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Production, decomposition, and heterotrophic utilization of the seagrass *Halophila decipiens* in a submarine canyon

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ABSTRACT: We examined the net production, decomposition, and microbial utilization of the seagrass *Halophila decipiens* during a 6.5 d period in May 1985 in the Salt River Canyon, St Croix, US Virgin Islands. *H. decipiens* covered 37 % of the Canyon floor between depths of 14 and 32 m with a biomass of 9.15 g dry wt m^{-2}; its net productivity was ca 0.145 g C m^{-2} d^{-1}. Turnover time, estimated by 2 independent methods, was 10.7 d. After 6.5 d *H. decipiens* incubated in litterbags buried in the sediment lost 56 % of their original ash free dry weight (AFDW) while litterbags incubated on the sediment surface lost only 28 % of their original AFDW. Bacteria grew rapidly on the detritus, doubling in 3.1 d in the surface bags and 3.7 d in the buried bags. Per-cell thymidine incorporation rates peaked within the first 13 h in both treatments but declined thereafter. Final incorporation rates were highest in surface bags. Mean bacterial cell size and bacterial abundance associated with degrading *H. decipiens* were larger in the buried litterbags. Bacterial biomass, however, was only 29.3 mg cell C g^{-1} AFDW in buried bags and 17.5 mg C g^{-1} AFDW in surface bags. Using bacterial production averaged for the 6.5 d, we estimate that only about 0.26 % of the daily detrital input from *H. decipiens* is converted daily into bacterial biomass attached to the degrading plant material. We conclude that, unless the bacterial community on *H. decipiens* detritus were to use the organic matter more efficiently and were heavily grazed upon, attached bacteria would not make a significant contribution to a deposit-feeding detritivore's energy demands.

INTRODUCTION

Highly productive seagrass communities occur in coastal waters throughout the Caribbean Sea and the Gulf of Mexico (Zieman & Wetzel 1980, Zieman 1982). Despite their wide distribution only a few herbivores feed directly on seagrasses (Zieman 1982, Thayer et al. 1984b). Nonetheless, the diversity, abundance, and biomass of seagrass-associated faunal communities almost always exceeds those of unvegetated subtidal habitats and it is believed that seagrass meadows are vital nursery habitats for valuable commercial and recreational fisheries (Kikuchi & Peres 1977, Zieman 1982, Thayer et al. 1984a). This has presented both an interesting question and something of a dilemma: why is such an abundance of animals sustained in a system where the primary source of organic matter is only minimally utilized by direct herbivory?

One of several proposed explanations for the relatively large faunal biomass and high secondary productivity of seagrass systems is that the plant material becomes nutritionally available to consumers after undergoing decomposition to either morphous particulate organic detritus or amorphous detrital aggregates (Odum & de la Cruz 1967; Odum et al. 1971, Robertson et al. 1982). Detritus is defined as dead organic matter in various stages of decay with its associated microorganisms, and is formed from complex physical and chemical interactions mediated by the environmental conditions of the sediment or water column as well as the metabolism of micro- and macroorganisms closely associated with detritus (Odum et al. 1971). In subtidal sediments bacteria and bacterial consumers are an important intermediary in the transformation of organic matter to organic detritus (Fenchel 1977, Klug 1980). Bacteria are capable of metabolizing dissolved organic compounds released from living and detrital seagrass (Moriarty & Pollard 1982, Robertson et al. 1982, Kenworthy & Thayer 1984, Moriarty et al. 1986). Bacteria also have enzymes for degrading refractory particulate

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organic compounds and are capable of altering the physical composition of detritus (Klug 1980). Since detritivores reportedly assimilate the plant fraction of detritus with efficiencies less than 5.0 %, but may assimilate microflora at efficiencies exceeding 50.0 % (Hargrave 1976, Yingst 1976, Lopez et al. 1977, Cammen 1980, Bianchi & Levinton 1984), it has been argued that a portion of a detritivore's nutritional requirements are met by the microbial component of detritus (for review see Lopez & Levinton 1987). Hence, bacteria function in mediating the recycling of nutrients and may be important in regulating the flow of energy from seagrass detritus to consumer organisms (Fenchel 1977, Klug 1980, Robertson et al. 1982).

Recent studies in the Salt River Submarine Canyon at St Croix, US Virgin Islands show that the seagrass *Halophila decipiens* Ostenfeld is an important source of organic matter and detritus for the Canyon (Josselyn et al. 1983, Josselyn et al. 1986). Frequent disturbance by burrowing and foraging animals and wave surge continually uproot or bury entire plants (Williams et al. 1985, Josselyn et al. 1986). The buried plant material forms organic detritus that decomposes in the sediment while material on the sediment surface decomposes in place or is transported down the Canyon (Josselyn et al. 1983).

Halophila decipiens is commonly found in other locations with diminished levels of quantum solar irradiance, including offshore shelves in the Gulf of Mexico (Continental Shelf Associates and Martel Laboratories, Inc., 1985) and shallow turbid water (Birch & Birch 1984). *H. decipiens* has certain morphological and structural features enabling it to maximize its light harvesting capacity in a low light environment (Josselyn et al. 1986). Compared to many other seagrasses, it is a relatively short lived species, has a high fecundity and rapid rate of rhizome elongation which enable it to colonize disturbance sites and recover from perturbations within existing meadows. Together these attributes enable *H. decipiens* to occupy an ecological niche not easily filled by other slower-growing or longer-lived tropical seagrasses.

Results of previous studies (Josselyn et al. 1983, Josselyn et al. 1986) and our interest in examining trophic links between benthic primary production and fisheries organisms prompted us to continue research on vascular plant detritus in the Salt River Canyon. We utilized the National Oceanic and Atmospheric Administration's (NOAA) underwater habitat, Hydrolab, between May 13 and May 28, 1985 to examine: (1) the distribution and abundance of *Halophila decipiens*; (2) net production and turnover time of *H. decipiens* at depths between 14 m and 32 m; (3) decomposition of *H. decipiens* in litterbags deployed on the sediment surface and buried in the sediment; and (4) abundance, biomass and heterotrophic activity of bacteria associated with living and decomposing *H. decipiens*.

MATERIALS AND METHODS

Study site. Salt River Canyon extends seaward from a shallow lagoon on the north shore of St Croix, US Virgin Islands (Fig. 1). The width of the Canyon floor is ca 100 to 150 m at water depths between 10 and 30 m and is bordered by coral reefs on the eastern and western perimeters. A narrow channel in the fringing reef connects the Canyon with Salt River Bay.

Distribution and abundance of *Halophila decipiens*. At the initiation of the study 2 aquanauts (divers working under N_2 saturation and living for the duration of the study in Hydrolab) laid out a transect parallel to the base of the west wall of the Canyon. The transect was flagged at 1 m intervals between the 14 and 32 m

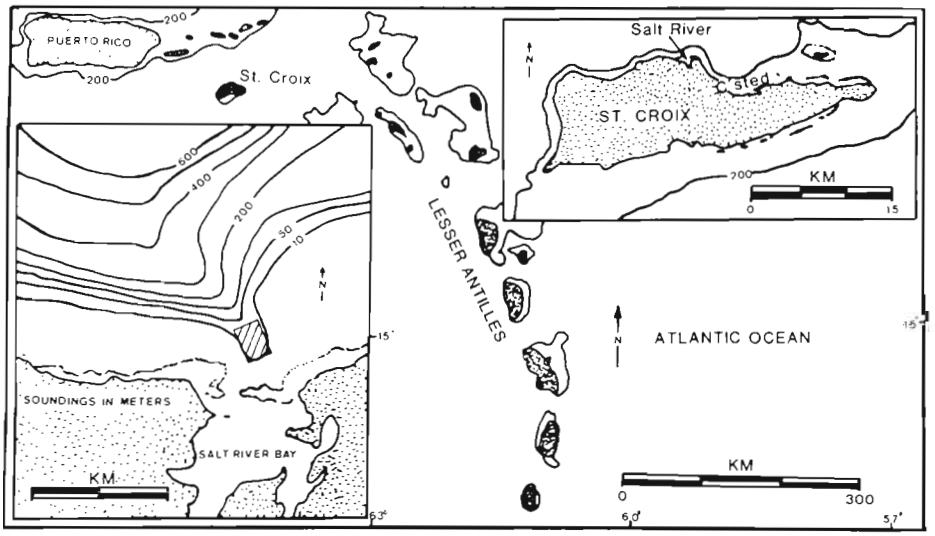

Fig. 1. Study site showing the island of St Croix and the Salt River Canyon

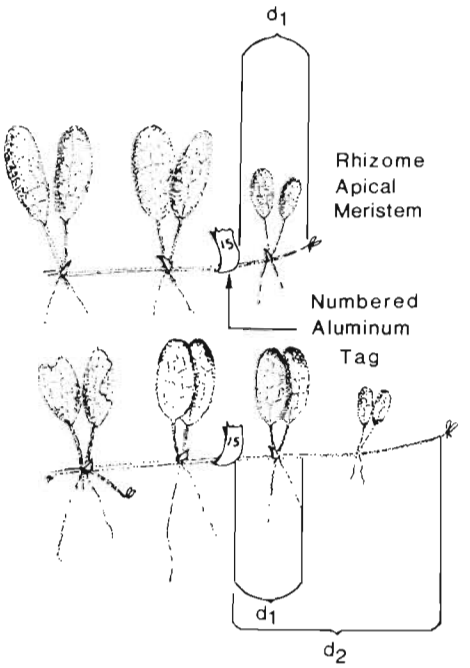

Fig. 2. *Halophila decipiens*. Morphology and marking technique used to measure net shoot production. d: distance in cm

depths; these depths were identified as the respective upper and lower limits of *H. decipiens* distribution at that time. The Canyon floor was divided into 10 by 10 m grid sections, and 46 intersection points in the grid were randomly selected. Using the west wall transect line, a compass for perpendicular orientation, and a measuring rod, each of the 46 points was located and all plant material within a 100 cm^2 quadrat at each point was collected. The depth at each collection was recorded and the plant material was sent to the surface, washed, sorted by species, dried and weighed to the nearest 0.001 g. The frequency of seagrass found in these random quadrats provided an estimate of percent cover. The number of seed pods and apical meristems of *H. decipiens* also were recorded.

Net shoot production of *Halophila decipiens*. Net shoot production of *H. decipiens* was estimated at 3 depths in the Canyon: 15, 21, and 27 m. Production was estimated by an in situ marking technique (Josselyn et al. 1986). At each depth station ca 100 individual rhizomes of *H. decipiens* were tagged with a small strip of numbered aluminum tape placed behind the terminal leaf pair of each rhizome (Fig. 2). After tagging each shoot the aquanauts recorded the length of rhizome from the apical meristem to the tag (d_1). The tagged plants were recovered 4 d later at the 27 and 21 m stations and 5 d later at the 15 m station. The number of new leaf pairs was recorded as well as the total new length from the tag to the apical meristem (d_2). The original length (d_1) was separated and discarded. The remainder, $d_2 - d_1$, was retained and weighed as an estimate of net production. The biomass increase per shoot was multiplied by the rhizome apical meristem density and divided by the number of days in the observation period to determine daily areal productivity of both above- and belowground components in vegetated areas of the Canyon. Total Canyon production per day was estimated by multiplying the average production of vegetated areas times the acreage of *H. decipiens* cover in the Canyon.

Turnover of *Halophila decipiens*. We estimated the turnover time of *H. decipiens* by 2 methods. For one estimate we divided the biomass (g dry wt m^{-2}) by the productivity (g dry wt m^{-2} d^{-1}). The second method consisted of combining data from the productivity stations with observations of the initiation of leaf senescence on a shoot. The average rate at which new leaf pairs were generated was determined from the production measurements and was multiplied by the number of leaf pairs from the meristem at which leaf deterioration was identified in a senescence survey conducted in situ by the aquanauts. In the senescence survey the aquanauts examined 25 intact *H. decipiens* rhizomes with apical meristems at each of the productivity stations. On each rhizome we identified the position of the following leaf pair categories: (1) the first branch position; (2) the first visible epiphytes; (3) the first indication of leaf loss; and (4) the first indication of leaf deterioration. The average of Categories 3 and 4 was computed and used as the indication of the initiation of leaf pair senescence. The average of Categories 3 and 4 was divided by the average rate (number of days) at which new leaf pairs were generated to estimate the time in days it took a leaf pair to form and pass naturally into senescence.

Decomposition of *Halophila decipiens* in litterbags. The decomposition of particulate organic matter and the formation of organic detritus originating from *H. decipiens* was investigated using 2.0 mm mesh fiberglass litterbags. Fresh, living *H. decipiens* (leaves, roots and rhizomes) was collected from the Canyon at the 15 m depth and retained in seawater. Approximately 10 g wet weight (0.635 g dry wt) of plant material was placed in each litterbag. Seventy-two bags were deployed at a site in the Canyon west of the habitat at the 15 m depth in an existing *H. decipiens* bed. One-half of the bags were threaded onto a monofilament line and suspended at the sediment surface while the remaining bags were buried ca 5 cm deep in the sediment. Surface and buried treatments were intended to approximate the major pathways for the formation of *H. decipiens* detritus on the Canyon floor (Josselyn et al. 1986). A wet to dry weight ratio was determined from 10 subsamples of the original plant material for estimation of the dry weights of plant material placed in the litterbags. Subsamples of the

original plant material were dried and split for carbon analysis with a Carlo Erba model 1106 elemental analyzer and combusted in a muffle furnace at 550 °C for 24 h to determine ash free dry weight (AFDW).

Litterbags were recovered from the Canyon station at various times between 7 and 156 h after deployment. At each sampling time 6 bags from each treatment were arbitrarily collected and transferred to the shore-based support facility. Three bags from each of the 2 treatments were subsampled for heterotrophic activity measurements, bacterial abundance and bacterial biomass. The remaining 3 bags from each treatment were dried to obtain a measure of dry weight loss and their contents were homogenized with a mortar and pestle. Subsamples of the homogenized material were combusted at 550 °C to determine ash content for estimates of AFDW during decomposition.

Abundance of bacteria. One weighed subsample, ca 0.1 g wet wt, was removed from each of 3 replicate litterbags and placed in a separate vial with 0.5 ml glutaraldehyde (25 %, v/v) and 4.5 ml 0.2 µm Nuclepore filtered seawater (FSW) to obtain a final concentration of 2.5 % glutaraldehyde. The preserved plant material was homogenized in 17 ml of FSW and 1 ml of 25 % glutaraldehyde for 30 s in a Polytron tissue homogenizer. A subsample of the homogenate was filtered for acridine orange direct counts (AODC) of bacteria as described in Hobbie et al. (1977) using prestained 0.2 µm Nuclepore filters. We counted one filter from each preserved subsample of homogenized plant material (Kirchman et al. 1982b). Ten to 20 fields were counted on each filter in order to count a minimum of 200 cells per filter. Four hundred or more cells were counted for most samples. FSW and AODC blanks were prepared daily. We estimated the density of bacteria on a gram ash free dry weight basis (g AFDW) from the original 0.1 g wet wt subsample.

Cell sizing and biomass of bacteria. Bacteria were sized on preserved subsamples from Canyon litterbags at times 0, 13, 32, 56, 80, 104, and 156 h. At least 40 cells in each subsample were sized, therefore 120 cells per treatment at each of the above sampling times were examined. An eyepiece grid with smallest divisions of 0.96 µm was used to measure the length and width of bacteria cells. Cell volumes were calculated using one of the following formulas: (1) sphere volume = $4/3\ \pi\ r^3$; (2) rod volume = $\pi\ r^2(L-2/3\ r)$; or (3) prolate spheroid volume = $4/3\ \pi\ L/2\ r^2$ (Fuhrman 1981, CRC Standard Mathematical Tables 21st ed, p. 13). Cell carbon biomass was calculated using the conversion factor 2.2×10^{-13} g C μm^{-3} (Bratbak 1985).

Net bacterial growth and production. The estimated bacterial density in a given bag was multiplied by the ash free dry weight of the contents of the bag to obtain an adjusted value equal to the total number of cells per litterbag. An average of the total number of cells for the 3 replicate bags at each sample time was calculated (Tables 4, 5). Doubling times for bacteria were computed for the 6.5 d period. A minimum estimate of bacterial carbon production was calculated from the increase in bacterial carbon during the 156 h litterbag incubations.

Heterotrophic activity; [^{3}H] thymidine incorporation. The heterotrophic activity of bacteria on fresh *Halophila decipiens* standing stock and detritus from subsamples of litterbags was measured using [^{3}H]-thymidine (Kirchman et al. 1982a, Kirchman et al. 1984). At the initiation of the litterbag experiment and at each sampling time, one subsample (ca 0.8 g wet wt) from each of 3 litterbags per treatment was gently rinsed in seawater, patted to remove excess water and weighed wet. Each subsample of plant material was placed in a clean glass vial with 5 ml of FSW. Subsamples from buried bags were incubated in degassed FSW (dissolved $O_2 < 2.0$ ppm). Incubations were begun by adding [methyl-^{3}H]-thymidine (specific activity 77.8 Ci $mmol^{-1}$; New England Nuclear) to a concentration of 10 nmol labeled thymidine. Vials were incubated for 60 min in the dark at in situ temperature (28 ± 1°C). Incubations were terminated by chilling the samples on ice followed by the addition of 10 ml ice-cold 5.0 % trichloroacetic acid (TCA) (Kirchman et al. 1984). After 30 min extraction the cold TCA-insoluble fraction was collected on a 0.45 µm Millipore filter A 3 ml cold TCA rinse of the incubation vial was added, and the filter washed twice more with 3 ml of ice-cold 5.0 % TCA. Filters were placed in clean glass scintillation vials and refrigerated for transport to Beaufort, North Carolina. Filter columns and supports were rinsed between samples with deionized water. Controls were prepared with the addition of 2.0 % glutaraldehyde to 0.8 g wet wt subsamples and were processed with the same protocol at each sampling time to correct the subsamples for abiotic adsorption of [^{3}H]-thymidine.

The labeled plant material was hydrolyzed at 100 °C with 1 ml of 1*N* HCl for 30 min prior to radioassay (Kirchman et al. 1984). Ten ml of Aquasol-2 was added to each incubation vial and radioactivity was assayed with a Beckman LS 200B scintillation counter using external standards. A quenching factor was determined for the plant material by adding whole *Halophila decipiens* plants to [^{3}H] toluene standards.

RESULTS

Distribution and abundance of *Halophila decipiens*

In the biomass survey, 17 of the 46 random quadrats (100 cm^2) contained living *Halophila decipiens* for an estimated coverage of 37 % of the Canyon floor (Table

Table 1. Distribution, abundance and biomass (mg dry wt) of plant material originating from seagrass and macroalgae in the Salt River Canyon. –: none present

Station	Depth (m)	Abundance of *Halophila decipiens* (no. 100cm^{-2})			Biomass of plant material (mg 100cm^{-2})				
		Apicals	Leaf pairs	Seed pods	Living *H. decipiens*	*H. wrightii* detritus	*S. filiforme* detritus	*T testudinum* detritus	Macroalgae
1	15.2	39	129	37	201.0	55.0	71.0	58.5	–
2	16.8	3	9	1	13.0	1.7	3.0	–	11.0
3	18.3	–	–	–	–	1.9	–	–	–
4	19.8	29	91	19	145.8	331.7	443.0	283.0	46.5
5	20.1	8	23	7	41.6	–	1.7	–	1143.0
6	20.1	3	11	8	30.6	0.5	–	–	
7	20.1	some *Halimeda*		–	–	–	–	–	176.0
8	20.4	3	7	3	–	–	–	–	–
9	20.4	25	60	18	197.0	3.1	9.0	–	–
10	20.4	11	36	13	77.0	6.4	–	–	–
11	20.7	19	47	15	112.0	3.5	–	132.5	–
12	21.0	–	3	2	8.1	–	–	–	–
13	21.9	7	22	4	31.9	2.5	–	–	–
14	22.3	–	–	–	–	–	–	–	1739.6
15	22.6	8	36	14	74.5	6.0	8.3	–	–
16	22.9	12	56	21	109.0	–	1.2	–	–
17	24.1	25	86	32	209.0	18.8	31.0	–	24.4
18	24.1	14	51	36	132.0	5.7	4.0	–	4.0
19	24.7	3	13	7	31.9	2.5	–	–	78.03
20	26.5	7	22	11	37.0	–	–	–	0.83
21	no data	13	40	15	104.0	–	1.0	–	–
$\bar{X}$		13.7	41.2	14.6	91.5	33.80	58.02	170.75	331.53
SD		10.34	33.78	11.12	67.22	90.69	136.96	158.74	626.75
N		17	18	18	17	13	10	2	11
m^{-2} [a]		1370	4120	1460	9.15	3.38	5.8	17.08	33.15

[a] Values for m^{-2} were obtained by multiplying the mean values for 100cm^{-2} by 100

1). Where *H. decipiens* occurred, the biomass was estimated to be 9.15 g dry wt m^{-2} and the density of leaf pairs 4120 m^{-2}. The total area of the Canyon available for *H. decipiens* was estimated to be 3.4×10^5 m^2. Based on a coverage of 37 %, 1.26×10^5 m^2 of the canyon was vegetated by *H. decipiens* with an estimated total biomass of ca 1.15×10^6 g dry wt (1150 kg). Thus, areal biomass of *H. decipiens* for the entire Canyon was 3.38 g dry wt m^{-2} with an areal density of 1514 leaf pairs m^{-2}.

Living algae, as well as plant debris originating from *Halodule wrightii* Ascherson, *Syringodium filiforme* Kütz and *Thalassia testudinum* König were present (Table 1). *Halodule* debris was the most widely distributed, followed by *Syringodium* and *Thalassia*. Concentrations of whole seagrass leaf debris were large in the troughs of sand ripples and in pockets at the base of the west wall. Also present were ovoid aggregations of *Halodule* leaves (10 cm × 5 cm) that rolled along the canyon floor; these often were concentrated in the troughs of sand ripples.

Table 2. *Halophila decipiens*. Daily net production at 3 depths in Salt River Canyon between May 17 and 22, 1985. Mean ($\bar{x}$) and standard deviation (SD) are reported

Station	No. of samples	Net production (mg dry wt shoot^{-1} d^{-1})
15 m	60	$\bar{x}$ = 0.740 SD = 0.520
21 m	72	$\bar{x}$ = 0.590 SD = 0.340
27 m	64	$\bar{x}$ = 0.545 SD = 0.385
Mean of all depths	196	0.625

Net production of *Halophila decipiens*

Net productivity of *Halophila decipiens* ranged between an average of 0.545 mg dry wt shoot^{-1} d^{-1} at the 27 m station and 0.740 mg dry wt shoot^{-1} d^{-1} at the 15 m station (Table 2). The 21 m station was intermedi-

Table 3. *Halophila decipiens*. Senescence survey at 3 depths in Salt River Canyon. Each station was located in close proximity to productivity stations. Mean and standard deviation of 25 rhizomes examined by the aquanauts at each depth are reported

Station		Average number of leaf pairs from apical meristem for: 1st branch (1)	1st epiphytes (2)	1st leaf loss (3)	1st deterioration of leaf structure (4)
15 m	$\bar{x}$	4.45	4.29	6.56	6.12
	SD	0.68	1.12	1.68	1.61
21 m	$\bar{x}$	4.33	3.55	6.42	6.17
	SD	0.68	1.10	1.71	1.75
27 m	$\bar{x}$	4.2	3.79	6.56	5.86
	SD	0.65	0.88	1.68	1.25
All depths	$\bar{x}$	4.33	3.88	6.23	6.05

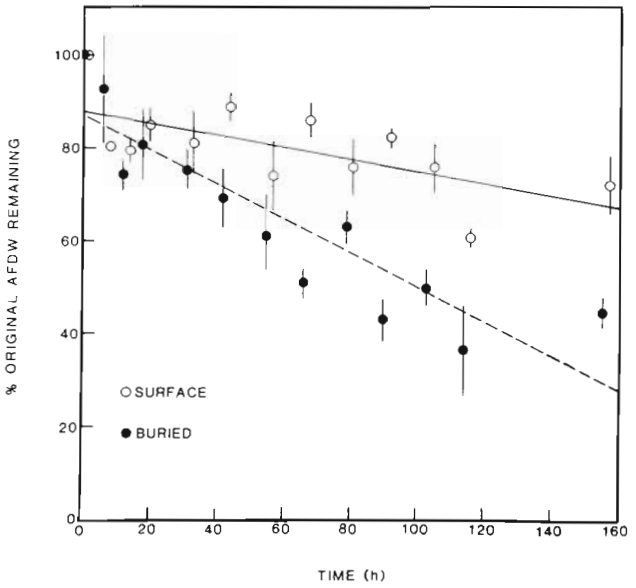

Fig. 3. *Halophila decipiens*. Weight loss (ash free dry weight, AFDW) of sea grass placed in litterbags and either buried in the sediment (●) or suspended on the sediment surface (○) in Salt River Canyon

ate: 0.590 mg dry wt shoot^{-1} d^{-1}. Using an apical meristem density of 1370 m^{-2} (Table 1), productivity where *H. decipiens* occurred was estimated to be 0.856 g dry wt m^{-2} d^{-1}. The organic matter content of *H. decipiens* was 42.5 % and the organic matter was 40 % carbon, so that 145 mg C m^{-2} d^{-1} or ca 0.1 mg C shoot^{-1} d^{-1} were produced where the plants occurred. *H. decipiens* productivity computed on the basis of the entire area of the Canyon (and not just where it occurred) was ca 0.05 g C m^{-2} d^{-1}. Based on our estimates of coverage (see previous section, 1.26 × 10^5 m^2) the total production of *H. decipiens* in the Canyon is ca 18 kg C d^{-1}.

Turnover of *Halophila decipiens*

The 2 methods for calculating turnover time of *Halophila decipiens* yielded similar estimates. The turnover time was 10.6 d based on the biomass to productivity ratio:

$$\frac{9.15 \text{ g dry wt m}^{-2}}{0.856 \text{ g dry wt m}^{-2} \text{ d}^{-1}}$$

Based on data from the senescence survey (Table 3), the first indication of leaf loss or deterioration of leaf structure occurred at leaf pairs 6.23 and 6.05, respectively. The average of these, 6.14, divided by the mean daily leaf pair formation rate (0.575 d^{-1}) resulted in a turnover value of 10.7 d.

Decomposition of *Halophila decipiens*

There was a difference in the rate of decomposition of surface and buried *Halophila decipiens*. Final weight for the surface bags averaged 28 % of the original material (Fig. 3). After an initial weight loss of 26 % during the first 16 h, the weight of the buried bags declined steadily so that at the final sampling (156 h) an average of 56 % was lost. An analysis of covariance (ANCOVA, $\alpha = 0.05$) indicated there was a significant

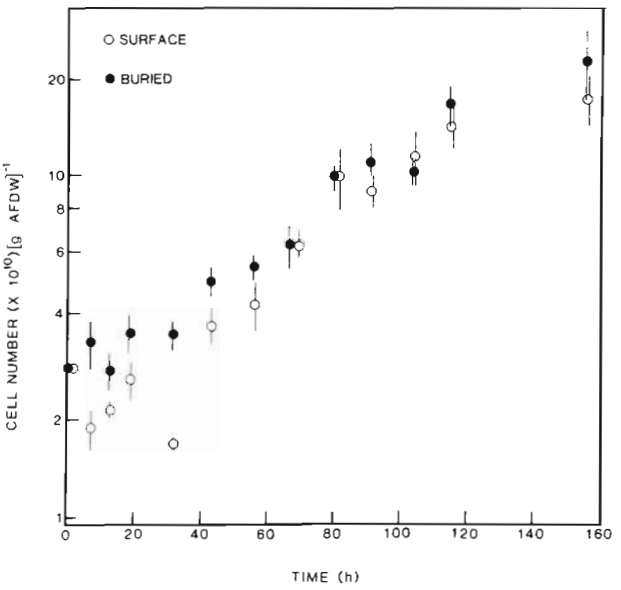

Fig. 4. Numbers of bacteria per g AFDW of *Halophila decipiens* placed in litterbags and either buried in the sediment (●) or suspended on the sediment surface (○) in Salt River Canyon

Table 4. Growth of bacteria in litterbags of *Halophila decipiens* suspended on the sediment surface reported as cell number (cells $\times 10^{10}$ [g AFDW]$^{-1}$) and bacteria cell carbon (mg C [g AFDW]$^{-1}$). Density values were adjusted to net growth by accounting for average weight lost during the 156 h experiment period to obtain total cells and total carbon

Sample time (h)	$\bar{x}$ % original AFDW remaining	Cell number		Cell carbon	
		Density (cells $\times 10^{10}$ [g AFDW]$^{-1}$)	Adjusted (total cells $\times 10^{10}$)	(mg bacteria C [g AFDW]$^{-1}$)	Adjusted (total C mg)
0	100	2.80	1.78	1.21	0.76
7	80	1.87	0.97		
13	79	2.12	1.06	1.43	0.71
19	84	2.59	1.41		
32	80	1.70	1.05	1.41	0.70
43	88	2.68	1.49		
56	73	4.27	1.99	3.10	1.44
67	85	6.32	3.41		
80	75	9.96	4.74	10.17	4.84
91	82	8.91	4.69		
104	75	11.30	5.45	14.00	6.76
115	60	13.70	5.30		
156	71	16.50	7.48	17.57	7.97

Calculation of doubling time:
$\text{Log}_2\ 1.78 \times 10^{10} = 34.05$
$\text{Log}_2\ 7.48 \times 10^{10} = 36.12$
$36.12 - 34.05 = 2.07$
$\frac{2.07}{156\ \text{h}} = 0.013\ \text{dbl h}^{-1}$ or $0.319\ \text{dbl d}^{-1}$
$\frac{1}{0.319} = 3.1\ \text{d} = \text{net doubling time}$

Table 5. Growth of bacteria in litterbags of *Halophila decipiens* buried in the sediment reported as cell number (cells $\times 10^{10}$ [g AFDW]$^{-1}$) and bacteria cell carbon (mg C [g AFDW]$^{-1}$). Density values were adjusted to net growth by accounting for average weight lost during the 156 h experiment period to obtain total cells and total carbon

Sample time (h)	$\bar{x}$ % original AFDW remaining	Cell number		Cell carbon	
		Density (cells $\times 10^{10}$ [g AFDW]$^{-1}$)	Adjusted (total cells $\times 10^{10}$)	(mg bacteria C [g AFDW]$^{-1}$)	Adjusted (Total C mg)
0	100	2.80	1.78	1.21	0.76
7	92	3.30	2.88		
13	74	2.75	1.86	3.42	2.32
19	80	3.53	1.79		
32	75	3.48	1.63	4.22	1.98
43	68	4.97	2.17		
56	60	5.43	2.07	8.01	3.06
67	51	6.23	2.01		
80	62	9.77	3.83	12.74	5.00
91	42	10.85	3.01		
104	50	10.16	3.20	15.30	4.81
115	36	15.91	3.71		
156	44	21.15	5.96	29.30	8.24

Calculation of doubling time:
$\text{Log}_2\ 1.78 \times 10^{10} = 34.05$
$\text{Log}_2\ 5.96 \times 10^{10} = 35.79$
$35.79 - 34.05 = 1.74$
$\frac{1.74}{156\ \text{h}} = 0.012\ \text{dbl h}^{-1}$ or $0.268\ \text{dbl d}^{-1}$
$\frac{1}{0.268} = 3.7\ \text{d} = \text{net doubling time}$

difference between the slopes of the regression lines of weight loss over time for the 2 treatments. The rate of weight loss in the buried treatments was significantly faster than in the surface treatments.

Bacterial abundance, growth, and net production

At the initiation of the litterbag incubations in the Canyon there were 2.8×10^{10} bacterial cells for each g AFDW of *Halophila decipiens*. During the first 29 h the increase in cell numbers may not have been as rapid as the increase between 32 and 116 h (Fig. 4). The cells in both treatments showed net doubling between samplings at 19 and 67 h and continued on an exponential increase until the 116 h sampling. The rate of increase in cell numbers declined between 116 h and the final sample at 156 h. Final cell abundances were 1.65×10^{11} per g AFDW in the surface bags and 2.12×10^{11} per g AFDW in buried bags. Overall bacterial net doubling times, estimated from the total number of cells, were 3.1 d for surface bags and 3.7 d for buried bags (Tables 4 and 5). Data from each treatment were log-transformed and compared using ANCOVA. There was no significant difference ($\alpha = 0.05$) between the slopes of the regression lines of cell numbers over time but there was a significant difference ($\alpha \leq 0.001$) in the adjusted group means. These results indicate there was no difference in the rate of increase in cell numbers between the 2 treatments but there were slightly greater numbers of cells in the buried bags.

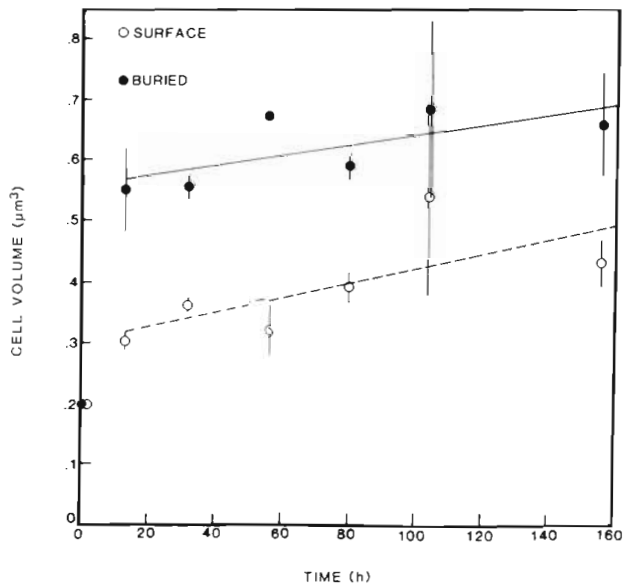

Fig. 5. Average volume (μm^3) of bacteria on *Halophila decipiens* in litterbags either buried in the sediment (●) or suspended on the sediment surface (○) in Salt River Canyon

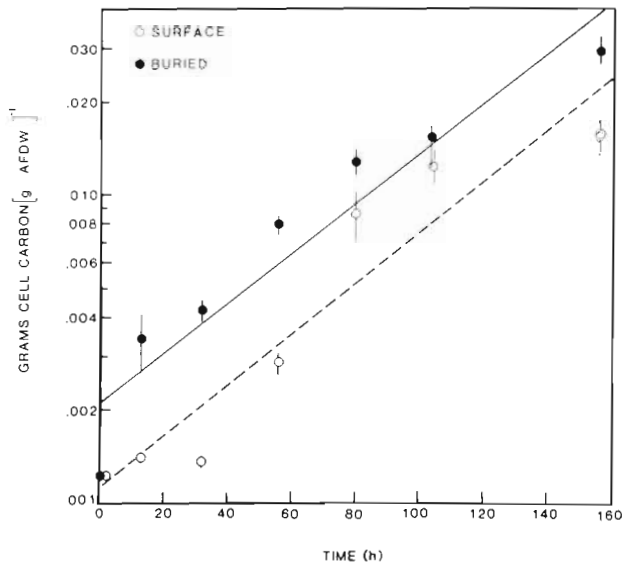

Fig. 6. Bacterial cell carbon per g AFDW of *Halophila decipiens* placed in litterbags and either buried in the sediment (●) or suspended on the sediment surface (○) in Salt River Canyon

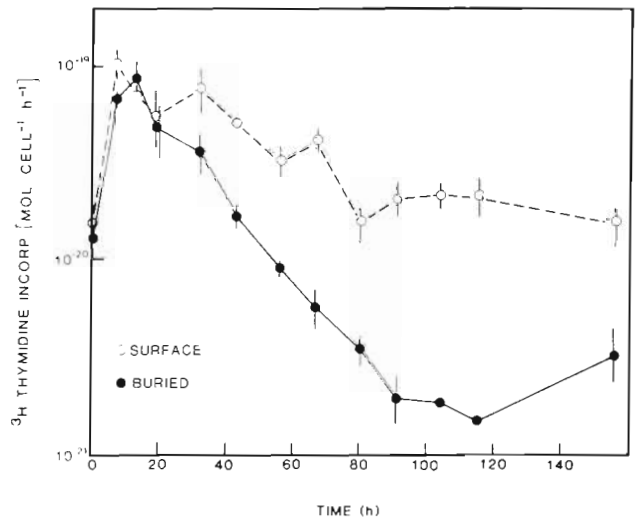

Fig. 7 [^{3}H] thymidine incorporation per cell for bacteria on *Halophila decipiens* placed in litterbags and either buried in the sediment (●) or suspended on the sediment surface (○) in Salt River Canyon

Initial mean cell size was 0.197 μm^3, and cell size increased immediately in both treatments (Fig. 5). Mean cell size continued to increase throughout the remainder of the expriment to 0.433 μm^3 in the surface bags and 0.611 μm^3 in the buried bags. Results of an ANCOVA comparing the 2 treatments showed there was no significant difference ($\alpha = 0.05$) between the slopes of the regression lines of cell size over time but that there was a significant difference in the adjusted group means. On the average, the cells were larger in the buried bags, and the difference in the treatments

were manifested during the first several hours of the experiment.

There was an initial exponential net increase in cell carbon per g AFDW reflecting the increase in cell number and cell size (Fig. 6). The rate of increase in bacterial carbon biomass was not as fast toward the latter part of the incubation with final values of 29.3 mg cell C per g AFDW for buried bags and 17.5 mg cell C per g AFWD for surface bags. The estimate of net carbon increase during the 156 h period was 7.21 mg C per surface litterbag and 7.48 mg C per buried litterbag (Tables 4 and 5).

Cell carbon data were log-transformed and the treatments compared with ANCOVA. There was no significant differences in the slopes of the regression lines of cell carbon over time but there was a significant difference between the adjusted group means indicating that, although the rates of carbon increase were similar, there was more bacterial biomass in the buried bags per unit weight of plant material.

Heterotrophic activity; [^{3}H]-thymidine incorporation in litterbags

The per-cell incorporation rate of thymidine increased in the first 7 h of the experiment for both treatments. This increase coincided with the increase in cell size. Thymidine incorporation rate then declined steadily until about 80 to 90 h when both rates stabilized (Fig. 7). The final rate in the buried treatment, 3.22×10^{-21} mol [^{3}H]-thymidine cell^{-1} h^{-1}, was substantially less than the initial rate, 1.25×10^{-20} mol [^{3}H]-thymidine cell^{-1} h^{-1}, while in the surface bags the final rate, 1.52×10^{-20} mol [^{3}H]-thymidine cell^{-1} h^{-1}, was nearly equivalent to the initial rate. On the basis of the AFDW content of the litterbags the incorporation rate of thymidine increased during the first 13 h in both treatments (Table 6). Thereafter the rates fluctuated but remained consistently higher in the surface bags.

DISCUSSION

Distribution, abundance and growth of *Halophila decipiens*

Halophila decipiens, allochthonous seagrass detritus, and macroalgae are the major sources of primary production, organic matter and vegetated habitat in the Salt River Canyon (Table 1) (Josselyn et al. 1983, Josselyn et al. 1986, Williams et al. 1985). The potential importance of *H. decipiens* may be illustrated by a comparison of its daily areal net productivity (50 mg C m^{-2} d^{-1}) with that of *Caulerpa* spp. (0.3 to 1.0 mg C m^{-2} d^{-1}), the dominant rhizophytic algae in the Canyon (Williams et al. 1985).

In locations where the seagrass occurred, *Halophila decipiens* biomass (9.15 g dry wt m^{-2}; Table 1) was similar to that reported by previous Hydrolab missions conducted in 1983 (7.0 g dry wt m^{-2}) and 1984 (8.1 g dry wt m^{-2}) (Josselyn et al. 1986). During our 1985 mission, net productivity in seagrass beds was 145 mg C m^{-2} d^{-1} which was lower than in July 1983 (238 mg C m^{-2} d^{-1}) but similar to August 1984 (144 mg C m^{-2} d^{-1}). It is difficult to ascertain whether these differences reflect real year-to-year variation or are due to seasonal cycles in growth. Our mission in 1985 was conducted in the latter part of May while missions in 1983 and 1984 were conducted in July and August, respectively. The lower value in August 1984 may indicate short-term fluctuations due to extreme environmental conditions. Josselyn et al. (1986) reported that during the 1984 mission the shallow head of the Canyon was very turbid. The solar irradiance reaching the bottom was actually higher at greater depths in the Canyon. This reduction in light transmittance corresponded with a sharp depression of the growth of *H. decipiens* at the 15 m station compared to the 21 and 27 m sites in the 1984 mission. An examination of Table 3 in Josselyn et al. (1986) shows that the rhizome elongation rate at 15 m was reduced by about 65 % of the 1983 value. Generally, the maximum daily irradiance during our study in 1985 reached 400 to 750 µE m^{-2} s^{-1}, which should not cause light-limited growth for *H. decipiens* (Dennison 1987).

Halophila decipiens net productivity and biomass is much lower than the larger, more robust Caribbean seagrasses *Thalassia testudinum, Syringodium filiforme* and *Halodule wrightii* (Zieman & Wetzel 1980).

Table 6. (^{3}H) thymidine incorporation rates (nmol [^{3}H] thymidine [g AFDW]$^{-1}$ h^{-1}) of bacteria growing on *Halophila decipiens* in litterbags either suspended at the sediment surface or buried in the sediment. Rates are derived from the average of three replicate litterbags

Sample time (h)	Surface	Buried
0	0.42	0.35
7	1.85	2.21
13	1.51	2.27
19	1.34	1.57
32	1.27	1.20
43	1.90	0.81
56	1.30	0.48
67	2.52	0.33
80	1.50	0.33
91	1.76	0.20
104	2.31	0.18
115	2.52	0.23
156	2.31	0.59

However, the turnover time for *H. decipiens* is faster. On the average, a new leaf pair emerged about every 1.7 d, whereas most other seagrasses have leaf emergence rates on the order of 9 to 16 d (Patriquin 1973, Zieman & Wetzel 1980, Thayer et al. 1984a, Fonseca et al. 1987). *H. decipiens* leaves begin to show senescence and substantial deterioration when they are only 10 to 11 d old, while most other seagrass leaves live and remain attached to the shoot for more than 25 d and frequently for as many as 40 to 50 d (Sand-Jensen 1975, Zieman 1975, Jacobs 1979, Thayer et al. 1984a).

Decomposition of *Halophila decipiens*

Our results indicate that measurable changes in plant composition and the microbial community occurred within 7 h after litterbag deployment. Litterbag experiments are typically sampled weeks or months after deployment, in contrast to the 6 to 12 h sampling period we followed. We based our sampling schedule on the relatively labile composition of *Halophila decipiens* and on previous observations that buried *Halophila* was decomposed beyond recognition after 48 h (M. Fonseca & M. Josselyn pers. obs.).

Disturbance and burial of plant material on the Canyon floor is a dynamic and important mechanism influencing the distribution of *Halophila decipiens* and the disposition of organic matter (Williams et al. 1985, Josselyn et al. 1986). Two important sources of disturbance are wave surge accompanied by sand movement, and burrowing and bottom feeding activities of macrofauna which uproot and frequently bury *H. decipiens* (Williams et al. 1985). Burial of plant material is important for at least 2 reasons. During high energy storm events a net down-Canyon flow of bottom current is responsible for bedload transport of organic matter out of the Canyon (Josselyn et al 1983). Burial offsets export by retaining organic matter in the Canyon and enhancing its decomposition and turnover rates.

According to our results and those of previous missions (Josselyn et al. 1986), when *Halophila decipiens* is buried, the plant tissue degrades faster than has been reported for other seagrasses (Thayer et al. 1984a). In just 5 d, percent weight loss in the buried bags was similar to that which typically occurs in 1 to 4 mo of decomposition for other species (Thayer et al. 1984a). When the plants are buried, the reduction of light and the anaerobic environment initiate almost immediate death and degradation. The weight loss in the surface bags was significantly slower and resembled the pattern more typical of seagrasses and other submerged vascular plants that initially lose about 10 to 20 % of their organic matter during the earliest stage of degradation.

Bacterial abundance and growth

The occurrence of large bacteria, a rapid bacterial net growth rate, and a substantial initial plant weight loss (ca 50 % of original) suggest that *Halophila decipiens* detritus is a readily available substrate for heterotrophic bacteria. Bacteria have responded similarly to exudation of organic substrate during plant metabolism or the initial stages of decay when dissolved organic matter was leached (Harrison & Mann 1975, Moriarty & Pollard 1982, Robertson et al. 1982, Kenworthy & Thayer 1984, Kirchman et al. 1984, Moriarty et al. 1985b, Moriarty et al. 1986). The large bacterial cell sizes we observed, especially for the buried *H. decipiens* are indicative of elevated concentrations of dissolved organics, nutrient-enriched environments, high metabolic activity, and rapid growth (Donachie et al. 1976, Pierucci 1978, Hagström et al. 1984, Palumbo et al. 1984). The average size of the bacterial communities in both treatments increased sharply during the first 13 h; however, the mean cell size in the buried bags was nearly twice that of the surface bags and remained so throughout the experiment. The maximum densities of cells attained in each litterbag treatment, i.e. 1.65×10^{11} (g AFDW)$^{-1}$ in the surface bags and 2.12×10^{11} (g AFDW)$^{-1}$ in the buried bags, exceeded the abundance of bacteria on the standing stock of *H. decipiens* (5.29 to 7.74 $\times 10^{9}$) by about 2 orders of magnitude and are greater than or equal to bacterial cell densities reported for detritus of other seagrass (Fenchel 1970, Newell 1981, Robertson et al. 1982, Rublee & Roman 1982, Kenworthy et al. 1987). Cell volume in both surface and buried bags also was larger than cell volumes reported for bacteria attached to *Zostera marina* leaves, the roots and rhizomes of temperate and tropical seagrasses, suspended particles, and sediments (Newell 1981, Rublee 1982, Kirchman 1983, Kenworthy et al. 1987). The estimated net doubling times, 3.1 and 3.7 d for surface and buried bags respectively, is within the broad range of 3 h to 21 d found in published studies of gross bacterial production (Newell 1981, Fuhrman & Azam 1982, Moriarty & Pollard 1982, Findlay & Meyer 1984, Hagström et al. 1984, Kirchman et al. 1984, Moriarty et al. 1985a, b, Fallon & Newell 1986, Moriarty et al. 1986) and net bacterial production (Newell et al. 1983). Since our methods were not suited for assessing the effects of grazing on the abundance of bacteria in the litterbags our estimates probably underestimate growth. Given that most grazing studies have emphasized pelagic bacteria and not cells attached to plant detritus we have little basis for drawing any conclusions or making any assumption about grazing in our experiments. However, 2 studies which examined the growth and abundance of attached bacteria and microheterotrophic grazers on vascular plant

detritus (Robertson et al. 1982, Newell et al. 1983) show a lag time of 5 to 12 d before the effects of grazing were evident. The fact that we observed logarithmic growth throughout the 6.5 d period in our study suggests that grazing may have been negligible.

Heterotrophic activity; [^{3}H]-thymidine incorporation

Differences in the heterotrophic activity (thymidine incorporation) between surface and buried litterbags and fluctuations in the per-cell incorporation rates within each treatment may be attributed to differences in the microbial communities and changes in their metabolism. Initially there was a sharp increase in per-cell thymidine incorporation and cell volume. The cells may have been preparing for a period of exponential growth during which bacteria may double or quadruple their nuclear material (Doetsch & Cook 1973). This would result in an increase in the cellular content of DNA and its precursors which would correlate with an increase in the thymidine incorporation rate (Kirchman et al. 1982a). After an initial increase in both treatments the per-cell incorporation of thymidine declined. Rates in the surface bags returned to their initial values but the buried bags continued to decline and reached a nearly constant value much lower than the initial rates. We attribute the decline in the buried bags to the presence of bacteria cells incapable of thymidine uptake. For example, *Pseudomonas* species (Ramsay 1974), anaerobic marine bacteria with special nutrient requirements (e.g. sulfate reducers), and bacteria on sediment incubated under anaerobic conditions may not incorporate measurable thymidine (Pollard & Moriarty 1984, Fallon & Newell 1986, McDonough et al. 1986). Although cell numbers increased exponentially in the buried bags we suspect that the total population incorporating thymidine was decreasing in conjunction with the development of an anaerobic community. After ca 80 h the per-cell incorporation rates in the surface bags reached a nearly constant value. It may have been that by this time the microbial communities associated with the decomposing litter had either adjusted to the initial disturbance of preparing the litterbags and/or had made a complete shift to a new equilibrium community with a different metabolism.

The constancy of a per-cell incorporation rate is a key assumption for deriving accurate bacterial production estimates from thymidine incorporation in mixed microbial assemblages (Kirchman et al. 1982a). Clearly, this was not the case in the litterbags. In addition, we were unable to empirically derive a factor for converting thymidine incorporation into bacterial cells. These, combined with other recently identified problems concerning incorporation of thymidine into proteins and inefficient extracton of radiolabeled macromolecules (Fallon & Newell 1986, Hollibaugh 1988), precluded an estimation of bacterial production on *Halophila decipiens* detritus using the thymidine data.

Heterotrophic utilization of *Halophila decipiens* detritus

We estimated bacterial net production based on the numerical abundance and cell size data from which we computed an increase in bacterial carbon (Tables 4 and 5). These values are conservative estimates of bacterial net production since we do not account for losses from the litterbags due to grazing and transport of small particles out of the bags. From 1 g AFDW of *Halophila decipiens* detritus the bacteria produced an average of 7.35 mg C (1.13 mg C d^{-1}) in both the buried and surface bags. During the same period *H. decipiens* produced ca 50 mg C m^{-2} d^{-1} or 119 mg AFDW m^{-2} d^{-1} areal production (includes the entire canyon floor area). Assuming that during this same period the *H. decipiens* biomass was near steady-state, and all plant material was retained in the canyon, then plant production would approximate the input of *H. decipiens* detritus. Given an input to the detrital pool of 119 mg AFDW m^{-2} d^{-1}, the estimated daily bacterial net production from new sources of detritus would equal 0.119 g m^{-2} d^{-1} × 1.13 mg C g^{-1} or 0.13 mg C m^{-2} d^{-1}. Thus, a conservative estimate of bacterial production on the detritus would be ca 0.26 % (0.132 ÷ 50) of daily net primary production of *H. decipiens*, much lower than values reported for estuarine and oceanic planktonic systems where the proportion of bacterial net production to primary production may exceed 40 % (Ducklow 1983), but comparable to other macrophyte detrital systems where the proportion of bacterial production is also lower (Newell et al. 1983, Findlay & Meyer 1984).

Despite the likelihood that a large fraction of the initial weight lost from the detritus was dissolved organic carbon (DOC), the attached bacteria utilized the substrate very inefficiently. Dividing the average carbon loss from the litterbags by the bacterial carbon yield, we estimate a net carbon conversion efficiency of 6 % for surface bags and 3 % in buried bags. Even though the contribution of bacteria growing on *Halophila decipiens* would extend beyond the initial 6.5 d period we would predict that as the detrital material aged and the rate of the release of dissolved organic matter declined, the growth rate of the attached cells would decline as well. Given the known ingestion rates and absorption efficiencies of deposit feeders, the microbial abundance on the particulate *H. decipiens* detritus could not make a significant contribution to a macrofaunal detritivore's energy

demands (Cammen 1980, Findlay & Meyer 1984, Lopez & Levinton 1987, Blum et al. 1988). Unless the attached bacteria were to use the organic matter more efficiently as it aged and were heavily grazed by meiofauna or microfauna they would not likely make a significant contribution to energy flow and secondary production (Fenchel & Jørgensen 1976, Fenchel 1982, Findlay & Meyer 1984, Linley & Newell 1984, Caron 1987). On the other hand, we did not measure bacterial growth based on DOC or fine particulate matter that escaped the litterbag, both of which could make additional contributions to secondary production.

Summary and conclusions

Although its net production is less than the other Caribbean seagrasses, *Halophila decipiens* is a major source of primary production on the Salt River Canyon floor. *H. decipiens* has adapted to low light levels and disturbed environments with a rapid growth rate, fast turnover time, and a reduced plant structure. *H. decipiens* biomass enters the detrital pool throughout the growing season and its labile composition results in rapid decomposition. Burial of *H. decipiens* through wave action and animal activities increases the rate of detrital input and retains the detritus within the Canyon. Buried detritus decomposes faster, and contains a greater bacterial biomass per g AFDW than material degrading on the sediment surface. However, in terms of recycling primary production within the Salt River Canyon, utilization of *H. decipiens* detritus by attached bacteria does not represent an efficient, tightly-coupled system. Future research on the particulate detritus of submerged aquatic vascular plants should examine the fate of bacterial production and the disposition of bacterial biomass during both the early and later stages of decay with emphasis on the utilization of bacteria by microheterotrophic grazers.

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LITERATURE CITED

Bianchi, T. S., Levinton, J. S. (1984). The importance of microalgae, bacteria, and particulate organic matter in the nutrition of *Hydrobia totteni*. J. mar. Res. 39: 547–556

Birch, W R., Birch, M. (1984). Succession and pattern of tropical intertidal seagrasses in Cockle Bay, Queensland, Australia: a decade of observations. Aquat. Bot. 19: 343–367

Blum, L. K., Mills, A. L., Zieman, J. C., Zieman, R. T (1988). Abundance of bacteria and fungi in seagrass detritus. Mar. Ecol. Prog. Ser 42: 73–78

Bratbak, G. (1985). Bacterial biovolume and biomass estimations. Appl. environ. Microbiol. 49: 1488–1493

Cammen, L. (1980). The significance of microbial carbon in the nutrition of the deposit feeding polychaete *Nereis succinea*. Mar. Biol. 61. 9–20

Caron, D. A. (1987). Grazing of attached bacteria by heterotrophic microflagellates. Microb. Ecol. 13: 203–218

Continental Shelf Associates, Inc., and Martel Laboratories, Inc. (1985). Florida Big Bend seagrass habitat study narrative report, a final report. Submitted to the Mineral Management Service, Metairie, La. Contract No. 14-12-0001-30188

CRC Standard mathematical tables. Chemical Rubber Co., Cleveland, Ohio, 21st edn. p. 13

Dennison, W. C. (1987). Effects of light on seagrass photosynthesis, growth and depth distribution. Aquat. Bot. 27: 15–26

Doetsch, R. N., Cook, T M. (1973). Introduction to bacteria and their ecobiology. University Park Press, Baltimore, p. 61

Donachie, U. D., Begg, K. J., Vincente, M. (1976). Cell lengths, cell growth and cell division. Nature, Lond. 264: 328–333

Ducklow, H. W (1983). Production and fate of bacteria in the oceans. Bioscience 33: 494–501

Fallon, R. D., Newell, S. Y (1986). Thymidine incorporation by the microbial community of standing dead *Spartina alterniflora*. Appl. environ. Microbiol. 52: 1206–1208

Fenchel, T (1970). Studies on the decomposition of organic detritus derived from turtle grass *Thalassia testudinum*. Limnol. Oceanogr 15: 14–20

Fenchel, T (1977). Aspects of the decomposition of seagrasses. In: McRoy, C. P., Helfferich, C. (eds.) Seagrass ecosystems, a scientific perspective. Marcel Dekker, New York, p. 123–145

Fenchel, T (1982). Ecology of heterotrophic microflagellates. IV Quantitative occurrence and importance as bacterial consumers. Mar. Ecol. Prog. Ser. 9: 35–42

Fenchel, T., Jørgensen, B. B. (1976). Detritus food chains of aquatic ecosystems and the role of bacteria. Adv. microb. Ecol. 1: 1–79

Findlay, S., Meyer, J. L. (1984). Significance of bacterial biomass and production as an organic carbon source in lotic detrital systems. Bull. mar Sci. 35: 318–325

Fonseca, M. S., Thayer, G. W., Kenworthy, W. J. (1987). The use of ecological data in the implementation and management of seagrass restorations. In: Durako, M. J., Phillips, R. C., Lewis, R. R. (eds.) Fla Mar Res. Publ. 42: 175–188

Fuhrman, J. A. (1981). Influence of method on the apparent size distribution of bacterioplankton cells: epifluorescence microscopy compared to scanning electron microscopy. Mar. Ecol. Prog. Ser. 5: 103–106

Fuhrman, J. A., Azam, F. (1982). Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters. Evaluation and field results. Mar Biol. 66: 109–120

Hagström, Å., Ammerman, J. W., Henrichs, S., Azam, F. (1984). Bacterioplankton growth in seawater 2. Organic matter utilization during steady-state growth in seawater cultures. Mar Ecol. Prog. Ser 18: 41–48

Hargrave, B. T (1976). The central role of invertebrate feces in sediment decomposition. In: Anderson, J. M., MacFayden,

A. (eds.) The role of terrestrial and aquatic organisms in decomposition processes. Blackwell, Oxford, p. 301–321

Harrison, P., Mann, K. H. (1975). Detritus formation from eelgrass (*Z. marina* L.): the relative effects of fragmentation, leaching, and decay. Limnol. Oceanogr. 20: 924–934

Hobbie, J. E., Daley, R. J., Jasper, S. (1977). Use of nuclepore filters for counting bacteria by fluorescence microscopy. Appl. environ. Microbiol. 33: 1225–1228

Hollibaugh, J. T. (1988). Limitations of the [^{3}H] thymidine method for estimating bacterial productivity due to thymidine metabolism. Mar Ecol. Prog. Ser 43: 19–30

Jacobs, R. P. W M. (1979). Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. Aquat. Bot. 7: 151–172

Josselyn, M. N., Calliet, G. M., Niesen, T M., Cowen, R., Hurley, A. C., Conner, J., Hawes, S. (1983). Composition, export and faunal utilization of drift vegetation in the Salt River Submarine Canyon. Estuar coast. Shelf Sci.17: 447–465

Josselyn, M. N., Fonseca, M., Niesen, T., Larson, R. (1986). Biomass, production and decomposition of a deep water seagrass, *Halophila decipiens* Ostenf. Aquat. Bot. 25: 47–61

Kenworthy, W. J., Currin, C., Smith, G., Thayer, G. W. (1987). The abundance, biomass, and acetylene reduction activity of bacteria associated with decomposing rhizomes of two seagrasses, *Zostera marina* and *Thalassia testudinum*. Aquat. Bot. 27: 97–119

Kenworthy, W. J., Thayer, G. W. (1984). Aspects of the production and decomposition of the roots and rhizomes of seagrasses, *Zostera marina* and *Thalassia testudinum*, in temperate and subtropical marine ecosystems. Bull. mar. Sci. 35: 364–379

Kikuchi, T., Peres, J. M. (1977). Consumer ecology of seagrass beds. In: McRoy, C. P., Helfferich, C. (eds.) Seagrass ecosystems: a scientific perspective. Marcel Dekker, New York, p. 147–193

Kirchman, D. (1983). The production of bacteria attached to particles suspended in a freshwater pond. Limnol. Oceanogr. 28: 858–872

Kirchman, D. K., Ducklow, H. W., Mitchell, R. (1982a). Estimates of bacterial growth from changes in uptake rates and biomass. Appl. environ. Microbiol. 44: 1296–1307

Kirchman, D. L., Mazzella, L., Alberte, R. S., Mitchell, R. (1984). Epiphytic bacterial production on *Zostera marina*. Mar. Ecol. Prog. Ser. 15: 117–123

Kirchman, D. L., Sigda, L., Kapuscinski, R., Mitchell, R. (1982b). Statistical analysis of the direct count method for enumerating bacteria. Appl. environ. Microbiol. 44: 376–382

Klug, M. J. (1970). Detritus-decomposition relationships. In: Phillips, R. C., McRoy, C. P. (eds.) Handbook of seagrass biology, an ecosystem perspective. Garland STPM Press, New York, p. 225–246

Linley, E. A. S., Newell, R. C. (1984). Estimates of bacterial growth yields based on plant detritus. Bull. mar. Sci. 35: 409–425

Lopez, G. R., Levinton, J. S. (1987). Ecology of deposit feeding animals in marine sediments. Q. Rev. Biol. 62: 235–260

Lopez, G. R., Levinton, J. S., Slobodkin, L. B. (1977). The effect of grazing by the detritivore *Orchestra grillusa* on Spartina litter and its associated microbial community. Oecologia 30: 111–127

McDonough, R. J., Sanders, R. W., Porter, K. G., Kirchman, D. L. (1986). Depth distribution of bacterial production in a stratified lake with an anoxic hypolimnion. Appl. environ. Microbiol. 52: 992–1000

Moriarty, D. J. W., Boon, P. I., Hensen, J. A., Hunt, W G., Poiner, I. R., Pollard, P. C., Skyring, G. W., White, D. C. (1985a). Microbial biomass and productivity in seagrass beds. Geomicrobiol. J. 4: 21–51

Moriarty, D. J. W., Iverson, R. L., Pollard, P. C. (1986). Exudation of organic carbon by the seagrass *Halodule wrightii* Aschers and its effect on bacterial growth in the sediment. J. exp. mar. Biol. Ecol. 96: 115–126

Moriarty, D. J. W., Pollard, P. C. (1982). Diel variation of bacterial productivity in seagrass *(Zostera capricorni)* beds measured by rate of thymidine incorporation into DNA. Mar. Biol. 72: 165–173

Moriarty, D. J. W., Pollard, P. C., Hunt, W. G. (1985b). Temporal and spatial variations in bacterial production in the water column over a coral reef. Mar. Biol. 85: 285–292

Newell, S. Y (1981). Fungi and bacteria in or on the leaves of eelgrass (*Zostera marina* L.) from Chesapeake Bay. Appl. environ. Microbiol. 41: 1219–1224

Newell, R. C., Linley, E. A. S., Lucas, M. I. (1983). Bacterial production and carbon conversion based on saltmarsh plant detritus. Estuar. coast. Shelf Sci. 17: 405–419

Odum, E. P., de la Cruz, A. (1967). Particulate organic detritus in a Georgia salt marsh-estuarine system. In: Lauff, G. H. (ed.) Estuaries. AAAS Publ. 83, p. 383–388

Odum, W E., Zieman, J. Z., Heald, E. P. (1971). The importance of vascular plant debris to estuaries. In: Proceedings of the Second Coastal Marsh and Estuary Management Symposium. L.S.U. Press, Baton Rouge, La., p. 91–114

Palumbo, A. V., Ferguson, R. L., Rublee, P. (1984). Size of suspended bacterial cells and association of heterotrophic activity with size fractions of particles in estuarine and coastal water Appl. environ. Microbiol. 48: 157–164

Patriquin, D. G. (1973). Estimation of growth rate, production and age of the marine angiosperm *Thalassia testudinum* Konig. Caribb. J. Sci. 13: 111–123

Pierucci, O. (1978). Dimensions of *Escherichia coli* at various growth rates. Model for envelope growth. J. Bacteriol. 135: 559–574

Pollard, P. C., Moriarty, D. J. W. (1984). Validity of the tritiated thymidine method for estimating bacterial growth rates: measurement of isotope dilution during DNA synthesis. Appl. environ. Microbiol. 48: 1076–1083

Ramsay, A. J. (1974). The use of autoradiography to determine the proportion of bacteria metabolizing in an aquatic habitat. J. gen. Microbiol. 80: 363–373

Robertson, M., Mills, A. L., Zieman, J. C. (1982). Microbial synthesis of detritus-like particles from dissolved organic carbon released by tropical seagrasses. Mar. Ecol. Prog. Ser. 7: 279–285

Rublee, P. A. (1982). Bacteria and microbial distribution in estuarine sediments. In: Kennedy, V S. (ed.) Estuarine comparisons. Academic Press, New York, p. 159–181

Rublee, P. A., Roman, M. R. (1982). Decomposition of turtlegrass (*Thalassia testudinum* Konig) in flowing sea-water tanks and litterbags: compositional changes and comparison with natural particulate matter. J. exp. mar Biol. Ecol. 58: 47–58

Sand-Jensen, K. (1975). Biomass, net production and growth dynamics in an eelgrass (*Zostera marina* L.) population in Vellerup Vig. Denmark. Ophelia 14: 185–201

Thayer, G. W., Bjorndal, K. A., Ogden, J. C., Williams, S. L., Zieman, J. C. (1984b). Role of larger herbivores in seagrass communities. Estuaries 7: 351–376

Thayer, G. W., Kenworthy, W. J., Fonseca, M. S. (1984a). The ecology of eelgrass meadows of the Atlantic Coast: a community profile. U. S. Fish Wildl. Serv. FWS/OBS-84/02

Williams, S. L., Breda, V A., Anderson, T. W., Nyden, B. B.

(1985). Growth and sediment disturbances of *Caulerpa* sp. (Chlorophyta) in a submarine canyon. Mar. Ecol. Prog. Ser 21. 275–281

Yingst, J. Y. (1976). The utilization of organic matter in shallow marine sediments by an epibenthic deposit-feeding holothurian. J. exp. mar. Biol. Ecol. 23: 55–69

Zieman, J. C. (1975). Quantitative and dynamic aspects of the ecology of turtle grass, *Thalassia testudinum*. In: Cronin, L. E. (ed.) Estuarine research, Vol. 1, Chemistry, biology and the estuarine system. Academic Press, New York, p. 541–562

Zieman, J. C. (1982). The ecology of the seagrasses of South Florida: a community profile. U. S. Fish Wildl. Serv. FWS/OBS-82/85

Zieman, J. C., Wetzel, R. G. (1980). Productivity in seagrasses: methods and rates. In: Phillips, R. C., McRoy, C. P. (eds.) Handbook of seagrass biology, an ecosystem perspective. Garland STPM Press, New York, p. 87–116

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