Hungry Hungry Honu: East Hawai'i Island green turtle (*Chelonia mydas*) diet determination utilizing stable isotopes $(\delta^{13}C \text{ and } \delta^{15}N)$

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Abstract:

Stable carbon (δ^{13} C) and nitrogen (δ^{15} N) isotopes are frequently utilized to determine the origin of nutrients in the diets of wildlife. The consumption of organic matter throughout an animal's life results in the deposition of isotopic signatures which can elucidate the prey and trophic level an animal feeds on. Adult green turtles (*Chelonia mydas*) are considered herbivorous animals that feed primarily on coastal seagrasses and macroalgae, but juveniles are opportunistic omnivores. Green turtles throughout their lives may feed on protein-rich items such as fish bait when the opportunity allows. Samples of skin were analyzed from 17 green turtles that had stranded between March 2020 to June 2022 from eight locations on the east coast of Hawai'i island. The turtles ranged in size from 36.1 - 78.5 cm curved carapace length (CCL) indicating size classes of juvenile to sub-adult. Mean δ^{13} C ‰ was - 15.9 ± 1.55 SD and mean δ^{15} N ‰ was 8.63 ± 1.41 SD. These values for east Hawai'i Island turtles are similar to those in previous studies on green turtles found at Palmyra Atoll, Fiji, and the Eastern Pacific. These values are consistent with a marine plant diet. The conservation of marine plant populations in the Hawaiian Islands is essential for the management of healthy green turtle populations.

Keywords - Feeding Ecology, Food Web, Diet Determination, Primary Consumer, Isotope Cycling

Introduction

Since the late 1970s, stable carbon and nitrogen isotopes have been utilized to determine the origin of nutrient resources in the diets of wildlife (DeNiro & Epstein 1978). The consumption of organic matter throughout an animal's life results in the deposition of isotopic profiles within the tissue (Seminoff et al. 2009). Carbon and nitrogen isotopes are deposited in tissue over time and can give information on longer term diet than other methods i.e. gut analysis, mouth sampling, crop lavages, and direct observation (DeNiro & Epstein 1981). Samples from multiple specimens within a population provide data on consumption patterns at a specific trophic level (Seminoff et al. 2009). For sea turtles, stable isotopes have been used to study migratory paths and to map feeding locations during their life history (Ceriani et al. 2012, Vander Zanden et al. 2015, Haywood et al. 2020).

The ratios of δ^{13} C (ratio of 13 C: 12 C) and δ^{15} N (ratio of 15 N: 14 N) are the two most frequently utilized isotopes to study dietary interactions (Post 2002). The δ^{13} C is used to identify the primary producers because this form of carbon remains unchanged throughout a food chain (Post 2002). However, nitrogen ratios are enriched in organisms higher in the food chain because 14 N isotopes are excreted preferentially, thus leaving higher 15 N levels within the organisms (DeNiro and Epstien 1989).

Epidermis tissue (subsequently referred to as 'skin') samples provide a recent history of feeding preferences; however, there have been no studies that directly determine the isotopic replenishment rate or turnover for adult sea turtle skin. However, adult freshwater pond sliders (*Trachemys scripta*) which are commonly used as a surrogate for sea turtles exhibit an estimated isotopic turnover rate in their skin of approximately four to six months (Seminoff et al. 2007, Seminoff et al. 2012). Based on tissue turnover rates in hatchlings and small juvenile sea turtles in captivity, isotope ratios are estimated to reflect habits at least four months prior to sampling (Reich et al. 2008, Seminoff et al. 2007, Reich et al. 2010, Ceriani et al. 2014)

After leaving their natal beach, green turtles spend the first period of their life in the open ocean. During these three to five years, the juvenile green turtles are opportunistic omnivorous feeders and consume a varied diet of pelagic planktonic items (Bolten 2003, Cardona et al. 2010). After their pelagic period, juvenile green turtles migrate to coastal environments where they transition to an herbivorous diet (Bjorndal 1980, Bjorndal and Bolten 1988, Bolten 2003, Balazs and Chaloupka 2004a, Reich et al. 2007, Arthur and Balasz 2008). According to previous stable isotope analysis studies (Godley et al. 1998, Hatase et al. 2006, Cardona et al. 2010) and gut content analysis (Limpus et al. 1994, Seminoff et al. 2002, Amorocho and Reina 2007), the exact

1.

time frame of diet change is variable among individuals when they make the switch. Turtles are thought to make this transition to nearshore environments when their straight carapace length (SCL) is around 35 cm in length (Zug et al. 2006). Adult green turtles migrate incredible distances between reproductive and feeding grounds (Hays and Hawkes 2018). Despite the distance, sea turtles are able to display high levels of site fidelity to specific feeding areas despite completing multiple migratory events within their life without issue (Shimada et al. 2020).

The switch to a herbivorous diet remains permanent throughout the remaining life of green turtles; this diet is the foundation of the common perception of sea turtles grazing on coastal macroalgae and seagrasses (Bjorndal 1980). The ecological impact of green turtles as megaherbivores in seagrass meadows is well documented (Frazier 1971, Hirt et al. 1973, Bjorndal 1980, Mortimer 1981, Bjorndal & Bolten 2003, McClenachan et al. 2006, Heithaus et al. 2008, Vander Zander et al. 2013, Heithaus et al. 2014). Seagrasses are the primary diet in populations of green turtles located on the coast of the Mediterranean (Margaritoulis & Teneketzis 2003, Cardona 2010), atolls in the Indian Ocean (Hasbún et al. 2000, Whiting et al. 2007), coastal areas of Australia (Arthur et al. 2009), and the Caribbean (Mortimer 1981).

In areas where seagrasses are sparse, turtles consume a diet either supplemented or primarily composed of macroalgae (Balazs 1976, Garnett et al. 1985, Limpus et. al 2005, Shimada et al. 2014, Whiting et al. 2014). Mangrove leaves and propagules are frequently found in diet analysis of green turtles found in some locations (Limpus & Limpus 2000, Arthur et al. 2009). In Hawai'i, coastal terrestrial grass, terrestrial leaves, and other items are occasnionally found within sea turtle stomachs (Russell et al. 2011) Other reports suggest adults may opportunistically feed on on invertebrates when available such as sponges, molluscs, fish, or macrozooplankton (Mortimer 1981, Bjorndal 1997, Burkholder et al. 2011, Russell et al. 2011, Fukuoka et al. 2016, Piovano et al. 2020). Preference for certain plant food items has been demonstrated in populations found in Australia (Brand-Gardner et al. 1999), but, diet selection is thought to be driven by availability of items (Forbes 1996)

In the main Hawaiian islands, green turtles primarily consume abundant red macroalgae (*Rhodophyta*) (Arthur & Balazs 2008). Green (*Chlorophyta*) and brown (*Phaeophyta*) macroalgae are also consumed by turtles when available (McDermid et al. 2007). Two seagrasses, *Halophila decipiens* and *H. hawaiiana* have also been reported to make up a substantial portion of turtle's diet, but only in areas that provide habitat for seagrass growth, e.g. near O'ahu (Russell et al. 2003). In a study conducted with turtles taken from Pālā'au, Moloka'i, the red algaes *Acanthrophora spicifera, Amansia glomerata, Gracilaria salicornia, Hypnea*

cervicornis, Hypnea musciformis and *Spyridia filamentosa* were commonly occurring species found to be consumed by turtles (Balazs et al. 1987, Russell & Balazs 2009).

The present study used stable isotope analysis of skin samples to investigate the diets of green turtles from the east coast of Hawai'i Island. The hypothesis was that the δ^{13} C and δ^{15} N values indicate a macroalgal diet and that the isotope ratios would not differ significantly from values reported from other green turtle populations.

Methods

2.

Seventeen samples of *Chelonia mydas* skin were obtained from turtles that stranded between March 2020 and June 2022, from eight separate locations on the east coast of Hawai'i Island (Figure 1). Stranding reports contained data on date, location, curved carapace length (CCL), current condition, and tag number if present. CCL was utilized as a proxy for age; individuals with a CCL less than 70 cm were considered juveniles, individuals with a CCL of 70 to 86 cm were grouped as sub-adults, and individuals with a CCL of over 87 cm were recognized as adults (Balazs 1980).



Figure 1: Stranding locations of green turtles (*Chelonia mydas*) on the east coast of Hawai'i Island.

The deceased turtles were taken to the University of Hawai'i at Hilo and frozen for preservation until transport to National Marine Fisheries Service on O'ahu on June 23, 2022 where necropsies were conducted on August 11, 2022. Skin samples were removed from the hind flippers close to the tail with a scalpel, and frozen in individual, labeled Whirlpak bags, and then

transported back to the Marine Science Department at the University of Hawai'i at Hilo on August 18, 2022.

Skin samples were rinsed with deionized water, before being weighed on a Scout Pro Model SP 402 for wet weights. Samples were then diced with a scalpel and dried in aluminum weighing dishes at approximately 60°C for a minimum of 24 hours in a FisherSci model oven.

The skin samples were dried to a constant weight and dry weights were recorded. Samples were ground with a mortar and pestle by hand into a fine powder. Some samples were pulverized in a Wig-L-Bug Grinding Mill to improve grinding. Powdered samples were returned to weigh boats in the oven temporarily until they were loaded into sterilized tin capsules. Between processing steps, samples were kept stored in the oven to prevent rehydration. (Seminoff et al. 2006)

Prepared samples in tin capsules were analyzed by the Analytical Laboratory at the University of Hawai'i at Hilo. Nitrogen and carbon were assayed using a Thermo Delta V IRMS machine. Some samples were randomly picked and processed as duplicates to test for consistency of ratio values, but were not used during data analysis.

The abundance of stable isotopes were reported as δX with X representing either ¹³C or ¹⁵N. To represent the ratio of isotopes, the R_{sample} and R_{standard} concept is used with respect to the heavy and light isotopes (¹³C/¹²C and ¹⁵N/¹⁴N). δX values past tense recorded as per mil (parts per thousand difference from international standard) and were calculated using the formula: $\delta X = 1000 \text{ x} ([(R_{sample} / R_{standard}] - 1))$

Results of isotope ratios were compared to the standards set forth by the United States Geological Survey (USGS). The R_{standard} for ¹³C was Vienna PeeDee Belemnite (VPDB) [40 (δ^{13} C vs VPDB = -26.4) & USGS 41 δ^{13} C vs. VPDB = 37.6)], and R_{standard} for ¹⁵N was normalized to atmospheric nitrogen [USGS 40 (δ^{15} N vs. Air = -4.5) & USGS 41 (δ^{15} N vs Air = 47.6)]. Both R_{standards} were accurate to 0.2‰. Two laboratory standards were run alongside the samples to verify the accuracy and precision of the spectrometer.

Results are reported as mean ± standard deviation (SD). Statistical analysis was performed using RStudio program version 1.4.1106 and GoogleSheets.

Results

3.

Skin samples (n = 17) from turtles that were found stranded at eight different locations on the east coast of Hawai'i Island (Table 1) were analyzed. The wet weight of samples ranged from 0.07 g to 0.31 g, after drying samples weighed from less than one gram to 0.14 g. The curved carapace lengths (CCL) of 16 turtles ranged from 36.1 - 75 cm in length (mean \pm SD = 57 \pm 15 cm) (Figure 2). One turtle (H391/H392 (MIS)) was recorded with a straight plastron length. This

choice in measurement method lacks a conversion method to curved carapace length (CCL), and has been omitted from size-related data as a result. Based on CCL measurements, juvenile turtles comprised of 65% (n = 11) used in this study of the stranded individuals, and the remaining 35% (n = 6) were classified as sub-adults (Table 2).

		Date Collected	CCL
Location Collected	Sample ID	(YYYY/MM/DD)	(cm)
Lili'uokalani Park and Garden	8		
	H341	2020/04/16	41
	H343	2020/05/18	41
	H359	2021/04/12	45
Moku Ola			
	H386 (MIS)	2022/03/02	45.5
	H387	2022/03/08	49.5
Onekahakaha Beach Park			
	H346	2020/07/31	78
	H371	2021/10/03	56
Private Residence			
	H391/H392 (MIS)	2022/05/07	
Punalu'u Beach Park			
	H374 (N799)	2021/12/02	75
Reed's Bay			
	H339	2020/03/24	55.5
	H380	2021/12/12	42
Richardson's Ocean Park			
	H354	2021/02/02	53.5
	H360	2021/04/15	78.5
	H361	2021/04/21	74
	H375	2021/12/10	41
	H383	2022/02/08	68.25
Wailoa River State Park			
	H400	2022/06/27	71

Table 1: Stranded green turtles (*Chelonia mydas*) found along the east coast of Hawai'i island between 2020 and 2022 categorized by the locations stranding occurred at. Curved carapce length (CCL) is given in centimeters.



Figure 2: The curved carapace length (CCL) of stranded green turtles (*Chelonia mydas*) found along the east coast of Hawai'i island between 2020 and 2022 that were utilized in this study as a proxy for age.

	Average CCL (cm)	Average δ ¹³ C	Average δ ¹⁵ N
Juveniles (<70 cm CCL) (n = 11)	47 (6.2)	-15.3 (1.43)	9.1 (1.6)
Subadults (71-86 cm CCL) (n = 6)	74 (4)	-16.9 (1.44)	7.9 (0.75)

Table 2: Mean curved carapace length (CCL) measurements (\pm SD) and mean skin tissue isotopic signatures (\pm SD) from age classes of stranded green turtles (*Chelonia mydas*) found along the east coast of Hawai'i island between 2020 and 2022 Age classes were defined as juvenile (> 65 cm CCL) and sub-adult (65 - 83 cm CCL).

The average value of δ^{13} C found within the samples was -15.9 (± 1.55), with values ranging from -14.3 to -18.0 (Figure 3). The average value of δ^{15} N was 8.6 (± 1.41), with values ranging from 6.2 to 11.9 (Figure 4).



Figure 3: The composition of δ^{13} C (± SD) in skin tissue samples from stranded green turtles (*Chelonia mydas*) found along the east coast of Hawai'i island between 2020 and 2022



Sample ID

Figure 4: The composition of $\delta^{15}N (\pm SD)$ in skin tissue samples from stranded green turtles (*Chelonia mydas*) found along the east coast of Hawai'i island between 2020 and 2022

Level recorded of δ^{15} N and δ^{13} C varied based on individuals. The turtle with the highest value of δ^{15} N was Turtle H371 (-12) (Figure 7), while Turtle H383 had the lowest value (-18)

(Figure 8). The turtle with the lowest value of δ^{13} C was Turtle H354 (6.2) (Figure 6) while Turtle H386 (MIS) had the highest value (11.9) recorded (Figure 8).



Figure 5: The composition of δ^{15} N and δ^{13} C in skin tissue samples taken from stranded turtles H339, H341, H343, and H346.



Figure 6: The composition of δ^{15} N and δ^{13} C in skin tissue samples taken from stranded turtles H354, H359, H360, and H361.



Figure 7: The composition of δ^{15} N and δ^{13} C in skin tissue samples taken from stranded turtles H371, H374 (N799), H375, H380.



 $\bullet \delta^{15} \mathsf{N} \bullet \delta^{13} \mathsf{C}$

Sample ID

Figure 8: The composition of δ^{15} N and δ^{13} C in skin tissue samples taken from stranded turtles H383, H386 (MIS), H387, H-391/392 (MIS), and H400.

4.

Discussion

The results of isotope levels are consistent with prior assumptions that after recruiting from the pelagic environment, sea turtles in Hawai'i primarily consume macroalgae. The lower nitrogen values that are present in subadults, and enriched in juveniles can be explained by this transition from animal to plant items in their diet. The existence of depleted values in juveniles or enriched subadults can be explained by either these individuals still consuming an omnivorous diet with a late dietary switch or a more recent transition to the neritic environment. East Hawai'i turtles may also supplement their diets with higher trophic level dietary items when opportunities are present.

The juvenile turtles presented with the most depleted carbon values. This can be indicative of a recent dietary shift from pelagic planktonic items to a coastal marine plant diet. However, the juvenile signatures were not significantly different from the sub-adult turtles which were slightly more enriched with carbon. Both the juvenile and subadult carbon values are indicative of a macroalgae diet. According to Arthur and Balazs (2008), macroalgae is a prey source that is considered to be further depleted in δ^{13} C when compared to seagrasses.

The subadult turtles possessed an overall depleted nitrogen value than the juvenile turtles. This suggests that the subadults were feeding on a higher trophic level than the juveniles prior to stranding (Arthur et al. 2009) The proteins in prey items are the main source for ¹⁵N, while ¹³C is able to be extracted from proteins, lipids, and carbohydrates. As a result, the turnover rate of epidermis layers, the dietary quantity of proteins in the individual turtle's diet, and turnover of protein consumption can affect the isotopic accumulation rate more frequently for nitrogen than carbon (Robbins et al. 2005, Robbins et al. 2010). In turtles, stable carbon ratios are reported to be enriched at levels approximately 0 - 1‰ higher than their prey (Seminoff et al. 2006) while nitrogen may be enriched at levels closer to 0.22 - 2.92‰ than prey (Seminoff et al. 2006).

As no prey samples were collected during the time frame of strandings for the turtles utilized in this study, no direct comparison of values could be made to showcase the variability in the diet. However, other studies conducted are able to indicate the values of carbon and nitrogen isotopes found with other populations which can be indicative of what can be expected from turtles who are consuming a diet of other items (Arthur et al. 2009, Kelly 2012) (Table 3).

Although isotopic signatures can not be directly compared across regions of feeding because of variables of baseline isotopic values by location or prey type, inferences of dietary preference indications can be made from literature analysis of generalized results of species' isotope levels. Showed turtles taken from Australia (Arthur et al. 2009) and Palmyra Atoll (Kelly 2012) all possessed enriched carbon values when compared to the individuals from east Hawai'i turtles. Hawai'i turtles consume a diet of macroalgae, rather than seagrasses unlike Australian and Palmyra turtles (Arthur et al. 2009, Kelly 2012). Differences can be attributed to environmental conditions differing isotopic signatures within regions (Pajuelo et al. 2012), location of sampling, and preferential consumption differences.

Food Source Option	δ ¹³ C	(‰)	δ ¹⁵ N	[(‰)
(Prey)	Mean	±SD	Mean	±SD
Values taken from Literature				
Macroalgae	-15.0	7.05	6.55	2.28
Chlorophyta	-15.97	6.54	6.22	2.10
Phaeophyta	-11.52	4.89	7.14	3.00
Rhodophyta	-17.72	5.34	6.84	1.18
Invertebrates	-11.69	5.21	9.52	0.29
East Hawaiʻi turtles				
Green Turtle ($n = 17$)	-15.9	1.55	8.6	1.41

Table 3: Mean isotopic values of prey items taken from the literature (Appendix A) to compare with east Hawai'i turtles values. Prey groups include Macroalgae (green algae (*Chlorophyta*), brown algae (*Phaeophyta*), red algae (*Rhodophyta*)), Seagrasses, Mangroves, Zooplankton, and Invertebrates. Mean \pm SD skin isotopes for sampled green turtles within the study from east Hawai'i also included for visual comparison.

No significant differences were found in nitrogen and carbon values among species. Small sample sizes from locations or different prey availability could explain the lack of statistical significance with isotope values. Further research can be conducted to explore the values of nitrogen and carbon isotopes within local Hawai'i macroalgal populations.

Hawai'i Island turtles may face physiological factors affecting the processing of proteins or other molecules into tissues which would affect the levels of isotopes present within tissue (Seminoff et. al 2006). Differences in individuals' growth, age, and dietary preferences and compositions may also exist between the populations referenced in the study (Seminoff et al. 2006, Arthur et al. 2008, Reich et al. 2008, Kelly 2012) which would affect the isotope values. Prey groups in literature frequently overlap and are not considered to be significantly different in many cases which limits accuracy. Incorporation of more species or groups for comparison may be beneficial for future studies.

Understanding the importance of marine plants in the diet of green turtles is essential in managing turtles as an endangered species. Sea turtles play an important position in the coastal marine ecosystem as a herbivore, and it is critical to maintain suitable habitats for their feeding to occur. The body condition of turtles living within a region can also provide researchers with an idea of the overall health of an ecosystem, by judging the success of a primary consumer (Wabnitz et al. 2010). To regulate the threat of human activities to ecosystems, potential solutions include creating more Marine Protected Areas (MPAs) in critical habitat locations and implementing local beach restoration efforts. Proper resource management is needed to maintain the protection of these vulnerable areas to prevent habitat loss.

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Prey Group	Source	Species	Sampling Location	δ ¹³ C (‰)	± SD	δ ¹⁵ N (‰)	± SD
Chlorophyta				-15.9 7	6.54	6.2 2	2.10
Avrainaville				-19.9		8.0	
а	Kelly 2012		Palmyra Atoll	2		3	
				-14.0		6.0	
	Kelly 2012		Palmyra Atoll	0		4	
				-163		67	
Bryonsis	Kelly 2012		Palmyra Atoll	-10.5		4	
Dijopolo	110119 2012		1 4111 / 14 1 10011	173		73	
	Kelly 2012		Palmyra Atoll	-17.5		8	
	11011y 2012		i unitytu i ttori	-		-	
				10.0			
Caulama	Kaller 2012		Delmarma Atell	-12.2		5.3	
Caulerpa	Kelly 2012		Palmyra Atoli	/		0	
	V 11 2012			-11.2		6.1	
	Kelly 2012		Palmyra Atoli	9		0	
	W 11 0010			-13.9		5.3	
	Kelly 2012		Palmyra Atoll	0		8	
				-15.4		7.0	
	Kelly 2012		Palmyra Atoll	0		6	
				-14.1		5.3	
	Kelly 2012		Palmyra Atoll	7		1	
	Hyndes &	С.	nearshore waters,				
	Lavery 2005	gemminata	SW Australia	-13.4		5.5	
	Hyndes &		nearshore waters,				
	Lavery 2005	C. flexilis	SW Australia	-12.6			

Raven et al. 2002	C. cactoides	Coobowie Bay, SA, Australia	-21.3 5
Raven et al. 2002	C. flexilis	Coobowie Bay, SA, Australia	-32.9 8
Raven et al. 2002	C. microphysa	W Flower Garden, Gulf of Mexico (GoM)	-22.7 9
Raven et al. 2002	C. microphysa	W Flower Garden, GoM	-20.3
Raven et al. 2002	C. microphysa	Sonnier, GoM	-19.6
Raven et al. 2002	C. microphysa	Stetson, GoM	-19.9 4
Raven et al. 2002	C. microphysa	Stetson, GoM	-20.9 7
Raven et al. 2002	C. microphysa	E Flower Garden, GoM	-19.9 9
Raven et al. 2002	C. obscura	Stragglers, WA, Australia	-20.3 3
 Raven et al. 2002	C. obscura	Carnac Island, WA, Australia	-30.1 8

Prey				δ ¹³ C	±	δ ¹⁵ Ν (‰	±
Group	Source	Species	Sampling Location	(‰)	SD)	SD
			Carnac Island, WA,	-29.5			
	Raven et al. 2002	C. obscura	Australia	9			
			Hamelin Bay, WA,	-31.3			
	Raven et al. 2002	C. obscura	Australia	3			
			Mewstone, WA,	-28.9			
	Raven et al. 2002	C. obscura	Australia	9			

Raven et al. 2002	C. obscura	Mewstone, WA, Australia	-28.5 9	
Raven et al. 2002	C. obscura	Stragglers, WA, Australia	-30.1 2	
Raven et al. 2002	C. obscura	Stragglers, WA, Australia	-28.3 9	
Raven et al. 2002	C. obscura	The Lumps,WA, Australia	-25.9 2	
Raven et al. 2002	C. obscura	The Lumps, WA, Australia	-31.3 8	

8.2

Cladopho

ra	Kelly 2012		Palmyra Atoll	-9.12	0
	Kelly 2012		Palmyra Atoll	-9.57	7.4 4
	Kelly 2012		Nursery	-15.1 4	6.6 4
	Dailer et al. 2010	C. sericea	NW Maui		0.2
	Vizzini & Mazzola 2003	Cladophora sp.	Lake of Sabaudia, Italy	-15.9	5.9
	Lepoint et al. 2000	C. proliphera	Gulf of Calvi, Corsica	-17.5	4
	McClelland et al. 1998	C. vagabunda	Pond/River, Mass., USA	-15.2	5.4
	Maberly et al. 1992	C. sericea	Tentsmuir Drift, East Coast Scotland	-19.3 5	
	Maberly et al. 1992	C. rupestris	Mid-Shore, East Coast Scotland	-16.6 6	
	Maberly et al. 1992	C. rupestris	Sheltered Rock Pool, , East Coast Scotland	-13.3 3	

Raven et al. 2002	C. albida	Filey, England	-10.8 3
Raven et al. 2002	C. hutchinsonia	Filey, England	-12.1 5
Raven et al. 2002	C. rupestris	Fifeness, England	-14.0 2
Raven et al. 2002	C. rupestris	Filey, England	-18.0 9
Raven et al. 2002	C. rupestris	East Sands, Scotland	-15

Prey Group	Source	Species	Sampling Location	δ ¹³ C (‰)	± SD	δ ¹⁵ N (‰)	± SD
	Raven et al. 2002	C. rupestris	East Sands, Scotland	-15.3 7			
	Raven et al. 2002	C. rupestris	Hemsdale, Scotland	-14.3 3			
	Raven et al. 2002	Cladophora sp.	Gran Canaria	-16.1 2			
Codium	Kelly 2012		T.H.	-9.82		7.4 7	
	Kang et al. 2008	C. arabicum	Samchoek Coast, Korea	-10.3		3.8	
	Lepoint et al. 2000	C. bursa	Gulf of Calvi, Corsica	-10.3		3.1	
	Hydes & Lavery 2005	C. duthaeie	SW Australia (Nearshore)	-15.5		4.8	
	Maberly et al. 1992	C. fragile	Rockpool, East Coast Scotland	-15.0 1			

Maberly et al. 1992	C. fragile	Sheltered Rockpool, East Coast Scotland	-14.0 8
Maberly et al. 1992	C. fragile	Sheltered Rockpool, East Coast Scotland	-10.2 3
Maberly et al. 1992	C. fragile	Fife Ness, East Coast Scotland	-15.3 8
Raven et al. 2002	C. convulutum	Brighton Beach / Papatowai Beach, New Zealand	-14.5 4
Raven et al. 2002	C. fragile	California, USA	-11.7
Raven et al. 2002	C. fragile	California, USA	-11.1 5
Raven et al. 2002	C. fragile	Brighton Beach / Papatowai Beach, New Zealand	-12.0 4
Raven et al. 2002	C. fragile	Brighton Beach / Papatowai Beach, New Zealand	-15.4 6
Raven et al. 2002	C. fragile	Helmsdale, Scotland	-12.8 7
Raven et al. 2002	C. fragile	St. Andrews, Scotland	-13.2 6
Raven et al. 2002	C. hubsii	Catalina Island, CA	-8.17
Raven et al. 2002	Codium sp.	Fifeness, Scotland	-10.8 6
Raven et al. 2002	Codium sp.	Gran Canaria	-9.86
Raven et al. 2002	Codium sp.	Gran Canaria	-14.4 7

			Sampling	δ ¹³ C	±	$\delta^{15}N$	±
Prey Group	Source	Species	Location	(‰)	SD	(‰)	SD

	Raven et al. 2002	Codium sp.	Hampton Bay, Long Island, NY	-15.7 6	
	Wang & Yeh 2003	C. mamillosum	sublittoral, North Taiwan	-14.2	
Dictyosphae					
ria	Kelly 2012		Palmyra Atoll		
	Kelly 2012		Palmyra Atoll		
	Raven et al. 2002	D. sericea	Rottnest Island, WA, Australia	-6.33	
Halimeda	Kelly 2012		Palmyra Atoll	-11.2 5	6.66
	Kelly 2012		Palmyra Atoll	-4.86	10.0 2
	Kelly 2012		Palmyra Atoll	-7.86	8.05
	Kelly 2012		P.S.	-4.76	8.60
	Lepoint et al. 2000	H. tuna	Gulf of Calvi, Corsica	-19.3	1.3
	Raven et al. 2002	Halimeda sp.	Gran Canaria	-11.3 3	
	Raven et al. 2002	Halimeda sp.	Singapore	-6.83	
	Wang & Yeh 2003	H. macroloba	Tidal Pool, South Taiwan	-21.2	
	Wang & Yeh 2003	H. opuntia	Tidal Pool, South Taiwan	-19.7	
Unknown				-10.7	
sp.	Kelly 2012		Palmyra Atoll	5	7.02

				-11.8			
Valonia	Kelly 2012		Palmyra Atoll	2		8.06	
				-16.8			
	Kelly 2012		Palmyra Atoll	4		8.82	
	Raven et al.			-14.8			
	2002	V. clavata	Gran Canaria	3			
				-11.5			3.0
Phaeophyta				2	4.89	7.14	0
				12.5			
Acathophora	Kelly 2012		Palmyra Atoll	0		8.58	
			Nearshore reef,				
	Lin & Fong	4	Opunohu Bay,			C	
	2008	A. spicifera	Moorea			6	
	Wang & Vah	1 anicifaua	Upper-tidal pool,	12.0			
	wang & Yen	A. spicijera	East Taiwaii	-13.9			
Dotyophycu							
S	Kelly 2012		Palmyra Atoll	-7.96		8.86	
							±
Prey	~	~ .	~	δ ¹³ C	~~	δ ¹⁵ N	S
Group	Source	Species	Sampling Location	(‰)	± SD	(‰)	D
Dictvota	Lepoint et al. 2000	Dictvota spp	Gulf of Calvi, Corsica	-174		36	
,	Umezawa et al		Offshore Reef	- / • •		2.0	
	2002	Dictyota spp.	Ishigaki Island, Japan			2	
	Umezawa et al.	_	Nearshore Reef,			_	
	2002	Dictyota spp.	Ishigaki Island, Japan			8	
	Newell et al.			-19.9		10.3	
	1995	D. dicotoma	Peninsular Malaysia	4		6	

	Raven et al.	D.		-15.0	
	2002	cervicornus	Stetson, GOM	6	
	Raven et al. 2002	D. dichotoma	N of Oban. Scotland	-18.4 3	
	Raven et al.	D diabatama	N of Ohan Sactland	-19.6	
	Raven et al.	D. dichotoma	Filoy England	-13.0	
	Raven et al. 2002	D. dichotoma	Finnov Norway	-12.0 6	
	Raven et al. 2002	D. menstrualis	W Flower Gardens, GOM	-11.0 6	
	Raven et al. 2002	D. menstrualis	Stetson, GOM	-10.0 6	
	Raven et al. 2002	D. menstrualis	Stetson, GOM	-9.06	
	Raven et al. 2002	D. menstrualis	Stetson, GOM	-8.06	
	Raven et al. 2002	D. pfaffi	Stetson, GOM	-7.06	
	Raven et al. 2002	D. pfaffi	E Flower Garden, GOM	-6.06	
	Raven et al. 2002	D. pulchella	Stetson, GOM	-5.06	
	Raven et al. 2002	D. menstrualis	E Flower Garden, GOM	-4.06	
Dotyophyc					
us	Kelly 2012		Palmyra Atoll	-7.96	8.66
Turbinaria	Kelly 2012		Palmyra Atoll	-8.46	9.70

Rhodophyt a				-17.7 2	5.34	6.84	1. 18
Asparagos p-sis	Kelly 2012		Palmyra Atoll	-17.0 9		7.96	
	Raven et al. 2002	A. armata	Stricland Bay, WA, Austrailia	-29.7 1			
	Raven et al. 2002	A. armata	Stricland Bay, WA, Austrailia	-29.5 5			
	Raven et al. 2002	A. taxixformis	Catalina Island, CA	-28			

Prey Group	Source	Species	Sampling Location	δ ¹³ C (‰)	± SD	δ ¹⁵ N (‰)	± SD
				-15.6			,
Ceramium	Kelly 2012		Palmyra Atoll	7			
				-14.5			
	Kelly 2012		Palmyra Atoll	7			
	Kelly 2012		Palmyra Atoll	-8.91			
	Kelly 2012		Palmyra Atoll	-8.68			
			Rockpool,				
	Maberly et al.		East Coast	-13.0		7.4	
	1992	C. rubrum	Scotland	9		7	
			Tentsmuir drift,				
	Maberly et al.		East Coast	-19.5			
	1992	C. rubrum	Scotland	6		3.8	
	Raven et al.			-18.2			
	2002	C. rubrum	Bergen, Norway	9		3.1	

	Raven et al. 2002	C. shuttleworth- ianum	Bergen Store Kalsoy, Norway	-19.2 6	4.8
	Raven et al. 2002	C. shuttleworth- ianum	Flamborough England	-19.1 3	
Galaxaura	Kelly 2012		Palmyra Atoll	-11.3 4	7.7 7
Guiunuuru	Wang & Yeh 2003	G. marginata	Tidal pool, East Taiwan	-16.2	
	Kelly 2012		Palmyra Atoll	-10.5 8	7.8 0
	Kelly 2012		Palmyra Atoll	-16.4 0	6.4 3
	Raven et. al 2002	Gelidiopsis sp.	Stetson, GOM	-19.6 8	
	Kelly 2012		Palmyra Atoll	-15.2 2	6.3 4
	Kelly 2012		Palmyra Atoll	-17.4	5.6 3
	Dailer et al. 2010	H. musciformis	Kahana, West Maui		6.6
	Dailer et al. 2010	H. musciformis	South Maui		6.8
	Hyndes & Lavery 2005	Hypnea sp A	SW Australia	-19.8	6.8
	Hyndes & Lavery 2005	Hypnea sp B	SW Australia	-19.6	5.4

Raven et al. 2002	H. volubilis	Stetson, GOM	-19.4 2
Raven et al. 2002	H. volubilis	Stetson, GOM	-21.0 9
Raven et. al 2002	H. volubilis	E Flower Garden, GOM	-18.5 6
Raven et al. 2002	Hypnea sp.	Gran Canaria	-21.7 5

Prey Group	Source	Species	Sampling Location	δ ¹³ C (‰)	± SD	δ ¹⁵ N (‰)	± SD
	Wang & Yeh 2003	H. spinella	Sublittoral, North Taiwan	-19.8			
	Wang & Yeh 2003	H. japonica	Sublittoral, North Taiwan	-21.2			

7.5

Jania	Kelly 2012		Palmyra Atoll	-7.49	3
	Raven et al. 2002	J. micrathandia	Rottnest Island, WA, Australia	-22.5 5	
	Raven et. al 2002	J. rubeus	S Coast of Devon, UK	-12.5 7	
Spirulina	Kelly 2012		Palmyra Atoll		
Spyridia	Kelly 2012		T.H.		
Gelidium	Kang et al. 2008	G. amansii	Samchoek Coast, Korea	-16.8	4.7

	Raven et. al		Bergen Store	-15.8		
	2002	G. latifolium	Kalsoy, Norway	6		
Invertebrate				-11.6 9	9.5 5.22 2	; 0.29
Black Sponge	Kelly 2012	Gelidiopsis sp.	Palmyra Atoll	-4.29	9.3 9	5
	Kelly 2012		Palmyra Atoll	-15.8 9	9.1 9	
Clay Colored Sponge	Kelly 2012		Palmyra Atoll	-8.96	9.7 2	1
Orange				-16.5	9.2	2
Sponge	Kelly 2012		Palmyra Atoll	6	3	
Purple	Valler 2012		Dalmarma Atall	8 00	9.8	8
runicates	Keny 2012		Paimyra Atoil	-8.90	/	
Red						_
Tunicates/	W 11 0010			-15.5	9.7	1
Sponge	Kelly 2012		Palmyra Atoll	5	4	

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