Microbial Metabolism and Incorporation by the Polychaete *Capitella capitata* of Aerobically and Anaerobically Decomposed Detritus*

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ABSTRACT: Detritus derived from *Spartina alterniflora* (cordgrass), *Gracilaria foliifera* (red seaweed), and periphyton (mixed algae) was decomposed aerobically and anaerobically for various lengths of time and then fed to the polychaete *Capitella capitata* in flow-through microcosms. Rates of detrital mineralization (CO_2 production), microbial respiration (O_2 consumption) and biomass (adenosine triphosphate and total adenylates, A_t), and net incorporation by *C. capitata* varied with detrital source and length of pre-aging. Oxygen consumption per unit microbial biomass (μmoles $\mu gA_t^{-1} d^{-1}$) increased linearly with age of the detritus: periphytic algal detritus had the highest daily increase of 4 %, followed by *G. foliifera* and *S. alterniflora* detritus at 1 % and 0.3 % respectively. Metabolic respiratory quotient (CO_2/O_2), which varied from < 1 to about 50 . 1, was a function of detrital source and age; it indicated that anaerobic bacteria were important decomposers of detritus. Net incorporation rates by *C. capitata*, microbial biomass, and O_2 consumption rates did not differ among *G. foliifera* detritus aged under oxic and anoxic conditions. Rates of CO_2 production, however, were up to 6 times higher for *G. foliifera* detritus aged anaerobically. The results suggest that anaerobic metabolism, which causes a high CO_2 production, could represent a significant loss of carbon from benthic food webs.

INTRODUCTION

Many factors regulate the decomposition and transformation of plant detritus. Microbial conversion, at least of more refractory detritus, is necessary before detritus is available as food for meiofauna and macrofauna (Fenchel, 1972; Tenore, 1976; Fenchel, 1978; Tenore and Rice, 1980). Following death of a plant, soluble organics leach from the detritus and are rapidly utilized by aerobic bacteria (Burkholder and Bornside, 1957; Gosselink and Kirby, 1974; Fallon and Pfaender, 1976). However, in salt marshes the bulk of vascular plant detritus is particulate and remains in low redox sediments for as long as a year (White et al., 1978; Hackney and de la Cruz, 1980; MacCubbin and Hodson, 1980), whereas seaweed and algae decompose within a few weeks to a month (Josselyn and Mathieson, 1980; Tenore and Hanson, 1980). The rate at which microbes decompose and detritivores utilize

particulate detritus depends on such factors as available caloric and nitrogen content, lignin and lignin-cellulose content, external nitrogen supply, particle size, and presence of oxygen and other terminal electron acceptors (Burkholder and Bornside, 1957; Gunnison and Alexander, 1975; Harrison and Mann, 1975; Haines and Hanson, 1979; Rich, 1979; MacCubbin and Hodson, 1980; Hanson, 1981; Tenore, 1981). Chemical inhibitors in the detritus may also influence decomposition rates and might depress consumption by macroconsumers (Valiela et al., 1979).

The marsh grass *Spartina alterniflora* has been regarded as a major food source for secondary consumers (Teal, 1962; Odum and de la Cruz, 1967). However, *S. alterniflora* detritus had the slowest decomposition rate and the highest conversion efficiency to microbial nitrogen among three marsh plants tested (Haines and Hanson, 1979). Thus, *S. alterniflora* detritus might be suitable as food for detritivores after it is converted to microbial biomass.

Incorporation of detritus by *Capitella capitata* and the rate at which detritus is oxidized and converted to microbial biomass in flow-through microcosms with

periphyton, *Gracilaria foliifera* or *Spartina alterniflora* detritus were related to decay resistance and age of the detritus (Tenore and Hanson, 1980). However, total microcosm respiration and CO_2 production rates were not reported because of possible differences in reduced end-products and mixed aerobic-anaerobic metabolism during aging of the different detrital types. Therefore, the influence of aerobic and anaerobic decomposition of detritus on the respiration and oxidation of the detritus was assessed by aging *G. foliifera* detritus in continuous cultures under oxic and anoxic conditions. The results describe microbial metabolism during aging of these sources of detritus and incorporation of aerobically and anaerobically aged detritus by *G. foliifera*.

MATERIALS AND METHODS

Detritus Aging for Microcosms

Periphyton, *Gracilaria foliifera* and *Spartina alterniflora* were grown to produce homogeneously-^{14}C-labeled detritus (Tenore and Hanson, 1980). Periphyton (an algal mat composed of diatoms, green and blue-green algae) and *G. foliifera* were cultured in illuminated tanks with seawater containing [14C]NaHCO$_3$. Labeled *S. alterniflora* detritus was prepared from plants grown for 3 months in an enclosed chamber with [14C]CO$_2$. Plant material was harvested, washed with seawater, rinsed quickly with 10 % HCl to remove surface-absorbed ^{14}C, rinsed with fresh water, freeze-dried, and ground to pass through a 250 μm mesh.

The different types of labeled detritus were aged at 20 °C in 7 l Plexiglas cylinders. The cylinders continuously received 9 l d^{-1} of 0.45 μm filtered seawater Inorganic nitrogen (145 μmoles NH$_4$Cl l^{-1}) was added to the water so that nitrogen would not limit decomposition. A circular Plexiglas plate moving vertically over the detritus ensured adequate water mixing above the detritus.

Detritus (including the microbial component) was removed from the cylinders at different times, freeze-dried, and kept frozen until used. We did not measure the microbial activity in these aging cultures. Because of this treatment before the detrital complex was introduced into microcosms, the activity in the microcosms was due to previous biochemical changes in the detritus-microbial complex.

Aged periphyton, *Gracilaria foliifera* and *Spartina alterniflora* detritus was added to 1.5 l microcosms (0.018 m^2 surface area) with a layer of clean, fine sand (< 0.3 mm; 250 cm^3) and 1.5 g dry wt. of labeled detritus. After *Capitella capitata* (75 worms micro-

cosm^{-1}) were added, the microcosms were covered with airtight lids. Filtered (1 μm) estuarine water, was pumped through the sealed microcosms at a rate of 35 l d^{-1} to ensure an adequate supply of oxygen. The experiments were run in the dark at 20 °C for 4 d. The term 'microcosm' refers to the community consisting of the detritus-microbial complex and the polychaete *C. capitata* only.

Gracilaria foliifera detritus was aged aerobically (bubbled with air) and anaerobically (bubbled with N$_2$ gas) in 18-l flow-through chambers (Fig. 1). Detritus that washed out with the effluent was trapped in small
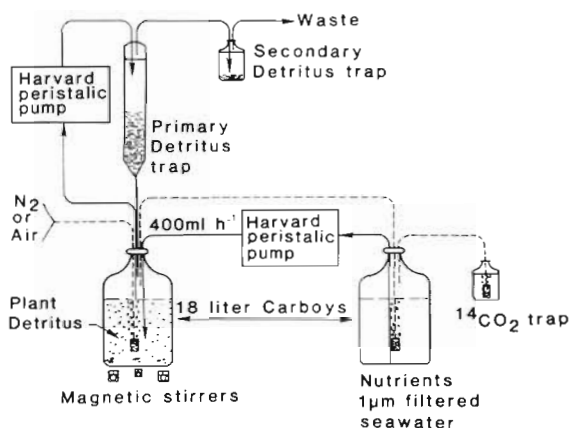

Fig. 1. Culturing system used to produce aerobically or anaerobically aged detritus

reservoirs and returned to the cultures daily. Sufficient inorganic nitrogen (NH$_4$NO$_3$, 150 μmoles l^{-1}) was added to the water, so that ammonium and nitrate would not limit decomposition and anaerobic metabolism respectively. This detritus was prepared as described above and then added to small 1.0-l microcosms (0.009 m^2) with 50 cm^3 of sand and 0.75 g dry weight of labeled *G. foliifera* detritus. *Capitella capitata* (37 ind. microcosm^{-1}) were added and the microcosms sealed. Seawater was pumped through these microcosms at a rate of 9 l d^{-1}.

Microbial and Macroconsumer Activity Measurements

Metabolic activity of microbes and macroconsumers in the microcosms was estimated from the difference in carbon dioxide and oxygen concentrations in water entering and leaving the microcosm on Days 3 and 4 of the experiment (Hanson, 1981). Bubble-free water samples were collected in 50 cm^3 syringes and injected into He-flushed serum bottles. Water samples were analyzed for CO_2, O_2 and N$_2$ by stripping the gasses from the acidified water (pH 2) into the helium-filled

head space. Samples for gas analysis varied by less than 4 % on a Carle Analytical Gas Chromatograph (columns: Molecular sieve 13A and a mixed Porapak N [60 %] and S [40 %]; temperature, 40 °C) with a thermal conductivity detector, which was connected to a Laboratory Data Control dual input integrator From the volume of water passed through each microcosm daily, microcosm respiration (O_2) and detritus oxidation (CO_2) rates were calculated.

Oxidation rates (mg detritus dry wt^{-1}) of the labeled detritus were estimated daily by measuring inorganic $[^{14}C]CO_2$ in effluent from the microcosms (Tenore et al., 1979).

After 4 d, the microcosms were opened and 1 cm^3 of surface sediment was taken by a small corer for adenylate extraction (Bancroft et al., 1976) and analysis (Tenore et al., 1979). The hot extracts were cooled in crushed ice, centrifuged, and the supernatant stored at −20 °C. Samples that contained worms were not included in total adenylate (A_t) estimations of microbial biomass. A Chem-Glow Photometer (American Instr. Co.) coupled to a digital integrator-timer (American Instr Co.) set for peak height analysis was used to measure the bioluminescence after injecting a firefly lantern tail extract into the sample extract.

Capitella capitata were picked from the sand, allowed to void their guts in seawater for 5 h, quickly rinsed with 10 % HCl and distilled water, and dried (Tenore and Hanson, 1980). The worms were divided into groups of 4 to 5 to facilitate weighing and isotope counting. Worm tissue and detritus were combusted in a Packard sample oxidizer before liquid scintillation counting.

Rates of O_2 consumption and the standing stock of microbial biomass were used to calculate specific rates of respiration (μmoles O_2 μg A_t^{-1} d^{-1}). In previous work under similar conditions (Tenore, 1977), microcosms with or without *Capitella capitata* showed no significant changes in detrital oxidation rates ($^{14}CO_2$). Thus, *C. capitata* contribute little to the rates of respiration in the microcosms. Further, *C. capitata* biomass (numbers) was constant in all microcosms so that the observed changes reflect microbial activity due to detrital source and age.

Metabolic 'respiratory' quotient (MRQ, CO_2/O_2) for the detrital types of different ages were calculated from O_2 consumption and CO_2 production rates. The MRQ describes the anaerobic to aerobic respiratory balance in the microcosm. If O_2 was the sole terminal electron acceptor, then a MRQ near 0.85 would be expected (see Discussion). The magnitude of MRQ depends on (1) the nature of the oxidizing agent being reduced by microbes in oxidative and substrate phosphorylation, (2) the biochemical composition of the detritus.

Microbial deoxyribonucleic acid (DNA) synthesis was estimated by ^{3}H-thymidine incorporation into DNA (Tobin and Anthony, 1978). ^{3}H-thymidine (0.04 ml of 5 μCi ml^{-1} solution) was added to 1 cm^3 of sediment (triplicates with a formalin-killed control) from each microcosm. Samples were incubated for 2 h and then 'killed' with 1 ml of 5.7 % formalin. The samples were washed free of unassimilated ^{3}H-thymidine and the nucleic acids solubilized overnight in 10 ml of 0.3 M NaOH. Extracts were centrifuged at 18,000 $\times$ g for 30 min and then transferred to clean tubes with 0.2 ml of carrier DNA ($\sim$ 200 μg). The DNA was neutralized with 1 ml of 3N HCl and precipitated with 1.2 ml of 50 % TCA. The extract was placed on ice for 30 min, half the volume was filtered on a 0.4 μm polycarbonate filter, washed twice with 4 ml of 5 % TCA, and half the volume was heated at 85 °C for 30 min, iced for 30 min, filtered and washed. Filters were dissolved in Soluene-350 and then counted by liquid scintillation. The difference in the counts between the 2 filters was taken as ^{3}H-thymidine incorporation into DNA. Internal standards were used to correct for quench and to convert counts to dpm cm^{-3} h^{-1}.

RESULTS

Temporal Changes in Microbial Activity

Microcosms

Changes in oxygen consumption indicated that utilization of oxidizable organics by microbes varied with detrital type and age (Fig. 2A). The rates of O_2 consumption correlated positively with estimates of microbial biomass (total adenylates, Fig. 3, in Tenore and Hanson, 1980). Microcosms with periphytic algal detritus had the highest initial rates of respiration indicating a rapid depletion of readily oxidizable organics during aging. Respiration rates in the microcosms with *Gracilaria foliifera* detritus suggest that 2 different energy pools became available or that there was a succession of decomposing organisms during aging. On the other hand, rates of respiration associated with *Spartina alterniflora* detritus were low during the first 100 d of aging and did not support high rates of respiration until after 6 months of aging.

When the rates of respiration were normalized for microbial biomass, the specific rates of respiration (μmoles O_2 μgA_t^{-1} d^{-1}) increased linearly with the age of each detrital type (Fig. 2B). We attribute the initial high rates for periphytic algal and *Gracilaria foliifera* detritus (5 d aged) to readily-assimilable organics in the detritus. Periphytic algal detritus had the highest daily increase in specific respiration of 4 %, followed
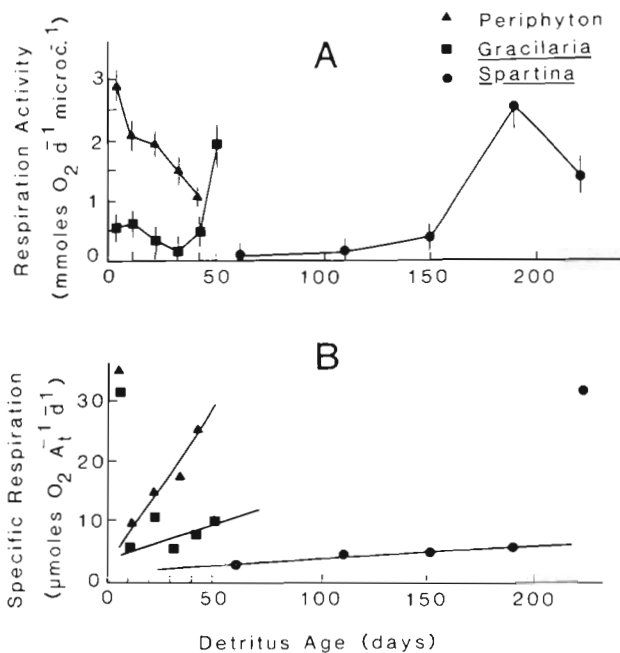
Fig. 2. Changes in respiration activity due to aging of detritus derived from different sources. Respiration rates are mean values ± S. E., based on 8 measurements from duplicate microcosm. Respiration rates (A) were converted to specific respiration rates (B) based on microbial biomass (A_t) in each microcosm
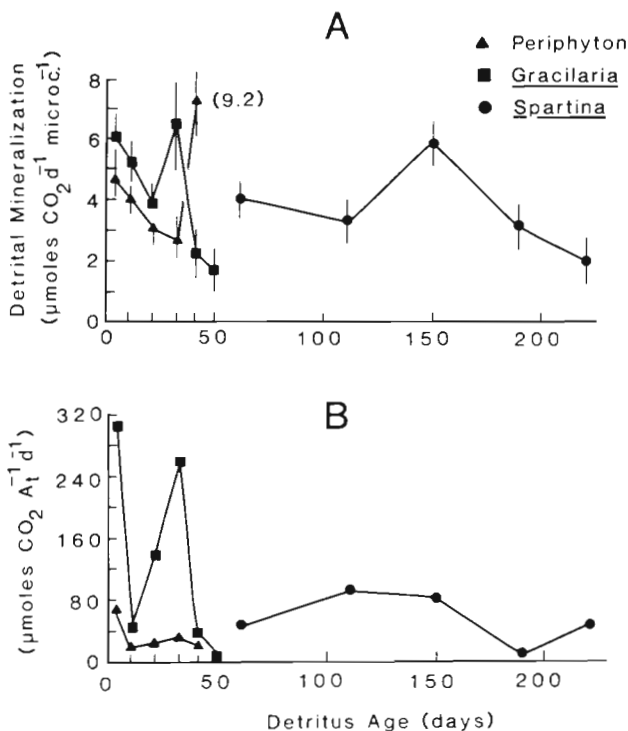

Fig. 3. Changes in mineralization due to aging of detritus derived from different sources. Same replication as in Fig. 1 Detrital mineralization (A) was converted to specific mineralization rates (B) based on microbial biomass (A_t) in each microcosm

by *G. foliifera* (1 %) and *Spartina alterniflora* detritus (0.3 %). We attribute these differences in specific respiration of the aerobic microbes to the resistance to decay and the biochemical composition of the detritus.

Gracilaria foliifera and periphytic algal detritus mineralized rapidly whereas *Spartina alterniflora* detritus did not (Fig. 3A). In general, total CO_2 production curves resembled those for detritus oxidation, determined from $^{14}CO_2$ production (Fig. 1 in Tenore and Hanson, 1980). When the rates were normalized for microbial biomass, specific rates of mineralization (Fig. 3B) generally followed the incorporation of detritus by *Capitella capitella* (Fig. 1 in Tenore and Hanson, 1980).

Metabolic 'respiratory' quotients (MRQ, total CO_2/O_2) for the detritus-microbial complex were greater than 0.85 (Fig. 4A), suggesting participation of anaerobic metabolism in the decomposition of detritus. The MRQ varied with the source of detritus and its age. During early stages of decomposition, microcosms with periphyton detritus had the lowest MRQ (< 2), whereas those with *Gracilaria foliifera* and *Spartina alterniflora* detritus had the highest MRQ. During later
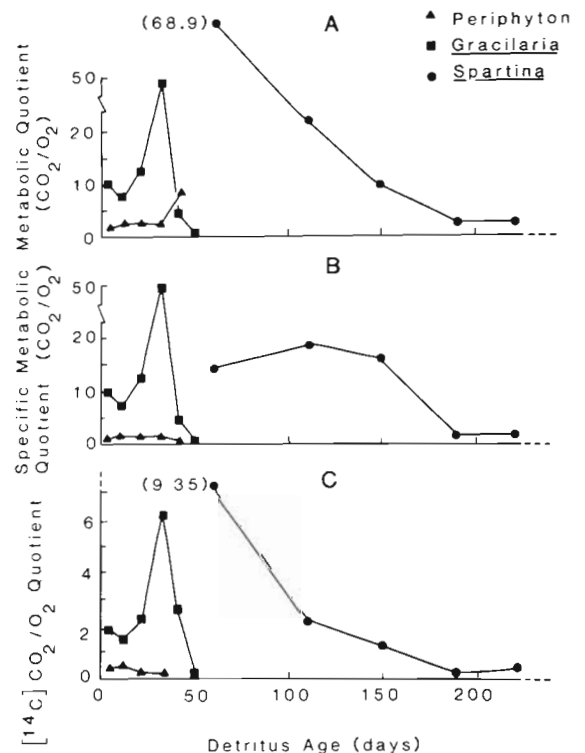

Fig. 4. Changes in metabolic quotient due to aging of detritus derived from different sources. A: metabolic quotient computed from respiration (Fig. 2A) and mineralization (Fig. 3A) rates. B: specific metabolic quotient computed from specific respiration (Fig. 2B) and mineralization (Fig. 3B) . C: detritus oxidation ($^{14}CO_2$) to respiration ratio computed from oxidation rates (reported in Tenore and Hanson, 1980) and respiration rates (Fig. 2A)

stages of decomposition, MRQ for these latter detrital sources approached values of 2 or less. When the specific rates of respiration and mineralization were used to compute the MRQ, the specific MRQ values (Fig. 4B) were similar to the total CO_2/O_2 quotient (Fig. 4A). We also computed, for comparison, a metabolic quotient based on the rates of detritus oxidation ($[^{14}C]CO_2$, Table 1 in Tenore and Hanson, 1980). The temporal changes (Fig. 4C) were similar to those in Fig. 4A but the values were much lower.

Aerobic Versus Anaerobic Decomposition

Culture

Aging of *Gracilaria foliifera* detritus under oxic and anoxic conditions suggested that anaerobic bacteria did not assimilate the detritus as efficiently as the aerobic bacteria (Fig. 5). After 24 h, bacterial biomass
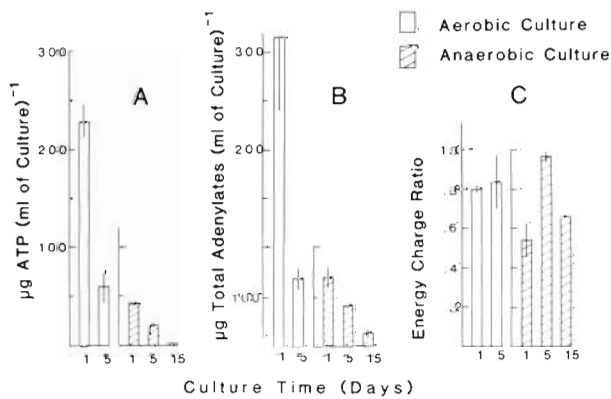

Fig. 5. Comparison of microbial biomass (ATP and A_t) and physiology of the microbiota decomposing *Gracilaria foliifera* detritus under strictly oxic or anoxic conditions. Means ± S. D. of 4 to 5 observations

(ATP and total adenylates, A_t) in aerobic culture was nearly 5 times greater than the biomass in the anaerobic culture (Fig. 5A, B). Biomass declined with aging in both cultures, and the biomass in the anaerobic culture never reached the biomass concen-

trations in the aerobic culture. In addition, the detritus in the aerobic culture was almost completely mineralized after 10 d, whereas detritus still remained in the anaerobic culture and therefore this culture was continued for another 10 d. The adenylate energy charge (AEC) ratio of 0.8 suggests that the bacterial growth in the aerobic culture remained in exponential phase during the aging of the detritus. However, in the anaerobic culture, the AEC ratio was initially low (~ 0.55); it increased to the physiological state of the aerobic culture after 5 d of aging. This suggests that the anaerobic bacteria took longer to develop on the detritus and that anaerobic metabolism became efficient in generating energy during the latter stages of detrital decomposition even though biomass was low.

Microcosms

When equal amounts of the detritus from the cultures were placed in the microcosms and aged for an additional 4–5 d, equivalent microbial biomass (Fig. 6A and B) and AEC ratio (Fig. 6C) were found for the 5 d aerobically and anaerobically aged detritus. This suggests that the microbes could efficiently utilize the detritus and end-products from anaerobic metabolism from the anaerobic culture. Because the anaerobic bacteria in the culture never attained the biomass concentration found by the aerobic bacteria, there was sufficient detritus (carbon) remaining for utilization by microbes in the microcosms. This was indicated by the high AEC ratio of ~ 0.8 for the microbes in the microcosms with anaerobically aged detritus (Fig. 6C).

Rates of O_2 consumption in these microcosms with *Gracilaria foliifera* detritus aged under oxic or anoxic conditions (Fig. 7A) were not significantly different from those in microcosms with detritus aged under mixed conditions (Fig. 2A). In addition, microcosms with either the aerobically or anaerobically aged detritus showed a slight increase in O_2 consumption after 10 d of aging. This similarity in the data suggests that reduced end-products from anaerobic metabolism was not a significant factor in the O_2 consumption
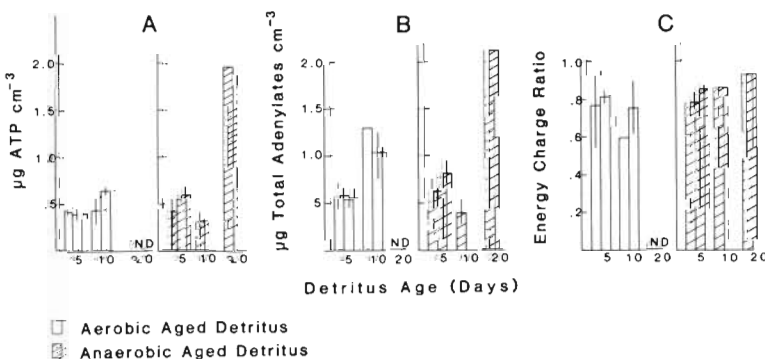

Fig. 6. Comparison of microbial biomass (ATP and A_t) and physiology (adenylate energy charge ratio) in microcosms with either aerobically or anaerobically aged *Gracilaria foliifera* detritus. ND: no data
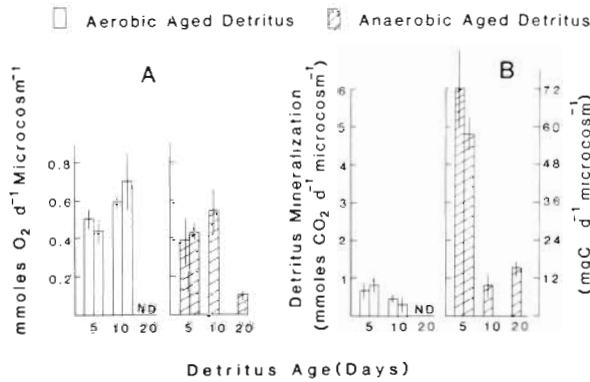
Fig. 7. Comparison of respiration (A) and detritus mineralization (B) in microcosms with either aerobically or anaerobically aged *Gracilaria foliifera* detritus. ND: no data

rates. However, aging the detritus anaerobically for 15 d in the culture resulted in rates of respiration that were significantly reduced (Fig. 7A).

Rates of CO_2 production in microcosms with anaerobically aged *Gracilaria foliifera* detritus (Fig. 7B) were similar to those for mixed conditions (Fig. 3A), but 2 to 6 times higher than those observed for aerobically aged detritus (Fig. 7B). Consequently, the metabolic 'respiratory' quotients for anaerobically aged detritus (Fig. 8) were similar to those for detritus
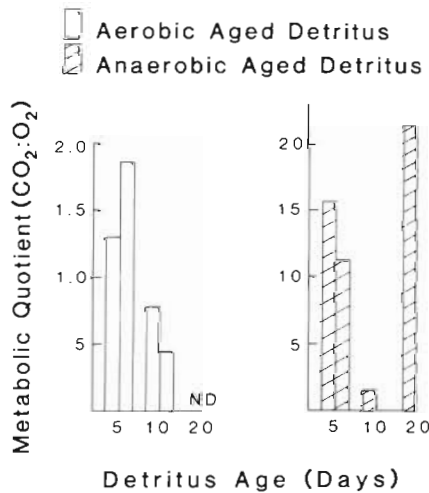

Fig. 8. Comparison of metabolic quotients in microcosms with either aerobically or anaerobically aged *Gracilaria foliifera* detritus. ND: no data

aged under mixed conditions (Fig. 4A). These observations suggest that anaerobic bacteria originated from the aging cultures and were active in the mineralization of the detritus.

The rates of detritus oxidation ($^{14}CO_2$) and incorporation by *Capitella capitata* of aerobically and anaerobically aged detritus are shown in Fig. 9. In general, rates of oxidation were similar for both aerobically and anaerobically aged detritus, and the rates decreased
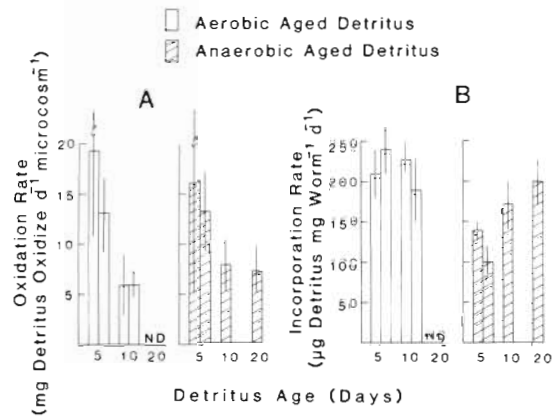

Fig. 9. Comparison of detritus oxidation (A) and net incorporation (B) rates of aerobically or anaerobically aged *Gracilaria foliifera* detritus by *Capitella capitata*. Oxidation values are means $\pm$ S. D. based on 15 observations. Net incorporation values are based on at least 15 observations (each 4 to 5 individual worms pooled) for each of 2 replicate microcosms. ND: no data

with aging time (Fig. 9A). *C. capitata*, on the other hand, incorporated the aerobically aged *Gracilaria foliifera* detritus at rates initially higher (47 %) than the anaerobically aged detritus (Fig. 8B). However, after 20 d of aging, *C. capitata* incorporated the anaerobically aged *G. foliifera* detritus as well as aerobically aged detritus.

Rates of thymidine incorporation into microbial DNA decreased over time for *Gracilaria foliifera* detritus aged aerobically whereas DNA synthesis increased over time for *G. foliifera* detritus aged anaerobically (Fig. 10). This trend resembles the rates at which *Capitella capitata* incorporated anaerobically aged
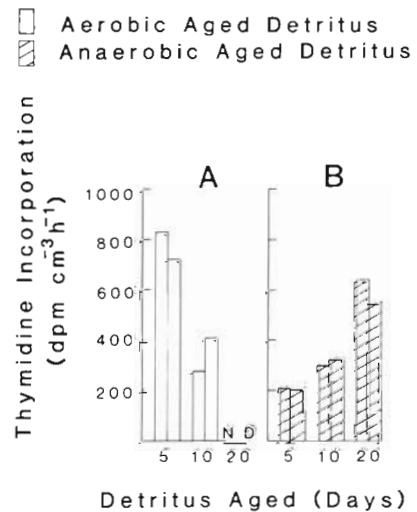

Fig. 10. Comparison of thymidine incorporation into the DNA of the microbiota in microcosms with either aerobically or anaerobically aged *Gracilaria foliifera* detritus. ND: no data

detritus (Fig. 9B). Apparently, the anaerobically aged detritus possessed carbon pools even after 20 d of aging for microbial and *C. capitata* growth.

DISCUSSION

The rates of microbial activity associated with aging detritus derived from periphytic algae, *Gracilaria foliifera* and *Spartina alterniflora* (Fig. 2A) describe (1) the relative structural complexity of biochemical composition of these detrital types, and (2) the availability of the carbon components over time to aerobic and anaerobic microbes. Because rates of respiration correlated with the concentration of microbial biomass associated with the detritus (Tenore and Hanson, 1980), fluctuations could be caused by resistance to decay and/or turnover of microbial populations. By normalizing rates of respiration to microbial biomass and perhaps metabolism can be nullified. Thus, the rates of respiration per unit of biomass (referred to as the specific rates of respiration) describe resistance to decay of each detrital type over time. Two aspects worth noting are: (1) even during the latter stages of decomposition and periods of low microbial biomass, the activity of microbes was higher than during periods of high biomass in the early stages of decomposition, i. e. the specific rates of respiration of the microbes increased; (2) the daily increase in the specific rate of respiration was linear over most of the aging period.

Structural cellulose and lignin content probably contributes to the relative resistance of the different detrital types to decay. In *Spartina alterniflora*, lignocellulose and lignin content represents 75 and 15 % respectively of the ash-free dry weight (MacCubbin and Hodson, 1980). However, available caloric content of detrital sources may also influence decomposition and utilization (Tenore, 1981; Hanson, in press). Available calories in *Gracilaria foliifera* and *S. alterniflora* stocks are 1.89 and 0.75 Kcal g^{-1}dry wt. or 57 % and 17 % of the total calories respectively (Tenore, 1981). Thus, *S. alterniflora* detritus with high lignocellulose and low available caloric content resists decomposition and conversion to microbial carbon (Haines and Hanson, 1979; Tenore et al., 1979; MacCubbin and Hodson, 1980; Hanson, 1980).

The similarity between increase in the specific rate of respiration (Fig. 2B) and in the P : O ratio, the ratio of detrital incorporation into *Capitella capitata* production (P) to the oxidation (O) of labeled detrital carbon (Fig. 2, Tenore and Hanson, 1980), suggests that either *C. capitata* production was coupled to microbial conversion and utilization of these detrital types or both were competing for similar nutrients in the detritus. The P : O ratio is defined as a measure of the cost

efficiency of the microcosm to produce macroconsumers (Tenore and Hanson, 1980). Daily increases in P : O ratios were 0.3 %, 1.2 % and 2.3 % for *Spartina alterniflora*, *Gracilaria foliifera* and periphytic algal detritus respectively. The daily change in the specific rate of respiration and P : O ratio also corresponds to daily changes in A_t : O ratios (Fig. 4 in Tenore and Hanson, 1980). Daily changes in A_t : O ratios in microcosms with *Spartina alterniflora*, *Gracilaria foliifera* and periphytic algal detritus were 0.8 %, 4.3 % and 8.4 % respectively, suggesting that microbial activity is important in the decomposition of the detritus and in production of the polychaete *Capitella capitata*.

The rates of mineralization (CO_2) of the 3 types of detritus did not correlate exactly with the rates of detritus oxidation ([^{14}C]CO_2; Tenore and Hanson, 1980). Possible causes are: (1) there was an external carbon source (DOC) in the 1 μm-filtered, estuarine water flushing the microcosm; (2) detritus was not uniformly labeled. We estimated that less than 1 to 10 % of the mineralization rates was due to DOC. However, DOC may be a significant carbon source to microorganisms when structural components of the detritus resist decay. We felt that the detrital carbon was uniformly labeled because of the similarity in the CO_2/O_2 and $^{14}CO_2/O_2$ quotients over time, and because specific rates of mineralization resembled temporal changes in A_t : O ratios (Fig. 4 in Tenore and Hanson, 1980).

Anaerobic bacteria contributed mostly to the CO_2 produced in the microcosms. Respiratory quotients (RQ) of eukaryotes and aerobic procaryotes utilizing carbohydrates at steady-state are about 0.7 to 0.85 (Payne, 1970; Boyd, 1973). However, the quotient is greatly affected by anaerobic metabolism. In mixed aerobic and anaerobic communities the metabolic 'respiratory' quotient (not synonomous with RQ) is usually greater than 0.85 (Rich, 1979). Therefore, the magnitude of the MRQ indicates a balance between aerobic respiration (O_2) and the respiratory demand on other terminal electron acceptors (NO_3^-, $SO_4^=$, CO_2 and oxidizable organics). The high MRQ for these detrital types in our microcosms are similar to the MRQ for many shallow marine and freshwater benthic systems (Park et al., 1958; Odum et al., 1963; Wood and Verduin, 1972; Rich, 1975, 1979; Hanson et al., 1981).

Because of high metabolic 'respiratory' quotients in well-aerated microcosms, we suspected that anaerobic bacteria survived pretreatment, e. g. freeze-drying and rehydration, and low oxygen or anoxic condition existed in localized niches within detrital aggregates. We examined this possibility with *Gracilaria foliifera* detritus aged under oxic and anoxic conditions. The results indicate that anaerobic aging of the detritus increased the magnitude of the metabolic quotients.

Therefore, we attributed the high quotients to metabolism by anaerobes associated with the detritus.

Even though 3 detrital types were decomposed under mixed aerobic and anaerobic processes, *Capitella capitata* incorporated the anaerobically aged *Gracilaria foliifera* detritus at the same magnitude as aerobically aged detritus. Oxic or anoxic aging made little difference in the suitability of the detritus to *C. capitata*. However, *G. foliifera* detritus from anaerobic cultures did require a longer period of aging before incorporation rates of anaerobically aged detritus by *C. capitata* approached those of the aerobically aged detritus. The results suggest that the aerobic culture had the highest conversion efficiency of the detritus to microbial carbon. Contrarily, the anaerobic culture had the lowest efficiency based on the low biomass and AEC ratio but became active after several days of aging.

Because of the low conversion and decomposition of *Gracilaria foliifera* detritus under anoxic conditions this detritus retained sufficient carbon reserve for further microbial metabolism and *Capitella capitata* production. For example, in microcosms with anaerobically aged detritus, microbial DNA synthesis increased with time and coincided with the increase in incorporation by *C. capitata*. On the other hand, microbial DNA synthesis decreased with time in the microcosms with aerobically aged detritus and *C. capitata* incorporation rates remained unchanged. In these microcosms, microbial biomass remained sufficiently high to support *C. capitata* activities. In addition, changes in DNA synthesis in microcosms with aerobic and anaerobic aged detritus followed the AEC ratio which is a relative measure of microbial growth rate (Wiebe and Bancroft, 1975). Therefore, if microbial biomass is high, *C. capitata* production is not tightly coupled to microbial production. Contrarily, if microbial biomass is low, *C. capitata* production is tightly coupled to microbial production.

Our results confirm the resistance of *Spartina alterniflora* detritus to decay and that the transfer of decay-resistant detritus to secondary consumers is mediated by microbes (Tenore and Hanson, 1980). Further, we show that anaerobic metabolism limits the flow of particulate carbon in the detrital food web. The carbon shunt results from the loss of CO_2 carbon during anaerobic metabolism and conversion of detritus to microbial carbon. Therefore, if the CO_2 escapes fixation by benthic chemoautotrophs, then CO_2 ebullition from the sediments would represent a significant loss of carbon from the food web.

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