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M. Alber · I. Valiela

Incorporation of organic aggregates by marine mussels

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Abstract Two marine mussels, *Geukensia demissa* (Dillwyn) and *Mytilus edulis* (L.) collected in 1990 in Old Silver Beach, Falmouth, Massachusetts, incorporated nitrogen when fed ^{15}N-labelled organic aggregates produced from dissolved organic nitrogen released by the brown seaweed *Fucus vesiculosis*. Uptake of ^{15}N on the aggregate diet was linear over the course of 24 h, and unincorporated ^{15}N was eliminated from the gut after 48 h. Both species of mussels incorporated approximately five times more N when they were fed organic aggregates than when they were fed either ^{15}N-labelled dissolved organic material (DOM) or particulate detritus, both of which were also derived from the seaweed. Nitrogen uptake was greatest in controls fed the diatom *Thalassiosira weissflogii*; mussels fed phytoplankton incorporated seven times more nitrogen than those fed aggregates. However, aggregates could supply an estimated 7 to 14% of the N requirements for both mussels, whereas DOM or particulate detritus could only supply 1 to 3%. These data provide evidence that a food web pathway exists from primary producer to released dissolved organic nitrogen to microbial organic aggregate to metazoan consumer, and, further, that it can be more important in a detrital food web than either particulate detritus or DOM.

Introduction

Very little of the macrophyte production in near-shore environments is grazed directly. Rather, an estimated 80 to 90% enters detrital food webs as either particulate or dissolved non-living organic material (Mann 1972). This detritus can be used by metazoan consumers via three distinct trophic pathways. First, consumers can take up dissolved organic material (DOM), which is released by both live and decaying producers. Second, consumers can ingest particulate detritus. Particulate detritus, the most commonly studied form of detritus, results from fragmentation of producers into small particles that still retain recognizable cellular structure. The third route for the consumption of detritus is via ingestion of organic aggregates.

Organic aggregates are detrital particles that form from the DOM released by producers. In previous work, we have produced aggregates from the DOM released by five decomposing macrophytes (*Fucus vesiculosis, Gracilaria tikvahiae, Ulva lactuca, Spartina alterniflora*, and *Zostera marina*, Alber and Valiela 1994 a). We have evidence that these aggregates are biotic in nature, as they contain large numbers of bacteria and their biochemical composition is closer to that of bacteria than to the macrophyte from which the DOM was derived (Alber and Valiela 1994 a, b). Although there are also reports that aggregates can be formed abiotically (Kepkay and Johnson 1988), the bacterial aggregates we have produced are similar to those described by others in both laboratory (Biddanda 1986) and field (Linley and Field 1982) settings.

The use of organic aggregates as a food resource by consumers has long been hypothesized (Baylor and Sutcliffe 1963), and there are some suggestions that the aggregate, or "amorphous," detrital pathway may be more important for the flow of material from producers to consumers than the particulate, or "morphous," detrital pathway (Bowen 1984; Mann 1988). In a freshwater system, tadpoles (*Bufo americanus*) fed amorphous detritus lived longer than either starved controls (Ahlgren and Bowen 1991) or those fed morphous detritus (Bowen 1984). The relative importance of the three detrital pathways has never been directly studied in marine systems. The present study was therefore designed to evaluate organic aggregates, particulate detritus, and DOM as food sources for two marine mussels, *Geukensia demissa* and *Mytilus edulis*.

Mussels, the dominant suspension-feeding consumers in many near-shore marine ecosystems, derive some of their nutrition from detritus. In separate studies of the

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M. Alber (✉)[1] · I. Valiela
Boston University Marine Program, Marine Biological Laboratory, Woods Hole, Massachusetts 02543, USA

[1] *Present address*: Marine Sciences Department, University of Georgia, Athens, Georgia 30602, USA

stable isotope composition of *Geukensia demissa* growing along transects in two different salt marshes (Peterson et al. 1985; Langdon and Newell 1990), those ribbed mussels growing in areas well within the marshes had isotope values suggesting that they derived 50 to 80% of their carbon and sulphur from *Spartina alterniflora*, whereas those living nearer the sea derived only 40%. *Mytilus edulis* collected outside the marshes derived 30% or less material from *S. alterniflora*, but it is unclear whether this lower value was due to the fact that the blue mussels were collected outside the marshes or because they are a different species. Although these studies provide evidence that mussels can assimilate macrophyte detritus, they do not indicate the route the material took through the food web or the relative importance of the various detrital pathways.

There is evidence that both mussels have the capacity to use particulate detritus in their diets: both *Geukensia demissa* and *Mytilus edulis* contain enzymes that can be used to hydrolyze starch, cellulose and laminarin (Lucas and Newell 1984; Brock et al. 1986). These carbohydrases demonstrate that bivalves are capable of digesting detrital material produced from vascular plants, green or brown algae, although the presence of specific enzymes does not necessarily indicate the use of a given substrate as a food resource (Newell and Langdon 1986). Kreeger et al. (1988) used radiolabelled cellulosic material from *Spartina alterniflora* to demonstrate that *G. demissa* can absorb refractory lignocellulosic carbon with an efficiency of 13 to 14%.

Bivalves can absorb DOM directly (for reviews see Wright and Manahan 1989; Gorham 1990). Uptake is an active process in which dissolved substances are selectively incorporated, even against a concentration gradient, and then processed (Manahan et al. 1983; Wright and Pajor 1989).

There have been no studies that examined whether mussels can incorporate amorphous organic aggregates. If such aggregates are comprised of live bacteria, dead bacteria, and bacterial exudation products, as we have hypothesized (Alber and Valiela 1994 a, b), then the most relevant studies are those that examined incorporation of bacteria by bivalves. Bivalves are capable of digesting bacteria. A survey of 33 species, including *Mytilus edulis*, all contained lysozyme-like enzymes that could digest the cell walls of bacteria (McHenery et al. 1979, 1986). Wright et al. (1982) found that *Geukensia demissa* captured bacterioplankton much more efficiently than did *M. edulis*. However, *M. edulis* is also capable of incorporating bacteria (Hollibaugh et al. 1980; McHenery and Birkbeck 1985). Prieur (1981) used histological and scanning electron micrographic techniques to provide direct observations of bacterial cells in the stomach of *M. edulis*. The observation that the bacteria in the stomach were in microcolonies or "mucus bacteria agglomerates" is particularly interesting in light of our hypothesis concerning aggregate composition.

In the present study, we used ^{15}N to trace nitrogen from a brown seaweed, *Fucus vesiculosis*, to *Geukensia demissa* and *Mytilus edulis* via detrital diets of organic aggregates, particulate detritus, or DOM. *F. vesiculosis* was chosen because it is commonly found in the same habitats as both mussel species. A diatom, *Thalassiosira weissflogii*, was also fed to the mussels to compare detritus utilization with direct grazing of phytoplankton.

Materials and methods

Juvenile *Geukensia demissa* (Dillwyn) and *Mytilus edulis* (L.) were collected in June 1990 in a small salt marsh estuary in Old Silver Beach, Falmouth, Massachusetts, USA. Mussels were maintained in a common tank in running seawater at ambient temperature (22 °C) for 3 wk and then used in the experiment. At the time of the experiment, *G. demissa* averaged 38.5 ± 4.7 mm in length (±SD) and 0.28 ± 0.11 g dry weight (g dry wt) and *M. edulis* averaged 34.8 ± 2.9 mm in length and 0.30 ± 0.09 g dry wt.

Mussels were fed one of four ^{15}N-labelled treatment diets: aggregates, DOM, particulate detritus, or phytoplankton. Mussels maintained in unlabelled 0.22-μm filtered seawater (FSW) were used as unfed controls.

Preparation of ^{15}N-labelled diets

Young, intact fronds of *Fucus vesiculosis* were collected from a submerged jetty in Woods Hole, Massachusetts. The alga (800 g wet wt) was distributed in two well-lit 76-liter tanks. Tanks stood in running seawater to maintain ambient temperature and were bubbled with aquarium filters to maintain oxygen concentration. Three times per week over a period of 2 wk, new seawater was allowed to flow through each tank for 3 h, followed by the addition of 0.3 g 99% $^{15}NH_4Cl$ (Cambridge Isotope Lab, Woburn, MA). At the end of the labelling period, algal biomass had increased to 1030 g (wet wt). Labelled algae were stored frozen (–20 °C) until use.

Labelled aggregates, DOM, and particulate detritus were produced from labelled *Fucus vesiculosis* fronds. Aggregates were made by leaching six 50 g (wet wt) subsamples of whole, labelled algal fronds in the dark in glass jars containing 500 ml of 0.22-μm FSW for 5 d. At the end of the leaching period, the algae was removed from the water, the leachate was centrifuged (4500 rpm for 20 min), and then the supernatant was filtered through a GF/F (Whatman) filter (median pore size 0.7 μm). The labelled leachate was bubbled in the dark with aquarium bubblers (fitted with in-line 0.22-μm filters) for 6 d, at the end of which time aggregates were present in all jars. For a more detailed description of aggregate production, see Alber and Valiela (1994 a). The aggregate treatment diet consisted of the suspension of labelled leachate plus aggregates present after 6 d of bubbling.

Labelled DOM treatment was made from two of the replicate jars of labelled aggregates. Material in the jars was centrifuged (4500 rpm for 20 min), and the supernatant was filtered through a GF/F filter (median pore size 0.7 μm). The filtrate was operationally defined as DOM in our study.

Particulate detritus was produced by drying (60 °C oven) samples of the *Fucus vesiculosis* that were removed from the water at the end of the leaching period. This material was ground in a Wiley mill (250-μm mesh) and mixed with 0.22-μm FSW just before being fed to mussels.

A diatom, *Thalassiosira weissflogii*, was labelled with ^{15}N for the phytoplankton treatment. Culture medium (f/2, Guillard and Ryther 1962) was prepared in Fernbach flasks without a nitrogen source and with silica added. Just prior to inoculating cultures, 99% $^{15}NH_4Cl$ was added to the flasks. Cultures were grown for 3 to 5 d before harvesting, at which time cells had reached concentrations of 10.7×10^4 cells ml^{-1}. Cell counts were made using a haemocytometer (a minimum of 100 cells were counted on at least two replicate slides).

Samples of the aggregate, particulate detritus and phytoplankton treatment diets were measured for $\%^{15}N$ using a dry combustion technique (Dumas procedure) and atomic emission spectroscopy. The dry combustion method cannot be used on soluble material, so we did

not measure the $\%^{15}N$ of the DOM diet directly (although see Bronk and Glibert 1991). However, since the DOM diet was prepared from the centrifuged, filtered leachate, its $\%^{15}N$ was assumed to be the same as that of the aggregates prepared from similar material. Biochemical characteristics of the diets are presented elsewhere (Alber and Valiela 1994b).

Experimental apparatus and protocol

The experiment was run in a flow-through system that delivered 0.22-μm FSW at a rate of 70 ml min^{-1} into 8-cm diameter funnels that were used as experimental tanks. Funnels were stoppered at the bottom and drained through an outlet port positioned at a level that maintained the water volume at 1 liter. Mussels were placed on mesh platforms inside the funnels, so that uneaten food and fecal material fell to the bottom.

Treatment diets were held in 4-liter glass jars and stirred with magnetic stirrers to keep them in suspension. Diets were dripped from the jars into the funnels via a peristaltic pump at a rate of 2.6 ml min^{-1}. The aggregate, particulate detritus, and phytoplankton diets were each dripped in at a concentration of 35 μg dry wt ml^{-1}, to make a final concentration of approximately 1.3 μg material ml^{-1} in the funnel. The weight of the aggregate diet was determined by filtering a known volume (5 to 15 ml) of the aggregate suspension and drying the filter overnight (60 °C). This protocol meant that the aggregate concentration during the experiment was determined based on samples obtained the previous day. The average concentration of the aggregate diet in the funnels during the experiment was 1.6 μg dry wt ml^{-1} (SD = 0.6, $n = 2$). The DOM diet was delivered at the same rate as the aggregate diet. Particulate detritus was weighed and then mixed into FSW. The final concentration of the phytoplankton diet in the funnels was approximately 4000 cells ml^{-1}, which is equivalent to 1.3 μg dry wt ml^{-1} (calculated based on data in Epifanio 1979 and Davis 1982).

At the beginning of the experiment, mussels were conditioned for 48 h with unlabelled *Thalassiosira weissflogii*, delivered at a concentration of 4500 cells ml^{-1}. After the conditioning period, mussels received treatment diets. During the feeding period, mussels were open and visibly filtering. Four individual mussels from each species were fed each of the treatment diets for 15 h and then allowed to depurate in FSW for 48 h. These time intervals were chosen based on previous experiments performed with *Argopecten irradians* (Alber 1992). To be sure that they were appropriate for mussels, both an uptake and a depuration time-course were performed with mussels that were fed aggregates. To test whether uptake of ^{15}N was linear during the feeding experiment, two ribbed and two blue mussels were fed aggregates for 5, 10, or 24 h and then allowed to depurate for 48 h. To determine whether the $\%^{15}N$ in the gut was eliminated after 48 h, six mussels of each species were fed aggregates for 15 h and then allowed to depurate for 0, 12, or 24 h. Data from mussels fed aggregates for 15 h and depurated for 48 h as part of the main experiment were included in each time-course.

After the appropriate depuration period, the $\%^{15}N$ of mussel tissues (oven-dried at 60 °C) were measured by atomic emission spectroscopy. Atom percent enrichments of the tissue of mussels fed the DOM and particulate detrital diets were below the detection limit (0.01%) of the atomic emission spectrometer in most cases. Therefore, atom $\%^{15}N$ of these mussels, the unfed controls, and those mussels fed aggregates for 15 h were analyzed on the more sensitive (0.0001%) mass spectrometer (Boston University Stable Isotope Laboratory). A Perkin Elmer Model 240C elemental analyzer was used to determine %N of mussel tissue.

Atom percent enrichment was calculated by subtracting the atom $\%^{15}N$ of control mussels from that of treatment mussels. Specific nitrogen uptake was calculated as follows:

$$\text{Specific nitrogen uptake} = \frac{\%^{15}\text{N (treatment mussel)} - \%^{15}\text{N (control mussel)}}{\%^{15}\text{N (treatment diet)} - \%^{15}\text{N (treatment mussel)}}, \quad (1)$$

$$= \frac{\text{g N incorporated}}{\text{g N in mussel}}. \quad (2)$$

Specific nitrogen uptake can be expressed in terms of the mussel's dry weight by multiplying by the % N of the tissue:

$$\frac{\mu\text{g N incorporated}}{\text{g dry wt}} = \frac{\text{g N incorporated}}{\text{g N in mussel}} \times \frac{\text{g N in mussel}}{\text{g dry wt of mussel}} \times \frac{10^6\,\mu\text{g}}{\text{g}} \quad (3)$$

Results

Atom % enrichment of mussels fed ^{15}N-labelled aggregates increased over the time-course of the feeding experiment (Fig. 1). Enrichment increased linearly over time (regression analysis, Table 1, $p < 0.0001$). Although there is an indication that *Geukensia demissa* was incorporating nitrogen more slowly than was *Mytilus edulis*, there was not a significant difference between species (Table 1, $p < 0.12$); the common slope for all mussels was 0.006.

The results of the depuration time-course suggest that whatever ^{15}N was present in the guts of the mussels was released after 48 h (Fig. 2). The *Geukensia demissa* data do not show any clear decrease over the depuration period, whereas the *Mytilus edulis* data show an initial peak, possibly due to the presence of undigested material in the gut, which disappeared after 24 h.

Specific nitrogen uptake for mussels fed phytoplankton, aggregates, DOM or particulate detritus was calculated using atom percent ^{15}N measured in treatment diets and mussels (Table 2). Specific nitrogen uptake was greatest for mussels fed phytoplankton, lower for those fed ag-

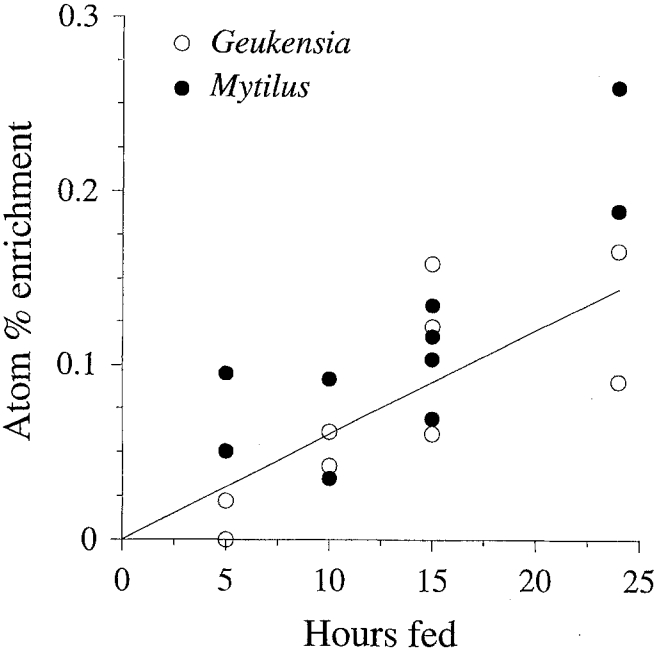

Fig. 1 *Geukensia demissa* and *Mytilus edulis*. Atom percent enrichment in mussels fed organic aggregates for 0, 5, 10, 15, or 24 h. All mussels depurated for 48 h. Equation for regression line is atom % enrichment = 0.006 × h fed

Table 1 *Geukensia demissa* and *Mytilus edulis*. Regression analysis results for time fed labelled aggregates versus atom percent enrichment measured in mussels. Two mussels from each species were fed aggregates for 5, 10, or 24 h; three *G. demissa* and four *M. edulis* fed for 15 h

(a) Analysis of variance

Source	SS	DF	*F*	*P*
Regression	0.231	2	75.639	0.0001
Error	0.026	17		
Total	0.257	19		

(b) Regression coefficients

Variable	Coefficient	SD	*P*
Hours fed	0.0064	0.0008	0.0001
Species	0.0265	0.0164	0.1247

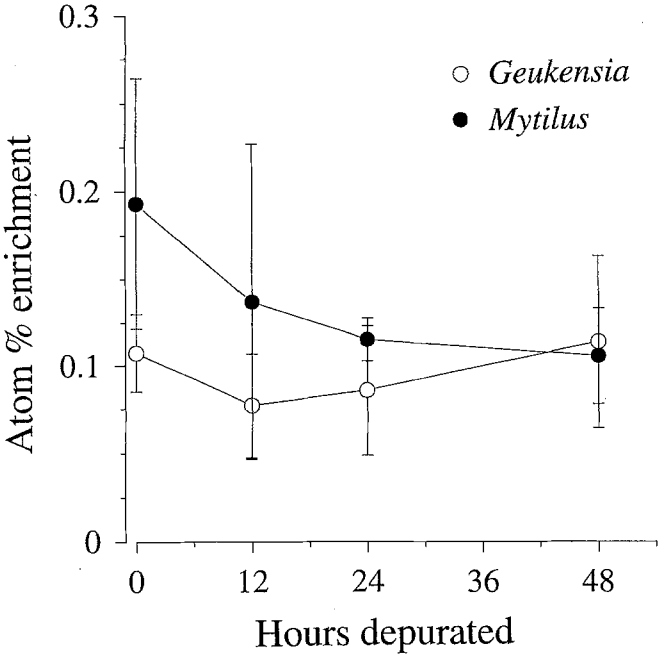

Fig. 2 *Geukensia demissa* and *Mytilus edulis*. Atom percent enrichment in mussels fed organic aggregates for 15 h and then depurated for 0, 12, 24, or 48 h. Bars represent SD. Two of each species of mussel were analyzed after 0, 12, and 24 h; three *G. demissa* and four *M. edulis* analyzed after 48 h

Table 2 *Geukensia demissa* and *Mytilus edulis*. Atom $\%^{15}N$ (±SD) measured in treatment diets and in tissues of mussels fed each diet. Atom $\%^{15}N$ of treatment diets and mussels fed phytoplankton analyzed by atomic emission spectrometry with a precision of 0.01%; remaining mussel samples analyzed by mass spectrometry with a precision of 0.0001%. Three samples of the particulate detritus and aggregate diets were analyzed, and ten samples of the phytoplankton diet. The $\%^{15}N$ of the dissolved organic matter diet was assumed to be the same as that of the aggregate diet. Four mussels from each species analyzed for each treatment diet ($n=4$), with the exception of *G. demissa* fed aggregates, where $n=3$

Diet	Diet $\%^{15}N$	Mussel $\%^{15}N$	
		G. demissa	*M. edulis*
Filtered seawater		0.377±0.002	0.381±0.007
Particulate detritus	13.8±2.8	0.381±0.004	0.391±0.011
Dissolved organic matter	27.6	0.387±0.006	0.392±0.010
Aggregates	27.6±2.2	0.470±0.054	0.479±0.013
Phytoplankton	74.3±1.4	2.2±0.2	2.0±0.2

Table 3 *Geukensia demissa* and *Mytilus edulis*. Specific nitrogen uptake and nitrogen incorporation g^{-1} dry wt h^{-1} (±SD) measured in mussels fed each treatment diet for 15 h. Number of observations as per Table 2

Diet	Specific N uptake ($\times 10^{-4}$)		µg N incorp. g^{-1} dry wt h^{-1}	
	G. demissa	*M. edulis*	*G. demissa*	*M. edulis*
Particulate detritus	3±3	7±8	1.7±1.7	3.7±4.4
Dissolved organic matter	3±2	4±4	1.9±1.3	2.2±1.9
Aggregates	34±20	36±5	18.3±10.7	19.3±26.3
Phytoplankton	260±33	244±84	139±18	131±45

Table 4 *Geukensia demissa* and *Mytilus edulis*. Analysis of variance results for specific nitrogen uptake rate measured in mussels fed four treatment diets (phytoplankton, aggregates, particulate detritus or dissolved organic matter). Data square-root transformed to meet assumption of homogeneity of variance. Number of observations as per Table 2

Source	SS	DF	*F*	*P*
Diet	0.095	3	165.199	< 0.001
Species	< 0.001	1	0.456	0.507
Species × Diet	< 0.001	3	0.597	0.624
Error	0.004	21		

gregates and lowest for those fed DOM or particulate detritus (Table 3). Analysis of variance of these measurements (Table 4) showed a significant diet effect but no species effect. A post-hoc Scheffé test of the diet effect indicated that the values fell into three significantly different ($p<0.001$) groups: the first contained phytoplankton-fed mussels, the second aggregate-fed mussels, and the last contained mussels fed either DOM or particulate detritus.

Specific nitrogen uptake rates of mussels fed each treatment diet for 15 h were converted to µg N incorporated g^{-1} dry wt h^{-1} based on the average %N measured in body tissue (8.0±0.6, $n=6$) (Table 3). Mussels fed aggregates incorporated about five times more nitrogen than mussels fed DOM or particulate detritus; mussels fed phytoplankton incorporated approximately seven times more nitrogen than those fed aggregates.

Nitrogen incorporation rates were used to make two independent estimates of the contribution that the various diets could potentially make to a mussel's metabolic requirements (Table 5). First, we compared the rate of nitro-

Table 5 *Geukensia demissa* and *Mytilus edulis*. Estimation by two different methods of the contribution of the various treatment diets: phytoplankton (*PHY*), aggregates (*AGG*), particulate detritus (*PAR*), and dissolved organic material (*DOM*) to the nutritional requirements of mussels. See "Results" for details

Method Diet	Diet	Species	
		G. demissa	*M. edulis*
Method 1			
(1) Specific N uptake (μg N incorporation g^{-1} dry wt h^{-1})			
	PHY	139	131
	AGG	18	19
	PAR	2	4
	DOM	2	2
(2) Nitrogen required (μg N g^{-1} dry wt h^{-1})			
		168	268–137
(3) Nitrogen incorporation as % N required [(1)/(3)×100]			
	PHY	83	49–96
	AGG	11	7–14
	PAR	1	1–3
	DOM	1	1
Method 2			
(4) Protein uptake [(1)×6.25]			
	PHY	869	819
	AGG	112	119
	PAR	11	23
	DOM	12	14
(5) Oxygen required (μl O_2 g^{-1} dry wt h^{-1})			
		803	1150
(6) Protein incorporated as % O_2 required [(4)/(5)×100]			
	PHY	100	71
	AGG	14	10
	PAR	1	2
	DOM	1	1

gen incorporation measured here with published estimates of nitrogen requirements. For *Geukensia demissa*, we used weight-standardized rate relationships for ammonia excretion, biodeposition, and byssal thread secretion (Jordan and Valiela 1982) to estimate the nitrogen requirements of a 0.3-g mussel for the summer season. For *Mytilus edulis*, we used the range of nitrogen absorption rates reported by Hawkins et al. (1986). Second, we compared the rate of nitrogen incorporation with that of oxygen consumption. Oxygen consumption for a 0.3 g dry wt mussel of each species at 22 °C was estimated from Read (1962) and converted to protein incorporation h^{-1} by assuming it takes approximately 1 ml of oxygen to oxidize 1 mg protein. Nitrogen incorporation was multiplied by a conversion factor (6.25) to calculate mg protein incorporated h^{-1}. This second estimate is based on oxidative metabolism only and does not include energy costs of growth or anaerobic metabolism. To make them comparable, all data are expressed on a g^{-1} dry wt basis.

The two methods of estimation yielded similar results, with very little difference between mussel species (Table 5). The phytoplankton diet could supply 49 to 100%; aggregates could supply 7 to 11%; and particulate detritus and DOM could supply only 1 to 3% of the requirements of both *Geukensia demissa* and *Mytilus edulis*.

The incorporation rates used in the above estimates should be interpreted with caution. Some of the incorporated nitrogen was probably metabolized and subsequently released as $^{15}NH_4$ during the 48-h flushing period before ^{15}N measurements were made. Although this loss of $^{15}NH_4$ does not affect comparisons between the diets since all mussels were treated equally, it would result in an underestimate of nitrogen incorporation and consequently of the potential contribution of the various diets to the requirements of the mussels. A second caveat is that some of the differences between incorporation rates may have been due to differences in particle size and shape, both of which can affect retention efficiency (for review, see Hawkins and Bayne 1992). To the extent that particles in either the aggregate or particulate detritus treatment were either too small or too large for effective filtration by mussels, these estimates would again be conservative. The particulate detritus passed a 250-μm mesh sieve, whereas aggregates were all retained by a 0.7-μm filter. It was not possible to determine the size frequency of aggregates, as they both clumped and broke up when sampled. We estimate that aggregates ranged in size from 1 to 500 μm in diameter. Although the experimental diets were delivered at the same mass loading rate, these other factors could have affected the ability of the mussels to effectively retain particles.

Discussion

Both *Geukensia demissa* and *Mytilus edulis* incorporated ^{15}N-labelled nitrogen when fed aggregates derived from DOM released by labelled macrophytes (Table 2), demonstrating that nitrogen can in fact be transferred from decomposing macrophytes to suspension-feeding consumers via the aggregate, or amorphous, detrital pathway. Moreover, both species of mussels incorporated significantly more nitrogen when they were fed aggregates than when they were fed either DOM or particulate detritus (Tables 3, 4). These results are consistent with previous evidence that aggregates are a better food source than particulate, or morphous, detritus: aggregates formed from five species of macrophytes were lower in C:N and higher in protein than morphous detritus (Alber and Valiela 1994 b). Specifically, aggregates derived from *Fucus vesiculosis* had C:N ratios of 6 and were 19% protein whereas morphous detrital particles had C:N ratios of 25 and were 9% protein. In addition, both sheepshead minnows, *Cyprinodon variegatus*, and bay scallops, *Argopecten irradians*, also incorporated more nitrogen when fed organic aggregates than when fed morphous detritus (D'Avanzo et al. 1991; Alber 1992). Taken together with the present results, these data suggest that the amorphous detrital pathway may be a more efficient link between producers and suspension-feeding consumers in detrital food webs than the two other pathways.

The relatively low uptake rates reported here for mussels that fed on the particulate detritus are consistent with

previous conclusions that detritus is poor quality food. For example, particulate detritus derived from *Spartina alterniflora* does not support the growth of *Mytilus edulis* (Williams 1981). However, it should be noted that some detritivores depend on decomposing microbes to alter the quality of the detritus, increasing both its nitrogen content and availability to consumers. Oysters, *Crassostrea virginica*, assimilated refractory *S. alterniflora*-derived detritus alone with an efficiency of 2.7%, whereas material that was colonized by bacteria was assimilated with an efficiency of 10.3% (Crosby et al. 1990). Since the particulate detritus used in this experiment was not aged, its contribution to the mussels' diet would be expected to increase as the material decomposes.

We estimated that the DOM diet could contribute only 1% of the mussels' requirements (Table 5). This is much lower than previous estimates, which ranged from 10 to 34% (Manahan et al. 1983; Siebers and Winkler 1984; Gorham 1988). As noted earlier, the estimates calculated here are conservative since some of the ^{15}N incorporated by the mussels in the present study was probably metabolized and released during the 48-h flushing period. In addition, the DOM treatment diet used here consisted of material that remained in solution after *Fucus vesiculosis* had been leached for 5 d, followed by a 6-d bubbling period to create aggregates. It, therefore, presumably did not consist of the more labile fraction of the leachate.

Previous estimates of DOM uptake, however, may have been high. They were based on the net difference between incurrent and excurrent amino acid concentrations during the short time interval (s) it took for water to pass over mussels. The potential contribution of DOM to a mussel's requirements was extrapolated from these short-term experiments by assuming the mussels were at steady state, were continuously pumping water and extracting amino acids, and that all of the amino acids removed from the water were incorporated. However, there is limited information on the actual metabolic fate of transported substances (Wright and Manahan 1989), and it is known that ventilation rates in bivalves vary with factors such as oxygen tension and temperature (Bayne et al. 1976). In contrast, DOM incorporation in the present study was measured directly as ^{15}N in mussel tissues. Our estimates of the potential contribution of DOM to the mussels were based on a feeding trial that lasted 15 h, which allowed for a long integration of natural variations in filtration rates. Ferguson (1982) estimated that free amino acids could meet from 3 to 19% of the metabolic needs of bivalves, using rates derived from experiments lasting 1 h. The actual contribution of DOM to a mussel's requirements probably lies somewhere between the previous high estimates and our low estimates.

Specific nitrogen uptake rate of mussels fed aggregates was 13 to 15% of that of mussels fed phytoplankton (Table 5). Phytoplankton is higher quality food for bivalves than aggregates: *Argopecten irradians* also assimilated phytoplankton with greater efficiency than they assimilated aggregates (Alber 1992). The relative importance of each diet in the field, however, depends not only on the ability of mussels to take up the potential foods but also on their relative abundance. Phytoplankton is often only a small percentage of the particulate organic matter (POM) available in the water. Van Valkenberg et al. (1978) found that POM in Chesapeake Bay averaged 77% non-living detrital particles and 23% phytoplankton. Moreover, variation in detrital POM is usually less than the marked seasonal variability of phytoplankton (Van Valkenberg et al. 1978; Langdon and Newell 1990). Phytoplankton concentrations off the west coast of Cape Peninsula, South Africa also showed short-term variations and accounted for an average of only 14% of the POM year-round (Seiderer and Newell 1985).

The relative importance of DOM, morphous and amorphous detrital diets in the field remains difficult to quantify. The data presented here demonstrate that organic aggregates can be used and that the amorphous pathway represents a route in the detrital food web whereby DOM that is not absorbed directly can potentially be repackaged and funnelled back into metazoan food chains. The fact that mussels incorporated approximately 5 to 10 times more nitrogen when fed aggregates than when fed either DOM or particulate detritus suggests that aggregates could make an equal contribution to a consumer's requirements even if they represented only a small proportion of the detritus available in the water. The processes that govern organic aggregates in the water column is an area of active study (e.g. Smith et al. 1992; Lampitt et al. 1993). Their role in the food web remains an important topic for the next decade of research in detrital systems.

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