Utilization of shallow-water seagrass detritus by Caribbean deep-sea macrofauna: δ^{13}C evidence

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Abstract—Three dives were made using the DSRV *Alvin* in the deep-sea basin north of St. Croix, Virgin Islands. Detrital seagrasses and macrofaunal distributions at 2455 to 3950 m depth were assessed quantitatively. Counts of the manatee grass *Syringodium filiforme* (*ca.* 5 to 100 blades m^{-2}) contrasted sharply with those of the turtle grass *Thalassia testudinum* (*ca.* 0.1 to 2.0 blades m^{-2}), reflecting an abundance proportional to previously reported export rates of the same species from Tague Bay, a nearby shallow source lagoon.

Of the macrofaunal consumers that could potentially utilize this detrital nutrient source, three species of holothurians (*Mesothuria verrilli, Psychropotes semperiana*, and *Benthodytes linqua*) and two species of sea urchins (*Hygrosoma petersi* and *Salencidaris profundi*) were collected and/or observed. Gut content analyses revealed that all three holothurians deposit-feed on sediment and at least one species of sea urchin (*H. petersi*) feeds almost exclusively on *Syringodium*.

Carbon:nitrogen analyses of naturally occurring abyssal *Thalassia* detritus showed very low nitrogen content (0.21% N) and a high C:N ratio (214.8), thus yielding a low nutritional value. Fresh *Thalassia* blades held in a litter bag experiment (by R. D. Turner) at 3950 m changed little in nitrogen content and C:N ratio after four years.

A comparison was made of the stable carbon isotope ratios of ^{13}C:^{12}C for abyssal seagrass detritus and other potential carbon sources with those for tissues from the holothurian and urchin consumers. The results indicate that a significant proportion of the nutrition of both groups is derived from detrital seagrasses either by direct consumption (sea urchins) or indirectly by deposit-feeding on sediments enriched by decomposed seagrasses (holothurians).

INTRODUCTION

ALTHOUGH the importance of detrital plant material (especially seagrasses) to the dynamics of near-shore communities has been recognized since the turn of the century (BOYSEN-JENSEN, 1914; PETERSEN, 1918) its significance has only recently gained the attention it deserves (MELCHIORRI-SANTOLINI and HOPTON, 1972; KLUG, 1980; SUCHANEK, 1983). It is becoming evident that seagrass detritus may be the single most important element in the cycling of nutrients in seagrass communities. In the tropics living seagrasses are grazed directly by a variety of herbivores such as sea urchins, gastropods, turtles, manatees, dugongs, and fish (OGDEN, 1980). Of the total productivity of seagrasses, such as the turtle grass *Thalassia testudinum* Banks ex König (0.6 to 16.0 g C m^{-2} day^{-1}) and the manatee

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grass *Syringodium filiforme* Kutzing (0.6 g C $^{-2}$ day^{-1}) (McRoy and McMillan, 1977; Zieman and Wetzel, 1980), only *ca.* 5% annually is believed to be utilized directly by these consumers. The remainder enters the detrital pathway and is either utilized within the seagrass ecosystem or exported. Estimates for seagrass export from source beds range from 1% of leaf productivity (Zieman *et al.*, 1979) to 9.5% (Greenway, 1976) for *Thalassia* and from 60 to 100% for *Syringodium* (Zieman *et al.*, 1979).

Exported detrital seagrasses often escape lagoonal environments, especially during winter storms, and are channeled into the deep sea. For example, rafts of drifting *Thalassia ca.* 50 m in diameter were noted in the Florida current after a hurricane (Menzies *et al.*, 1967). Subsequent dredging operations on the deep-sea floor off North Carolina revealed substantial drift detrital *Thalassia* 550 to 1100 km from any known source region (Menzies and Rowe, 1969). In addition, abundant seagrass detritus has been noted in the deep sea in the Gulf of Mexico (Pequegnat *et al.*, 1972), the Cayman and Puerto Rican trenches (Pratt, 1962; Moore, 1963; Wolff, 1976) and the Virgin Islands basin (Roper and Brundage, 1972). However, little quantitative or qualitative evaluation of seagrasses has been done. Few investigators have speculated on the role of seagrass detritus as a source of nutrition as shown by Wolff's (1979, 1980) reviews on micro- and macrofaunal utilization of detrital plant material (of both terrestrial and marine origin) in the deep sea. In addition, the origin of the organic carbon utilized by deep-sea organisms has not been identified, except by direct evidence of gut contents and inference from shallow-water relatives. For example, it is unclear whether the deep-sea echinoids that Mortensen (1938) described were utilizing the land plants and algae in their guts or the epibionts on the leaves for nutrition.

With the relatively recent advances in the development of isotopic carbon ratio analysis, it is now possible to determine more precisely the source of organic material utilized by a consumer (DeNiro and Epstein, 1978; Haines and Montague, 1979; Teeri and Schoeller, 1979). Specifically, the use of ^{13}C:^{12}C ratios (δ^{13}C units) can help 'fingerprint' an organism's source of nutrition.

In this study we have asked what contribution detrital plant material (especially seagrass) makes to deep-sea macrofaunal heterotrophic nutrition. To answer this question we (1) ascertained the density and availability of shallow-water-derived organic detritus in the deep sea off St. Croix, Virgin Islands, (2) determined the C:N ratio of the organic detritus as an estimate of nutritional value, (3) identified the macrofauna that could be using this nutrient source, and (4) compared the carbon isotopic ratios of detrital source material with those of tissues from deep-sea macrofaunal heterotrophs. Our preliminary findings on the processes that determine the fate of shallow-water sediment and organic detritus in the deep sea off St. Croix (Hubbard *et al.*, 1982) have been extended. Here we present data showing that organic detritus derived from seagrasses contributes significantly to the metabolism of several deep-sea macrofauna.

METHODS

Study area

Using the Deep Submergence Research Vessel (DSRV) *Alvin*, three dives (1101, 1102, 1103) in January and February 1981 were made in the basin just north of St. Croix, Virgin Islands, to depths of 2455 to 3950 m (Fig. 1). The dive sites represent areas associated with contrasting potential source regions for seagrass detritus. Dive 1101 (maximum depth—3950 m) occurred off Christiansted submarine canyon, a moderate-sized feature pre-
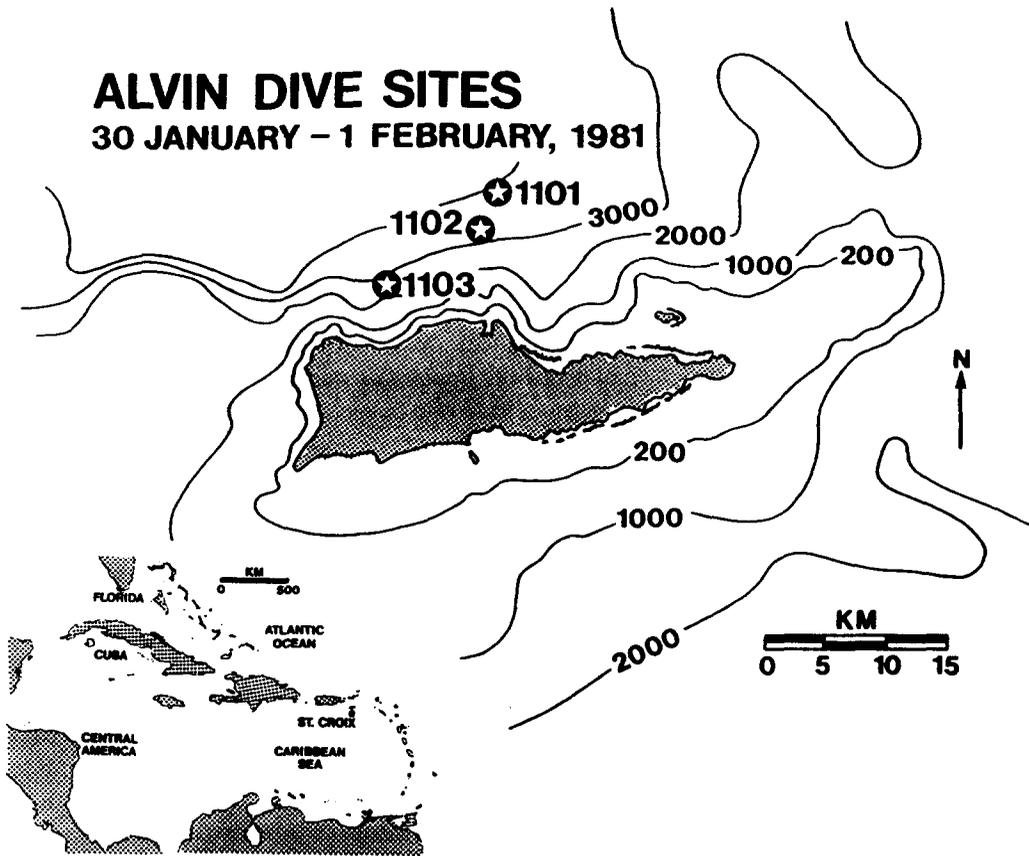
Fig. 1. *Alvin* dive sites: stars, dives 1101, 1102, and 1103, St. Croix, Virgin Islands. Depth contours in meters.

viously hypothesized to funnel shallow-water sediments and seagrass to the basin floor (HUBBARD *et al.*, 1982). Dive 1102 (maximum depth—3526 m) was near a smaller canyon system that could not be traced into the basin. Dive 1103 (maximum depth—3235 m) was made in an area off a shelf with no known associated canyon connections.

Survey and collection techniques

Densities of the two detrital seagrasses *Thalassia* and *Syringodium* were estimated visually on all three 1981 dives. In addition, an external Benthos ™ 35 mm camera was periodically cycled at 4- to 6-s intervals along several transects on each dive. Seagrass densities were estimated from calibrated counting fields on the resulting color transparencies using an ocular micrometer and dissecting microscope.

A variety of methods were employed for the collection of detrital seagrasses, including an unsuccessful technique using modified wire brush collectors to 'stab' the blades. The most successful involved use of the manipulator arms of the submersible to operate sweep nets and to collect individuals of the holothurian *Mesothuria verrilli* (Theel), which consistently had many (1 to 20) blades (mostly *Thalassia*) attached to them. In addition to collecting 11

specimens of several species of holothurians, three specimens of the urchin *Hygrosoma petersi* Agassiz were also collected using the manipulator arms. Gut content analyses were performed on all specimens using a dissecting microscope.

Additional material

Live *Thalassia, Syringodium,* and *Sargassum* were collected from the shallow lagoon of Tague Bay, St. Croix (Fig. 1) in December 1978 for use in a 'litter bag' experiment conducted by R.D. Turner. The plants were placed in plastic onion bags (with 1.0 cm stretched mesh), held at 3950 m depth in Christiansted Canyon for *ca.* four years, and collected in November 1982 using the DSRV *Alvin* (dive 1288).

Additional samples of *Thalassia* blades for δ^{13}C analysis were collected from Christiansted Canyon on supplemental dive 1297 (maximum depth—2000 m). Comparative shallow lagoon samples of *Thalassia* detritus were also collected by SCUBA from the sediment surface of Tague Bay (maximum depth—5 m).

Carbon isotope analysis

After being acidified for 5 min in 10% HCl to remove carbonates, all samples were lyophylized for 45 h and analyzed using methods given in FRY and PARKER (1979). Final δ^{13}C units are expressed relative to the carbonate standard PDB (CRAIG, 1957).

Carbon and nitrogen analysis

Detrital samples were lyophylized for 45 h, finely ground, and analyzed in a Perkin–Elmer 240B Elemental Analyzer calibrated with acetanilide. Epiphyte material (including carbonates) was not removed prior to analysis because it was considered part of the detrital source of carbon and nitrogen available to consumers. The absolute accuracy of the method is ±0.3%. *Thalassia* leaves from the litter bag experiment were similarly treated before analysis, except that a Carlo Erba Model 1106 Elemental Analyzer calibrated with atropine was used in the analyses.

RESULTS

Seagrass distribution

On all three 1981 dives seagrass detritus was found in low abundance except in shallow depressions or downslope channels. Data from Benthos ™ camera slides showed that *Syringodium* was considerably more abundant than *Thalassia* on all three dives, generally increasing in abundance upslope to a mean of 30 to 40 blades m^{-2} at 3000 m depth, whereas *Thalassia* was widely scattered on all dives, never exceeding 1 to 2 blades m^{-2} (Fig. 2).

Both *Syringodium* and/or *Thalassia* blades could almost always be found on the holothurian *Mesothuria verrilli*. Although *Thalassia* was considerably less dense on the sea floor, *Mesothuria* seemed to prefer it over *Syringodium* as cover.

The appearance of the detrital seagrasses was variable. Many blades collected from the greatest depths (*ca.* 4000 m) were brown or black, consisting of little more than structural components. At shallower depths (2500 to 3000 m) some greener or greenish-brown blades were found.

Estimates based on analysis of photographic slides were consistently much lower, especially for *Syringodium*, than direct observer counts, which ranged from 0.1 to 2.0 blades m^{-2} for *Thalassia* and 5 to 150 blades m^{-2} for *Syringodium* (Fig. 2). The discrepancy
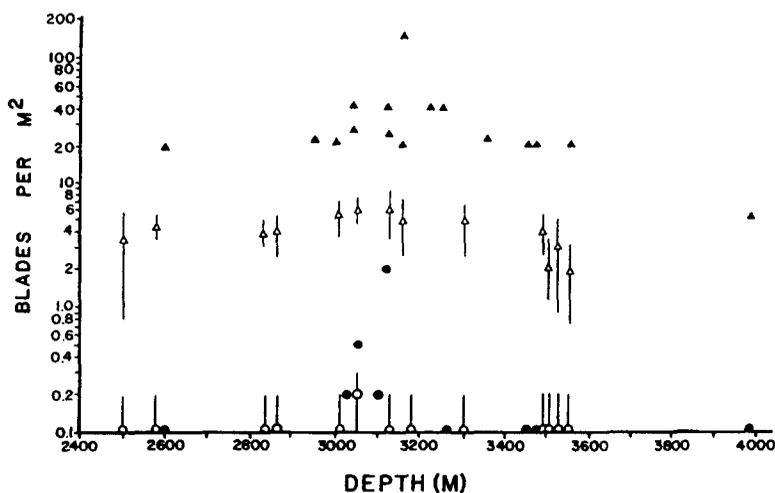
Fig. 2. Abundance of the seagrasses *Syringodium* (triangles) and *Thalassia* (circles) from the cumulative data of *Alvin* dives 1101, 1102, and 1103 plotted on a log ordinate *vs* depth. Solid symbols represent visual counts by observers in the submersible, open symbols are quantitative estimates (with bars representing ±1 s.d.) derived from colour transparencies (see Methods).

between direct observer counts and counts from photographic slides undoubtedly reflects the resolution (down to *ca.* 2 cm) of the film. The densities shown in Fig. 2 are directly proportional to the export rates of *Thalassia* and *Syringodium* from the shallow lagoon at Tague Bay (the presumed source) reported by ZIEMAN *et al.* (1979).

Macrofauna distribution and gut contents

Information on the three species of holothurians (*Benthodytes linqua, Mesothuria verrilli,* and *Psychropotes semperiana*), and the two species of sea urchins (*Hygrosoma petersi* and *Salencidaris profundi*) observed and/or collected during the three *Alvin* dives in 1981 is listed in Table 1. Photographs of macrofauna studied in detail are provided in Fig. 3. *B. linqua* was relatively common on all dives, reaching a maximum abundance during the shallowest portion of dive 1103. Although the abundance of *M. verrilli* was variable, densities of 1 to 2 per m² were sometimes reached. *P. semperiana*, which has a characteristic dorsal or bivium 'sail', was comparatively less common but present on all three dives. The sea urchin *H. petersi* was sighted only three times on each of dives 1101 and 1102 and five times on dive 1103, whereas *S. profundi,* although patchy in distribution, often occurred in aggregations of several hundred individuals. These groups, usually several meters across, were often separated by distances of 30 to 50 m.

The gut contents of 11 macrofauna were examined for the presence of seagrass detritus (Table 1). None was found in the eight holothurians examined. However, an analysis of gut contents from three specimens of the urchin *H. petersi* yielded predominantly seagrasses, over 95% being *Syringodium* (Table 2). A measure of food acceptance values, calculated as an 'electivity' coefficient or preference index (IVLEV, 1961), showed that this species does not discriminate between seagrasses, i.e., it consumes them in direct proportion to their abundance in the environment. In contrast, the holothurian *M. verrilli* displayed a significant preference for *Thalassia* blades as cover by disproportionately selecting them over

Table 1. *Statistics on holothurians and urchins collected (or observed*) from deep-sea sites off St. Croix*

|	Length (cm)	Height (cm)	(n)	Attached seagrass	Exterior	Color	Gut contents	Observed depth range (m)
Holothuroidea								
Benthodytes linqua	38.0 ± 2.8	8.0	(2)	No	Smooth with tubercles	Purple	Sediment	2628–3810
Mesothuria verrilli	17.3 ± 0.7	8.0 ± 0.9	(5)	Yes	Rough or smooth	Brown	Sediment	2618–3720
Psychropotes semperiana	9.0	7.0	(1)	No	Smooth with sail	Purple	Sediment	3429–3701
Echinoidea	Test diameter (cm)	Test height (cm)						
Hygrosoma petersi	11.8 ± 1.3	4.3 ± 0.3	(3)	No	Leathery test	Maroon	Seagrasses	2528–3800
Salencidaris profundi*	ca. 1–2	ca. 1–2	(100's)	No	—	White	—	2528–3329
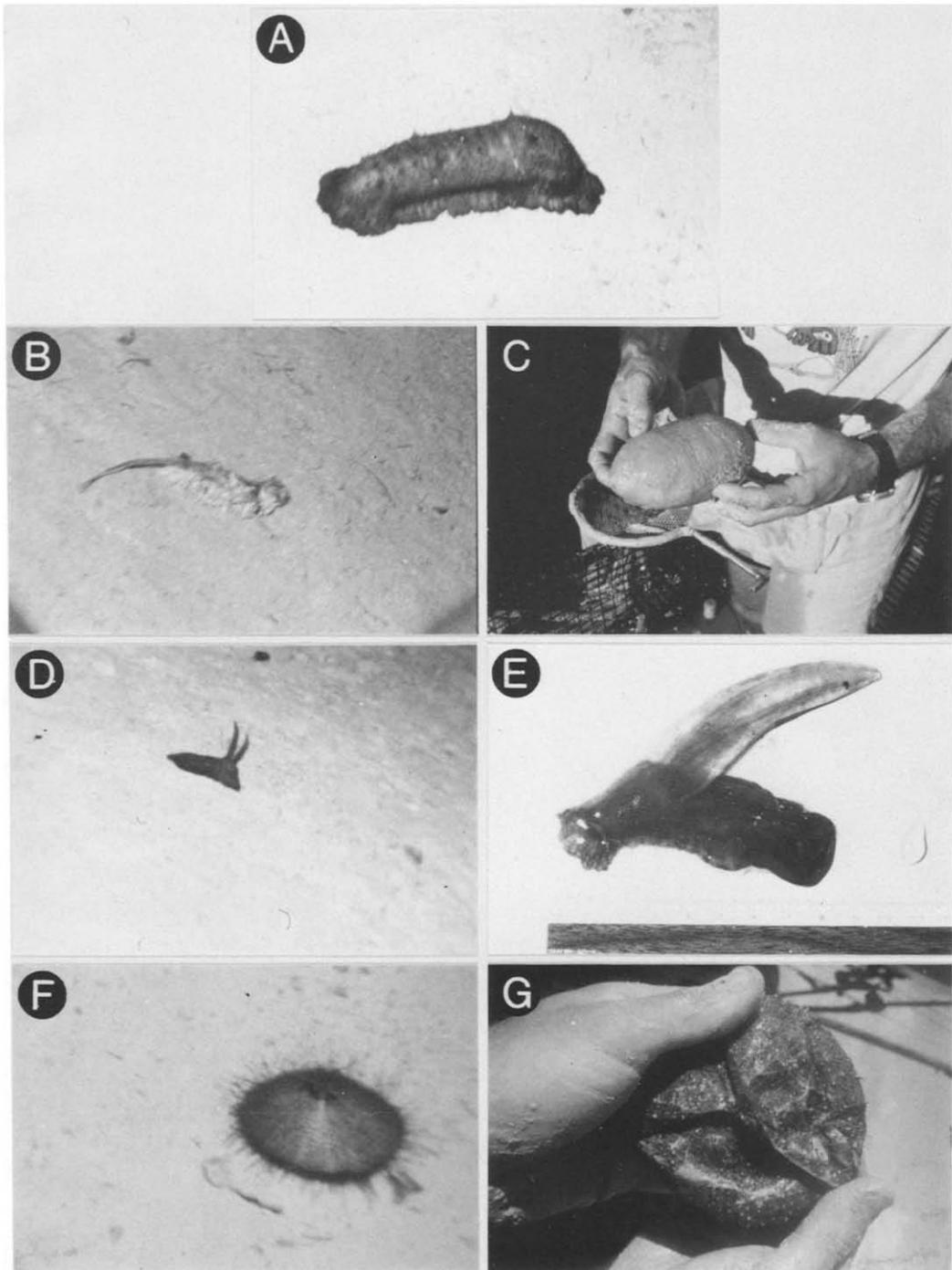
Fig. 3. The deep-sea macrofauna studied in detail. (A), (B), (D), and (F) Animals on the sea floor. (C), (E), and (G) The same species after retrieval. (A) *Benthodytes linqua*, (B) and (C) *Mesothuria verrilli*, (D) and (E) *Psychropotes semperiana*, (F) and (G) *Hygrosoma petersi*. Note that in (B) *M. vernilli* is covered by detrital seagrasses and shell material (in this case *Thalassia* and brachiopod shells); in (D) the second 'sail' is a shadow produced by the photographic strobe; the leathery test in (G).

Table 2.   Gut contents of the sea urchin Hygrosoma petersi. *Sample size* = 3, *from* 2814 *to*
2930 m *depth*

% Gut contents	Description
95.7 ± 3.1	*Syringodium filiforme* pieces, 1.8 to 9.0 mm long, mostly blades, some short shoots, and rhizomes.
	Epibiota on *Syringodium*:
	hydroids, sponge, bryozoa, and algae: *Dictyota* sp., *Cladophora* sp., *Hersiphonia segunda*, *Hypnea musciformis*, *Ceramium* sp., crustose coralline algae.
4.3 ± 3.1	*Thalassia testudinum* blades, short shoots, and some rhizomes.
	Epibiota on *Thalassia*:
	sponge, hydroids, filamentous blue-green algae, and encrusting coralline algae.
	Halodule wrightii blades
	Epibiota on *Halodule*:
	unidentified sponge
	Sargassum vulgare and/or *S. polyceratium* blades and bladders

Syringodium blades (SUCHANEK, in preparation). The reason for this selection is unknown, but because *Thalassia* has a wider blade it may offer better coverage.

Carbon: nitrogen analysis

The differences in %N, %C, and C:N atomic ratios between *Thalassia* leaves drifting out from the lagoon and those deposited in the abyss were significant (*t*-test; $P < 0.01$, 0.001, 0.001, respectively). Abyssal *Thalassia* detritus had lower nitrogen and higher carbon contents than drift material (Table 3).

Thalassia that remained in litter bags at 3950 m for four years (neither *Syringodium* nor *Sargassum* were found) was greenish, resembling living more than detrital *Thalassia*. Although the fresh *Thalassia* placed in the litter bags was not analyzed, the carbon and nitrogen content of the retrieved *Thalassia* was not very different from values typical for living *Thalassia* (PATRIQUIN, 1972; KNAUER and AYERS, 1977; KLUG, 1980).

Table 3.   Carbon and nitrogen content of Thalassia testudinum *detritus from St. Croix. Mean value* ± 1 s.d.
(sample size). C:N *ratio is atomic*

Source	%N	%C	C:N
Tague Bay Lagoon drift leaves	0.51 ± 0.24 (9)	26.07 ± 2.67 (9)	83.34 ± 55.23 (9)
Abyssal leaves	0.21 ± 2.28 (6)	34.69 ± 2.28 (9)	214.80 ± 65.45 (6)
Abyssal rhizomes	0.25 ± 0.31 (5)	26.80 ± 4.37 (5)	153.59 ± 111.15 (5)
Leaves (from 4-year litter bag experiment)	0.93 ± 0.16 (12)	20.54 ± 0.71 (12)	26.65 ± 4.96 (12)

Stable carbon isotope analysis

The δ^{13}C values of *Thalassia* from the abyss were similar to those found in the lagoon of its probable origin (MCMILLAN *et al.*, 1980). Unfortunately, the unsuccessful collection of abyssal *Syringodium* precluded analysis. The very negative values of the miscellaneous leaves and twigs verify their terrestrial origin (SACKETT *et al.*, 1965).

The δ^{13}C values of abyssal macrofauna (Table 4) ranged from -9.1 to $-17.7‰$, being slightly more depleted than the *Thalassia* leaves collected there (-9.0) and considerably more depleted than *Syringodium* collected from the shallow lagoon at Tague Bay (-4.0 to -5.1). The range of values within individuals is typical of known values, especially those of gonad tissue which is likely to be lipid-rich (MCCONNAUGHEY and MCROY, 1979; FRY, 1981).

Table 4. ^{13}C : ^{12}C *ratios of potential carbon sources and consumers in the deep-sea.*
δ^{13}C *values are expressed as ‰ relative to the carbonate standard PDB*

Potential carbon sources	δ^{13}C
Syringodium filiforme (seagrass)	
Lagoon: leaves only	-4.0 to -5.1^*
Thalassia testudinum (seagrass)	
Lagoon: leaves only	$-9.9, -10.0^*$
Abyss: rhizomes only	$-6.4, -5.8$
Abyss: leaves only	-9.0
Sporobolus virginicus (marsh grass)	
Abyss: rhizomes	-11.4
Miscellaneous leaves and twigs – abyss	-28.0
Plankton	$-23.3, -22.0†$
	-19.8 to $-22.5‡$
	$-20.6§$
Particulate organic carbon	-22.0 to $-24.3‖$
	-20.1 to $-28.2¶$
Dissolved organic carbon	-21.2 to $-24.4‖$

	Specimen number		
Abyssal consumers	1	2	3
Holothuroidea:			
Mesothuria verrilli:			
Epidermis	-13.0	-12.2	-12.6
Longitudinal muscles		-13.8	-13.5
Respiratory tree		-13.4	-16.0
Benthodytes linqua:			
Epidermis	-13.3	-13.8	
Longitudinal muscles	-12.9		
Gonad (eggs)	-17.7		
Intestinal wall	-13.1		
Echinoidea:			
Hygrosoma petersi:			
Epidermis	-9.1		
Gonad (eggs)	-14.6		

* MCMILLAN *et al.* (1980).
† MCCONNAUGHEY and MCROY (1979).
‡ DEGENS *et al.* (1968).
§ SACKETT *et al.* (1965).
‖ WILLIAMS and GORDON (1970).
¶ JEFFREY *et al.* (1983).

Although gut contents of the urchin *H. petersi* were 95 to 99% *Syringodium*, the δ^{13} C values were considerably more negative than would be expected if its nutrition was derived solely from this source. Holothurian δ^{13}C values ranged from −12.2 to −17.7, indicating a probable mixed origin for the carbon in their diet as well. If the ingested sediments were solely enriched from plankton or particulate or dissolved organic carbon, then the δ^{13}C values should be considerably more negative (on the order of −20 to −24). If, on the other hand, the carbon comes mostly from deteriorating seagrass, one would expect the values to approach −5 to −10.

DISCUSSION

Our most convincing evidence for utilization of detrital seagrasses as a metabolized food source by deep-sea macrofauna is derived from gut contents and δ^{13}C analysis. The sea urchin *H. petersi* had the gut filled with *Syringodium* except for a minor amount of *Thalassia*, although other investigators have found the gut contents of this species to be packed with mud (MORTENSEN, 1935), "bits of plants" (MORTENSEN, 1938) and/or a mixture of mud, *Sargassum*, and *Thalassia* (PAWSON, 1982). That the detrital seagrasses from the gut contents of our specimens were in the same proportion in the gut as they occur in the deep-sea habitats indicates little or no feeding selectivity on the part of *H. petersi*.

Stable carbon isotope analysis of animal tissues lends further support to the idea of macrofaunal consumption and utilization of seagrass detritus in the abyss (Table 4). Our specimens showed δ^{13}C values close to nearby plant material, with the exception of the miscellaneous leaves and twigs of terrestrial origin. The δ^{13}C values of the seagrass material in turn were similar to those of the nearshore seagrasses at St. Croix (MCMILLAN *et al.*, 1980). The δ^{13}C values of the animal tissues being slightly more negative than marine vascular plant detritus may indicate a small\dietary input from carbon sources such as plankton or terrestrial leaves and twigs, both of which have more negative values than those of seagrasses.

The C:N values of *Thalassia* that we collected drifting out of the shallow lagoons were higher than other values reported for typical *Thalassia* detritus (KNAUER and AYERS, 1977). We suggest the following reasons for this difference. Because *Thalassia* detritus sinks, the samples from Tague Bay may have undergone extensive degradation while enroute from the seagrass beds (ZIEMAN *et al.*, 1979). We also suggest that the microbial depletion of detrital nitrogen may be greater in severely nutrient-limited tropical waters than in temperate waters which have more available nitrogen and where the detritus studies cited above were performed.

The detritus on the deep-sea floor was even lower in nitrogen than previously reported for *Thalassia* detritus. Fresh *Thalassia* allowed to age at abyssal depth, however, showed little change after four years. Based on nitrogen contents reported for fresh seagrass, we estimate that about half of the original nitrogen was lost after four years (HARRISON and MANN, 1975; KNAUER and AYERS, 1977; THAYER *et al.*, 1977). The four-year litter bag experiment further supports the idea that bacterial action on the deep-sea floor is much slower than at shallow depths (JANNASCH *et al.*, 1971; JANNASCH and WIRSEN, 1977; MORITA, 1979). In addition, our results suggest that the naturally occurring detritus collected from the deep-sea floor was very ancient or had been extensively degraded prior to arrival.

The C:N ratio of detritus has been used as an indicator of the potential food value for consumers (MANN, 1972; TENORE, 1977; THAYER *et al.*, 1977). An earlier view that the C:N ratio of detritus decreases with aging as a result of microbial colonization, thereby increasing

its nutritive quality, is now being revised (TENORE and RICE, 1980; RICE and TENORE, 1981; RICE, 1982). The abyssal animals collected were consuming seagrass detritus which apparently represents a poor source of nitrogen. Several possible reasons are suggested for this behavior. First, the consumers may have evolved an ability to select fresher detritus and those *Thalassia* blades that we collected and analyzed from the deep-sea were atypical of that being consumed. Second, the metabolism of deep-sea fauna, including deposit feeders, may be modified to enable existence on low-nitrogen food. WOLFF (1980) presents evidence that the sediments next to a clump of low-nitrogen abyssal *Thalassia* were even lower in nitrogen. Third, it is also possible that the animals require high-nitrogen food only periodically. High-nitrogen food falls occur rarely in the deep sea (STOCKTON and DELACA, 1982). but may be frequent enough to support these fauna. An analogy would be that humans could exist on a junk-food diet if we periodically ate steak. Fourth. nitrogen may be supplemented from other sources on a continual but low level basis. We have reported elsewhere that the dissolved organic nitrogen concentrations in the water directly above the bottom at these study sites were above 30 μM (HUBBARD *et al.*, 1982) and it is well known that species from nearly all invertebrate phyla, including echinoderms, have the ability to uptake dissolved nitrogen (STEPHENS and SCHINSKE, 1961; STEWART, 1979). Finally, nitrogen-fixing bacteria, possibly associated with the digestive tracts of consumers, may also contribute to the nutritional value of the otherwise nitrogen-poor food. This phenomenon has been shown to be widespread among many shallow-water tropical sea urchins (GUERINOT *et al.*, 1977; GUERINOT and PATRIQUIN, 1981).

To summarize our findings, the relative distribution of blades of the seagrasses *Thalassia* and *Syringodium* on the deep-sea floor were in direct proportion to the export rates reported from one nearby source lagoon, Tague Bay. Gut contents and/or δ^{13}C analyses indicate that at least one species of urchin and two species of holothurians consume and metabolize abyssal seagrass detritus (either directly or indirectly) even though it contained <1% nitrogen. Avenues for future research on the utilization of seagrass detritus by macrofauna in the deep sea are the determination of their metabolic rates, more sophisticated analyses of seagrass detritus as a food source (e.g., protein analysis) and quantification of the processes of aging of seagrass detritus from its source to its deposition on the deep-sea floor.

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