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Stable carbon isotopic profiles of sea turtle humeri: implications for ecology and physiology

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Abstract

Analyses of sequential growth layers of marine turtle humeri indicate that diet is the primary influence on the carbon isotopic composition of sea turtle bone carbonate. However, secondary physiological and geographical factors, such as foraging locality, migratory range, physiological interactions with ocean water, and especially respiratory physiology, also influence carbon isotope values of biogenic structural carbonate. The difference in carbon isotope compositions between diet and bone structural carbonate is consistently smaller in the deep-diving leatherback (*Dermochelys coriacea*) and olive ridley (*Lepidochelys olivacea*) turtles than in the shallow-diving green turtle (*Chelonia mydas*). Although diet has considerable influence on sea turtle bone carbonate $\delta^{13}C$, respiration appears to be an additional influence, because of the accumulation of respired CO_2 in blood during extended breath-hold diving and the concomitant incorporation of blood-CO_2 into bone carbonate. Preliminary analyses of collagen and muscle tissue do not show evidence of respiratory effects on their carbon isotope compositions.

Keywords: Carbon isotopes; Bone; Carbonate; Diet; Respiration; Turtles

1. Introduction

Sea turtles spend most of their lives submerged in the ocean. Adult sea turtles are migratory animals that may travel thousands of kilometers between foraging grounds and nesting beaches (Carr and Hirth, 1962; Pritchard, 1973). Male sea turtles rarely return to land after leaving their natal beaches as hatchlings and females return only to nest (McCarthy, 1996). Therefore, it is difficult to study sea turtles in the wild and most sea turtles studied are reproductive-aged females returning to their natal beaches to nest.

Stable carbon isotopic values of sea turtle humeri and of sea turtle epibiota should reflect the conditions in which they were formed. These conditions, in turn, are dependent on physiology, behavior, and ecology. In order to understand the factors that influence stable carbon isotope variation in sea turtle bone carbonate, three species of sea turtles with differing diets, migratory ranges, foraging habitats, and respiratory physiology were analyzed. Carbon isotopes in calcite shells of commensal barnacles collected from the same turtle species were analyzed for comparison with turtle bone carbonate isotopic composition.

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1.1. Carbon isotope variation in marine organisms

Because ^{12}C is utilized preferentially over ^{13}C in photosynthesis, organic matter derived from photosynthesis is ^{13}C-depleted relative to dissolved inorganic carbon in seawater (e.g., Boutton, 1991b). After animals ingest organic matter in the ocean, internal fractionation occurs as carbon becomes incorporated into their tissues. In a single animal, muscle tissue is generally ^{13}C-enriched by ~1‰ relative to diet, whereas bone carbonate is ^{13}C-enriched by up to ~12‰ relative to diet (Koch et al., 1994). Further ^{13}C-enrichment occurs progressively at each trophic level (Koch et al., 1994) as higher-level consumers develop their tissues. The ratio of ^{13}C to ^{12}C is expressed in $\delta^{13}C$ values, where δ is the deviation in per mil (‰) of the $^{13}C/^{12}C$ ratio of the sample of interest from the carbonate standard of Vienna Pee-Dee belemnite, or V-PDB (Gonfiantini et al., 1995). $\delta^{13}C$ is defined as follows:

$$\delta^{13}C = [(({}^{13}C/{}^{12}C)_{SAMPLE} - ({}^{13}C/{}^{12}C)_{V-PDB}) / ({}^{13}C/{}^{12}C)_{V-PDB}] \times 1000‰.$$

The $\delta^{13}C$ values of whole animal tissue are predominantly related to the food consumed by the animal over weeks or months, and therefore, reflect an average diet (Gearing, 1991). The carbon isotope composition of the structural carbonate in teeth and bones is enriched by ~9‰ in marine mammals (e.g., Roe et al., 1998) and ~9‰ to 14‰ in terrestrial vertebrates (e.g., Ambrose and Norr, 1993; Koch et al., 1994; Sillen and Lee-Thorp, 1994) and sharks (e.g., Vennemann et al., 2001), relative to diet.

The geographical range of a marine organism and the locality of its food source influence the organism's carbon isotope composition. The $\delta^{13}C$ values of phytoplankton, at the base of the marine food chain, are approximately 5‰ higher at low latitudes than phytoplankton from high latitudes (Rau et al., 1982; Descolas-Gros and Fontugne, 1990; Boutton, 1991b). As a result, ^{13}C-enrichment also occurs in animals at higher trophic levels feeding at low latitudes as compared to similar animals feeding at high latitudes. Likewise, nearshore feeders have higher $\delta^{13}C$ values than offshore feeders within a given trophic level (Burton et al., 2001).

The isotopic composition of animal tissue is also affected by respiratory physiology. During breath-hold dives by pulmonate marine vertebrates, such as marine mammals or sea turtles, CO_2 accumulates in the body as oxygen is consumed (Truchot, 1987; Randall, 1988; Lutz and Storey, 1997). While diving, marine reptiles have increased resistance to blood flow in the pulmonary vascular bed, resulting in intracardiac shunting (Truchot, 1987; Lutcavage and Lutz, 1997), which may favor greater accumulation of CO_2 in body fluids than in lung gas during a dive (Ackerman and White, 1979). In the blood, CO_2 reacts with water to form carbonic acid, which dissociates into carbonate and bicarbonate ions. The predominant form of CO_2 in blood is bicarbonate, HCO_3^- (Randall, 1988). Sea turtle dives are almost invariably aerobic with moderate cycling of CO_2 partial pressure (PCO_2) and pH, suggesting an efficient CO_2/bicarbonate and ionic exchange system (Lutcavage and Lutz, 1997).

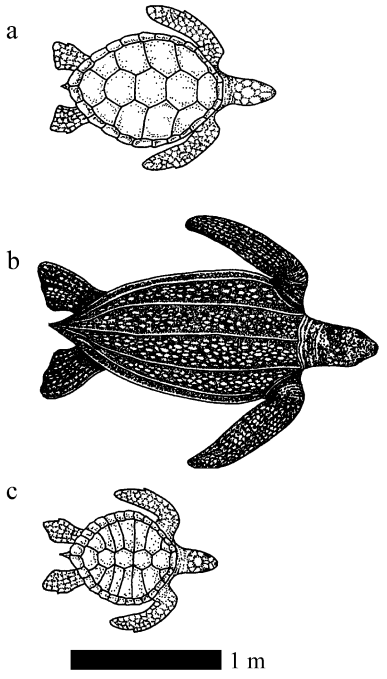

Fig. 1. The sea turtles in this study (drawn to scale): (a) the green turtle (*C. mydas*); (b) the leatherback (*D. coriacea*); and (c) the olive ridley (*L. olivacea*). Average sizes of the green turtle, the leatherback, and the olive ridley are based on data from National Marine Fisheries Service and U.S. Fish and Wildlife Service (1991, 1992, 1998), respectively.

Vertebrates possess large buffer reserves, such as calcium carbonate and calcium phosphate in mineralized structures (Truchot, 1987). In mammals, bone CO_2 comprises more than 80% of total body CO_2 stores (Truchot, 1987; Bushinsky and Frick, 2000). Thirty percent of bone CO_2 is present as bicarbonate surrounding hydroxyapatite crystals and the remaining as structural carbonate, fixed within the bone structure (Poyart et al., 1975a). As blood circulates, blood-CO_2 exchanges slowly with bone carbonate (Poyart et al., 1975b), although rapid exchange may occur during metabolic acidosis (Freeman and Fenn, 1953; Bushinsky and Frick, 2000). During long-term submergence of the freshwater turtle *Chrysemys picta bellii* at low temperature, an increase in plasma calcium occurred, suggesting exchange with bone carbonate (Jackson and Ultsch, 1982; Jackson et al., 1984). McConnaughey et al. (1997) suggested that most vertebrate bone carbonate is derived from CO_2 produced by respiratory processes. Because respired CO_2 is ^{13}C-depleted (McConnaughey et al., 1997), the amount of respired CO_2 incorporated into an animal's bone carbonate should negatively correlate with bone carbonate $\delta^{13}C$ values.

1.2. Species of interest

Three species of sea turtles, the green turtle (*Chelonia mydas*), leatherback (*Dermochelys coriacea*), and olive ridley (*Lepidochelys olivacea*) (Fig. 1), were the focus of this study, because they frequent a diversity of habitats, have varying diets, and engage in long-range migratory activity (National Marine Fisheries Service and U.S. Fish and Wildlife Service, 1991, 1992, 1998). *D. coriacea* is the only living taxon within the family Dermochelyidae, whereas all other extant sea turtles belong to the family Cheloniidae (Gaffney and Meylan, 1988). Skeletal growth characteristics vary between the two families of sea turtles. The skeleton of *D. coriacea* exhibits mammal-like growth, remains extensively cartilaginous throughout adulthood, and the diaphyses of the humerus is derived from a combination of endochondral and periosteal membranous growth

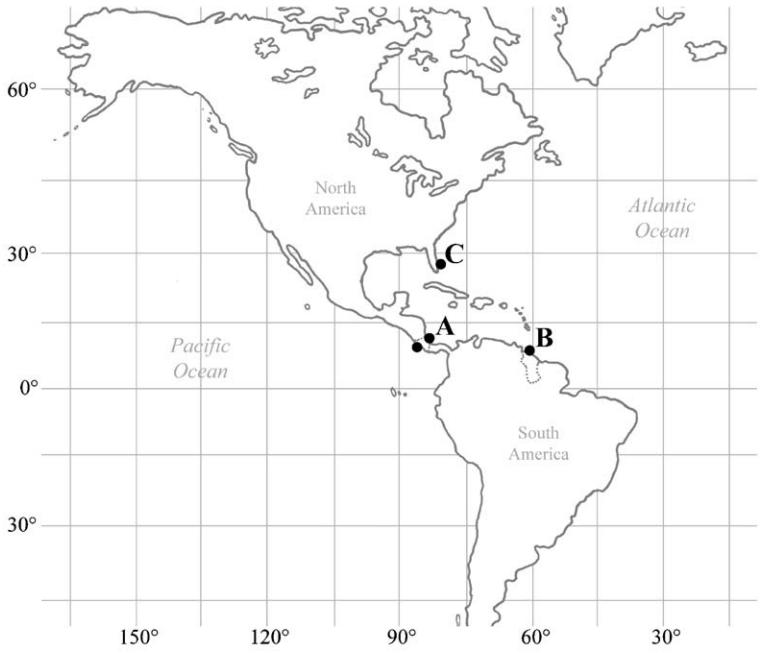

Fig. 2. Collection localities. (A) Costa Rica. *C. mydas* and *D. coriacea* specimens were collected in Tortuguero on the Caribbean coast, and *L. olivacea* humeri were collected from Ostional along the Pacific coast; (B) Guyana. *D. coriacea* humeri were collected along the central and northwest coast; (C) Florida. One *D. coriacea* humerus was collected from the Port St. Lucie region.

with no remodeling occurring in the periosteal regions (Rhodin et al., 1981). Turtles within the family Cheloniidae have humeri with distinct periosteal layers; each layer is associated with a single growth season, although bone remodeling, famine, injury, or disease may affect the seasonality of the growth layers (Zug, 1991; Bjorndal et al., 1998).

2. Methods

2.1. Sample collection and preservation

Humeri from *C. mydas* ($n=7$), *D. coriacea* ($n=1$), and *L. olivacea* ($n=3$) were collected from the coasts of Tortuguero and Ostional, Costa Rica (Fig. 2A). Flesh was removed from the bones by mechanical means at the site of collection, and then by placement on ant beds or burial at the collection locality. All specimens were preserved in ethanol, and then dried in a fume hood at room temperature. *D. coriacea* humeri ($n=3$) were also collected in Guyana (Fig. 2B) by the Chelonian Research Institute. An additional *D. coriacea* humerus was collected in St. Lucie County, Florida (Fig. 2C), by the Sea Turtle Stranding and Salvage Network and was preserved by freezing. The barnacles *Chelonibia testudinaria* ($n=2$) and *Platylepas coriacea* ($n=1$) were collected from deceased *C. mydas* in Tortuguero and a nesting *D. coriacea* in Florida, respectively. Tables 1 and 2 list specimen details. The seagrass *Thalassia testudinum* was collected from Atlantic coastal waters off Nicaragua by

Table 1
Collection data for turtle specimens analyzed in this study

Sample number	Collection date	Collection locality	Taxon (M/F if known)	Element/length (cm)	Curved carapace length (cm)	State[a] of turtle
T-5RH	6/17/2000	Tortuguero, Costa Rica 10 23.92N / 83 25.22W	F. green turtle (*Chelonia mydas*)	R. Humerus/17.3	93.0	1, 2
T-3LH	6/15/2000	Tortuguero, Costa Rica 10 28.42N / 83 27.96W	Green turtle (*Chelonia mydas*)	L. Humerus/19.4	Unknown	4
T-4LH	6/15/2000	Tortuguero, Costa Rica 10 30.65N / 83 29.17W	Green turtle (*Chelonia mydas*)	L. Humerus/19.8	Unknown	4
T-7LH	6/17/2000	Tortuguero, Costa Rica 10 26.73N / 83 27.00W	Green turtle (*Chelonia mydas*)	L. Humerus/19.3	Unknown	4
T-7RH	6/17/2000	Tortuguero, Costa Rica 10 26.73N / 83 27.00W	Green turtle (*Chelonia mydas*)	R. Humerus/19.3	Unknown	4
T-9LH	7/1/2000	Tortuguero, Costa Rica 10 28.97N / 83 28.28W	F. green turtle (*Chelonia mydas*)	L. Humerus/22.0	108.0	1, 2
T-12LH	7/4/2000	Tortuguero, Costa Rica	M. green turtle (*Chelonia mydas*)	L. Humerus/19.2	97.5	1, 2
CRI-4RH	Unknown	Guyana	Leatherback (*Dermochelys coriacea*)	R. Humerus/26.2	Unknown	Unknown
G-1LH	8/9/2000	Gwenie Beach, Guyana 7 53.12N / 58 59.49W	Leatherback (*Dermochelys coriacea*)	L. Humerus/24.1	Unknown	4
F-1LH	3/2/2001	Port St. Lucie, Florida	M. leather back *(D. coriacea)*	L. Humerus/30.0	166.5	2
T-51RH	5/7/2001	Tortuguero, Costa Rica 10 25.17N / 83 26.05W	Leatherback *(D. coriacea)*	R. Humerus/25.9	Unknown	4
A-1LH	8/16/2000	Almond Beach, Guyana	Leatherback *(D. coriacea)*	L. Humerus/27.0	Unknown	4
O-1LH	6/21/2000	Playa Guiones/ near Ostional 9 56.36N / 85 40.05W	Olive Ridley *(L. olivacea)*	L. Humerus/13.4	66.0	3
O-3LH	6/22/2000	Playa Ostional, Costa Rica 9 58.73N / 85 41.31W	Olive Ridley *(L. olivacea)*	L. Humerus/15.5	Unknown	4
O-7LH	6/23/2000	Playa Guiones/ near Ostional 9 56.85N / 85 40.39W	Olive Ridley *(L. olivacea)*	L. Humerus/14.1	66.5	3

[a] Turtle decompositional state: 1, recent jaguar kill; 2, moderate decomposition; 3, dry carcass; 4, scatted bones.

Table 2
Collection data for barnacles analyzed in this study

Sample number	Collection date	Collection locality	Barnacle/host turtle (turtle no.)	Rostro-carinal diameter (mm)
T-16B	7/1/2000	Tortuguero, Costa Rica 10 28.97N/83 28.28W	*Chelonibia testudinaria*/ Stranded *Chelonia mydas* (T-9)	36
T-17B	7/1/2000	Tortuguero, Costa Rica 10 28.97N/83 28.28W	*Chelonibia testudinaria*/ Stranded *Chelonia mydas* (T-9)	28
F-77B	4/11/2001	Juno Beach, Florida	*Platylepas coriacea*/Nesting *Dermochelys coriacea*	11

Cynthia Lagueux of the Wildlife Conservation Society and was preserved in isopropyl alcohol.

2.2. Sample preparation and analytical methods

Slices were cut perpendicular to the longitudinal midline from the diaphyses of *C. mydas* and *L. olivacea* humeri using a slow-speed diamond saw. X-ray analyses were performed on *D. coriacea* humeri to determine areas of high bone density and slices were cut slowly with a coping saw from these areas. Slices from *C. mydas* and *D. coriacea* humeri were treated in 5% reagent-grade sodium hypochlorite for ~20 h at room temperature and slices from *L. olivacea* humeri were treated for 8 h at room temperature to remove organic material from the bone. The barnacles were treated in 5% reagent-grade sodium hypochlorite for ~24 h at room temperature. The bones and barnacles were rinsed for several days in ~50 aliquots of deionized water at ambient (room) temperature to remove the sodium hypochlorite, air-dried at room temperature, and individual growth layers of cortical bone and barnacles were sampled by hand-filing, shaving, or slow-speed drilling. Muscle tissue was removed from a *D. coriacea* humerus, dried at 25 °C, and ground into a coarse powder. Dried tendon fibers were removed from *C. mydas* and *L. olivacea* humeri and ground into coarse powder. Seagrass samples were dried in an oven at 60 °C and ground into a coarse powder. Scanning electron microscopy and X-ray diffraction analyses of bone slices, before and after treatment with sodium hypochlorite, revealed no secondary calcium carbonate formation or other compositional alterations.

The samples were analyzed using standard techniques. Bone and shell carbonate was converted to CO_2 by reaction with 100% phosphoric acid for ~16 h at 25 °C (McCrea, 1950). Organic samples were converted to CO_2 by dry combustion in an excess of oxygen with CuO as the oxygen source (Boutton, 1991a). The CO_2 from all samples was cryogenically purified and analyzed on a Finnigan-MAT 251 mass spectrometer in the stable isotopes lab at Southern Methodist University Department of Geological Sciences. Precision on replicate isotopic analyses was better than 0.1 ‰ for $\delta^{13}C$.

3. Results

Mean carbon isotope values for bone carbonate and muscle or tendon tissue from three extant species of sea turtles from Costa Rica, Guyana, and Florida and their respective foraging information are presented in Table 3. The bone carbonate $\delta^{13}C$ values of individual growth layers of humeri from seven *C. mydas* turtles from Tortuguero range from −0.7 ‰ to 1.7 ‰, with a mean value of 0.4 ‰. These values are in the same range as those for their commensal barnacles, but are significantly higher than the mean $\delta^{13}C$ values of *D. coriacea* and *L. olivacea* bone carbonate. The $\delta^{13}C$ value for tendon tissue from *C. mydas* is −7.5 ‰, which is 9 ‰ lower than the mean bone carbonate $\delta^{13}C$ value of the same turtle.

The mean $\delta^{13}C$ value for bone carbonate from three *D. coriacea* turtles from Guyana is −8.4 ‰, and $\delta^{13}C$ values of individual growth layers range from −9.8 ‰ to −5.6 ‰ among individuals. The mean $\delta^{13}C$ value for bone carbonate from a single *D. coriacea* individual from Tortuguero is −10.6 ‰ and the $\delta^{13}C$ value of an individual from St. Lucie County, Florida is −12.3 ‰. The $\delta^{13}C$ value for muscle tissue from the Florida *D. coriacea* is −18.1 ‰, which is

Table 3
Foraging information and mean carbon isotope compositions of various tissues for sea turtles in this study

Species	Diet	Foraging location	Maximum/ routine dive depth	Collection locality	Tissue[j]	Sample number	*N* (# growth layers sampled)	Average $\delta^{13}C_{V\text{-}PDB}$ (‰) (mean ± S.D.)
Green turtle (*Chelonia mydas*)	Primarily, sea grass and algae[a]	Throughout the Caribbean, but mainly along the coast of Nicaragua[d]	110 m/ 20–50 m[g]	Tortuguero, Costa Rica	Bone	T-5RH	4	0.8 ± 0.2
					Bone	T-3LH	2	0.4 ± 0.1
					Bone	T-4LH	2	− 0.4 ± 0.0
					Bone	T-7LH	2	− 0.5 ± 0.2
					Bone	T-7RH	8	0.6 ± 0.4
					Bone	T-9LH	6	1.5 ± 0.3
					Bone	T-12LH	4	0.6 ± 0.1
					Tendon	T-9RH	1	− 7.5
Leatherback turtle (*Dermochelys coriacea*)	Primarily, jellyfish and pelagic tunicates[b]	Nearshore and offshore; in surface waters and at great depth; at high and low latitudes[e]	>1000 m/ 50–84 m[h]	Guyana	Bone	CRI-4RH	23	− 6.2 ± 0.3
					Bone	G-1LH	9	− 9.4 ± 0.3
					Bone	A-1LH	2	− 9.7 ± 0.2
				Tortuguero, Costa Rica	Bone	T-51RH	2	− 10.6 ± 0.1
				St. Lucie County, Florida	Bone	F-1LH	3	− 12.3 ± 0.2
					Muscle	F-1LH	1	− 18.1
Olive ridley turtle (*Lepidochelys olivacea*)	Varied carnivorous diet, including crabs, tunicates, shrimp, and fish[c]	Deep water, pelagic habitats, and shallow benthic environments[f]	290 m/ unknown[i]	Ostional, Costa Rica	Bone	O-1LH	2	− 6.8 ± 0.1
					Bone	O-3LH	3	− 7.4 ± 0.3
					Bone	O-7LH	2	− 8.9 ± 0.1
					Tendon	O-7LH	2	− 13.9 ± 0.1

Diet information was summarized from: [a]Bjornal (1980, 1982) and Pritchard and Trebbau (1984); [b]Bleakney (1965), Davenport and Balazs (1991), Den Hartog (1980), Eisenberg and Frazier (1983), and Grant and Ferrell (1993); [c]Carr (1961), Montenegro et al. (1986), and Mortimer (1982). Foraging locations were summarized from: [d]Carr and Hirth (1962), and Carr et al. (1978); [e]Den Hartog (1980), Lazell (1980), Leary (1957), and Lee and Palmer (1981); and [f]Hughes (1974), Plotkin et al. (1994), and Pritchard and Trebbau (1984). Dive depth information was summarized from: [g]Berkson (1967), Brill et al. (1995), and Hays et al. (2000); [h]Eckert et al. (1989) and Eckert et al. (1986); and [i]Plotkin (1994). [j]Tissues analyzed; bone refers to bone carbonate.

5.8 ‰ more ^{13}C-depleted than the bone carbonate from the same turtle.

The mean $\delta^{13}C$ value for bone carbonate from three *L. olivacea* turtles from Ostional is − 7.7 ‰, with $\delta^{13}C$ values of individual growth layers ranging from − 9.0 ‰ to − 6.9 ‰ among individuals. The mean $\delta^{13}C$ value for tendon tissue from *L. olivacea* is − 13.9 ‰, which is 5 ‰ lower than the mean bone carbonate $\delta^{13}C$ value for the same turtle.

Mean $\delta^{13}C$ values for shell carbonate (calcite) from two extant species of barnacles from Costa Rica and Florida are presented in Table 4. The mean $\delta^{13}C$ value for shell carbonate from two *Chelonibia testudinaria* barnacles recovered from the carapace of a stranded

Table 4
Mean carbon isotope compositions of barnacles analyzed in this study

Barnacle species	Host-turtle	Collection locality	Sample number	*N* (# growth layers sampled)	Average $\delta^{13}C_{V\text{-}PDB}$ (‰) (mean ± S.D.)
Chelonibia testudinaria	Stranded green turtle (*Chelonia mydas*)	Tortuguero, Costa Rica	T-16B	28	0.6 ± 0.4
			T-17B	15	1.0 ± 0.2
Platylepas coriacea	Nesting leatherback turtle (*Dermochelys coriacea*)	Juno Beach, Florida	F-77B	5	− 0.6 ± 0.2

green turtle in Tortuguero is 0.8‰, with $\delta^{13}C$ values of individual growth layers ranging from −0.4‰ to 1.2‰ among the two individuals. *Platylepas coriacea*, a barnacle recovered from a leatherback that stranded in Florida, has a mean shell carbonate $\delta^{13}C$ value of −0.6‰.

4. Discussion

4.1. Implications of stable carbon isotopes for sea turtle diet, respiratory physiology, and habitat

The diets of animals are the principal influence on the carbon isotope composition of biogenic carbonate (DeNiro and Epstein, 1978; Lee-Thorp and Van der Merwe, 1987; Quade et al., 1992; Koch et al., 1994), with a $\Delta^{13}C_{bc-f} \approx +9$‰ to 14‰ for terrestrial vertebrates (e.g., Ambrose and Norr, 1993; Koch et al., 1994; Sillen and Lee-Thorp, 1994), where $\Delta^{13}C_{bc-f} = \delta^{13}C_{bc} - \delta^{13}C_f$; $\delta^{13}C_{bc} = \delta^{13}C$ of biogenic carbonate and $\delta^{13}C_f = \delta^{13}C$ of food. Sillen and Lee-Thorp (1994) noted that carbon isotopic fractionation in apatite is similar for terrestrial carnivores and herbivores, with an ~12‰ ^{13}C-enrichment as compared to diet. Collagen is ^{13}C-enriched by approximately 5‰ and muscle tissue is ^{13}C-enriched by 1‰ to 3‰ compared to diet in terrestrial herbivores and carnivores (Koch et al., 1994; Sillen and Lee-Thorp, 1994). $\Delta^{13}C_{bc-f} \approx +8$‰ to 9‰ for carnivorous marine mammals (e.g., Rau et al., 1983; Abend and Smith, 1997; Roe et al., 1998; Kelly, 2000; and Burton et al., 2001) and $\Delta^{13}C_{bc-f} \approx +10-16$‰ for carnivorous sharks (e.g., Rau et al., 1983;Vennemann et al., 2001). In both marine mammals and sharks, collagen is ^{13}C-enriched by approximately 5‰ and muscle tissue is ^{13}C-enriched by 1‰ to 2‰ compared to diet (e.g., Rau et al., 1983; Abend and Smith, 1997; Roe et al., 1998; Vennemann et al., 2001).

When comparing offsets among diets and tissues of vertebrates, $\Delta^{13}C_{bc-f}$ values for shark teeth are larger at low and middle latitudes than those of terrestrial vertebrates, whereas $\Delta^{13}C_{bc-f}$ values for marine mammal bones or teeth are smaller than those of terrestrial vertebrates. CO_2 in aquatic (non-pulmonate) vertebrate tissue isotopically equilibrates with environmental CO_2 more thoroughly than in air-breathing vertebrates (McConnaughey et al., 1997), and dissolved CO_2 in the ocean is ^{13}C-enriched relative to atmospheric CO_2 (Boutton, 1991b). Furthermore, atmospheric CO_2 is ^{13}C-enriched relative to respired CO_2 in air-breathing vertebrates. Because respired CO_2 accumulates in blood and contributes more to the biogenic carbonate of pulmonate taxa than to that of non-pulmonates, as a result of reduced gas exchange in air-breathing organisms (McConnaughey et al., 1997), bone carbonate of gill-respiring marine vertebrates should be more ^{13}C-enriched relative to diet than that of pulmonate vertebrates. This holds true for sharks at low and middle latitudes (e.g., Vennemann et al., 2001) relative to terrestrial and marine air-breathing vertebrates and explains the reduced offset of $\delta^{13}C$ between diet and bone carbonate in marine mammals as compared to sharks. Summaries of carbon isotope fractionation within tissues of marine turtles are presented in Fig. 3 for comparison.

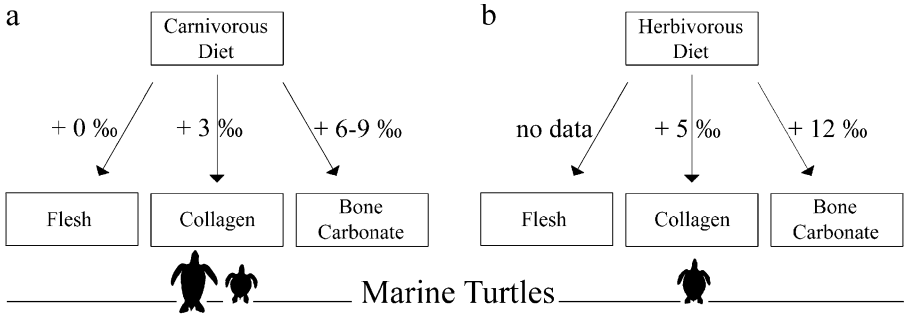

Fig. 3. A preliminary model for carbon isotope fractionation in various tissues of marine turtles: (a) *D. coriacea* and *L. olivacea* and (b) *C. mydas*. Diet $\delta^{13}C$ values are based on data from Rau et al. (1983), Fry (1984), Schoeninger and DeNiro (1984), Fry (1988), Hobson (1990), Minagawa (1992), Van der Merwe et al. (1993), Koch et al. (1994), Abend and Smith (1997), Bonsall et al. (1997), Ginzburg (1999), Vennemann et al. (2001) and this study. Tissue $\delta^{13}C$ values are based on data from this study.

4.1.1. $\delta^{13}C$ variation in bone carbonate from C. mydas humeri

$\delta^{13}C$ values for food sources of sea turtles are shown in Fig. 4. The mean $\delta^{13}C$ value for *C. mydas* bone carbonate is approximately 12‰ higher than the value for its primary food source, *T. testudinum* (Bjorndal, 1980, 1982). This 12‰ difference in value between food source and bone carbonate also occurs in terrestrial herbivores (Koch et al., 1994; Sillen and Lee-Thorp, 1994) and in some other marine vertebrates (e.g., Vennemann et al., 2001). Because green turtles in the Atlantic also ingest algae and small crustaceans (Bjorndal, 1980; Pritchard and Trebbau, 1984), which are ^{13}C-depleted relative to *Thalassia* (e.g., Fry, 1984, 1988; Boutton, 1991b), the 12‰ offset may be a low estimate of the actual ^{13}C-enrichment. Because *C. mydas* neither lives on land nor respires through gills, the magnitude of the offset in bone carbonate $\delta^{13}C$ cannot be the result of *C. mydas* having a respiratory physiology that is similar to sharks or identical to terrestrial vertebrates.

In *C. mydas*, the lung oxygen store is larger than the blood and tissue oxygen store by at least a factor of two, whereas in *D. coriacea* the blood and tissue oxygen store is larger than the lung oxygen store, an adaptation for deep-diving (Lutcavage and Lutz, 1997; Hays et al., 2000). Because *C. mydas* stores a greater percentage of oxygen in the lungs, blood must continually obtain oxygen from the lungs during diving, while lung PO_2 and blood pH are declining. Therefore, the Bohr effect (decreased O_2 affinity of hemoglobin with decline in pH for more efficient release of the last traces of O_2) is decreased in *C. mydas* relative to *D. coriacea*, and oxygen uptake is favored over oxygen release. This enables oxygen stored by the lungs to be used during a dive (Lutcavage and Lutz, 1997). The decreased Bohr effect and higher blood oxygen affinity in *C. mydas* relative to *D. coriacea* results in *C. mydas* having a decreased rate of respiration, reducing the accumulation of respired CO_2 in its blood, which is reflected in bone carbonate $\delta^{13}C$ values (McConnaughey et al., 1997). Therefore, *C. mydas* bone carbonate should be more ^{13}C-enriched relative to diet than that of *D. coriacea* (Fig. 4).

Assume that bone carbonate forms in a locally closed-system, and that this formation occurs as a result of the incorporation of two isotopically distinct blood bicarbonate end members. The first, most ^{13}C-depleted end member, is blood bicarbonate derived from a maximum amount of respired CO_2 (the amount of respired CO_2 accumulated in the body of a deep-diving individual). The second, most ^{13}C-enriched end member, is blood bicarbonate derived from a minimum amount of respired CO_2 (the amount of respired CO_2 accumulated in the body of a shallow-diving individual). The amount of respired CO_2 accumulated in the body is not constant because sea

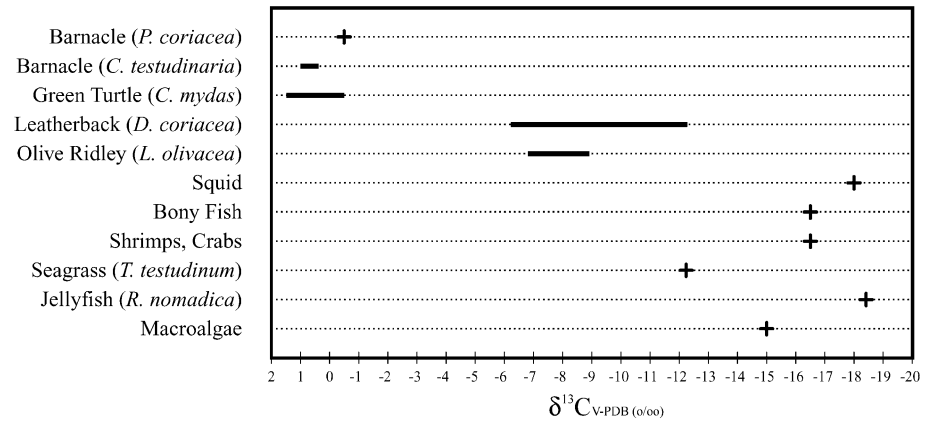

Fig. 4. Mean $\delta^{13}C$ values (+) and ranges (bold lines) for sea turtle bone carbonate, epizoic barnacle carbonate, and soft tissues of common sea turtle food sources. Sea turtle and barnacle data are from this study. Diet $\delta^{13}C$ data are from Rau et al. (1983), Fry (1984), Schoeninger and DeNiro (1984), Fry (1988), Hobson (1990), Minagawa (1992), Van der Merwe et al. (1993), Koch et al. (1994), Abend and Smith (1997), Bonsall et al. (1997), Ginzburg (1999), Vennemann et al. (2001) and this study.

turtles expel respired CO_2 when breathing and dive duration varies for any given individual. Therefore, the actual $\delta^{13}C$ value of blood bicarbonate would lie between the $\delta^{13}C$ values of the end members. This hypothetical relationship can be described with a simple mass balance equation:

$$\delta^{13}C_m = X_d\delta^{13}C_d + X_s\delta^{13}C_s \qquad (4-1)$$

where $\delta^{13}C_m$ = measured $\delta^{13}C$ value of blood bicarbonate; $\delta^{13}C_d = \delta^{13}C$ value of blood bicarbonate derived from a maximum amount of respired CO_2 accumulated in the body of a deep-diving individual; $\delta^{13}C_s = \delta^{13}C$ value of blood bicarbonate derived from a minimum amount of respired CO_2 accumulated in the body of a shallow-diving individual; X_d = mole fraction of blood bicarbonate derived from a maximum amount of respired CO_2; and X_s = mole fraction of blood bicarbonate derived from a minimum amount of respired CO_2. In this two-component mixing model, the sum of X_d and X_s must equal 1, and, therefore, $X_s = 1 - X_d$. Eq. (4-1) can be simplified as follows:

$$\delta^{13}C_m = X_d\delta^{13}C_d + X_s\delta^{13}C_s,$$

therefore,

$$\delta^{13}C_m = X_d\delta^{13}C_d + (1 - X_d)\delta^{13}C_s,$$

and

$$\delta^{13}C_m = (\delta^{13}C_d - \delta^{13}C_s)X_d + \delta^{13}C_s. \qquad (4-2)$$

If we assume that diet and respiration are the only influences on bone carbonate $\delta^{13}C$ values, and that deep-diving pulmonate marine vertebrates remain at depth during bone carbonate formation, their bone carbonate $\delta^{13}C$ values should be $\sim 1‰$ higher than diet $\delta^{13}C$ values (allowing for a 1‰ fractionation during bone carbonate precipitation). Because ^{12}C, which is expelled preferentially by respiratory processes, cannot be expelled from these animals at depth, the isotopic signature of diet should be preserved in the bone carbonate. Conversely, if air-breathing marine vertebrates remain above the ocean surface during bone carbonate formation, expelling respired CO_2 at approximately the same rate as do terrestrial vertebrates, then their bone carbonate $\delta^{13}C$ values should be ^{13}C-enriched relative to diet by approximately the same amount as that in terrestrial vertebrates.

The diet $\delta^{13}C$ value of *D. coriacea*, which is approximately $-18‰$, based on the measured value of muscle tissue in this study, is assumed to approximate the $\delta^{13}C_d$ value for that species. Based on measured values of diet, the $\delta^{13}C_d$ value for *C. mydas* is estimated to be $-12‰$. For *L. olivacea*, the $\delta^{13}C_d$ value is estimated to be $-17‰$, based on diet $\delta^{13}C$ values. All measured values are for bone carbonate rather than blood bicarbonate, therefore all $\delta^{13}C_d$ values must be corrected by 1‰ to account for fractionation during bone carbonate precipitation from blood bicarbonate. Because *C. mydas* is the shallowest-diving sea turtle analyzed in this study, its mean bone carbonate $\delta^{13}C$ value, $\sim 0‰$, approximates the $\delta^{13}C_s$ value for sea turtles. Insertion of the two end-member values, $\delta^{13}C_d$ and $\delta^{13}C_s$, for each species into Eq. (4-2), yields the expressions:

$$\text{for } C.\ mydas\text{: } \delta^{13}C_m \approx -[11‰]X_d, \qquad (4-3a)$$

$$\text{for } D.\ coriacea\text{: } \delta^{13}C_m \approx -[17‰]X_d, \qquad (4-3b)$$

$$\text{and for } L.\ olivacea\text{: } \delta^{13}C_m \approx -[16‰]X_d. \qquad (4-3c)$$

Given that the mean bone carbonate $\delta^{13}C$ value measured ($\delta^{13}C_m$) for *C. mydas* $\approx 0‰$, then $X_d \approx 0$ and $X_s \approx 1$. For *D. coriacea*, the mean $\delta^{13}C$ value for bone carbonate $= -10.4‰$. Therefore, $X_d \approx 0.6$ and $X_s \approx 0.4$. For *L. olivacea*, whose mean $\delta^{13}C$ value $= -7.7‰$, $X_d \approx 0.5$ and $X_s \approx 0.5$. Because *D. coriacea* is the deepest-diver and *L. olivacea* dives deeper than *C. mydas*, the X_d and X_s values for the three species of sea turtles appear to be reasonable.

Because *C. mydas* is a marine vertebrate that spends only 3% to 6% of its lifetime above the ocean surface (Lutcavage and Lutz, 1997), it is unlikely that it expels respired CO_2 at the same rate as do terrestrial vertebrates. Therefore, the relatively higher $\Delta^{13}C_{bc-f}$ of *C. mydas* can possibly be explained by influences additional to diet or respiration, such as by relatively slower metabolic processes, or by the incorporation of dissolved

inorganic carbon from ocean water into its tissues. The mean $\delta^{13}C$ value for *C. mydas* bone carbonate, 0.4 ‰, is within the range of ocean water dissolved inorganic carbon $\delta^{13}C$ values (e.g., Anderson and Arthur, 1983) and barnacle shell carbonate $\delta^{13}C$ values (0 ± 1 ‰). Because barnacles precipitate calcium carbonate shells from ocean water bicarbonate, the $\delta^{13}C$ values of barnacle shells reflect ocean water values. The similar $\delta^{13}C$ values between barnacle shell carbonate and bone carbonate from *C. mydas* suggest that water bicarbonate may be a source for sea turtle bone carbonate, as sea turtles ingest ocean water. It is also a possibility that in *C. mydas*, bone carbonate precipitates only while the turtle is at the surface breathing, thus giving *C. mydas* the same $\delta^{13}C_{bc-f}$ value as that in terrestrial vertebrates.

4.1.2. $\delta^{13}C$ variation in bone carbonate from L. olivacea and D. coriacea humeri

In contrast to *C. mydas*, *L. olivacea* has a varied carnivorous diet, primarily in pelagic environments, but also is known to forage in nearshore waters (Pritchard and Trebbau, 1984; Plotkin, 1994; Bjorndal, 1997). Therefore, its dietary $\delta^{13}C$ value is an average of $\delta^{13}C$ values for the fish and crustaceans that comprise its diet (e.g., Fig. 4). Assuming that the mean $\delta^{13}C$ value for the diet of *L. olivacea* is -17 ‰, then the mean $\delta^{13}C$ value of *L. olivacea* bone carbonate is approximately 9 ‰ higher than the value for its diet. This is comparable to the 9 ‰ ^{13}C-enrichment of cetacean tooth or bone carbonate (e.g., Roe et al., 1998) relative to diet. The mean bone carbonate $\delta^{13}C$ value for *D. coriacea* from Guyana and Tortuguero is 9 ‰ and 8 ‰ higher, respectively, than the $\delta^{13}C$ value (~ -18.5 ‰) found for jellyfish (Ginzburg, 1999), its primary diet (Bleakney, 1965; Den Hartog, 1980; Eisenberg and Frazier, 1983). However, the *D. coriacea* individual from Florida has a mean bone carbonate $\delta^{13}C$ value that is approximately 6 ‰ higher than the value for its diet.

D. coriacea has bone carbonate $\delta^{13}C$ values that are consistent with deep-diving cetacean bone carbonate $\delta^{13}C$ values (e.g., Roe et al., 1998) and hematocrit values that are larger than any other reptile (32% to 38%) and approach the volumes measured in marine mammals (Lutcavage and Lutz, 1997). Therefore, respiration may play a considerable role in the relative ^{13}C-depletion of *D. coriacea* bone carbonate as compared to the other sea turtle species (Table 3). Because *L. olivacea* dives much deeper than *C. mydas* (e.g., Plotkin, 1994; Brill et al., 1995; Hays et al., 2000), *L. olivacea* would be expected to have physiological adaptations similar to those of *D. coriacea*, such as a large blood and tissue oxygen store and an increased respiratory rate, causing a greater accumulation of blood CO_2 during breath-hold dives, resulting in a smaller offset between diet and bone carbonate as compared to *C. mydas.* Because the bone carbonate in *L. olivacea* appears to be more isotopically similar to that in *D. coriacea* than to the bone carbonate in *C. mydas*, it is not apparent that the differences in skeletal growth characteristics between the families Dermochelyidae and Cheloniidae have an effect on carbon isotope compositions.

The *D. coriacea* individual collected in Florida was a large adult male, compared to the other *D. coriacea* specimens collected for this study, which were smaller adult females. Because of the larger size of the male specimen, it is possible that the male may have foraged at higher latitudes, resulting in a lower bone carbonate $\delta^{13}C$ value relative to its diet as compared to the female specimens. Additionally, although not conclusive as a result of the current sample size, the average $\delta^{13}C$ values of *D. coriacea* bone carbonate decrease with increasing latitude of the beaches from which the bones were collected (Fig. 5).

The mean bone carbonate $\delta^{13}C$ value for *L. olivacea*, -7.7 ‰, is approximately 8 ‰ lower than the mean bone carbonate $\delta^{13}C$ value for *C. mydas* but is 1 ‰ to 5 ‰ higher than the mean bone carbonate $\delta^{13}C$ values of the three different populations of *D. coriacea*. Although respiratory physiology appears to affect bone carbonate $\delta^{13}C$ values, most of the difference between the $\delta^{13}C$ values of *L. olivacea* and *C. mydas* can be explained by diet and foraging locality. The diet of *L. olivacea* is, on average, at least 5 ‰ lower in $\delta^{13}C$ than that of *C. mydas* (e.g., Fig. 4). This accounts for approximately 5 ‰ of the 8 ‰ difference in mean $\delta^{13}C$ values between *L. olivacea* and *C. mydas*. Because *L. olivacea* primarily forages offshore (Hughes, 1974; Pritchard and Trebbau, 1984; Plotkin et al., 1994) and *C. mydas* forages nearshore (e.g., Carr and Hirth, 1962), the bone carbonate $\delta^{13}C$ value is expected to be additionally decreased by 1–2 ‰ in

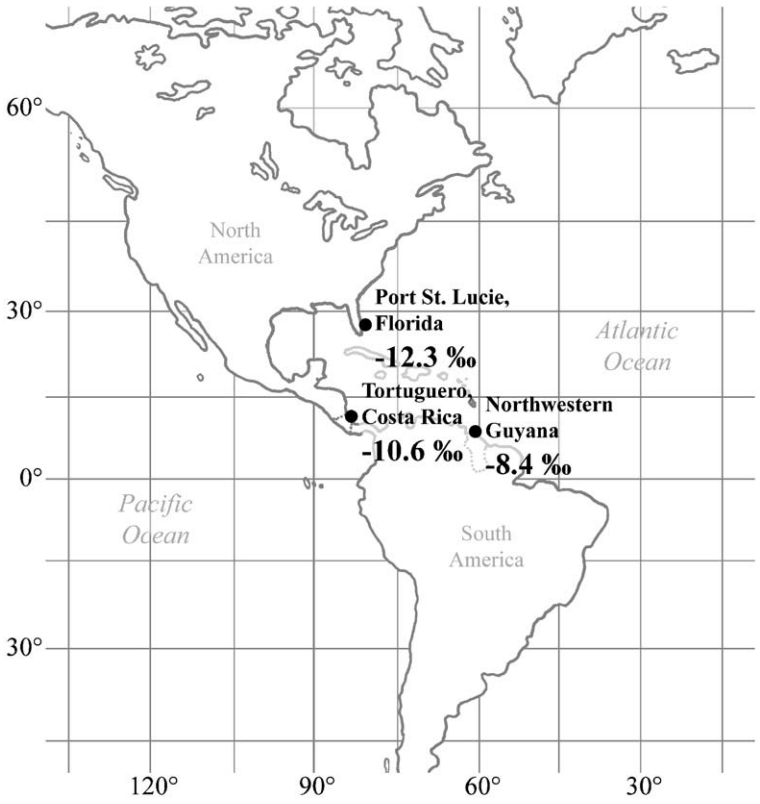

Fig. 5. $\delta^{13}C$ values of bone carbonate from *D. coriacea* humeri decrease with increasing latitude of collection site. Numerical values represent the deviation, in per mil, of $^{13}C/^{12}C$ of the sample from that of the standard V-PDB.

L. olivacea relative to *C. mydas*. The same argument holds true for *D. coriacea*, a frequent offshore feeder (Pritchard and Trebbau, 1984), relative to *C. mydas*. Likewise, because *D. coriacea* often forages at higher latitudes than *C. mydas* and *L. olivacea* (e.g., Den Hartog, 1980; Pritchard and Trebbau, 1984), the $\delta^{13}C$ value of *D. coriacea* is expected to be decreased by 1–2 ‰ as compared to the $\delta^{13}C$ values of *C. mydas* and *L. olivacea*.

5. Conclusions

Bone carbonate appears to be a reliable source material for carbon isotopic analyses of modern taxa. The carbon isotope composition of sea turtle bone carbonate is primarily a function of diet, but is also affected by respiratory physiology. The data in this study show that the offset between diet $\delta^{13}C$ and bone carbonate $\delta^{13}C$ is greatest in *C. mydas*, the shallowest-diving turtle, and lowest in the deep-diving turtles, *L. olivacea* and *D. coriacea*. Because deep-divers incorporate more respired CO_2 into their bone carbonate, which should reduce the offset between diet $\delta^{13}C$ and bone carbonate $\delta^{13}C$, the data supports the hypothesis that respiratory effects are evident in bone carbonate $\delta^{13}C$ values. Therefore, isotopic analyses of structural carbonate can be an important tool in understanding respiratory physiology.

In contrast, the carbon isotope compositions of bone collagen and muscle tissue do not appear to be affected by respiration. Therefore, bone collagen and muscle tissue should more accurately indicate the isotopic composition of diet. Other factors that influence the carbon isotopic composition of sea turtle bone carbonate are foraging proximity to coastline, geographical range, and physiological interactions with water bicarbonate.

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