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Restricted diet in a vulnerable native turtle, *Malaclemys terrapin* (Schoepff), on the oceanic islands of Bermuda

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***Abstract.*—Diamondback Terrapins (*Malaclemys terrapin*) are native to Bermuda, presently inhabiting only four small brackish-water ponds. Their foraging ecology was investigated using direct observation, fecal analysis, and necropsy. They do not have as varied a diet as reported from their North American range. Small gastropods (<3 mm shell height) were found in 66.7% of fecal samples and made up 97.3% of animal material dry mass, thus dominating their diet. Scavenged fish and other vertebrates (19% of samples overall), plus terrestrial arthropods (14.3% of samples) were other common items. Polychaete worms and bivalves each occurred in less than 3% of fecal samples. Pond sediment was found in 74% of the samples, probably incidentally ingested while foraging (by oral dredging) for the gastropods. The distribution and abundance of arthropods and molluscs within the terrapins' brackish-water environment were assessed in three different habitats; pond benthos, mangrove swamp, and grass-dominated marsh. These indicated that Bermuda's terrapins do not fully exploit the food resources present. On Bermuda *M. terrapin* is basically a specialist microphagous molluscivore and mainly forages by deposit-feeding on gastropods living in soft sediments. This dietary restriction has made them particularly vulnerable to environmental contamination.**

Keywords. Anchialine pond, Diamondback Terrapin, fecal analysis, feeding ecology, aquatic gastropod

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The Diamondback Terrapin *Malaclemys terrapin* is one of two emydid turtle species living in the inland pond environments of the oceanic islands of Bermuda. The other, *Trachemys scripta elegans*, is a widely-distributed introduced freshwater pest (Outerbridge 2008). Diamondback Terrapins are less abundant than the sliders and have a greatly restricted local brackish distribution (Davenport et al. 2005). Native to Bermuda (Davenport et al. 2005; Parham et al. 2008) they form the only known population outside of the USA.

Diamondback Terrapins have been identified as an important component of the trophic dynamics of the east coast USA salt marsh ecosystem (Silliman and Bertness 2002; Davenport 2011) and are carnivorous, feeding mostly upon a variety of marine molluscs and crustaceans throughout the North American range (Butler et al. 2006; Ernst and Lovich 2009). There is, however, a growing body of evidence to support the hypothesis that this terrapin species may be a dietary generalist that is opportunistic in its foraging habits (Spivey 1998; Petrochic 2009; Butler et al. 2012; Erazmus 2012). Diamondback Terrapins show resource partitioning, whereby individuals with wider heads (the largest females) consume larger snails and crabs than terrapins possessing smaller heads (Tucker et al. 1995). Diamondbacks appear to be predators that use visual cues while foraging, showing selectivity in the prey that they eat (Davenport et al. 1992; Tucker et al. 1995, 1997; Butler et al. 2012).

Though the diet of Diamondback Terrapins has been studied in various regions throughout their North American range, no studies have been conducted on Bermuda. Analysis of fecal material is a non-destructive and non-invasive way of examining dietary preference and has been used on several species of small turtles previously (Demuth and Buhlmann 1997; Lima et al. 1997), including Diamondback Terrapins (Tucker

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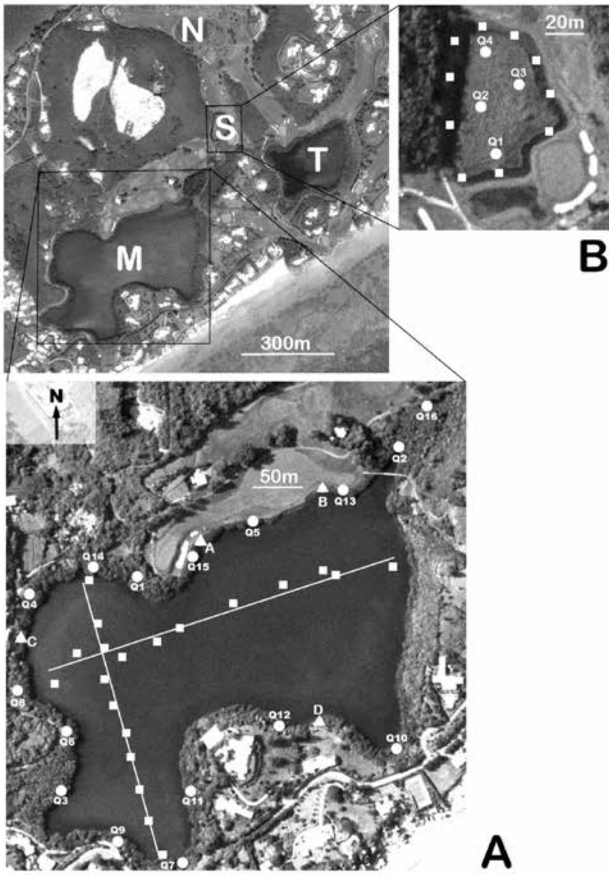

Fig. 1. Benthic survey locations in Mangrove Lake (A) and South Pond (B). Squares represent detritus sample locations along the belt transects; triangles represent the pond quadrat sample locations; circles represent the quadrat sample locations in the adjacent wetland communities. M = Mangrove Lake, T = Trott's Pond, S = South Pond, N = North Pond.

et al. 1995; Spivey 1998; Roosenburg et al. 1999; King 2007; Petrochic 2009; Butler et al. 2012; Erazmus 2012; Tulipani 2013; Tulipani and Lipcius 2014). This method of dietary determination has the added benefit of allowing multiple samples to be taken from a single individual over time. However, it is limited by the differential digestibility of the various hard and soft-bodied dietary components which in turn affects their representation within the feces.

The primary objective of the current investigation was to examine the diet and foraging ecology of Bermuda's terrapin population, with specific aims to assess food preferences within the land-locked, brackish-water pond environment, as well as assess the abundance and distribution of potential food items within the ponds and adjacent wetland communities. It was envisaged that detailed knowledge of terrapin diet in Bermuda would help appropriate conservation and management efforts to be directed towards protecting the areas in which they forage.

Materials and Methods

Study Site

Bermudian Diamondback Terrapins occur in four neighbouring brackish-water ponds: Mangrove Lake, South Pond, North Pond, and Trott's Pond (Fig. 1) situated on a private golf course located at the eastern end of the islands (32.32858°N, 64.70547°W; WGS 84). They move between these ponds (Outerbridge 2014). Mangrove Lake (10 ha area) and Trott's Pond (3 ha) are the largest of these and both are simple, shallow, anchialine basins fringed by Red Mangrove Trees (*Rhizophora mangle*) with deep benthic deposits of highly organic sediment (Thomas et al. 1992). Anchialine ponds are relatively small land-locked brackish bodies of water with subterranean connections to the sea (Holthuis 1973) and they show limited tidal influence. North Pond (0.4 ha) and South Pond (0.5 ha) are considerably smaller in area, shallower in depth, and lack mangrove vegetation. However, both have small central marshes dominated by grasses (*Cladium jamaicense* and *Paspalum vaginatum*). All ponds were incorporated into the golf course as water hazards during the 1920s, are situated upon a single square kilometer of land, and are only separated from each other by, at most, 380 m of land (straight-line distance between North Pond and Trott's Pond).

Fecal Analyses

Juvenile, immature, and adult Diamondback Terrapins were opportunistically captured using a long-handled dip net from Mangrove Lake, South Pond, North Pond, and Trott's Pond from March–September 2010 and January–October 2011. Maturity status was determined following Lovich and Gibbons (1990); individuals <91 mm straight plastron length (SPL) were classified as juveniles, males as sexually mature if SPL = 91–137 mm, females as sexually mature if SPL ≥ 138 mm. Females of SPL 91–137 mm were regarded as immature. After capture, each individual was kept outside in the shade for 48 h in covered, plastic storage bins (55 cm long × 45 cm wide × 30 cm deep). All fecal material collected in the 48 h period was strained through a one mm mesh-sized sieve, oven dried at 80 °C for 48 hours, and stored in a sealed glass vial for subsequent identification. Fecal samples were also collected from neonate terrapins (i.e., individuals that were less than one year old) that were followed as part of a radio-telemetry study (Outerbridge 2014). At the end of the tracking period, each individual was placed in a 500 ml plastic bowl containing enough freshwater to cover the carapace and held in a room with an ambient temperature of 30 °C for 48 hours. All fecal material collected in this period was strained through 47 mm filter paper to retain finer particles from smaller prey items consumed, allowed to air dry for 48 hours, and stored in a sealed glass vial. All terrapins captured during the fecal analysis investigation were released at their original capture location.

Each fecal sample was examined at magnifications between 10× and 25× using a stereoscopic microscope with an ocular scale. Food items were identified to the lowest possible taxonomic level, and weighed to the nearest 0.0001g. The shells of gastropods, when encountered whole, were counted and shell height (SH; maximum measurement along the central axis) was measured to the nearest 1.0 mm (note that some fecal samples only contained broken shells, the size of which could not be estimated). Quantification of dietary items was accomplished by determining the percentage dry mass of each item relative to the total dry mass of each sample. The relative frequency of occurrence of each dietary item was determined by calculating the percentage of turtles containing a given food type in relation to the total number of turtles examined.

Benthic Biotic Surveys within the Terrapins' Wetland Environment

Assessments of mollusc and crustacean abundance and distribution within the ponds and adjacent wetland environments were conducted to determine prey availability for Bermuda's Diamondback Terrapins. These assessments were accomplished by performing a series of benthic transects within three different habitats utilized by all size and age classes of Bermuda's Diamondback Terrapins; the sediment at the bottom of Mangrove Lake and South Pond, the Red Mangrove swamp community that surrounds Mangrove Lake, and the Saw-grass (*Cladium jamaicense*) marsh in the center of South Pond.

Pond Benthic Surveys

Two belt transect surveys of benthic biota were performed in Mangrove Lake and one belt transect survey was carried out in South Pond in July 2011. The Mangrove Lake transects were straight-line and followed an east-west direction (Transect 1) and a south-north direction (Transect 2), whereas the survey in South Pond was circular (Transect 3). Ten locations were haphazardly sampled along the path of each transect (Figs. 1A, 1B). The GPS coordinates were recorded at each location together with a brief description of the benthic characteristics. Collection consisted of sweeping a dip net with one mm mesh and a square opening of 25 x 25 cm for a distance of one m and a depth of approximately 2.5 cm at the surface of the sediment (thereby sampling a linear area of 0.25 m^2 at each location). The collected sediment was passed through a one mm mesh sieve at the surface of the pond and the material that remained was transferred into a one litre container. In addition to the belt transects, four replicate 25 x 25 cm quadrat surveys (A–D, Fig. 1A) were performed at random in sand, rock, and gravel areas of the margins of Mangrove Lake. The area defined by each quadrat was dredged to a depth of 2.5 cm and the contents transferred into a bucket and sorted by hand.

Mangrove Swamp Surveys

Sixteen replicate quadrat surveys were performed within the mangrove swamp that borders Mangrove Lake (Q1–Q16, Fig. 1A). The sites were haphazardly chosen, using an aerial map, at various locations around the periphery of the pond. Upon arrival in the field, a 25 × 25 cm quadrat was randomly placed upon the leaf litter immediately land-ward of the water-line. The area defined by each quadrat was dug to a depth of 2.5 cm and the contents transferred to a 3.8 liter sealable plastic bag. The contents of each bag were gently sifted in the laboratory using running water and a sieve with five mm mesh stacked on top of a one mm mesh-sized sieve.

Saw-grass Marsh Surveys

Four replicate quadrat surveys were performed within the saw-grass marsh at the center of South Pond (Q1–Q4, Fig. 1B). These sites were also haphazardly chosen using an aerial map. Upon arrival in the field, a 25 × 25 cm sample of saw-grass and turf was cut, to a depth of 2.5 cm, from the marsh at each of the four sites. The saw-grass blocks were transferred to separate 19 L buckets and taken to the laboratory for examination. Each sample was placed in a plastic bin (60 cm long × 40 cm wide × 14 cm deep), carefully broken apart and gently sifted in the laboratory using running water and a five mm sieve stacked on top of a one mm sieve. Shoot bundles were counted to determine saw-grass density.

All biological specimens from the belt transect and quadrat surveys were kept for subsequent identification in the laboratory, but only living specimens were counted and measured (i.e., empty gastropod shells were discarded). Live gastropods were counted, measured (total shell height mm), and frozen for eco-toxicological analyses (Outerbridge et al. 2016). All other living biological specimens were returned to their original locations and released after identification. All transect and quadrat survey results were standardized as values m^{-2} as depth was constant throughout.

Results

Fecal Analyses

A total of 54 Diamondback Terrapins were netted between March and September 2010 (*n* = 21) and January and October 2011 (*n* = 33), of which 42 (77.8%) produced fecal samples during the 48-hour confinement period (30 adults, four immature females, three juveniles of undetermined gender, and five neonates). Of the 54 terrapins, 30 were captured from South Pond (of which 23 (76.7%) produced fecal samples), 20 from Mangrove Lake (of

Table 1. *Malaclemys terrapin* dietary items obtained from 42 fecal samples (from females, males, juveniles and neonates combined) collected from inhabitants of four brackish ponds in Bermuda. Symbols: *n* = number of samples containing a given food type; % = percentage of samples containing a given food type in relation to the total number of samples. Presence (+) and absence (-) of dietary items' data for the various gender/age categories are given separately.

Dietary Item	*n* (%)	Adult females	Adult males	Juveniles	Neonates
Plants (grass, seeds, algae)	14 (33.3%)	+	+	+	-
Gastropoda	28 (66.7%)	+	+	+	+
Heleobops bermudensis	24 (57.1%)	+	+	+	+
Melanoides tuberculata	15 (35.7%)	+	+	+	-
Melampus coffeus	2 (4.8%)	+	-	-	-
Insecta	6 (14.3%)	+	-	+	+
Polychaeta					
Arenicola cristata	1 (2.4%)	-	+	-	-
Bivalvia					
Isognomon alatus	1 (2.4%)	+	-	-	-
Crustacea					
Armadillidium vulgare	1 (2.4%)	+	-	-	-
Osteichthyes					
Fundulus bermudae	5 (11.9%)	+	+	-	-
Amphibia/Reptilia					
Rhinella (syn *Bufo*) *marinus*	2 (4.8%)	+	+	-	-
Malaclemys terrapin	1 (2.4%)	+	+	-	-
Sediment	31 (73.8%)	+	+	+	-
Trash (cigarette filter)	1 (2.4%)	+	-	-	-

which 15 [75.0%] produced fecal samples), three from North Pond (all of which produced fecal samples), and one was captured from Trott's Pond (which also produced a fecal sample). Note that the small Bermudian terrapin population meant that some terrapins were netted more than once in this exercise; three females, one male, and one neonate were captured twice. One of the females was captured three times.

Of the 42 terrapins that produced fecal matter, 28 (66.7%) were classified as female (24 mature, four immature) ranging from 126–196 mm straight carapace length (SCL) (mean 172, SD 17.9) and six (14.3%) were classified as male (all mature) ranging from 114–134 mm SCL (mean 122, SD 8). Three (7.1%) were classified as juveniles (97–107 mm SCL, mean 102, SD 5), and five (11.9%) were classified as neonates (31–35 mm SCL, mean 33.7, SD 1.6).

Sediment occurred in 73.8% of the fecal samples, gastropods in 66.7%, plant material in 33.3%, fish and other vertebrate bones in 19%, terrestrial arthropods in 14.3%, polychaete worms, bivalves, terrestrial crustaceans, and trash (each 2.4% respectively) [Table 1]. The gastropods comprised three species: an endemic hydrobiid snail *Heleobops bermudensis*, the Red-rimmed Melania (*Melanoides tuberculata*), and the Coffee Bean Snail (*Melampus coffeus*). *Heleobops bermudensis* occurred in 57.1% of all fecal samples and was obtained from terrapins captured in South Pond, Mangrove Lake, and North Pond. *Melanoides tuberculata* occurred in 35.7% of the fecal samples but was only obtained from terrapins captured in South Pond, while *M. coffeus* only occurred in 4.8% of the fecal samples and was obtained from terrapins captured in Mangrove Lake.

The plant materials consisted mostly of mown grass fragments, saw-grass seeds, and green algae. None of the plant material appeared to have been digested and may have been ingested incidentally with animal prey (cf. Erazmus 2012). The terrestrial arthropods consisted of honey bees (*Apis mellifera*) (4.8% of the samples), small beetles (*Berosus infuscatus*), an isopod (*Armadillidium vulgare*), a millipede (*Julus* sp.), a big-headed ant (*Pheidole megacephala*), and an unidentified caterpillar (each represented in 2.4% of the samples). Vertebrate animal bones came from aquatic species and included fish from the family Cyprinodontidae—which occurred in 11.9% of the samples; an amphibian (the toad *Rhinella* [syn *Bufo*] *marinus*)—which occurred in 4.8% of the samples; and another terrapin (*Malaclemys terrapin*), probably scavenged—which occurred in 2.4% of the samples. The fecal samples containing arthropods and fish and vertebrate animal bones were acquired from terrapins captured in a variety of ponds. The samples that contained the burrowing polychaete worm (*Arenicola cristata*) and shell fragments from the Flat Mangrove Oyster (*Isognomon alatus*) all came from terrapins captured in Mangrove Lake. The single sample that contained a cigarette filter was obtained from a terrapin captured in South Pond. It is worth noting that most of the samples (n = 33 or 78.6%) that contained sediment also contained other dietary items, whereas nine samples

Table 2. Dry mass summary of all animal food items obtained from 33 fecal samples of Diamondback Terrapins collected from four sites combined (South Pond, Mangrove Lake, Trott's Pond, and North Pond).

	Melanoides dry mass (g)	*Heleobops* dry mass (g)	*Melampus* dry mass (g)	*Isognomon* dry mass (g)	Insect dry mass (g)	*Fundulus* bone dry mass (g)	*Rhinella* bone dry mass (g)	*Malaclemys* bone dry mass (g)	*Polychaete* dry mass (g)	TOTAL dry mass (g)
Proportion of	37.08	14.85	2.22	0.0595	0.117	0.139	1.17	0.0003	0.0153	55.65
total dry mass	66.6%	26.7%	3.99%	0.11%	0.21%	0.25%	2.1%	0.0005%	0.027%	100%

(21.4%) comprised only sediment. Female, male, and juvenile terrapins were all found to have ingested sediment, but none of the neonate terrapins produced feces that contained sediment.

Table 2 summarises the dry mass of all animal food items obtained from 33 terrapin fecal samples. It is evident that the three gastropod species made up most (97.3% of dry mass) of the collected material. Table 3 summarises their numbers and sizes. First, it can be seen that the terrapins ate very large numbers of *M. tuberculata* and *H. bermudensis*, and second that the gastropods were predominantly small in size (*M. tuberculata* mean SH 3.2 mm; *H. bermudensis* mean SH 1.7 mm). Thirdly, these data show that *H. bermudensis* had been consumed by all age classes (i.e., adults, juveniles, and neonates), whereas *M. tuberculata* had been consumed by adults and juveniles and the larger *M. coffeus* were found only in female adult samples. Most *H. bermudensis* measured <2 mm SH and *M. tuberculata* measured <3 mm SH. The majority (ca. 70%) of the *M. coffeus* snails ingested by the females measured 9–10 mm SH.

Further statistical analysis is compromised because a) many gastropod shells were broken, so unmeasureable, and b) there were not matched numbers of female, male, juvenile and neonate terrapins. However, it appears from Table 3 that adult females consumed rather larger prey than adult males. This is consistent with earlier studies of this markedly sexually-dimorphic species (Tucker et al. 1995).

Finally, it should be noted that the diet of neonate terrapins was extremely restricted (Table 1). Four out of five samples only contained remains of the gastropod *H. bermudensis*. The last sample also contained this species together with a little insect material. None of the neonate fecal samples contained sediment, presumably reflecting their terrestrial lifestyle.

Benthic Biotic Surveys within the Terrapins' Wetland Environments

Pond Benthic Surveys

Only two species of aquatic gastropods were encountered during the Mangrove Lake surveys; the False Horn Shell (*Batillaria minima*) and *H. bermudensis*. Two species of aquatic gastropods were also encountered during the South Pond surveys; *H. bermudensis* and *M. tuberculata*.

Table 4 summarises the gastropod survey data for all three transects in both ponds. Gastropod abundance in Mangrove Lake varied along Transects 1 and 2. *Batillaria minima* and *H. bermudensis* were encountered in relatively low numbers at locations that comprised sediment only (*B. minima* range 0–28 snails m^{-2}, mean 3.0, SD 7.2, *n* = 52; *H. bermudensis* range 0–192 snails m^{-2}, mean 27.0, SD 47.7, *n* = 424); however abundance increased significantly at locations where widgeon grass (*Ruppia maritima*) was found (*B. minima* range 0–56 snails m^{-2}, mean 33.0, SD 27.8, *n* = 132; *H. bermudensis* range 252–772 snails m^{-2}, mean 474, SD 221.5, *n* = 1,896). Shell height of *H. bermudensis* along both transects ranged from 1–4 mm (mean 1.7 mm, SD 0.5, *n* = 580); *B. minima* ranged from 6.5–11 mm (mean 8.9, SD 1.0, *n* = 46). Pooling the data for each of the two separate transects in Mangrove Lake shows that *H. bermudensis* was more abundant than *B. minima* along the central axes of the pond.

All of the sample locations along Transect 3 in South Pond comprised sediment and both snail species were encountered in low numbers (*H. bermudensis* 0–4 snails m^{-2}, mean 0.4, SD 1.3, *n* = 4; and *M. tuberculata* 4–20 snails m^{-2}, mean 13.2, SD 5.7, *n* = 132). Shell heights of *H. bermudensis* encountered along Transect 3 all measured one mm and the shell heights of *M. tubercu-*

Table 3. Pooled summaries of the total numbers (*n*) and sizes (shell height, SH) for whole *Melanoides tuberculata, Heleobops bermudensis,* and *Melampus coffeus* obtained from the 28 Diamondback Terrapin fecal samples that contained gastropods.

	Melanoides tuberculata				*Heleobops bermudensis*				*Melampus coffeus*			
Terrapin samples	*n*	Size Range (SH; mm)	Mean (SH; mm)	SD (mm)	*n*	Size Range (SH; mm)	Mean (SH; mm)	SD (mm)	*n*	Size Range (SH; mm)	Mean (SH; mm)	SD (mm)
All pooled	2224	1–18	3.2	2.1	1910	1–5	1.7	0.7	13	7–11	9.4	1.1
Female pooled	2112	1–18	3.3	2.1	1643	1–5	1.8	0.8	13	7–11	9.4	1.1
Male pooled	99	1–7	2.1	1.0	150	1–3	1.5	0.6	-	-	-	-
Juvenile pooled	13	1–3	2	0.6	77	1–3	1.2	0.4	-	-	-	-
Neonate pooled	0	-	-	-	40	1–2	1.2	0.4	-	-	-	-

Table 4. Summary of gastropod abundance (number of snails 0.25 m^{-2}) at each sampling site along Transects 1 and 2 in Mangrove Lake and Transect 3 in South Pond.

Site No.	Description	*Batillaria*	*Heleobops*	*Melanoides*
1-1	sediment	2	9	0
1-2	sediment	1	10	0
1-3	sediment	0	0	0
1-4	sediment	7	6	0
1-5	sediment	0	0	0
1-6	sediment	0	4	0
1-7	widgeon grass	14	123	0
1-8	widgeon grass	14	63	0
1-9	sediment	0	4	0
1-10	sediment	0	48	0
2-1	sediment	0	0	0
2-2	sediment	0	1	0
2-3	sediment	1	0	0
2-4	sediment	0	1	0
2-5	sediment	0	1	0
2-6	widgeon grass	0	193	0
2-7	widgeon grass	5	95	0
2-8	sediment	0	15	0
2-9	sediment	0	4	0
2-10	leaf litter	2	3	0
3-1	sediment	0	0	1
3-2	sediment	0	1	4
3-3	sediment	0	0	4
3-4	sediment	0	0	4
3-5	sediment	0	0	3
3-6	sediment	0	0	5
3-7	sediment	0	0	5
3-8	sediment	0	0	3
3-9	sediment	0	0	1
3-10	sediment	0	0	3

lata ranged from 1–11 mm (mean 3.1 mm, SD 2.0). The pooled data for Transect 3 shows that *M. tuberculata* was more abundant than *H. bermudensis* within the sediment of South Pond. Furthermore, *H. bermudensis* appeared to be more abundant within Mangrove Lake than in South Pond.

Further analyses of gastropod abundances along the three transects were attempted. The data were non-normal and variance was heterogenous whether the data were raw or square root transformed. The requirements of parametric statistics were therefore violated. Accordingly, a non-parametric approach was adopted. First, the abundances of *B. minima* were investigated. A Kruskall-Wallis test across the three transects showed that there were significant differences amongst the numbers of this species (Chi-Square = 7.885, df = 2, p = 0.019). Post-hoc tests using Mann-Whitney U tests were then conducted

Table 5. Summary of gastropod (*Batillaria minima*) and crustacean (*Alpheus armillatus*) total abundance (individ. m^{-2}) at each quadrat site (n = 4) within Mangrove Lake.

Site No.	Description	*Batillaria minima*	*Alpheus armillatus*
A	Sand and gravel	2128	0
B	Rocks	2000	48
C	Rocks	3504	32
D	Rocks	6752	0

to compare Transect 1 with Transect 2, Transect 1 with Transect 3 and finally Transect 2 with Transect 3. This is not an ideal approach as there is an attendant risk of Type 1 error (i.e., incorrect rejection of a null hypothesis), but no better alternative is available. These post-hoc tests indicated that there were no significant differences in numbers of *B. minima* between Transects 1 and 2 (both from Mangrove Lake) (Mann-Whitney U = 36.50, Wilcoxon W = 91.50, Z = -1.153, p = 0.315). There were no significant differences in numbers of *B. minima* between Transects 1 and 3 (Mann-Whitney U = 33.00, Wilcoxon W = 88.00, Z = -1.302, p = 0.218), but there were significant differences between Transects 2 and 3 (Mann-Whitney U = 12.00, Wilcoxon W = 67.00, Z = -2.954, p = 0.003).

Second, the same approach was adopted for the abundances of *H. bermudensis*. A Kruskall-Wallis test across the three transects showed that there were significant differences amongst the abundances of this species (Chi-Square = 12.76, df = 2, p = 0.002). Post-hoc Mann-Whitney tests showed that abundances of *H. bermudensis* did not differ between Transects 1 and 2 (Mann-Whitney U = 39.00, Wilcoxon W = 94.00, Z = -2.954, p = 0.436), but did differ significantly between Transects 1 and 3 (Mann-Whitney U = 11.00, Wilcoxon W = 66.00, Z = -3.229, p = 0.002) and between Transects 2 and 3 (Mann-Whitney U = 12.50, Wilcoxon W = 67.50, Z = -3.117, p = 0.003). Overall these tests indicate that there is strong (but not conclusive) support for the abundance trends identified above.

Table 5 shows the results of the four replicate quadrat surveys that were performed in the sandy, rocky, and gravelly marginal areas of Mangrove Lake. Only one species of gastropod (*B. minima*) and one species of crustacean (the Snapping Shrimp, *Alpheus armillatus*) were encountered. The snails were found most often attached to the rocky substrate, whereas the shrimp were found either buried within the gravel or hidden beneath rocks. The density of *B. minima* ranged from 2,000–6,752 snails m^{-2} (mean 3,596, SD 2,211.4) and their sizes ranged from 3.5–10 mm SH (mean 6.4); the density of *A. armillatus* ranged from 0–48 shrimp m^{-2} (mean 20, SD 24) and their total lengths (TL) ranged from 10–19 mm (mean 15.6). These data suggest that the density of *B. minima* surveyed upon the rocky shoreline habitat (mean 3,596 snails m^{-2}) was nearly 400 times more than the mean density of live

Table 6. Biotic summary of the quadrat surveys (n = 16) performed within the mangrove swamp around Mangrove Lake. *M.c.* = *Melampus coffeus, M.m.* = *Myosetella myositis*, *L.c.* = *Laemodonta cunensis*, *M.o.* = *Microtralia occidentalis*, *P.m.* = *Pedipes mirabilis*, Amp. = Amphipod spp., *L.b.* = *Ligia baudiniana*, *A.e.* = *Armadilloniscus ellipticus*, *A.v.* = *Armadillidium vulgare*, *B.i.* = *Bersos infuscatus*, Lep. = Lepidopteran larvae, *Jul.* = *Julus* sp., *A.m.* = *Anisolabis maritima*, *Fun.* = *Fundulus* eggs, Ara. = Arachnid spp., P = Earthworm sp.

	Gastropods					Crustaceans				Insects				Fish	Other	
	M.c.	*M.m.*	*L.c.*	*M.o.*	*P.m.*	Amp.	*L.b.*	*A.e.*	*A.v.*	*B.i.*	*Lep.*	*Jul.*	*A.m.*	*Fun.*	Ara.	P
Mean density (indiv. m^{-2})	282	53	5	3	3	371	4	197	8	4	1	17	10	313	9	9
Size range (mm)	2–15	1–6	1–3	6–7	2–3	-	-	-	-	-	-	-	-	-	-	-
Mean size (mm)	8.8	2.8	1.8	6.3	2.3	-	-	-	-	-	-	-	-	-	-	-
SD	3.2	1.2	0.8	0.6	0.6	-	-	-	-	-	-	-	-	-	-	-

B. minima found upon the sediment along the central axes of Mangrove Lake (9.2 snails m^{-2}).

Mangrove Swamp Surveys

Table 6 summarises the various aquatic and terrestrial species discovered during the quadrat surveys (n = 16) performed within this environment. A total of five gastropod species were encountered; all were found within the detritus of the intertidal zone and some individuals of *M. coffeus* were also encountered attached to Red Mangrove prop roots, usually in clusters, immediately above the water line of the pond. *Melampus coffeus* were most frequently encountered. Density for this species ranged from 0–1,168 snails m^{-2} (mean 282, SD 399.3, n = 4,512), and shell height ranged from 2–15 mm SH (mean 8.8, SD 3.2, n = 4,512). *Myosetella myosotis* was the second most frequently encountered gastropod, but only at one of the 16 locations. Sizes ranged from 1–6 mm SH (mean 2.8, SD 1.2, n = 848). *Laemodonta cubensis* was encountered in densities of 80 snails m^{-2} and all occurred in one location. Sizes ranged from 1–3 mm SH (mean 1.8, SD 0.8). *Microtralia occidentalis* and *Pedipes mirabilis* were infrequently encountered. Sizes of the former ranged from 6–7 mm SH (mean 6.3, SD 0.6, n = 48), and the latter ranged from 2–3 mm SH (mean 2.3, SD 0.6, n = 48).

In addition to the gastropods mentioned above, four species of crustaceans were encountered among the detritus (Table 5). The amphipods were the most abundant crustaceans encountered, being found in 81.3% of the quadrat locations. Densities ranged from 0–2,272 m^{-2} (mean 371, SD 656.8, n = 5,936). The isopod *Armadilloniscus ellipticus* was the second most frequently encountered crustacean, with densities of 0–1,008 m^{-2} (mean 197, SD 311.5, n = 3,152). *Ligia baudiniana* and *A. vulgare* were not commonly encountered.

Eggs (approx. two mm diameter) from the endemic Bermuda Killifish (*Fundulus bermudae*) were encountered in 25% of the quadrat surveys. Abundance varied from 0–3,824 eggs m^{-2} (mean 313, SD 958.5, n = 5,008). The eggs were usually found hidden within the leaf detritus, but also attached to the Red Mangrove prop roots at the high water mark. A variety of primarily terrestrial organisms were occasionally encountered in low densities within the 16 quadrat locations; these included millipedes, earwigs, small spiders, earthworms, small beetles, and a lepidopteran larva.

Saw-grass Marsh Surveys

Table 7 summarizes the aquatic and terrestrial species discovered during the quadrat surveys performed within this environment. Only one species of gastropod was found during the quadrat surveys (*H. bermudensis*). Densities ranged from 176–272 snails m^{-2} (mean 208, SD 43.3, n = 832), and shell heights ranged from 1–4 mm SH (mean 2.3, SD 0.7). Terrestrial organisms were infrequently encountered within the quadrats and consisted of millipedes and small spiders. The number of saw-grass shoot bundles ranged from 16–48 m^{-2}.

Discussion

The anchialine ponds inhabited by Bermudian Diamondback Terrapins are unusual habitats for the species. In the USA terrapins live predominantly in *Spartina* salt marshes and in the Everglades mangrove swamps of west Florida. The latter environments feature substantial allochthonous inputs from neighbouring marine and freshwater habitats as well as abundant autochthonous energy sources, so are amongst the most productive natural environments in the world, supporting diverse plant and animal communities (Schmalzer 1995; Whitney et al. 2004).

In contrast, energy sources of anchialine pools are

Table 7. Biotic summary of the quadrat surveys (n = 4) performed within the saw-grass marsh habitat at the center of South Pond. Note: results standardized to values m^{-2}.

Site No.	No. of grass shoot bundles	*Heleobops bermudensis*	Millipedes	Spiders
Q1	16	176	48	64
Q2	48	272	32	80
Q3	32	192	64	48
Q4	32	192	16	32

largely autochthonous. The Bermudian anchialine pools inhabited by terrapins proved to have limited faunal diversity. Over most of the area of Mangrove Lake (the largest pond), only two species of benthic gastropod snails were found; *H. bermudensis* and *B. minima*. Similarly, two species of aquatic gastropods were encountered during the benthic South Pond surveys; *H. bermudensis* and *M. tuberculata*. All three species are operculate deposit-feeders; *B. minima* and *H. bermudensis* are native, while *M. tuberculata* is primarily a freshwater (though salt-tolerant) species that is native to tropical and sub-tropical regions of southern Asia and northern Africa (Clench 1969), but widely-introduced to various regions via the aquarium trade. *Heleobops bermudensis* is a small endemic hydrobiid snail, limited to brackish-water ponds in Bermuda (see Pilsbry in Vanatta 1911), while *B. minima* is found also on local mudflats (Sterrer 1986).

The results of the quadrat and transect surveys revealed that the sediment surface in Mangrove Lake and South Pond generally showed relatively low densities of gastropods; however *B. minima* and *H. bermudensis* were both found to exist in higher densities in localized patches throughout Mangrove Lake. *Batillaria minima* was most often associated with sand, rock, and gravel substrate, reaching densities ca. 6,750 snails m^{-2}, whereas *H. bermudensis* was more commonly found within beds of widgeon grass in densities up to 772 snails m^{-2}. Benthic mapping of Mangrove Lake was not performed, but visual assessments of the pond in 2011 suggested that both the gravel/rock and widgeon grass environments comprised a very small proportion (< 5%) of the total pond area. Taken with the fecal sample results, it would appear that juvenile and adult terrapins on Bermuda rely heavily on benthic dredging of small gastropods (Outerbridge and Davenport 2013) from the large areas of pool bottoms, presumably because this unselective feeding behavior provides them with plenty of food.

Gastropods were more abundant and diverse within the mangrove and saw-grass marsh environments. Five species of gastropods (all pulmonates of the Family Melampidae) were encountered during the quadrat surveys within the detritus of the mangrove swamp intertidal zone around Mangrove Lake. *Melampus coffeus* grow to 20 mm SH, but the other species rarely exceed eight mm SH (Sterrer 1986). Thomas et al. (1992) and Herjanto (1994) reported that *M. coffeus* was frequently encountered upon the detritus and prop roots of mangrove trees in Mangrove Lake and Trott's Pond. The present investigation showed that gastropods within Bermuda's saw-grass marsh and mangrove swamp environments can reach densities of up to 1,168 snails m^{-2} (*M. coffeus*). However, it is evident that the adult and juvenile terrapins rarely, if ever, use this resource and are essentially aquatic foragers.

Crustaceans were rarely encountered within the aquatic environment of Mangrove Lake; only one species (*Alpheus armillatus*) was found in the rocky marginal habitats; no crustaceans were encountered within South Pond. However, crustaceans (mostly small amphipods and isopods) were frequently encountered (87.5%) in the quadrat surveys performed in the mangrove swamp surrounding Mangrove Lake. The Mangrove Crab (*Goniopsis cruentata*) was not encountered during the present study though it was reported to inhabit the intertidal zone of Mangrove Lake and Trott's Pond two decades ago (Thomas et al. 1992). Small numbers of terrestrial invertebrates were also found in the vegetated areas around the pools.

Some potential food organisms had been surveyed before this study. The Flat Mangrove Oyster (*Isognomon alatus*) grows in clumps on the submerged prop roots of red mangrove trees in Mangrove Lake and Trott's Pond and has been reported to reach densities of 250 oysters $root^{-1}$ or about 2,700 oysters m^{-2} of pond (Thomas and Dangeubun 1994); the Bermudian terrapins hardly use this resource. Fish have also been investigated; the endemic killifish (*Fundulus bermudae*) occurs in Mangrove Lake (estimated population about 11,000) and Trott's Pond (about 8,000) (Outerbridge et al. 2007). Killifish in Mangrove Lake are benthopelagic and are omnivorous opportunistic feeders. They are swift swimmers that form loose schools of similarly-sized fish (Rand 1981) and are probably difficult for terrapins to catch.

Overall, it appeared that the ponds themselves had low faunal diversities, but abundant supplies of small deposit-feeding gastropod snails; the neighbouring vegetated areas had rather higher diversities, but gastropods were again dominant. Given the small size of the terrapin population (ca. 100 individuals ≥ 81 mm straight carapace length, see Outerbridge et al., In Press), it was evident that plenty of food was available to them.

The benthic sediment in all of the terrapin ponds is gelatinous and extremely flocculent which allows the terrapins to both easily move through it and process it, apparently allowing them to consume *M. tuberculata*, the most frequently encountered gastropod within the pond's sediment (Outerbridge and Davenport 2013). In support of this hypothesis, fecal analyses from this study confirm that Bermuda's terrapins consume very high numbers of small (<2 mm) *M. tuberculata* and *H. bermudensis* together with large quantities of sediment. The sediment is believed to have been incidentally rather than deliberately ingested (as is probably the case for plant material too). It is evident that small gastropods form almost all of the adult and juvenile terrapins' animal diet (97.3% of dry mass).

All of the few insects recorded from fecal material were probably consumed after falling into the ponds, rather than having been ingested in the terrestrial environment (with the exception of those consumed by neonate terrapins which are residents of the intertidal mangrove and grass-dominated marsh environments adjacent to the ponds; Outerbridge 2014). The fish, toad, and terrapin bones discovered in some fecal samples indicate that Bermuda's terrapins also scavenge on animal remains. Carcasses of these species are periodically observed floating at the surface of the study ponds and it is likely that they are opportunistically ingested when encountered. Scavenging has been reported for other diamondback terrapin populations in the USA (Ehret and Werner 2004; Petrochic 2009; Butler et al. 2012).

Plant material (mown grass fragments, saw-grass seeds, algae) was found in small quantities in a third of fecal samples. All appear to have been incidentally ingested. Mown grass fragments presumably reflect the golf course management of the terrapins' habitat. The presence of seeds in feces has been reported before (Tulipani 2013; Tulipani and Lipcius 2014) from terrapins foraging in salt marshes in Virginia; in that case the turtles were shown to be significant in the dispersal of Eelgrass (*Zostera marina*) seeds.

It is interesting to note that Bermuda's Diamondback Terrapins apparently did not ingest or rarely ate some items common in their environment. There was no evidence that they ever ate the Snapping Shrimp *Alpheus armillatus*, though substantial numbers were available in rocky areas of the shoreline. They also ate few of the Mangrove Oysters (*Isognomon alatus*) despite the latter's high population densities on mangrove roots. There was little evidence of foraging amongst the mangrove vegetation; most of the pulmonate gastropod species (*M. coffeus* does not appear to be an important dietary food item for Bermuda's terrapins, and *M. myosotis*, *L. cubensis*, *M. occidentalis*, and *P. mirabilis* do not appear to be consumed at all), amphipods and isopods were not recorded in fecal samples.

The dietary specialization and restriction in Bermuda's terrapins carries penalties. It has been demonstrated that they are exposed to a wide range of toxic compounds (e.g., trace metals, gasoline-range, and diesel-range petroleum hydrocarbons and polycyclic aromatic hydrocarbons) via food-chain contamination, specifically through the ingestion of gastropods, but probably exacerbated by the high incidence of associated sediment intake. It has also been shown that these contaminants are transferred to terrapins eggs, which show low hatching rates and evidence of embryonic abnormalities (Outerbridge et al. 2016).

Conclusion

The field surveys and fecal analyses reported on here showed that Diamondback Terrapins in Bermuda are specialist microphagous molluscivores that do not exploit the full range of potential prey species available to them. The range of food items ingested is much narrower than reported from North American populations, but this is probably caused by the near absence of tidal action that permits the accumulation of organic-rich sediments browsed upon by abundant small gastropods. The anchialine pools and surrounding vegetated areas exhibit a low potential prey diversity in comparison with those found in the salt marshes of the eastern seaboard of the USA, but adult and juvenile terrapins evidently select preferentially within this low diversity for small gastropods of only two species (*M. tuberculata* and *H. bermudensis*).

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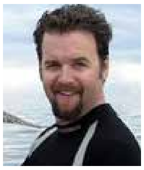

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