may drown (Stabenau et al. 1991; Mann 1995; Wood 1997; Radzio and Roosenburg 2005; Larocque et al. 2012). In order to reduce bycatch mortality, it is important to first understand the limits of survivable submergence.

The Diamondback Terrapin, *Malaclemys terrapin*, is an emydid turtle that inhabits brackish waters along the eastern coast of the United States from Cape Cod, MA, to Corpus Christi, TX (Iverson 1992). Although little is known of their diving physiology, juvenile and adult terrapins remain submerged for weeks or months each winter without drowning (Yearicks et al. 1981). Despite this, terrapins frequently drown in fishing gear during the warmer summer months (Roosenburg et al. 1997; Wood 1997; Hart and Crowder 2011) and sustained mortality

in fishing gear has been shown to impact population size and demographic structure (Roosenburg 2004; Dorcas et al. 2007; Wolak et al. 2010; Grosse et al. 2011). In states with a Blue Crab (*Callinectes sapidus*) fishery, incidental drowning in crab pots is considered to be the major threat to *M. terrapin* populations (Butler et al. 2006).

Commercial-style crab pots are typically set on the bottom of tidal creeks and open bays and may or may not be exposed to air at low tide. Terrapins, attracted to the bait, enter the crab pot through an underwater opening and become trapped (Bishop 1983). Bycatch reduction devices (BRDs) were first developed for crab pots in southern New Jersey (Wood 1997) and are required in many, but not all states within the range of the Diamondback Terrapin (Roosenburg 2004). BRDs constrain the entrance to the crab pot such that large female terrapins are excluded; however, males and subadult females readily enter (Mann 1995; Wood 1997; Roosenburg and Green 2000). It is unknown how long a terrapin can survive after entering a submerged crab pot, but the likelihood that a terrapin will drown increases when crab pots are not checked daily (Bishop 1983; Wood 1997; Grosse et al. 2009; Hart and Crowder 2011).

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determined empirically (Parker 1925; Belkin 1968), an alternate approach is to estimate survival time by integrating available data on the anatomy and physiology with field observations. One such measure, calculated aerobic dive limit (cADL), is computed by dividing the volume of oxygen stored in the body (i.e., lungs, blood, and muscle) by the rate of oxygen consumption. In this study laboratory experiments and field observations were combined to estimate cADL and predict the survival time for Diamondback Terrapins caught in crab pots. These data should inform state agencies as they establish gear requirements and soak times for coastal fisheries.

MATERIALS AND METHODS

We captured Northern Diamondback Terrapins (*Malaclemys terrapin terrapin*) in July, 2008, as part of a long-term population study in Cape May County, New Jersey (Wood 1997). We unmodified (i.e., BRDs) deployed no commercial-style crab pots (n = 7) baited with frozen Bunker (*Brevoortia tyrannus*) in two shallow tidal creeks (Josh and Charles Creeks) for a total of 42 trap days. Trapping dates for Josh Creek (1–3 July) were two weeks earlier than those for Charles Creek (15-17 July). In order to determine submergence time and water temperature, we affixed one TidBit temperature logger (Onset Computers, Pocassett, Massachusetts, USA) to the top corner of each crab pot and another near the entrance. The loggers recorded either water temperature (T_w) or air temperature (T_a) every 5 min, depending on the height of the tide. Crab pots were assumed to be submerged by high tides when the temperature difference (ΔT) between the top and bottom logger was less than 1.0° C, and we confirmed this by visual inspection. We checked and rebaited crab pots ~1 h before each high tide to minimize the risk of drowning terrapins.

Adult male and juvenile female terrapins are caught in crab pots with greater frequency than adult female terrapins (Mann 1995; Roosenburg et al. 1997; Wood 1997; Dorcas et al. 2007). For this reason, we selected seven adult males and five juvenile females obtained during the population survey and transported them to Widener University to determine voluntary dive times and rates of oxygen consumption.

Voluntary dive time.—We

While the lethal limits of submergence can be voluntary dive times by observing a subset of adult male (n = 4) and juvenile female (n = 5)terrapins in the laboratory. We placed each terrapin individually in an 80-L glass aquarium filled with room temperature water (~22° C) and video-recorded for up to 8 h. We recorded dives for each period of continuous submergence > 3min. We computed dive frequency and mean voluntary dive duration for each individual.

> *Metabolic rate, O₂ consumption.*—To estimate the rate that a submerged terrapin would deplete oxygen reserves, we measured oxygen consumption at two temperatures (10 and 20° C). We placed male (n = 7) and juvenile female (n = 7)5) terrapins individually in a custom made, (6.5)cm diameter \times 8 cm high), cylindrical, doublewalled glass metabolic chamber (Labglass, Vineland, New Jersey, USA) with a circulating water bath (Neslab RTE 211, Newington, New Hampshire, USA) to regulate temperature. We placed each animal in the darkened chamber for 30 min prior to data collection for acclimation to minimize activity during oxygen consumption However, insulating foam measurements. around the chamber prevented visual monitoring of activity during data collection. A mass flow controller (Sable Systems, Las Vegas, Nevada, USA) regulated the flow of excurrent air at 50 ml min⁻¹, resulting in a minimum final oxygen concentration of excurrent air no lower than 20.00%. Water and CO₂ were removed from air that had passed through the animal chamber by sequential columns of Drierite and soda lime before the air was sub-sampled into an Ametek S-3A one-channel oxygen analyzer (Ametek, Pittsburgh, Pennsylvania, USA). This system was controlled by Expadata (Sable Systems, Las Vegas, Nevada, USA) and data were recorded every second during a 15-min data collection run. We analyzed data using the Expadata software.

Lung volume.—Duration of aerobic dives in turtles is constrained by lung volume (Berkson 1966); therefore, we needed a reliable measure of lung capacity for terrapins to estimate dive time. We selected terrapins for necropsy from among hundreds that are struck and killed by motor vehicles in Cape May County each summer (Wood and Herlands 1997). Roadkill terrapins with minimal shell damage were brought back to the laboratory for dissection determined (Wood and Herlands 1997). We determined

laboratory by inflating lungs of terrapins (n =11). To accomplish this, we made a lateral incision across the ventral aspect of the neck to access the trachea. We ligated a 50 ml syringe to the trachea and slowly injected room temperature air into the lungs until the plunger could not be easily depressed. When lung volume (VL) exceeded 50 ml, the trachea was clamped with a hemostat while the syringe was refilled. In cases in which the specimen was found to be gravid, we surgically removed the eggs (Wood and Herlands 1997), and remeasured the lung volume. Finally, the lungs were dissected free from the carcass and inflated to obtain maximum lung volume (VL_{max}). Because body mass fluctuates with gravidity and changes in water balance, plastron length was used as a standard measure of body size for lung volume.

Blood sampling and lactate analysis.—We analyzed blood samples from terrapins (n = 16)to determine whether entrapped terrapins were accumulating lactate. Immediately after their removal from the crab pot, we drew blood from the caudal septum with a 1 ml syringe and placed each sample on ice (Werner et al. 2002). Terrapins were transported back to the laboratory and placed individually in 20 l plastic buckets and kept in a dark, quiet room at $\sim 22^{\circ}$ C. We drew a second set of blood samples ~12 h after the terrapins were removed from the traps. All samples were centrifuged to separate plasma from packed cells and the plasma was frozen and stored at -20° C.

We determined plasma lactate concentration by a colorimetric assay (Procedure No. 735, Trinity Biotech, Berkeley Heights, New Jersey, USA) adapted for a 96-well plate to accommodate small sample volumes. Briefly, we added 500 μ l of reagent to a 1 ml centrifuge tube containing 5 µl of plasma or lactate standard (40 mg d/l) and vortexed to mix. After allowing 10 min for a complete reaction, we transferred 200 µl of the reaction mixture to a 96-well plate with a clean pipette. Once all of the samples were transferred, we loaded the plate into a spectrophotomer (SpectraMax 340 PC. Molecular Devices, Sunnyvale, California, USA) and read the absorbance at 540 nm.

normality and analyzed with StatView (SAS not dive more frequently than juvenile females

mass-specific lung volume (ml kg⁻¹) in the Institute, Cary, North Carolina, USA). When normally distributed, samples were compared using Student's t-test or a two-way ANOVA, with temperature and sex as factors. When data were non-normal, we used the Wilcoxon ranksum test. We used a paired t-test to evaluate differences in plasma lactate values for blood samples from the same individuals taken immediately after removal from the trap and after 12 h recovery. We report significance when P < 0.05.

RESULTS

Population survey.—We captured 93 terrapins for an average of 2.2 terrapins per trap day. From this total, 90 (35 males, 55 females) could be sexed by external morphology and three were too small to determine sex. On average, the straight line carapace length (CL) of males (10.6 \pm 1.5 cm; n = 35) was smaller than that of females (12.5 \pm 2.3 cm; n = 55; U = 507; P <0.001). The majority of females (74.5%) were smaller than the minimum size (CL = 14.5 cm) for sexual maturity in our population (Fig. 1.).

Submergence times and water temperature.— Crab pots were assumed to be submerged when $\Delta T < 1.0^{\circ}$ C. As the tide receded, ΔT increased rapidly until both loggers were exposed to air at low tide (Fig. 2). Our study area has a mixed semi-diurnal tide cycle with two high tides and two low tides each day. During the trapping period, average duration of submergence for crab pots set in Josh Creek was longer during evening high tides $(365 \pm 42 \text{ min})$ than during morning high tides $(164 \pm 66 \text{ min}; t = 10.11, df = 32, P < 1000)$ 0.001). Water temperatures in Josh Creek during the period of submergence were higher during evening high tides $(27.0 \pm 0.6^{\circ} \text{ C})$ than those during the morning high tides $(24.2 \pm 0.7^{\circ} \text{ C}; t =$ 12.35, df = 32, P < 0.001). A similar pattern was observed for crab pots set in Charles Creek (Fig. 3). Although some of the terrapins that were removed from submerged traps appeared to be lethargic and disoriented, none died during the survey.

Laboratory dive data.—Terrapins spent little time swimming at the surface and undertook several dives of >3 min every hour. Males dove 5.3 ± 1.0 times per hour while juvenile females **Statistical analyses.**—Data were checked for dove 4.2 ± 0.4 times per hour. Male terrapins did



FIGURE 1. Distribution of body sizes for male (solid bars) and female (hashed bars) Diamondback Terrapins (*Malaclemys terrapin*) captured in unmodified commercial-style crab pots in Cape May County, NJ. Vertical red line indicates minimum size of maturity in females of this population.



FIGURE 2. Representative temperatures from data loggers affixed to the top (solid) and bottom (dashed) of a crab pot used to capture Diamondback Terrapins (*Malaclemys terrapin*) in Cape May County, NJ. Approximate times of high tides during the trapping period are denoted by the letter H.



FIGURE 3. Estimated submergence times (min) and mean water temperatures (°C) recorded by data loggers affixed to crab pots set in Charles (squares) and Josh (triangles) Creeks in Cape May County, NJ. Duration of submergence was longer with higher temperatures for evening high tides (filled symbols, circled) than morning high tides.

(t = 1.5, df = 7, P = 0.17). Mean voluntary dive times of 7.4 ± 3.4 min (n = 4) were observed for males and 9.2 ± 6.8 min (n = 5) for juvenile females. Juvenile female terrapins did not dive longer than adult males (t = 1.6, df = 7, P = 0.15). When combined, mean voluntary dive time for this size class of *M. terrapin* is 8.4 ± 5.7 min (n = 9). The longest voluntary dive observed in the laboratory was by a 197 g female that rested on the bottom for most of a 50 min dive.

Oxygen *consumption*.—Diamondback Terrapins exhibit discontinuous breathing with long periods of apnea. By averaging values over time, we obtained representative rates of oxygen consumption. A two-factor analysis of variance showed a significant effect of temperature (F =6.45, df = 1, 23, P = 0.02). Rate of oxygen consumption was higher at 20° C than at 10° C, but the effect of sex was not significant (F =0.31, df = 1, 23, P = 0.59), and there was no significant interaction between temperature and sex (F = 4.25, df = 1, 23, P = 0.052). When data for both sexes were combined, oxygen consumption increased from 0.10 ± 0.01 ml g h^{-1} at 10° C to 0.17 ± 0.01 ml g⁻¹ h^{-1} at 20° C yielding a Q_{10} value of 1.73.



FIGURE 4. Lung volume (ml) of Malaclemys terrapin as a function of plastron length (cm). Measurements were taken by inflating the lungs within intact specimens.

Lung volume.—Lung volume measurements were made during necropsies of gravid (n = 3)and non-gravid female terrapin carcasses (n = 8)and were then combined because they were not significantly different (U = 9.0; P = 0.345). Lung volume for 11 adult female terrapins was 175 ± 27 ml with a corresponding lung mass of 13.5 ± 2.8 g. Mass specific lung volume was 214 \pm 38 ml kg⁻¹. As expected, lung volume of terrapins increased with body size. However, log-log regression of lung volume against plastron length (Fig. 4) yielded a scaling exponent of 2.244. This finding is interpreted as negative allometry (i.e., lung volume decreased relative to body length) because the expected scaling exponent for isometry is 3.0 when a volume is regressed on a linear measurement (Schmidt-Nielsen 1984). The result was similar for analysis of lung volume against body mass (scaling exponent = 0.845, isometry = 1.0).

cADL for **M. terrapin**.—Assuming the air in fully-inflated lungs is 17.4% O₂ (Berkson 1966), a 200 g terrapin has 7.4 ml of oxygen in its lungs at the beginning of a dive. We did not quantify other body oxygen stores (i.e. blood, muscle), but Lutz and Bentley (1985) estimated that the lungs of *T. scripta* held 68.1% of oxygen stores with the remainder stored in blood (29.2%) and muscle (2.7%). If these proportions hold for *M. terrapin*, then a 200 g₁ terrapin consuming oxygen at 0.17 ml g⁻¹ h would deplete total oxygen stores in 19 min when diving at 20° C.

Baker et al.—Estimating survival times for terrapins.



FIGURE 5. Plasma lactate concentrations of terrapins sampled immediately after removal from crab pots set in two tidal creeks in Cape May County, NJ and after 12-h recovery in the laboratory. Mean (\pm S.E.) Asterisk above the symbols indicates a statistical difference after 12-h recovery (t-paired, P < 0.05).

Mass-specific cADLs were calculated for individual terrapins and compared to laboratory observations when data for both oxygen consumption and dive duration were available (Table 1). Although the majority of terrapins did not exceed cADL for any dives during the period of observation, three terrapins frequently dove beyond their cADL and one did occasionally.

Plasma lactate concentrations for trapped *turtles.*—We obtained blood samples from 16 terrapins from two creeks during the population survey. Because submergence time of crab pots was longer during evening high tide cycles, blood samples were analyzed by creek of origin and by time of capture. Plasma lactate concentrations were highest for terrapins recovered from traps during evening high tide In Josh Creek, lactate cycles (Fig. 5). concentrations were significantly higher for terrapins removed from traps during evening high tides $(38.5 \pm 13.9 \text{ mmol /l})$ than for those captured during morning high tides (5.4 ± 5.2) mmol/l; t = 5.46, df = 10, P < 0.001). Unfortunately, this comparison could not be made for Charles Creek because only one terrapin was sampled during the day. Lactate values for terrapins captured in Josh Creek were significantly lower (*t-paired* = 6.05; P = 0.0018) after 12-h recovery. This relationship was expected for terrapins from Charles Creek, but there was no difference (P = 0.104).

DISCUSSION

Diamondback Terrapins readily enter crab pots deployed in the tidal creeks they inhabit. Spatial overlap between terrapin activity and crab pots increases during the active season when water temperatures are higher (Harden and Southwood

TABLE 1. Calculated aerobic dive limits (cADLs), mean and maximum dive durations for male (n = 4) and female (n = 5) Diamondback Terrapins (*Malaclemys terrapin*).

Gender	Mass (g)	$VO_2 (ml g^{-1}h^{-1})^*$	VL (ml)**	cADL (min)	Dives	Mean Duration (min)	Maximum Duration (min)	% Dives exceeding cADL
М	216	0.27	46	11.8	39	8.7	20	30.7
Μ	151	0.15	32	21.3	23	7.4	12	0.0
М	136	0.25	29	12.8	23	6.4	18	4.3
М	286	0.08	61	39.9	25	7.0	18	0.0
F	299	0.10	64	31.9	38	8.0	19	0.0
F	199	0.21	43	15.2	19	12.5	50	26.3
F	212	0.18	45	17.7	17	8.7	21	23.5
F	296	0.10	63	31.9	23	9.7	23	0.0
F	169	0.12	36	26.6	25	7.1	20	0.0
Mean	218	0.16	47	23.2	26	8.4	22	10.3
S.D.	63	0.07	13	9.9	8	1.9	10.7	1.5

* rate of oxygen consumption at 20° C

** lung volume (ml) estimated from body size

Williard 2012). Without intervention, these airbreathing animals will be physiologically stressed within minutes and eventually drown.

Trapping dates for our study coincided with a new moon and full moon for Josh and Charles Creeks respectively. The high tidal amplitude associated with spring tides resulted in longer than anticipated submergence times, but fortunately all turtles survived. Trapping methods employed in our study differ from those of commercial watermen in that we intentionally deployed pots in locations where the trap would be exposed to air as the tide receded. In studies that replicate commercial fishing methods (i.e., deeper water, longer soak times), terrapins die (Mann 1995; Wood 1997; Grosse et al. 2011; Hart and Crowder 2011, Harden and Southwood Williard 2012). Wood (1997) reported 20% mortality for terrapins captured in unmodified crap pots checked two times per day. Higher mortality rates (up to 75%) were observed when pots equipped with BRDs were checked once a day (Wood 1997). Similarly, Hart and Crowder (2011) found mortality rates for terrapins caught in crab pots increased from 15% to 50% if soak times were increased from 1 to 5 d. This threat to terrapin populations is amplified when crab pots are lost or abandoned in shallow waters and become a permanent hazard (Bishop 1983; Mann 1995; Grosse et al 2009).

Voluntary dive times.—Voluntary dive times in this study were longer than those observed for *M. terrapin* in breeding pens in Beaufort, North Carolina (McCutcheon 1943). In that setting, terrapins made several short dives $(1-2 \min)$ and occasionally extended dives (3–10 min) where they rested on the bottom. Differences between these studies are likely explained by the higher ambient temperatures (29° C) in July in North Carolina. Studies of other turtle species suggest that short dives are usually terminated before oxygen supply is depleted and are therefore likely to be largely aerobic (Lutz and Bentley 1985; Wallace et al. 2005). Although it is not known what causes terrapins to return to the surface, Trachemys scripta appear to terminate their dives at a critical lung PO_2 of 22 torr (Ackerman and White 1979). The fime to reach a critical PO_2 is dependent on oxygen stores, body temperature, and activity rate. Dive data from free-ranging terrapins is desirable and should be investigated with time-depth recorders (e.g., Blumenthal et al. 2010) to better describe

voluntary dive durations under ecologicallyrelevant conditions. These data could provide additional support for the observation that Diamondback Terrapins surface more frequently in warm water (Harden et al. 2009) and, by extension, are stressed when forcibly submerged (e.g., trapped) beyond their aerobic dive limit.

Lung volume and other oxygen stores.—Lung volume determined from road kill female terrapins accords well with the maximum lung volume (VL_{max} = 262 ml kg⁻¹) for a closely-related freshwater turtle, *T. scripta* (Perry 1978). However, freshwater turtles alter their lung volume to achieve neutral buoyancy while diving (Jackson 1971), so VL_{max} necessarily overestimates the volume of air, and thus oxygen available to terrapins during a dive. Resting lung volumes for small T. scripta average 100 to 120 ml kg⁻¹ (Jackson 1971) and 160 ml kg⁻¹ in larger T. scripta (Crawford et al. 1976). Our finding that lung volume of *M. terrapin* scales negatively with increasing body size differs from the analysis of *T. scripta* by Perry (1978). While methodological differences exist between studies, another possible explanation for this discrepancy is that the large T. scripta (Crawford et al. 1976) are likely females whereas the smaller T. scripta studied by Jackson (1971) could be of mixed sex or all male. We recorded a lung volume of 40 ml for a 175 g adult male terrapin that was found dead in the salt marsh and assumed to have drowned. However. removing the datum for the male terrapin from our analysis did not change the results. Additional lung volume measurements for males and juvenile females would be useful in refining our estimates of lung volume at smaller body sizes and strengthen our cADL for the size classes most at risk of entrapment.

Non-pulmonary respiration via aquatic uptake of oxygen is well described for other turtle species (Belkin 1968; Reese et al. 2001; Gordos et al. 2004). The ability to maintain aerobic respiration while submerged at relatively high water temperatures (25° C) is probably best developed in the Fitzroy River Turtle (*Rheodytes leukops*), an Australian turtle with anatomical and behavioral adaptations that increase aquatic oxygen uptake (Gordos et al. 2004). Close relatives of the Diamondback Terrapin (e.g., *T. scripta*, *Graptemys geographica*) are known to extract oxygen by moving water across highly vascular surfaces in the buccal cavity (Belkin

1968; Reese et al. 2001). However, meeting active in a dry chamber. metabolic demands with oxygen supplied by non-pulmonary respiration is only possible for turtles inhabiting environments with highly oxygenated water or when metabolic rate is extraordinarily low (Crocker et al. 1999; Herbert and Jackson 1985). It is unknown whether hibernating Diamondback Terrapins can obtain enough oxygen from water to survive extended submergence at low temperatures; however, because trapped terrapins accumulate lactate we conclude that non-pulmonary respiration is not sufficient to meet aerobic demands of active *M*. *terrapin* during the summer.

Oxygen consumption and dive duration in *turtles*.—Metabolic aerobic scope determines the rate submerged terrapins consume oxygen. Oxygen consumption rates at 10 and 20° C observed in this study are higher than published values for other turtle species (Litzgus and Hopkins 2003; Reyes and Milsom 2010) and much higher than the range $(0.028-0.055 \text{ ml g}^{-1})$ h⁻¹) previously reported for *M. terrapin* (Bentley et al. 1967). Indeed, the rate of oxygen consumption observed in this study is comparable to that of maximal oxygen consumption by active and exercising turtles respiring in a dry chamber (Gatten 1974; Stockard and Gatten 1983; Bagatto and Henry 1999). Is it well known that activity in a metabolic chamber will substantially increase measured oxygen consumption (Gatten 1974; Stockard and Gatten 1983; Litzgus and Hopkins 2003). Although we placed terrapins in the chamber 30 min prior to measurement, it is likely they were still active and thus these values do not represent resting metabolic rate. However, resting metabolic rate is a poor estimate of oxygen consumption for a turtle trapped in a crab pot because resting or restrained turtles consume little oxygen relative to active turtles and can remain aerobic longer (Stockard and Gatten 1983). Metabolic rate is further depressed in quiescent turtles when tissue oxygen supply is reduced (Jackson 1968; Herbert and Jackson 1985). For this reason, cADLs based on resting metabolic rate may overestimate the duration of dives.

On the other hand, rates of oxygen consumption measured for active turtles can also be misleading. Stockard and Gatten (1983) found that oxygen consumption of active turtles (*Carretta carretta*) with total oxygen stores of

However, total metabolic demand in swimming turtles is higher and supported by increasing reliance on anaerobic metabolism (Stockard and Gatten 1983; Bagatto and Henry 1999). For this reason, lactate may begin to accumulate in the plasma while oxygen stores are available. Internal oxygen stores of T. scripta submerged at 24° C are depleted within the first hour of the dive (Jackson 1968; Robin et al. 1981). Yet, these turtles survive >4 h of submergence at 24° C (Jackson 1968). Subsequent studies have shown that T. scripta submerged in this manner accumulate significant concentrations of lactate (Bagatto and Henry 1999; Warren and Jackson 2007). Diving lactate threshold, defined as the time at which lactate begins to accumulate in plasma, is low relative to maximum dive duration for turtles (Herbert and Jackson 1985). Lactate accumulation is associated with a decrease in blood pH and negatively impacts physiological function; therefore, submergence that exceeds aerobic capacity is physiologically stressful to terrapins.

cADL as predictor of submergence time for turtles.—Aerobic dive limits for turtles are calculated by dividing oxygen stores by metabolic rate (Caligiuri et al. 1981; Fuster et al. 1997; Wallace et al. 2005). Critical oxygen tension, the PO_2 when metabolism switches from aerobic to anaerobic, is influenced by ambient temperature. Usable oxygen stores decrease as temperature increases (Fuster et al. 1997). For this reason, cADL overestimates the aerobic dive limit at higher temperatures.

Entrapment and entanglement in fishing gear is a major conservation concern for both freshwater and marine chelonians (Stabenau et al. 1991; Wood 1997; Snoddy et al. 2009, Larocque et al. 2012). We examined published data and estimates of cADL to compare aerobic dive limits among species. Using oxygen stores (3.1 ml) and oxygen consumption rate (0.22 cm^3) $O_2 g^{-1} h^{-1}$) for a Painted Turtle (*Chrysemys picta*) swimming in 25° C water (Stockard and Gatten 1983), the estimated cADL for a 100 g animal is 14 min. Caligiuri and colleagues (1981) estimated that a 1 kg Red-eared Slider (T. scripta) submerged at 24° C would deplete oxygen stores in 36 min. Lutz and Bentley (1985) estimated that a 20 kg Loggerhead Turtle is lower when swimming in water than when 22.2 ml O_2 kg⁻¹ could dive aerobically for 33

min. Wallace et al. (2005) used field metabolic first hour of submergence and a significant rates to estimate cADL for Leatherback Turtle (Dermochelys coriacea), one of the deepest diving vertebrates, to be from 12 to 44 min. Thus, a 1 kg *T. scripta* has a greater cADL (36 min) than that predicted for a 20 kg Loggerhead Turtle. Given the large mass specific lung volume recorded in this study and for related freshwater turtles (Patterson 1973), it is not surprising that the cADL for *M. terrapin* is comparable to that of much larger sea turtles (Hochscheid et al. 2007). Thus, despite a ~2000difference in body fold size between Diamondback Terrapins and Leatherback Turtles, the largest marine turtles have just 10 additional minutes of oxygen during a dive. These data suggest that the stress associated with prolonged submergence due to entanglement or entrapment in fishing gear is similar for turtles of all sizes and the window of opportunity for recovery is equally short.

Dive durations observed for terrapins in 22° C water in this study suggest that most voluntary dives are aerobic. The majority of dives by Loggerhead Turtles and Leatherback Turtles were also below cADL (Lutz and Bentley 1985, Wallace et al. 2005). Individuals that exceeded cADL in this study and that of Wallace et al. (2005) were the ones with the highest metabolic rate. Neither study measured metabolic rate exclusively during dives; therefore, the effect of non-diving activity may contribute to higher metabolic rates observed for these individuals and therefore underestimate cADL. Aerobic metabolism is a more efficient means of generating ATP to fuel physiological functions; therefore, foraging animals that dive aerobically may conserve energy for other purposes (Wallace et al. 2005).

Lactacidosis in forcibly submerged turtles.— Lactate accumulation and management of the associated acidosis is likely the limiting factor for terrapins submerged in crab pots. Temperature has a profound effect on the anaerobic metabolic rate, increasing by 1.3 orders of magnitude between 5 and 25° C (Herbert and Jackson 1985; Warren and Jackson 2007). In addition, the buffering capacity of shell and other skeletal elements that promotes long term survival during hibernation is sharply reduced as temperature increases (Warren and Jackson 2007). When submerged at 20° C, prolonged submergence if access to oxygen is turtles exhibit elevated plasma lactate after the restored. In our study, terrapins with the highest

decline in pH (Crocker et al. 1999). High plasma lactate concentrations in terrapins removed from crab pots support the observation that diving lactate threshold is low and exceeded relatively quickly. In Josh Creek, terrapins submerged for < 3-h at \sim 27° C had a mean plasma lactate concentration of $38.5 \pm 13.9 \text{ mmol/l}$. Assuming these terrapins were in the trap the entire time it was submerged, we calculated the minimum rate of lactate accumulation to be 12.8 mmol/l/h. By comparison, Crocker et al. (1999) found mean lactate concentrations of four freshwater turtle species to range between 10 and 30 mmol/l after 6 h of submergence at 20° C for an effective rate of lactate accumulation of 1.5 to 5 mmol/l/h. Baggato and Henry (1999) reported a 6.21 mmol increase in lactate in T. scripta during 1 h of forced submergence at $22-25^{\circ}$ C. Likewise, when submerged for 6 h at 24° C T. scripta accumulated lactate at 7.1 mmol/l/h (Robin et al. 1981). Whereas temperature effects account for some of the higher lactate levels observed in the present study, struggling to escape also likely increased the rate of lactate accumulation. In studies where submerged turtles are active or swimming, lactate accumulates more rapidly (Stockard and Gatten 1983; Bagatto and Henry 1999). Kemp's Ridley Turtles (Lepidochelys *kempi*) exhibited a six-fold increase in plasma lactate after 2.7 to 7.3 min of forced submergence in fishing gear (Stabenau et al. 1991). On average, these turtles experienced an 8.5 mmol increase in lactate in \sim 7 min of forced submergence; however, some individuals had ~ 10 mmol increases in lactate in only 3 min of submergence coupled with vigorous swimming. In a study of sea turtles entangled in gill nets, lactate and corticosterone levels were highest for turtles that struggled to reach the surface (Snoddy et al. 2009). A moribund terrapin, brought into our laboratory by a member of the public, was found to have a plasma lactate concentration of 140 mmol/l. This terrapin died shortly after the blood sample was drawn. Lethal acidosis for other species occurs at plasma lactate concentrations near 130 mmol/l (Jackson et al. 1996). With a rate of lactate accumulation of 12.8 mmol/l/h, a terrapin submerged in 27° C water will reach a lethal lactacidosis in less than 12 h.

Diamondback Terrapins may recover from

lactate levels had significantly lower lactate al. 2009). The results of this study support levels after 12-h of recovery. Painted Turtles fully restore their blood pH by the end of the first recovery hour following 2-h of anoxic submergence at 25° C; however, complete recovery from submergence stress takes 7–10-h (Warren and Jackson 2004). In the presence of oxygen, lactate that accumulated in the plasma and other tissues during submergence can be converted back to glucose and stored as glycogen (Warren and Jackson 2004). This process is inefficient and some energy is necessarily lost. Therefore, terrapins that survive prolonged submergence will have reduced energy stores that might otherwise have been used for growth or reproduction.

Neurobehavioral impairment has been observed for turtles recovered from fishing gear in this study and by others (Radzio and Roosenburg 2005; Snoddy et al. 2009; Stoot et al. 2013). Many of the terrapins captured in eel pots by Radzio and Roosenburg (2005) exhibited symptoms of submergence stress (e.g., lethargy, labored breathing, and greatly reduced motor response). In closely related species, these types of behavioral impairment are observed in less than 3 h of forced submergence (Stoot et al. 2013). Although it is unknown how long the terrapins in our study and that of Radzio and Roosenburg (2005) were actually submerged, their affect improved within a few hours. In our experience, impaired terrapins, even ones that appear dead, may recover if placed on an inclined surface with the head pointing downward such that water can drain from the lungs. Stressed turtles may not be capable of swimming or avoiding other potential hazards (e.g., boat strikes) in their environment (Snoddy et al. 2009) and should not be released until they have fully recovered. Future studies should incorporate an objective measure of neurobehavioral impairment (e.g., Stoot et al. 2013) to quantify submergence stress and recovery time. These data may be used to develop a protocol for safely releasing Diamondback Terrapins that have experienced submergence stress.

Conclusions.—Our experimental data support the widespread observation that, without intervention, Diamondback Terrapins trapped in submerged crab pots will rapidly exhaust oxygen stores and eventually drown (Bishop 1983; Roosenburg et al. 1997; Wood 1997; Grosse et

observations that terrapins may drown in 2 to 4h when temperatures exceed 20° C (Mann 1995; Roosenburg 2004). Ironically, the time to reach a lethal acidosis is, in part, dependent on how active the terrapin is in its attempt to escape. Fishing gear deployed for commercial purposes are set to maximize catch of animals (e.g., fish, crustaceans) that efficiently extract dissolved oxygen from water and have no need to access the surface. Terrapin mortality would likely be reduced by establishing or enforcing shorter (~24 h) soak times for crab pots (Wood 1997; Grosse et al. 2009; Hart and Crowder 2011). However, lethal acidosis can occur rapidly in warmer waters and every effort should be made to modify fishing gear to reduce the number of turtles that enter (Wood 1997; Roosenburg and Green 2000; Hart and Crowder 2011), design traps that allow access to the surface (Roosenburg et al. 1997; Bury 2011), and to periodically remove lost or abandoned fishing gear (Guillory et al. 2001).

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