

REVIEW

Utilization of detritus and bacteria as food sources by two bivalve suspension-feeders, the oyster *Crassostrea virginica* and the mussel *Geukensia demissa*

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ABSTRACT: The concentration and composition of suspended particulate food available to estuarine suspension-feeding bivalve molluscs varies temporarily and spatially. Non-algal food sources may be important to suspension-feeders when algal concentrations are seasonally low or where there are high concentrations of suspended detrital material and bacteria, as found within marshes. We carried out a series of laboratory experiments and field measurements to determine to what extent 2 common estuarine bivalve molluscs, the oyster *Crassostrea virginica* and the ribbed mussel *Geukensia demissa*, could utilize cellulose and bacteria from Canary Creek marsh, Delaware, USA. Endogenously produced extracellular cellulases of the oyster depolymerized ingested cellulose to soluble oligomers. Subsequent intracellular cleavage of the oligomers to glucose was limited. The oyster absorbed carbon from refractory cellulosic material with an efficiency of only 3%. In contrast, the ribbed mussel absorbed carbon from the same cellulosic material with an efficiency of 9% and this increased to 14% if mussels were subjected to a 6 h exposure/6 h submergence cycle, a typical exposure regime for this intertidal species. We estimated that suspended cellulosic carbon in Canary Creek marsh during summer could supply 0.7% and 8.6% of the respiratory carbon requirements of subtidal oysters and intertidal mussels, respectively. In laboratory feeding experiments, colonization of refractory cellulosic food material by cellulolytic bacteria isolated from the marsh resulted in the oyster indirectly assimilating cellulosic carbon with an efficiency of 10%. The oyster was able to filter free, unattached bacteria from suspension with an efficiency of only 5.0%, compared with an efficiency of 15.8% for the ribbed mussel. We estimated that both unattached and attached bacteria combined in Canary Creek marsh during summer provide only 5.5% of the oysters' metabolic carbon requirements but could provide 31.0% of an intertidal mussel's metabolic carbon requirements. Experiments with ¹⁵N labelled bacteria indicated that attached bacteria associated with the breakdown of cellulosic material could mediate the flow of dissolved inorganic nitrogen from seawater to the oyster. We estimated that unattached and attached bacteria in Canary Creek marsh during summer could contribute 26.7% and 70.6% of the metabolic nitrogen requirements of subtidal oysters and intertidal mussels, respectively. These results indicate that in this marsh, utilization of bacteria as a food source could make a significant contribution during the summer to the nitrogen requirements of the oyster and to the carbon and nitrogen requirements of the mussel. However, cellulosic detritus and bacteria do not appear to fully meet the requirements of these bivalve species for carbon and nitrogen and utilization of other food sources is required, such as phytoplankton, nanozooplankton or non-cellulosic particulate and dissolved organic matter

INTRODUCTION

Marine bivalve molluscs are an important and often dominant component of the macroinvertebrate biomass of coastal and estuarine ecosystems. Suspension-feeding bivalve molluscs often form an important link between the water-column and benthos by filtering suspended particles from the water column and producing large amounts of biodeposits which become incorporated in sediments. Populations of the ribbed mussel *Geukensia demissa* inhabiting marshes have been estimated to filter a daily volume of water in excess of the tidal volume of the marsh (Jordan & Valiela 1982). Kuenzler (1961) reported that up to one third of suspended particulate phosphorus was removed by mussels inhabiting a Georgian (USA) salt marsh. A major fraction of this filtered material was sedimented as biodeposits, thereby conserving this nutrient and other materials within the marsh.

Although there is a considerable body of information on bivalve nutrition, primarily based on laboratory studies of animals fed on algal diets (see reviews by Epifanio 1982, Webb & Chu 1982) there is little known about the effects of variation in food availability and quality on the nutritional status of bivalves in the natural environment. Information on the relative importance of phytoplankton and material derived from marsh plants in the nutrition of estuarine bivalves has been obtained from measurements of stable isotope ratios of carbon, sulfur and nitrogen (Montague et al. 1981, Peterson et al. 1985, 1986). However, although such tracer techniques enable the elemental origin of food material to be identified, they yield little information on the exact pathways and mechanisms that enable the material to be assimilated by bivalves in their natural habitat.

In this paper we briefly review temporal and spatial heterogeneity in food available to estuarine and marsh-inhabiting suspension feeders, such as the oyster *Crassostrea virginica* and the ribbed mussel *Geukensia demissa*. In addition, we present results of a series of experiments carried out in our laboratories, some of which have been previously published (Newell & Langdon 1986, Kreeger et al. 1988, Crosby et al. 1989, in press), that were designed to determine utilization of cellulosic detritus and bacteria as food sources by these bivalve species in a marsh environment. The potential importance of cellulosic detritus and bacteria in meeting the carbon and nitrogen requirements of mussels and oysters is then discussed.

VARIATION IN FOOD AVAILABILITY

Phytoplankton is considered to be a major source of nutrition for suspension-feeding molluscs. Seasonal

cycles in primary production of cold temperate waters associated with changes in temperature and light intensity are commonly observed (Eppley 1972). However, the winter minimum of phytoplankton production often has little effect on bivalve populations because many bivalve species are quiescent during this season due to low water temperatures (Newell 1979). In addition, bivalve species commonly accumulate nutrient reserves during periods of phytoplankton abundance which support maintenance metabolism and gametogenesis during these predictable periods of reduced food availability (Bayne 1976, Sastry 1979).

Variation in spring and summer primary production between years may have more significant repercussions on production of populations of suspension-feeders than the winter minimum. For example, in Broad Creek, Maryland (USA), a sub-estuary of Chesapeake Bay, high spring rainfall (March through May 1983) caused an abrupt decrease in salinity in spring 1983 (Fig. 1a). This high rainfall resulted in extensive flushing of phytoplankton from Broad Creek and the reduced salinity depressed autochthonous primary production. As a consequence, chlorophyll *a* concentrations between March and June (Fig. 1a) were an order of magnitude lower than during the same period in 1982 (Berg & Newell 1986). However, despite this lack of phytoplankton in 1983, spring concen-

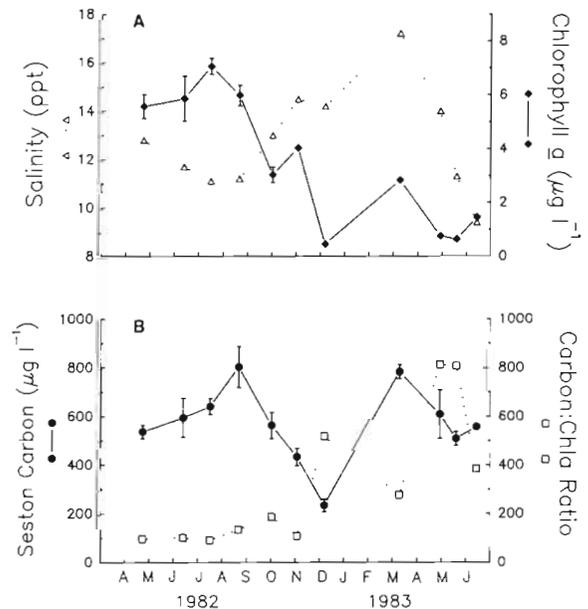


Fig. 1 Seasonal variation in seston composition at Broad Creek, Maryland. (A) Phytoplankton abundance (\bullet — \bullet), measured as chlorophyll *a* concentration ($\mu\text{g l}^{-1}$), and salinity (Δ — Δ). (B) Concentration of total organic carbon ($\mu\text{g l}^{-1}$; \bullet — \bullet) and the ratio of organic carbon to chlorophyll *a* (\square — \square). Values are means \pm 1 SD ($n=3$). For mean chlorophyll and carbon values without standard deviations error bars are smaller than the plotted symbol. Data from Berg & Newell (1986)

trations of total particulate organic carbon did not differ between years (Fig. 1b) indicating greater allochthonous inputs of carbon, or perhaps resuspension of sedimentary organic material, in 1983 than in 1982 (Berg & Newell 1986). High concentrations of suspended non-algal organic matter in spring 1983, Broad Creek, are also indicated by relatively high carbon to chlorophyll ratios (Fig. 1b). Values of ca 100 for the ratio of total suspended particulate carbon to chlorophyll *a* indicate that carbon is mainly associated with living phytoplankton cells, whereas values greater than 100 are indicative of the presence of higher proportions of non-living detrital carbon (Zeitzschel 1970). In Broad Creek the ratio was ca 100 throughout 1982. In contrast, carbon to chlorophyll ratios were much higher in 1983, reaching 800 in spring (April and May), indicating that the majority of suspended carbon was not from living phytoplankton but instead associated with detritus. Oysters inhabiting Broad Creek during spring 1983 would benefit if they were able to utilize detrital carbon in order to meet seasonally higher carbon demands associated with gametogenesis and growth.

In addition to seasonal and yearly variation in seston composition and concentration within one estuarine habitat, significant differences also occur between

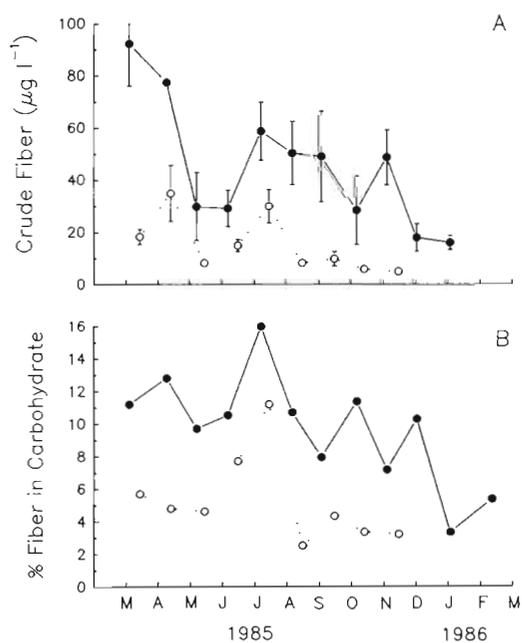


Fig. 2. Seasonal variation in seston composition at Broad Creek, Maryland (○-○; Crosby et al. in press), and Canary Creek marsh, Delaware (●-●; Kreeger et al. 1988). (A) Concentration of total crude fiber in the seston ($\mu\text{g l}^{-1}$). Values are means \pm 1 SD ($n = 3$). For means without standard deviations error bars are smaller than the plotted symbol. (B) Percentage contribution of crude fiber to the total carbohydrate fraction of the seston

habitats, in part due to the magnitude and composition of allochthonous carbon inputs. For example, the composition and concentrations of suspended detrital material in a system with limited tidal wetlands, such as Broad Creek, Chesapeake Bay, differ from those of Canary Creek, a sub-estuary of Delaware Bay, which drains extensive marshland dominated by the marsh-grass *Spartina alterniflora*. Total concentrations of crude fiber, estimated by the acid/alkali extraction procedure of Strickland & Parsons (1972), were considerably higher in Canary Creek than in Broad Creek (Fig. 2a). Furthermore, a higher proportion of total suspended particulate carbohydrate was made up of crude fiber in Canary Creek than in Broad Creek (Fig. 2b).

The high concentrations of crude fiber in the seston of Canary Creek, compared with those of Broad Creek, were probably due to inputs of lignocellulosic detritus from decomposing *Spartina alterniflora* from the surrounding marshland. Living *S. alterniflora* is composed of 70 to 82 % carbohydrate by dry weight (Squiers & Good 1974, Smith et al. 1979) and up to 99 % of the carbohydrate fraction is made up of cellulosic material (McIntire & Dunstan 1976, Maccubbin & Hodson 1980). Much of the decomposition and fragmentation of marshgrass lignocellulosic material occurs within the marsh (Smith et al. 1979, Benner et al. 1984, Newell et al. 1985), but some of the litter may be exported to adjacent estuaries during periods of high tides, unusual storms (Pickral & Odum 1976) or as a result of ice rafting (Heinle & Flemer 1976).

The concentration of cellulosic material in Canary Creek was determined by digesting filtered suspended material with cellulases and measuring the total release of glucose (Kreeger et al. 1988). Cellulose concentrations as high as $165 \mu\text{g l}^{-1}$ were found in winter (December to March), with an average annual concentration of 78 ± 47 (1 SD, $n = 3$) $\mu\text{g l}^{-1}$ (Fig. 3). About

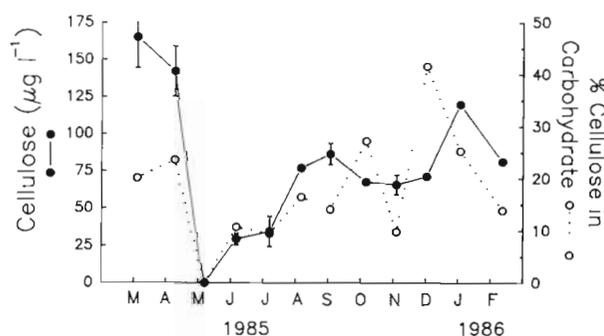


Fig. 3. Seasonal variations in cellulose concentration in the seston (mean \pm 1 SD [$n = 3$]; $\mu\text{g l}^{-1}$; ●-●) and the percentage contribution of cellulose to the mean total carbohydrate content of the seston at Canary Creek marsh, Delaware (○-○). For mean cellulose values without standard deviations error bars are smaller than the plotted symbol. Data from Kreeger (1986)

25 % of the total particulate carbohydrate in the seston was made up of cellulose in the spring and fall, with lower proportions occurring in summer (Fig. 3).

The average total concentration of bacteria in the Canary Creek marsh over a 10 mo period (Fig. 4) was 4.92 ± 1.20 ($n = 30$) $\times 10^6$ bacteria ml^{-1} (Kreeger 1986). Bacterial concentrations in Delaware Bay adjacent to Canary Creek inlet were measured during the same period by Coffin & Sharp (1987). The mean total bacteria concentrations for months when Canary Creek and the main stem were both sampled were 4.80 ± 1.42 ($n = 30$) and 3.87 ± 1.78 ($n = 12$) $\times 10^6$ bacteria ml^{-1} , respectively, indicating that the average concentration of bacteria in Canary Creek was 24 % higher than in Delaware Bay. An average of only 3.6 ± 1.2 % ($n = 30$) of suspended bacteria in Canary Creek was attached to seston particles, sampled over a 10 mo period (Kreeger 1986).

In summary, estuarine bivalves inhabit environments that exhibit temporal and spatial variability in concentration and biochemical composition of suspended particulate food resources. Non-algal foods, such as crude fiber, cellulose and bacteria may be important sources of nutrition to bivalves during periods of low phytoplankton abundance as well as in habitats receiving significant inputs of allochthonous material from marshes, such as Canary Creek, Delaware.

MARSHGRASS DETRITUS AS A FOOD SOURCE

The role of detritus derived from vascular plants, such as *Spartina alterniflora*, in the nutrition of suspension-feeding bivalves is equivocal. Attempts to culture the scallop *Argopecten irradians* (Kirby-Smith 1976) and the mussel *Mytilus edulis* (Williams 1981) on marshgrass detritus alone have been unsuccessful, although it is not clear from such studies whether poor growth was due to nutritional deficiencies of the detritus or due to its poor digestibility. Stuart et al. (1982) demonstrated that the mussel *Aulacomya ater* could digest and assimilate up to 50 % of detritus prepared from kelp. However, detritus from such macroalgae is more readily digestible than detritus from *S. alterniflora* (Findlay & Tenore 1982).

Stable isotope analyses have been used extensively to study the ability of natural populations of molluscs to utilize detritus derived from *Spartina alterniflora*. Haines and co-workers (see review by Montague et al. 1981) demonstrated that detritus originating from *S. alterniflora* was important in the nutrition of some species of invertebrates living within the marsh, but not important to *Crassostrea virginica* inhabiting creeks draining marshland. Peterson et al. (1985, 1986) reported that the diet of populations of the American

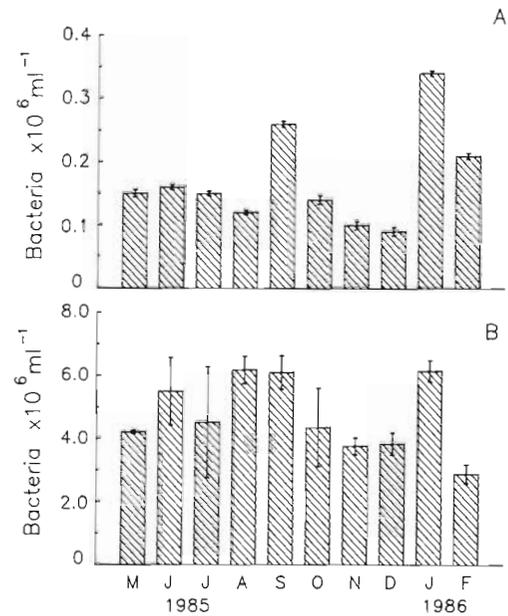


Fig. 4. Seasonal variations in concentration of bacteria (mean ± 1 SD) cells ml^{-1} . (A) Bacteria attached to seston particles in Canary Creek marsh. (B) Free, non-attached bacteria in Canary Creek marsh, Delaware. Data from Kreeger (1986)

oyster and ribbed mussel consisted of both phytoplankton and detritus originating from *S. alterniflora*. Mussels in the interior of the Great Sippewissett marsh had carbon and sulfur isotopic signatures which indicated that as much as 80 % of their diet originated from *S. alterniflora*. Conversely, ribbed mussels living at the mouth of the creek draining the marsh only obtained about 40 % of their nutrition from *S. alterniflora* (Fig. 5).

Using the methods described by Peterson et al. (1986) we determined carbon and sulfur isotopic signatures for ribbed mussels at 3 sites along a transect

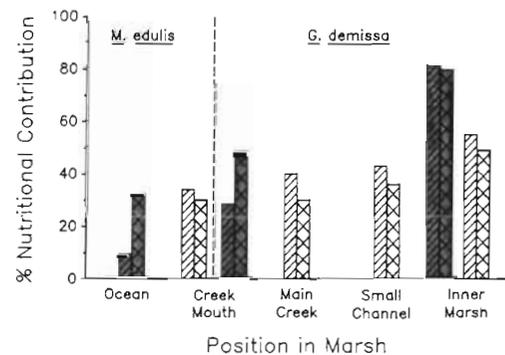


Fig. 5. Estimated percent contribution, based on stable isotope ratios (Fig. 6), of material derived from *Spartina alterniflora* to the nutrition of the blue mussel *Mytilus edulis* and the ribbed mussel *Geukensia demissa* based on sulfur (diagonal slashes) and carbon (broad cross hatching) ratios. Data for Great Sippewissett Marsh from Peterson et al. (1985) indicated by shaded bars, and data for Canary Creek from this study indicated by non-shaded bars

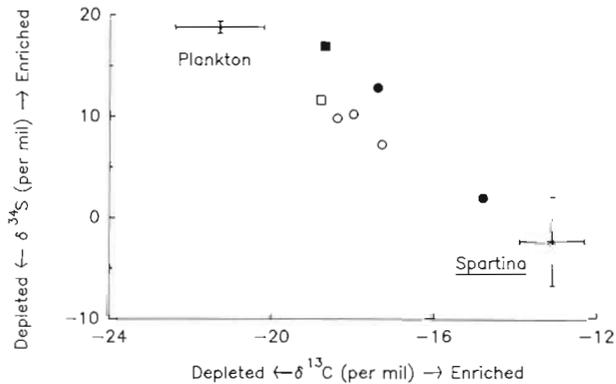


Fig. 6. Isotopic signatures for *Geukensia demissa* (○) and *Mytilus edulis* (□) collected along a transect through Canary Creek marsh, with ^{34}S plotted as a function of ^{13}C . Data for *G. demissa* (●) collected along a transect in Great Sippewissett Marsh and an open ocean population of *M. edulis* (■) from Peterson et al. (1985). Each of these points represents pooled samples of 10 to 200 individuals. Data for the isotopic signatures for *Spartina* and phytoplankton are taken from Peterson et al. (1985). Bars are means \pm 1 SD

from the mouth of Canary Creek to the innermost region of the marsh (Fig. 6). All stable isotope analyses were performed by the Ecosystem Center, Marine Biological Laboratory, Woods Hole. Results indicated that *Spartina alterniflora* provided ca 50 % of the carbon and sulfur in tissues of mussels living in the inner parts of Canary Creek marsh but less than 40 % of those elements for mussels living at the mouth of the creek (Fig. 5). These differences in the importance of *S. alterniflora* as a food source for mussels inhabiting various parts of Canary Creek marsh were not as pronounced as those reported by Peterson et al. (1986) for spatially separated populations of mussels from the Great Sippewissett marsh (Fig. 5). Blue mussels *Mytilus edulis* living at the confluence of Canary Creek and Delaware Bay had an isotopic signature indicative of them obtaining ca 30 % of their nutrition from material derived from *S. alterniflora* (Fig. 6), suggesting export of detritus of *S. alterniflora* from the mouth of Canary Creek marsh into Delaware Bay.

Stable isotope studies are useful in that they provide an integrated measure of the relative contributions of elements and food to consumers inhabiting ecosystems but they provide little information on the consumer's feeding behavior and physiology that may explain observed isotopic signatures.

UTILIZATION OF CELLULOSE

A second approach in assessing the potential importance of marshgrass detritus in the nutrition of bivalve suspension-feeders is to produce chemically defined, isotopically labelled detrital material, and to determine

the ability of bivalves to utilize this material under experimental conditions. We have used results from this kind of experiment, in conjunction with environmental measurements of the concentration of suspended cellulose, to estimate the importance of this food source in the nutrition of bivalves inhabiting Canary Creek marsh.

Radiolabelled *Spartina alterniflora*, grown in an atmosphere enriched with ^{14}C , was subjected to grinding and acid/alkali extraction to produce lignocellulosic material $< 20 \mu\text{m}$ in particle size (Newell & Langdon 1986). The composition of the prepared lignocellulosic material was characterized by a combination of chemical and enzymatic methods to determine the distribution of ^{14}C among biochemical fractions. Ninety-two percent of ^{14}C was present in the polysaccharide fraction, and 85 % of this fraction was digested by cellulases and, therefore, potentially biologically available to consumers (Newell & Langdon 1986). The remaining ^{14}C label was present in lignin (7.7 %), and lipid (0.1 %) fractions.

In vitro enzymatic studies (Newell & Langdon 1986) indicated that extracts of the oyster's style were able to break down both particulate amorphous cellulose and the prepared ^{14}C -labelled *Spartina alterniflora* material to soluble oligomers (Fig. 7) by the action of endogenously produced β -1,4-glucanase (C_x cellulase). However, extracellular C_1 -cellulase, that breaks down crystalline cellulose, was not detected in style extracts (Fig. 7). The absence of glucose release from cellobiose together with the low rate of glucose production from partially digested amorphous cellulose and *S. alterniflora* (Fig. 7), indicated that β -glucosidase (cellobiase) was not present in the style. However, complete intracellular breakdown of amorphous cellulose to glucose can probably occur in *Crassostrea virginica* because both β -1,4-glucanase activity (Brock et al. 1986) and β -glucosidase (cellobiase) activity (Mayasich

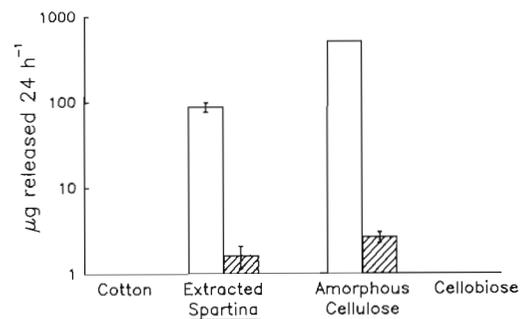


Fig. 7. *Crassostrea virginica*. Style cellulase activity. Mean (\pm 1 SD, $n = 4$) μg total carbohydrate (glucose equivalents) (open bars), and μg glucose (bars with diagonal slashes), released during 24 h incubation from various cellulosic substrates per mg protein of style homogenate. Data from Newell & Langdon (1986)

& Smucker 1986) have been reported in diverticula extracts of *C. virginica*.

In a series of feeding experiments, particulate ^{14}C -lignocellulosic material was either introduced directly by syringe into the stomach of oysters (Newell & Langdon 1986) or oysters were allowed to feed on a suspension of the material in flow-through chambers (Crosby et al. 1989). Despite the presence of extracellular β -1,4-glucanase and reported intracellular β -glucosidase activities (Mayasich & Smucker 1986), oysters absorbed ^{14}C from ingested lignocellulosic material with efficiencies of only $1.3 \pm 0.6 \%$ ($n = 11$) (syringe-fed oysters; Newell & Langdon 1986) and $2.7 \pm 1.8 \%$ ($n = 20$) (naturally fed oysters; Crosby et al. 1989). On the basis of estimates given in Table 1, cellulosic carbon would only contribute 0.7 % of the summer metabolic carbon requirements of oysters inhabiting Canary Creek.

In vitro rate measurements of both the production of

free reducing sugars from refractory cellulosic substrates by oyster style extracts and style turnover rates have been used by Lucas & Newell (1984) to estimate that detrital cellulosic material could contribute up to 40 % of the total carbon requirements of *Crassostrea virginica*. However, based on a re-evaluation by Fielding et al. (1986) of the biochemical assays used by Lucas & Newell (1984), it appears that Lucas & Newell's estimate of the contribution of cellulose to the oyster's carbon budget should only be 13 %. This latter corrected value may also be an overestimate because the rate of complete breakdown of amorphous cellulose to glucose is dependent on the combined activities of both β -glucosidase (cellobiase) and β -1,4-glucanase. In order to determine the rate of glucose production from ingested cellulose it is, therefore, necessary to consider the activities of both these enzymes.

Overall, it appears that extracellular β -1,4-glucanase activity associated with the style of *Crassostrea vir-*

Table 1. *Crassostrea virginica* and *Geukensia demissa*. Estimation of the contribution of cellulosic detritus and bacteria to metabolic requirements during summer in Canary Creek marsh, Delaware

	Cellulose C	Attached bacteria C N		Unattached bacteria C N	
Conc. (mg l^{-1}) in marsh	26.4 ^a	4.3 ^b	1.2 ^c	139.5	39.9 ^c
<i>C. virginica</i> (subtidal)					
$\mu\text{g filtered l}^{-1}$	26.4	4.3	1.2	7.0 ^d	2.0
$\mu\text{g absorbed l}^{-1}$	0.7 ^e	2.3 ^f	0.6	3.6 ^f	1.0
$\mu\text{g filtered \& absorbed per 12 h tidal cycle}$	42.0 ^g	138.0	36.0	216.0	60.0
% contribution to metabolic requirements per 12 h tidal cycle	0.7 ^h	2.1	10.0 ⁱ	3.4	16.7
<i>G. demissa</i> (intertidal)					
$\mu\text{g filtered l}^{-1}$	26.4	4.3	1.2	22.0 ^j	6.3
$\mu\text{g absorbed l}^{-1}$	3.8 ^k	2.3 ^l	0.6	11.4	3.3
$\mu\text{g filtered \& absorbed per 12 h tidal cycle}$	177.8 ^m	107.6	28.1	533.5	154.4
% contribution to metabolic requirements per 12 h tidal cycle	8.6 ⁿ	5.2	10.9 ^o	25.8	59.7

^a Mean summer cellulose concentration of $66 \mu\text{g l}^{-1}$ with 40 % of the cellulose as carbon (Fig. 3)

^b Average summer concentration of 5.58×10^6 unattached bacteria and 0.17×10^6 attached bacterial ml^{-1} . Bacterial carbon equals 25 femtograms cell^{-1} (Ducklow 1982, Rice & Hanson 1984, Nagata 1986)

^c C to N ratio for bacteria of 3.5 to 1 (Fenchel & Blackburn 1979)

^d Filtration efficiency of 5.0 % for unattached bacteria assuming that $3.92 \mu\text{m}$ beads are retained with 100 % efficiency (Fig. 6)

^e Carbon absorption efficiency of 2.7 % for cellulose (Crosby et al. in press)

^f Carbon absorption efficiency of 52 % for bacteria (Crosby 1987)

^g Filtration rate of $5 \text{ l h}^{-1} \text{ g}^{-1}$ tissue dry wt (Newell & Langdon 1986)

^h Respiration rate of $1.0 \text{ ml O}_2 \text{ h}^{-1} \text{ g}^{-1}$ tissue dry wt (= $537 \mu\text{g C h}^{-1}$; Newell & Langdon 1986)

ⁱ Nitrogen excretion rate of $30 \mu\text{g h}^{-1}$ for an oyster (R.I.E. Newell unpubl.) and a mussel (Jordan & Valiela 1982) of 1 g tissue dry wt

^j Filtration efficiency of 15.8 % for unattached bacteria compared with 100 % efficiency for $3.92 \mu\text{m}$ microspheres (Fig. 6)

^k Carbon absorption efficiency of 14.2 % for cellulose (Kreeger et al. 1988)

^l Assuming carbon and nitrogen absorption efficiencies of 52 % for bacteria i.e. similar to those for *C. virginica*

^m Filtration rate of 7.8 l h^{-1} for a mussel of 1 g tissue dry wt (Kreeger et al. 1988)

ⁿ Respiration rate of $0.41 \text{ ml O}_2 \text{ h}^{-1}$ (= $220 \mu\text{g C h}^{-1}$) and $0.23 \text{ ml O}_2 \text{ h}^{-1}$ (= $124 \mu\text{g C h}^{-1}$) for a submerged and exposed mussel, respectively, of 1 g tissue dry wt at 20°C (Widdows et al. 1979)

^o Assuming both nitrogen and oxygen requirements of exposed mussels are reduced to the same extent (56.4 %) compared with those of submerged mussels

ginica breaks down amorphous cellulose into soluble oligomers. These oligomers must be transported to the diverticula where intracellular β -glucosidase activity completes digestion, liberating glucose. However, cellulose is not efficiently used as a carbon source by *C. virginica*, possibly because intracellular β -glucosidase activity is rate limiting. Perhaps the main function of extracellular β -1,4-glucanase activity in *C. virginica* is the depolymerization of cellulosic cell walls of algae and cellulosic detritus particles with the consequent release and intracellular digestion of associated nutrients.

Whereas *Crassostrea virginica* is predominantly distributed in sub-tidal zones of the mid-Atlantic coast of the USA, *Geukensia demissa* is restricted to high intertidal zones of marshes and brackish estuaries, sometimes being submerged for only 4 h per tidal cycle (Jordon & Valiela 1982). Therefore, we compared the ability of mussels to use cellulose as a carbon source under simulated sub-tidal (continuous submergence) conditions versus simulated mid-intertidal (6 h submergence/6 h exposure) conditions (Kreeger 1986, Kreeger et al. 1988). Mussels held in the simulated mid-intertidal regime assimilated carbon from cellulose with an efficiency of 14.2 % which was significantly higher than an efficiency of 9.2 % for mussels held in the simulated subtidal conditions. On the basis of estimates given in Table 1, cellulosic carbon could contribute 8.0 % to the summer metabolic carbon requirements of mussels inhabiting the mid-intertidal zone of Canary Creek.

In vitro mussel cellulase activity has not been determined, but Brock et al. (1986) reported that β -1,4-glucanase activity in extracts of the diverticula of *Geukensia demissa* was about 2.5 times greater than in *Crassostrea virginica*, perhaps explaining the mussel's higher assimilation efficiency of carbon from cellulose compared with that for oysters. The higher carbon assimilation efficiency of intertidal mussels fed cellulose compared with that of sub-tidal mussels may be due to a prolonged gut residence time for ingested cellulose resulting in increased digestion efficiency. This hypothesis agrees with the suggestion of Bayne et al. (1988) that intertidal, suspension-feeding bivalve molluscs may physiologically compensate for reduced feeding periods by increasing gut residence time. Gillmor (1982) reported that intertidal populations of the ribbed mussel grew faster than subtidal populations. He suggested that higher growth rates of intertidal mussels were due to a requirement for a period of aerial exposure for co-ordination of digestive rhythms that, in turn, resulted in increased digestion efficiencies. Further experiments are required to determine the physiological basis of enhanced cellulose utilization in intertidal populations of *G. demissa*.

NUTRITIONAL ROLE OF BACTERIA

Although results from our experiments indicate insignificant direct utilization of cellulosic carbon by oysters in Canary Creek, bacteria associated with the decomposition of detrital material may facilitate transfer of carbon from particulate or dissolved sources to *Crassostrea virginica*. We examined this hypothesis by comparing ^{14}C assimilation efficiencies of *C. virginica* fed ^{14}C -labelled lignocellulose alone with those of oysters fed on cellulosic material pre-incubated with cellulolytic bacteria isolated from Canary Creek. Initial experiments indicated that suspended cellulolytic bacteria were utilized by *C. virginica* with a ^{14}C assimilation efficiency of 52 % (Crosby 1987, Crosby et al. in press). The bacteria/cellulose detrital complex was prepared by pre-incubating ^{14}C -labelled cellulose with the cellulolytic strain of bacteria for 2 wk (Crosby 1987, Crosby et al. in press). The measured ^{14}C assimilation efficiency of 10.3 % \pm 6.7 % ($n = 5$) for oysters fed on the bacteria/cellulose detrital complex was significantly greater than the efficiency of 2.7 % \pm 1.8 ($n = 20$) for oysters fed on ^{14}C -labelled cellulose alone.

It is possible to estimate the contribution of attached bacteria to the carbon requirements of *Crassostrea virginica* and *Geukensia demissa* living in Canary Creek marsh during the summer (June through September) when water temperatures exceed 20 °C. Using a mean concentration for attached bacteria of $1.7 \times 10^5 \text{ ml}^{-1}$ (Fig. 4) together with laboratory-determined assimilation efficiencies and respiration rates, we estimate that attached bacteria could contribute 2.1 % to the metabolic carbon requirements of subtidal oysters and 5.2 % to the metabolic carbon requirements of intertidal mussels over a complete tidal cycle (Table 1). It is apparent that cellulosic material (see previous section) and attached bacteria make a small contribution to the carbon requirements of intertidal mussels and an even smaller contribution to the requirements of subtidal oysters in Canary Creek (Table 1). Furthermore, the percentage contribution of cellulose and attached bacteria to the total carbon requirements of mussels and oysters will be even less than these estimates for metabolic carbon requirements because total carbon requirements are generally about 33 % greater than a bivalve's metabolic carbon requirements (Bayne & Newell 1983).

In other estuarine habitats, the contribution of attached bacteria to the carbon requirements of oysters and mussels may be higher than for populations inhabiting Canary Creek. For example, Crosby et al. (in press) estimated that attached bacteria could contribute 19.2 % to the total carbon requirements of *Crassostrea virginica* inhabiting the Chesapeake Bay because of high suspended bacteria concentrations

(1×10^7 cells ml^{-1}) and a high proportion (15 %) of attached bacteria. Only 6 % of the suspended bacteria in Canary Creek were attached. A similar low percentage (< 3 %) of suspended bacteria were attached in the Great Sippewissett marsh (Kirchman et al. 1984).

We have compared the abilities of *Crassostrea virginica* and *Geukensia demissa* to remove free bacteria from marsh water collected from Canary Creek. We held individual mussels and oysters in upweller columns (Langdon & Siegfried 1984) and added to the flowing seawater combinations of natural seston, free bacteria and 1.6 and 3.9 μm diameter 'Fluoresbrite' polystyrene fluorescent microspheres (Polyscience Inc.). The concentrations of particles in water samples collected from below and above the bivalves in the upweller columns were determined with a model ZB Coulter Counter. For the enumeration of bacteria and microspheres, water samples were filtered onto 0.2 μm 'Nuclepore' filters, bacteria were first stained with DAPI (Porter & Feig 1980) and then bacteria and microspheres were counted directly using an epifluorescent microscope. Control treatments (empty mussel shells glued together) were included in the experiments to allow correction for changes in particle concentration due to particle settlement or other factors. We found that mussels removed unattached bacteria from Canary Creek water with 15.8 % of the efficiency of removal for 3.9 μm diameter microspheres, whereas oysters filtered unattached bacteria with an efficiency of only 5.0 % that for 3.9 μm microspheres (Fig. 8). Similarly, Riisgård (1988) reported that the ribbed mussel retained < 5 μm sized particles more efficiently than the oyster although he did not obtain information on the retention of particles < 2 μm in diameter which is a particle size more representative of the dimensions of free bacteria. Wright et al. (1982) did not determine retention efficiencies for oysters fed on free bacteria

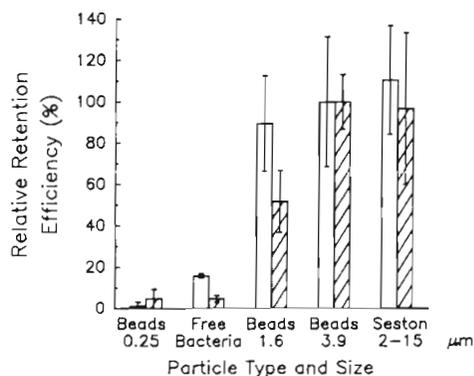


Fig. 8. Relative filtration efficiencies of *Crassostrea virginica* (bars with diagonal slashes) and *Geukensia demissa* (open bars). Retention efficiencies are mean values (± 1 SD, $n = 5$) for various sizes of suspended particles expressed relative to an assumed 100 % retention efficiency for 3.9 μm latex microspheres

but reported that *G. demissa* retained total bacteria (attached and non-attached combined) from marsh water with 18.4 % of the efficiency of retention for colloidal graphite (Aquadag) particles 1 to 2.3 μm in size. The total bacteria retention efficiency of *G. demissa* reported by Wright and co-workers is comparable to our value of 15.8 % for mussels fed on free bacteria (Fig. 8).

Using values for assimilation efficiencies of bacterial carbon (described above) for both oysters and mussels, unattached, free bacteria in Canary Creek could contribute 3.4 % and 25.8 % to the metabolic carbon requirements of subtidal oysters and intertidal mussels, respectively (Table 1). Therefore, unattached bacteria would appear to make a more significant contribution to the carbon requirements of mussels than to those of oysters.

Findlay & Tenore (1982) used ^{15}N tracer techniques to demonstrate that microbes associated with the breakdown of detritus could mediate the transfer of inorganic nitrogen from seawater to the polychaete *Capitella capitata*, thereby enriching the nitrogen content of the detrital particle. Using similar ^{15}N tracer experiments, we demonstrated that cellulolytic bacteria, associated with the breakdown of prepared *Spartina alterniflora* lignocellulosic material, incorporated inorganic nitrogen from seawater. However, oysters fed on the detrital complex only absorbed ^{15}N associated with the particle with an efficiency of $3.5 \pm 2.3 \%$ ($n = 5$) (Crosby et al. in press). Therefore, most of the particulate nitrogen associated with the detrital complex was nutritionally unavailable to the oyster. Only 6 % of detrital ^{15}N was estimated to be associated with bacterial cells. If the oyster's assimilation efficiencies for bacterial carbon and nitrogen are assumed to be similar at 52 % (Crosby et al. in press), utilization of bacteria cellular nitrogen alone could account for almost all of the oyster's observed absorption of nitrogen from the detrital complex.

A possible explanation for the oyster's low absorption efficiency for detrital nitrogen is that the majority (95 %) of the nitrogen associated with sediments is refractory and not metabolizable by invertebrates (Rice et al. 1986). Rice (1982) and Rice & Hanson (1984) suggested that refractory detrital nitrogen may be covalently bound as complex macromolecular material produced by condensation reactions between microbial proteinaceous exudates and reactive phenols or carbohydrates generated in the decomposing detritus matrix. Harvey & Luoma (1984) reported that sediment-bound and dissolved bacterial exopolymers did not appear to be directly metabolized by the deposit-feeding clam *Macoma balthica*. Nutritionally available nitrogen of detrital particles would, therefore, appear to be primarily associated with bacteria cells.

The estimated contributions of bacteria in meeting metabolic nitrogen requirements are 10 % (attached bacteria) and 16.7 % (unattached bacteria) for subtidal oysters compared with 11 % (attached) and 60 % (unattached bacteria) for intertidal *Geukensia demissa* in Canary Creek marsh during the summer (Table 1). A similarly significant contribution of bacteria to the nitrogen requirements of bivalves has been reported by Newell & Field (1983a, b) who estimated that suspended bacteria present in South African kelp beds provided 73 % of the nitrogen, but only 9 % of the carbon, required by bivalve suspension feeders. However, it is only in certain environments, such as eutrophic estuaries (Ducklow et al. 1988), kelp beds, and marshes that bacteria concentrations are sufficiently great for bacteria to contribute significantly to the nutrition of suspension-feeding bivalves. In contrast, bacteria are generally less abundant in open coastal and oceanic waters (Coffin & Sharp 1987) and in such habitats bacterial nitrogen is unlikely to be nutritionally significant for bivalves.

OTHER SOURCES OF NUTRITION

The results of the studies reviewed here indicate that the ribbed mussel, *Geukensia demissa*, is better able to filter bacteria from suspension and assimilate carbon from cellulosic detritus compared with the oyster, *Crassostrea virginica*. As a result of these physiological processes, *G. demissa* can potentially derive a greater proportion of its carbon and nitrogen requirements from cellulose and bacteria than the oyster. This conclusion is supported by stable isotope analyses which indicate that material derived from *Spartina alterniflora* is a more important dietary constituent for *G. demissa* than for *C. virginica* (Montague et al. 1981, Peterson et al. 1985, 1986). However, we estimate that direct utilization of cellulose and bacteria only accounts for 40 % of the summer metabolic carbon requirements of mussels inhabiting Canary Creek marsh with bacteria also supplying 71 % of the mussel's metabolic nitrogen requirements. This estimate of cellulose/bacterial carbon utilization by *G. demissa* is in agreement with our finding, based on stable isotope analysis, that *S. alterniflora* is providing between 30 and 50 % of the mussel's carbon requirement for growth (Fig. 5). In contrast Peterson et al. (1985) reported that mussels living in the inner regions of the Great Sippewissett marsh (Mass., USA) obtain at least 80 % of their carbon requirements from food originating from *S. alterniflora* (Fig. 5). This high contribution from *Spartina*-derived material may be due to mussels being exposed to concentrations of cellulosic detritus and bacteria that are higher in the Great Sippewissett marsh than those we measured in

Canary Creek marsh. Bacteria concentrations in the Great Sippewissett marsh vary according to tide and season but maximum summer concentrations (3.2×10^6 cells ml^{-1} ; Kirchman et al. 1984) are lower than summer concentrations in Canary Creek marsh. Kirchman et al. (1984) estimated that bacteria in the Great Sippewissett marsh supplied less than 10 % of the carbon required by *G. demissa* for growth during the summer.

Unfortunately, there are no reported data on cellulose concentrations for the Sippewissett marsh to compare with our data for Canary Creek and so it is impossible to estimate direct utilization of cellulosic carbon by bivalves in this marsh. Indirect utilization of material derived from *Spartina alterniflora* via consumption of nanozooplankton may be an important source of nutrition for mussels in the Great Sippewissett marsh, explaining the stable isotope signatures obtained by Peterson et al. (1986). Nanociliates and flagellates are important components of the nanozooplankton of estuarine waters and have been shown to feed primarily on bacteria (Fenchel 1982, Sherr et al. 1986, 1987). In salt marshes, Benner et al. (1988) demonstrated that protozoans are important consumers of bacteria associated with the decomposition of lignocellulosic material derived from *S. alterniflora*. Nanociliates and flagellates which are 2 to 20 μm in size can be more efficiently retained by suspension-feeding bivalves than unattached bacteria and hence may be an important link in the transfer of nutrients from bacteria to bivalves (Sherr et al. 1986). We know of no reported concentrations of nanozooplankton in Great Sippewissett marsh; however, Sherr et al. (1986) have reported that ciliates and flagellates attained a carbon biomass of 12.2 and 9.3 $\mu\text{g C l}^{-1}$, respectively, during August in tidal creeks draining the upper Duplin River salt-marsh in Georgia. If we assume that, (a) such concentrations of nanozooplankton are typical of marsh systems, (b) nanozooplankton can be filtered from suspension with 100 % efficiency by bivalves and, (c) cellular carbon is absorbed with 75 % efficiency (a typical efficiency for phytoplankton cells; Bayne and Newell 1983), we estimate, using additional data in Table 1, that nanozooplankton could contribute 15 % and 37 % to the summer metabolic carbon requirements of oysters and mussels, respectively, in Canary Creek.

Little is known of the potential contribution of dissolved organic matter (DOM) to the nutrition of marsh-inhabiting bivalves. Concentrations of DOM may be as high as 9 mg C l^{-1} in some marshes, i.e. 10 to 20 times that present in the open ocean (Pomeroy & Imberger 1981). Most of this material is thought to be refractory although a labile fraction is available to bacteria (Wiegert et al. 1981) and possibly to mussels and oysters which have been shown to absorb dissolved nutrients, such as amino acids, directly from seawater

(Wright 1982). Manahan et al. (1983) estimated that uptake of amino acids at ambient concentrations in seawater, could meet 34 % of the metabolic requirements of the mussel *Mytilus edulis*.

In summary, it is apparent that mussels and oysters inhabiting Canary Creek marsh must utilize food sources in addition to cellulose and bacteria in order to satisfy their summer carbon and nitrogen requirements. This conclusion agrees with that of Peterson et al. (1985, 1986) who determined that mussels in the Great Sippewissett marsh use a mixture of food sources to meet their nutritional requirements, with the proportion derived from *Spartina alterniflora* varying according to the mussel's location in the marsh and season.

Phytoplankton is probably the major source of nutrition for marsh-inhabiting bivalves, especially during periods of high phytoplankton abundance. During periods of low phytoplankton abundance, unattached bacteria may be an important source of nitrogen and carbon for mussels, and to a lesser extent for oysters. Cellulose appears to be a less important source of carbon than bacteria for mussels and oysters inhabiting Canary Creek during the summer, but nonetheless cellulose may indirectly contribute to their carbon requirements by acting as a carbon source for cellulolytic bacteria and perhaps nanozooplankton. This indirect contribution of material derived from *Spartina alterniflora* to the nutrition of bivalves inhabiting marshes would explain the results of stable isotope analyses which have indicated the importance of *S. alterniflora* in mussel nutrition.

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