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Utilization of Aged Detritus Derived from Different Sources by the Polychaete *Capitella capitata*

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Abstract

Because the rate of microbial degradation differs for the various sources contributing to the detrital pool in marine systems, their availability to detritivores might also vary. Carbon-14 tracer experiments were used to compare differences in the oxidation and net incorporation by the polychaete *Capitella capitata* of a nitrogen-rich, easily-decomposable detritus derived from the red macrophytic algae *Gracilaria* sp. versus a nitrogen-poor, decay-resistant detritus derived from the eelgrass *Zostera marina*. The net incorporation of *Gracilaria* sp. detritus by *C. capitata* reached a maximum (91 μg dry weight of detritus/mg dry weight of worm/day) after only 14 days of decomposition, whereas that of *Z. marina* detritus equaled this level after 30 days of aging, but continued to increase to 375 μg at 180 days. The oxidation rate of *Gracilaria* sp. detritus was consistently higher (peak of 61 mg dry weight of detritus/day at 30 day-aging) than *Z. marina* detritus, which reached this level only after 180 days of aging. The presence or absence of *C. capitata* did not significantly alter the oxidation rate. The above difference might be attributed to a rapid exploitation and mineralization by bacteria of the more available *Gracilaria* sp. detritus, but a slow, "controlled" utilization by the microbes of the less available *Z. marina* detritus, especially during the early stage of decomposition. This would allow maximum exploitation of the substrate by macroconsumers, resulting in more of the detrital resource being tied up in detritivore biomass rather than being rapidly mineralized to CO_2. Difference in the length of aging at which various detrital sources become available to detritivores could result in a temporal partitioning of food resources and should be considered in attempting to understand the dynamics of detrital-based food chains.

Introduction

The importance of detritus-based food chains in coastal marine environments has long been recognized (see reviews by Darnell, 1967; Mann, 1972; Tenore, 1976). Much indirect evidence is available suggesting that high secondary production is associated with the influx of large amounts of organic detritus into the benthic system.

However, equating nutritional importance solely with the quantity of detritus present in an environment can be misleading due to the heterogenous composition of the detrital pool. The major sources of detritus in coastal areas are decaying macrovegetation (seagrasses and seaweeds), fecal pellets and terrestrial runoff. These components have different biochemical characteristics that affect their nutritive value to detritivores. Because much detritus is comprised of nitrogen-poor, highly-complexed structural materials, Mare (1942) and other early workers had estimated only 10 to 20% of sediment organic matter was available to deposit feeders. Subsequent investigators have indeed substantiated that only 5 to 15% of the material ingested is utilizable by detrital feeders as a source of nutrition (George, 1964; Newell, 1964; Hargrave, 1970; Fenchel, 1972).

The availability of the detritus to macroconsumers is controlled in large part by microbial degradation and enrichment. A heterogeneous microbial flora develops on detrital particles and their activity is the initial step in detrital food chains. The bacteria are capable of decomposing and assimilating structural components of detritus while utilizing inorganic nitrogen from the seawater. The resulting microbial biomass is readily utilized by macroinvertebrates. Thus, there can be an increase in protein with aging of particles derived from nitrogen-poor macrophytes due to microbial development on the detritus (Fenchel, 1969;

Heald, 1971; De la Cruz and Poe, 1975). There is much experimental evidence that detritivores feed on microorganisms associated with detritus rather than on the particles themselves (Newell, 1964; Johannes and Satomi, 1966; Frankenberg *et al.*, 1967; Frankenberg and Smith, 1967; Fenchel, 1970, 1972; Hargrave, 1970; Yingst, 1976). Most macrobenthic "detritus feeders" are not capable of assimilating the structural components of detritus. For example, Hylleberg Kristensen (1972) measured the digestive carbohydrases of detrital feeders and found all deficient in hydrolyzing cellulose, xylon and other structural carbohydrates that comprise the bulk of detritus. Seki (1972) found that the brine shrimp *Artemia salina* was unable to survive on detritus until it was enriched by *Pseodomonas* sp.

The rate of microbial activity on various sources of the detritus can vary. Many freshwater macrophytes and seaweeds undergo rapid microbial degradation (Olah, 1972; Calow, 1975). In contrast, marsh and seagrasses that comprise a large portion of the detrital input into coastal marine environments are relatively decay-resistant and require considerable time (i.e., months) for decomposition and microbial development (Gosselink and Kirby, 1974; Harrison and Mann, 1975; Tenore, 1975). Even some microalgae withstand degradation for up to 1 month and show differing susceptibility to decomposition related to the relative biodegradabilities of specific components of the cell wall (Gunnison and Alexander, 1975).

In light of the above differences, the apparent discrepancies and contradictions in the literature regarding the nutritive value of detritus are understandable. The use of fresh detritus derived from decay-resistant sources such as eelgrass results in little or no growth of a detritivore (e.g. Prinslow *et al.*, 1974). However, in a series of tracer experiments, *Capitella capitata* and *Nephthys incisa* incorporated virtually no fresh material, but maximum amounts of 5-month aged labeled eelgrass detritus (Lee *et al.*, 1975; Tenore, 1975; Tenore *et al.*, 1977). In fact, actual growth of a deposit feeder on different detritus has been demonstrated by Tenore (1977). In a series of growth experiments of 3 months duration there was an increasing gradation in attainable standing crop of *C. capitata* cultured on 5 detrital sources ranging from lowest growth on nitrogen-poor, decay-resistant macrophytes (the cordgrass *Spartina alterniflora* and the eelgrass *Zostera marina*) to highest growth in the nitrogen-rich seaweeds (the rockweed *Fucus* sp. and the red macroalgae *Gracilaria* sp.).

Thus, the source and state of decomposition of detritus can affect its nutritional value in the detrital system. Therefore, I conducted a series of tracer experiments to compare differences in the availability to *Capitella capitata* of a nitrogen-rich, easily-decomposable detritus derived from *Gracilaria* sp. versus a nitrogen-poor, decay-resistant eelgrass detritus.

Materials and Methods

Labeled detritus derived from eelgrass and *Gracilaria* sp. were prepared using procedures reported in detail elsewhere (Tenore, 1975, 1977). Briefly, live intact plants were cultured in illuminated 8 l seawater tanks containing $NaH^{14}CO_3$. The water was periodically changed and the isotope replenished to minimize bacterial growth. At the end of 1 month the plants were washed with filtered seawater, rinsed quickly with 10% HCl to remove surface adsorbed cabon-14, rinsed with fresh water, freeze-dried and ground to 120 µm with a Wiley Mill. Although a completely homogenously-labeled material was not obtained, this procedure did produce detritus with a large percentage of label in structural components and minimal leaching of isotope when introduced into an aquatic medium.

Flasks containing 2 g of the detritus and 250 ml of 1 µm-filtered seawater enriched with *f*-medium (Guillard and Ryther, 1962) were placed on a shaker table for aging. Each week an additional 10 ml of nutrient-enriched filtered seawater was added to insure an adequate inorganic nutrient supply (especially nitrogen) to the microbiota. The flasks were aged for different lengths of time, were then centrifuged, the supernatant decanted, the particulates weighed and a subsample removed for dry weight and specific activity determinations.

The more decay-resistant eelgrass detritus was tested after 14, 30, 60, 120 and 180 days of aging; the faster decomposing *Gracilaria* sp. detritus was tested after 5, 14, 30 and 60 days. For each detrital age there were 2 replicated chambers with and without *Capitella capitata* (250 worms/chamber).

The bottom of 7 l volume chambers (0.07 m^2 surface area) were layered with clean fine (<0.3 mm) sand. Labeled detritus and *Capitella capitata* were added to the appropriate chambers, which were then sealed with an O-ringed cover. Seawater, filtered to 1 µm to prevent phytoplankton and meiofaunal contamination, was metered through the sealed chambers to insure adequate dissolved oxygen (ca. 40 l/chamber/day).

Table 1. *Capitella capitata*. Oxidation (O), turnover rates (T) and net incorporation (N) by the polychaete of variously aged detritus derived from the red algae *Gracilaria* sp. and the eelgrass *Zostera marina*. Oxidation rate = mg dry weight of detritus/day measured by CO_2 respired, given as mean value ± standard deviation based on number of observations in parentheses. Turnover rate = oxidation rate per day/total detritus present. Net incorporation rate = µg dry weight of detritus/mg weight of worm/day, given as mean value ± standard deviation based on number of observations in parentheses. Each of two replicate chambers contained 250 *C. capitata* that were grouped for activity determination

Aging period	*Gracilaria* sp. detritus		*Zostera marina* detritus	
	Without *C. capitata*	With *C. capitata*	Without *C. capitata*	With *C. capitata*
5 days				
O	52.1 ± 17.8(15)	64.0 ± 22.5(15)	23.6 ± 4.2(15)	
T	3.0%	3.7%	1.3%	
N		58.1 ± 15.8(39)		
14 days				
O	59.3 ± 19.8(15)	61.6 ± 21.9(14)	24.9 ± 4.6(15)	25.9 ± 4.0(15)
T	4.4%	4.6%	1.9%	2.0%
N		91.0 ± 42.1(70)		37.3 ± 8.0(25)
30 days				
O	61.0 ± 26.2(13)	58.7 ± 19.9(13)	27.6 ± 9.0(15)	26.9 ± 11.6(15)
T	5.5%	5.3%	2.2%	2.1%
N		73.5 ± 21.5(22)		41.3 ± 11.2(25)
60 days				
O	44.5 ± 11.1(12)	55.3 ± 15.0(13)	34.0 ± 10.9(15)	39.0 ± 17.5(15)
T	4.0%	5.0%	2.7%	3.1%
N		45.0 ± 20.4(34)		70.7 ± 25.4(59)
120 days				
O			37.3 ± 18.0(18)	32.5 ± 10.5(22)
T			3.1%	3.2%
N				123.7 ± 51.1(21)
180 days				
O			59.9 ± 21.3(22)	74.5 ± 21.7(17)
T			5.8%	7.3%
N				375.4 ± 116.3(46)

The oxidation rate (mg dry weight/day) of the labeled detritus was estimated from samples of the chamber effluent. Samples of the effluent were filtered and total activity (total inorganic ^{14}carbon and dissolved organic ^{14}carbon) of the filtered water determined. The water was then acidified with cold phosphoric acid and agitated to remove the inorganic ^{14}carbon fraction. The activity due to the remaining dissolved organic ^{14}carbon was counted and the total inorganic ^{14}carbon determined by difference. Knowing the volume passed through the chambers and the specific activity of the labeled detritus, one can calculate the oxidation rate of the detritus. Because there was a weight loss of the original 2 g of detritus in each flask we also calculated a turnover rate of oxidation rate/weight of detritus present.

The chambers were maintained for 5 to 10 days. Then the worms were removed, allowed to void their guts in seawater, quickly rinsed with 10% HCl and seawater and dried. The radioactivity of pooled samples of weighed tissue was determined and net incorporation rate of the detritus calculated. Tissue and filters were combusted on a Packard sample oxidizer for liquid scintillation counting. Water samples were counted with Aquasol. All values were corrected for quench, background and machine counting efficiency.

Results

The results (Table 1) show differences due to detrital aging between oxidation, turnover rates and net incorporation by *Capitella capitata* of *Gracilaria* sp. and *Zostera marina* detritus.

The net incorporation by *Capitella capitata* of *Gracilaria* sp. detritus reached a maximum (91 µg dry weight of detritus/mg dry weight of worm/day) after 14 days of decomposition and declined with further aging. In contrast, the net incorporation of *Zostera marina* detritus reached such levels only after 120 days of aging but continued to increase to 375 µg at 180 days.

The oxidation rate of *Gracilaria* sp. detritus was consistently higher than that of *Zostera marina* detritus and peaked (61 mg dry weight of detritus/day) at 30 days of aging. The oxidation rate of *Z. marina* detritus continuously increased with aging, but equalled this level only after 180 days of aging. Because there was a weight loss with decomposition, a comparison based on absolute oxidation rates can be misleading. Both detrital types showed a significant weight loss during the first 30 days of aging, with *Z. marina* detritus losing 36% and *Gracilaria* sp. 45% of their ash-free dry weight. After this initial rapid weight loss further changes were negligible. Even so, turnover times (% of available detritus oxidized/day) did reflect the same broad differences shown by oxidation rates – a higher turnover of *Gracilaria* sp. detritus peaking (5.5%) at 30 days whereas the turnover time of *Z. marina* detritus was only 1 to 3% until 180 days of decomposition. Oxidation rates were not significantly different with or without *Capitella capitata* present.

Discussion

Gracilaria sp. and *Zostera marina* probably represent extremes of detrital sources. *Gracilaria* sp. is composed of nitrogen-rich (>5%) and labile compounds that are readily decomposed by microbes. In contrast, *Z. marina* is nitrogen-poor (<2%) and contains refractive structural carbohydrates that are decay-resistant. Thus, one would expect a difference in the time required to decay these detrital types to a point where they are available to detritivores. Because of the rather arbitrary procedure of N addition with *f*-medium during aging of the detritus, one should not construe the decay rates as necessarily reflecting those occurring in nature. Further work must be carried out to ascertain the effect of differences in the available inorganic nitrogen to detrital enrichment and subsequent availability. But the fact of a decay period before availability characteristic for *Z. marina* detritus had already been documented (Tenore, 1975, 1977).

What were unexpected were differences in the relationship between oxidation and net incorporation rates of the two detrital types. The oxidation rate of *Gracilaria* sp. detritus was double that of *Zostera marina,* but the maximum net incorporation rate of *Z. marina* detritus by *Capitella capitata* was about four times greater than the peak for *Gracilaria* sp. detritus. This difference could be the result of energy allocation at the microbial level in detrital food chains. Macrobenthic detritivores are supported by the microbes that utilize detritus. Microbes are usually adept at substrate exploitation that results in the substrate being metabolically utilized and mineralized. Macroinvertebrates, although relatively slower in resource utilization, are characterized by a trophic energy partitioning that results in a greater amount of the resource being "stored" in biomass (i.e., not as rapidly recycled as in microbes). A readily available detrital source such as *Gracilaria* sp. might be so rapidly exploited and mineralized by microbes that a large proportion of the resource is not available for trophic growth of a macrodetritivore. In contrast, the decay resistance of a detrital source such as *Z. marina* could result in controlled substrate availability such that the utilization rate of the macrodetritivore keeps up with that of the microbial community. The results of the present experiment in no way directly address this hypothesis, but do suggest that such an avenue of research could be fruitful.

Differences in the age at which various detrital sources are maximally available to detritivores could result in a temporal partitioning of the food resource in detrital-based food chains. Much of the macrophytic material enters the detrital pool of coastal systems in autumn. Differential rates of decomposition and related availability to the macroconsumers might mitigate this pulse of food and assure a continual nutrient source to the benthos. In this regard, our usual treatment of the detrital pool in an ecosystem as a "black box" can obfuscate the delineation of food resource availability and exploitation. In the present experiment we did not equalize the food concentrations of the various ages of detritus but, in fact, wanted to emphasize any differential rate of use and subsequent loss of detrital sources. Future work will include the affect of food concentration on resource exploitation.

That the presence of the *Capitella capitata* did not significantly affect the oxidation rate of the detritus might be a summation of the polychaetes feeding activity on the microbes. The *C. capitata* are more than likely utilizing the bacteria on the detrital particles. The cropping activity of detrital feeders can enhance microbial activity and thus, increase oxygen consumption and standing crop (Hargrave, 1970; Fenchel, 1972). However, at the same time, more of the detrital substrate with associated bacterial biomass is tied up in particulate form in the *C. capitata* biomass and not as rapidly mineralized to CO_2. A prime target of future work in detrital food chains must be the interaction of microbial and macroconsumer components.

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Literature Cited

Calow, P.: On the nature and possible utility of epilithic detritus. Hydrobiologia *46*, 181-189 (1975)

Darnell, R.M.: Organic detritus in relation to the estuarine ecosystem. *In:* Estuaries, pp 376-383. Ed. by G.H. Lauff. Washington, D.C.: American Association for the Advancement of Science 1967. (Publs Am. Ass. Advmt Sci. No. 83)

De la Cruz, A.A. and W.E. Poe: Amino acids in salt marsh detritus. Limnol. Oceanogr. *20*, 124-127 (1975)

Fenchel, T.: The ecology of marine microbenthos. IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to the ciliated protozoa. Ophelia *6*, 1-182 (1969)

- Studies on the decomposition of organic detritus derived from the turtle grass, *Thalassia testudinum*. Limnol. Oceanogr. *15*, 14-20 (1970)
- Aspects of decomposer food chains in marine benthos. Verh. dt. zool. Ges. *65*, 14-22 (1972)

Frankenberg, D., S.S.L. Coles and R.E. Johannes: The potential trophic significance of *Callianassa major* fecal pellets. Limnol. Oceanogr. *12*, 113-120 (1967)

- and K.L. Smith, Jr.: Coprophagy in marine animals. Limnol. Oceanogr. *12*, 443-450 (1967)

George, J.D.: Organic matter available to the polychaete, *Cirriformia tentaculata* (Montagu) living in an interstitial mud. Limnol. Oceanogr. *9*, 453-455 (1964)

Gosselink, J.G. and C.J. Kirby: Decomposition of salt marsh grass, *Spartina alterniflora* Loisel. Limnol. Oceanogr. *19*, 825-831 (1974)

Guillard, R.R.L. and J.H. Ryther: Studies on marine planktonic diatoms. Can. J. Microbiol. *8*, 229-239 (1962)

Gunnison, D. and M. Alexander: Resistance and susceptibility of algae to decomposition by natural microbial communities. Limnol. Oceanogr. *20*, 64-70 (1975)

Hargrave, B.T.: The effect of a deposit-feeding amphipod on the metabolism of benthic microflora. Limnol. Oceanogr. *15*, 21-30 (1970)

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

Heald, E.J.: The production of organic detritus in a south Florida estuary. Tech. Bull. Sea Grant Progm Univ. Miami *6*, 1-110 (1971)

Johannes, R.D. and M. Satomi: Composition and nutritive value of fecal pellets of a marine crustacean. Limnol. Oceanogr. *11*, 191-197 (1966)

Hylleberg Kristensen, J.: Carbohydrates of some marine invertebrates with notes on their food and on the natural occurrence of the carbohydrates studied. Mar. Biol. *14*, 130-142 (1972)

Lee, J.J., K.R. Tenore, J.H. Tietjen and C. Mastroapolo: An experimental approach toward understanding the role of meiofauna in a detritus based marine food web. Proc. natn. Symp. Radioecol. U.S. atom. Energy Commn (Oak Ridge) *4*, 140-147 (1975)

Mann, K.H.: Macroscopic production and detritus food chains in coastal areas. Memorie Ist. ital. Idrobiol. *29* (Suppl.), 353-382 (1972)

Mare, M.F.: A study of a marine benthic community with special reference to the microorganisms. J. mar. biol. Ass. U.K. *25*, 517-554 (1942)

Newell, R.: The role of detritus in the nutrition of two marine deposit feeders, the prosobranch, *Hydrobia ulvae* and the bivalve, *Macoma balthica*. Proc. zool. Soc. Lond. *144*, 25-45 (1964)

Olah, J.: Leaching, colonization and stabilization during detritus formation. Memorie Ist. ital. Idrobiol. *29* (Suppl.), 105-128 (1972)

Prinslow, T.E., I. Valiella and J.M. Teal: The effect of detritus and ration size on the growth of *Fundulus heteroclitus*. J. exp. mar. biol. Ecol. *16*, 1-10 (1974)

Seki, H.: The role of microorganisms in the marine food chain with reference to organic aggregates. Memorie Ist. ital. Idrobiol. *29* (Suppl.), 245-259 (1972)

Tenore, K.R.: Detritus utilization by the polychaete, *Capitella capitata*. J. mar. Res. *33*, 261-274 (1975)

- Food chain pathways in detrital feeding benthic communities: a review with new observations on sediment resuspension and detrital recycling. *In:* Ecology of marine benthos, pp 31-54. Ed. by B.C. Coull. (Belle W. Baruch Library in Marine Science, No. 6). Columbia: University of South Carolina Press 1976
- Growth of the polychaete, *Capitella capitata* cultured on different levels of detritus derived from various sources. Limnol. Oceanogr. (In press). (1977)

-, J.H. Tietjen and J.J. Lee: Effect of meiofauna on incorporation of aged eelgrass detritus by the polychaete, *Nephthys incisa*. J. Fish. Res. Bd Can. *34*, 563-567 (1977)

Yingst, J.: The utilization of organic matter in shallow marine sediments by an epibenthic deposit-feeding holothurian. J. exp. mar. biol. Ecol. *23*, 55-70 (1976)

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