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Organism-Sediment Interactions

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Feeding Processes of Bivalves: Connecting the Gut to the Ecosystem

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Abstract: Bivalves exist in dense populations and may strongly affect the seston of coastal and estuarine water columns. Conversely, the seston content of such systems may affect the feeding behavior, particle processing, and digestive strategies of suspension feeders, both as individuals and within suspension-feeder communities such as oyster and mussel beds. It is an important objective to develop conceptual and mathematical models to describe both of these sets of interactions, but it is equally important to connect individual bivalve feeding selectivity and water column processes. Many models that consider feeding rates exist, often in the aquaculture literature, but the incorporation of selectivity needs to be addressed. In order to produce such models, we must know much more about particle selectivity and rates of particle processing in response to availability in the water column. We describe some methods and results demonstrating that (1) rate-limiting steps within bivalve feeding compartments might affect particle processing from the water column; (2) particle selectivity might strongly affect the composition of the seston in estuaries; and (3) resuspension of pseudofeces influences the role of bivalves in affecting the seston.

Introduction

Our purpose in this essay is to argue the necessity for connecting the factors that determine particle transfer functions within the various pallial cavity compartments of a suspension-feeding bivalve (Levinton et al. 1996) with the factors that regulate the abundance and particle composition of the water column seston. Bivalve molluscs are efficient suspension feeders and can strongly modulate the seston of estuaries, in those with sluggishly circulating coastal waters (Dame 1993a,b) as well as vigorously circulated coastal waters that are nevertheless trapped in circulating cells close to shore by confinements such as offshore bars (McLachlan 1980). For example, very dense coastal diatom blooms off the coasts of Oregon, USA, and South Africa are set off by a special set of circumstances that include restricted circulation and bivalve excretion (Lewin et al. 1975; McLachlan 1980).

The intimate relationship between particle processing by suspension-feeding individuals and the changing composition of seston suggests a number of questions:

(1) Does systematic rejection-acceptance of particles (i.e., selectivity among particle types), combined with resuspension processes, strongly affect the composition of particle types in the water column?

(2) Within bivalves, does particle transfer between organs in the pallial cavity (gills, palps, digestive tract) create rate-limiting steps that result in feedback to the seston in the water column?

Some of these questions have already been asked of the relationships between zooplankton grazers and phytoplankton dynamics (e.g., Frost 1972, 1987; Steele 1974). Also, there is a rich literature attempting to connect bivalve feeding to total phytoplankton concentration, especially in the context of mariculture. While we discuss some of the literature next, our main focus in this paper is to present new empirical approaches to bivalve feeding selectivity and adjustments of feeding rate that can eventually be integrated into more standard models of bivalve total feeding effects on estuaries and long residence time coastal waters. Are bivalves restricted to just feeding at a certain rate? Do they respond to changes in the seston and does this in turn affect the water column? These are questions that can be answered with studies of bivalve functional ecology and modeling of estuarine systems.

Past Work and Models on Bivalve Feeding Effects on Ecosystems

The objective of bivalve mariculture is to grow as many bivalves in a confined space as fast as possible, while maintaining a convenient means of recovering animals for harvest. Models predicting carrying capacity contrast the filtration rates of bivalve populations with factors that control phytoplankton supply rate (Grant et al. 1993; Heral 1993; Prins et al. 1998; Smaal et al. 1998). This objective is concordant with the objective of understanding how a "natural bivalve population" might influence the seston of an estuary or how the seston might affect the bivalve population dynamics and individual growth (Cloern 1982; Officer et al. 1982; Herman 1993).

To assess the interaction of a bivalve population with an estuary one must develop an ecosystem-based budget that relates phytoplankton production, water exchange, and bivalve feeding rate (e.g., Grant et al. 1993; Herman 1993; Prins et al. 1998). The simplest model extrapolates individual feeding rate, pseudofeces production rate, and resuspension to ecosystem and population levels. When compared with phytoplankton growth rate, a steady-state bivalve population size can be calculated if we know individual feeding rate and conversion efficiencies, which will enable calculation of scope for growth as a measure of individual energy balance. The natural ecosystem analogue to this was pioneered by Officer et al. (1982). Equations were developed that predicted phytoplankton change as a function of bivalve population density, and bivalve population density as a function of mortality and feeding rate. While it is doubtful that this model is very useful for bivalve population growth rate, it was still an excellent formulation to understand the potential for bivalve effects on phytoplankton dynamics and for the potential of bivalve self-limitation by overfiltration. A number of mariculture-based models have been developed to predict the so-called carrying capacity of a localized area. Some models use relatively few variables to model bivalves and water-column organisms (Grant et al. 1993), while others are elaborate with as many as 60 parameters that require extensive measurement (Campbell & Newell 1998).

Even with such models, many complexities complicate a simple extrapolation of individual feeding rates to the ecosystem. For example bivalve beds produce depletion boundary layers (Wildish & Kristmanson 1984; Frechette et al. 1989) and variations in water column stratification therefore require strong adjustments to such a simple model. Phytoplankton abundance varies seasonally in most locales, as does temperature. The concordance of a phytoplankton bloom with a seasonal larval release may strongly influence recruitment success.

It would be extremely useful if we could develop generalizations concerning the water exchange and phytoplankton dynamics that determine the importance of bivalve populations to the water column and vice versa. Dame and Prins (1998) employed Herman's (1993) simple model to characterize the carrying capacity of nearshore systems. They used three parameters to compare properties of estuaries (our notation differs somewhat):

Water residence time (T) is the time that it takes for the volume or mass of water, W , in a basin to be replaced by exchange at rate dW/dt with another body of water, such as open coastal waters.

$$T = \frac{W}{dW/dt} \quad (\text{units: hours} = \text{g/g h}^{-1})$$

Primary production time was defined (Dame & Prins 1998) as the ratio of yearly-averaged phytoplankton biomass (B) to primary production (P).

$$PPT = \frac{B}{P} \quad (\text{units: hours} = \text{g/g h}^{-1} = \text{h})$$

Finally, **bivalve population clearance time** CT (Smaal & Prins 1993) is the time needed to filter out one volume of the basin in question.

Assuming that phytoplankton production is the same inside and outside the water body in question, the carrying capacity clearance time, CT_K , can be related to the first two parameters:

$$CT_K \propto \frac{1}{PPT \times T}$$

As water residence time increases, phytoplankton influx from the outside will diminish, giving bivalves a greater opportunity to clear the water column. PPT and T are not independent of each other because as T decreases, the relative influence of PPT within the estuary diminishes. As PPT increases, the possibility for clearance will similarly increase. If open coastal water is relatively depleted in phytoplankton, then there will a complex interplay between water exchange from outside the estuary and phytoplankton growth within.

As mentioned, Clearance Time is probably a much more complex function of PPT , T , and other variables, as there are likely to be nonlinearities when relating clearance rates between large and small basins. Large basins (e.g., Chesapeake Bay) may have restricted circulation within the estuary and vertical stratification, making much of the phytoplankton inaccessible to bivalves on the bottom. Also, large basins probably have proportionally less water exchange with the open sea than smaller basins. Basins with relatively low primary production may find that bivalves reduce feeding rate as phytoplankton biomass falls below a threshold.

There are also, unfortunately, other parameters. For example, suitable habitat area should increase with basin size, most likely with area. If the semi-enclosed basin has a characteristic linear size scale, L , then the carrying capacity clearance time should be

$$CT_K \propto \frac{1}{L^2}$$

It is likely that larger basins have longer replenishment times: $T \propto L^2$, and therefore

$$CT_K \propto \frac{1}{T}$$

which might make *PPT* the only relevant parameter, because the effect of increasing bivalve space would be counteracted by the decreased replenishment of phytoplankton from the outside of the semi-enclosed basin.

Dame and Prins (1998) examined available data from a number of estuaries. While it is rather difficult to make effective comparisons, as localized effects (e.g., the very small oyster population in Chesapeake Bay) prevent the use of simple parameterization, they found that *T* is positively correlated with *PPT*. Large bivalve populations apparently thrive under conditions where $T < 2,400$ h and $PPT < 240$ h. My calculations suggest that there is a positive correlation between *T* and basin area, although Chesapeake Bay is off scale, perhaps owing to its large size and relatively restricted opening.

Two Connected Models

Modeling total feeding and the effects on total phytoplankton is important, but food quality is equally important to bivalves. Bivalve food quality must be described in terms of the composition of the seston, which includes both living and nonliving components. To connect bivalve functional morphology to processes affecting seston dynamics, we have constructed conceptual models to describe the dynamics of particle processing within a bivalve and within the water column. The challenge is then to connect the two systems, by theory and empirical study, to ask whether reciprocal effects are possible.

BIVALVE COMPARTMENT MODEL

Levinton et al. (1996) developed the beginnings of a compartment model for bivalve molluscs (Fig. 1a), which can be likened, with some modifications, to a box model in oceanography. In the bivalve compartment model, the input comes from the water column, with which an eventual connecting model must be made. Figure 1b shows examples of specific bivalve anatomies and their fit into the box model.

If the compartment model is a chain of reactions in equilibrium, then there should be a conservation of mass transfer from one compartment to the next. The rate of transfer from one box to the next (e.g., gill to palp) is

$$\frac{d \sum_i N_i}{dt} = \frac{\sum_i N_i}{T}$$

where N_i = the mass of particles of type *i* and *T* is the residence time of all particles in a compartment. We assume that all particles move in a single tract at the same velocity, and that the gill compartment therefore has a single residence time. This would apply to transport on the gills of *Mytilus* spp. (Ward et al. 1998a): particles are collected on the gill and transported ventrally. Alternatively, there may be some sorting within the gill, as occurs in oysters of the genus *Crassostrea* (Ward et al. 1998b) and in the zebra mussel, *Dreissena polymorpha* (Baker et al. 1998, 2000), and therefore different particle types may have differing residence times.

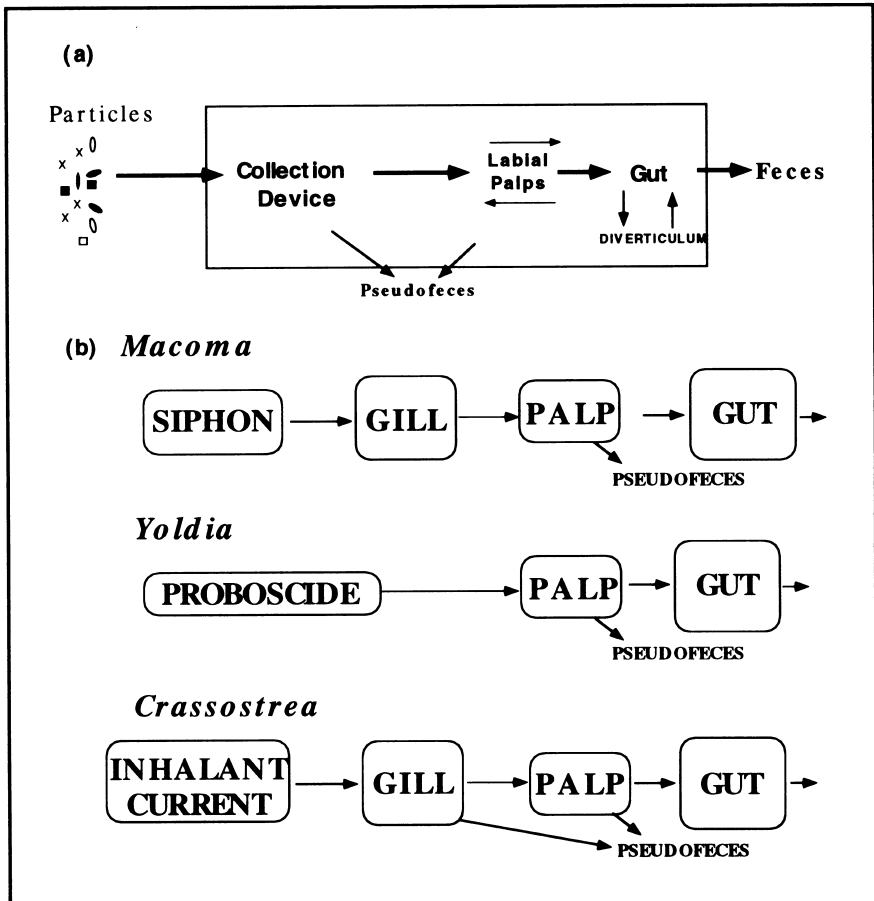


Fig. 1. (a) A bivalve compartment model, showing the important components and routes of transfer. (b) Three examples of the application of the compartment model to bivalves with differing anatomies and feeding styles (after Levinton et al. 1996).

This set of relationships would be in balance for the compartment model if the two degrees of freedom in a compartment—residence time and transfer rate to the next compartment—could be freely adjusted, or if a “downstream compartment” that is being overfilled or underfilled could exert feedback on “upstream” compartments. The simplest case would involve equality of residence times and transfer rates between compartments. Levinton et al. (1996), for example, demonstrated that residence times on gills and palps of *Macoma secta* are approximately equal, which implies that transfer rates are also equal. However, residence time in the gut is 60–240 times longer. To achieve balance with no other means implies that the mass of gut contents at steady state must be at least 60–240 times greater (or even more) than on the gills or palps (see Hylleberg & Gallucci 1975; Decho & Luoma 1991; Levinton et al. 1996). On the other hand, the equality of transfer from gills to palp and from palp to mouth suggests no feedbacks that cause cessation of particle transfer from gills to palps.

The balance model must accommodate at least two major sources of variability:

(1) Particle concentration entering the siphon may vary considerably, and individual species of suspension feeders appear to be adapted to variable particle concentrations (Iglesias et al. 1992).

(2) Food quality of the particles may vary, ranging from pure and readily digestible algae to virtually indigestible particles (Widdows et al. 1979; Berg & Newell 1986; Ward et al. 1998a,b), especially in nearshore habitats and in marsh creeks where relatively indigestible detrital particles and even toxic cells are mixed with far more digestible microorganisms.

Particle mixtures decline in food quality as the proportion of inert particles increases. Ingestion rate of the mussel *Mytilus edulis* increases with overall particle concentration, but then attains a plateau, suggesting a compensation of ingestion rate in response to high amounts of nonnutritious particles (Bayne et al. 1989). Such a plateau in ingestion may be compensated by the hard clam, *Mercenaria mercenaria*, by rejection of particles as pseudofeces or reduction of filtration rates (Bricelj & Malouf 1984). While cockles change filtration rate in response to changing particle concentrations of algae, they use production of pseudofeces to compensate for high concentrations of indigestible particles (Iglesias et al. 1992). While components of response have been studied in different species, it is likely that all suspension-feeding bivalves living in nearshore temperate environments have similar responses, with only the degree of response varying (Hawkins et al. 1998). Many nearshore bivalves can feed in the face of high particle concentrations, but the cockle *Cerastoderma edule* is particularly good at this, owing to its continual exposure to near-bottom resuspension of sediment (Navarro et al. 1998). At present it is not clear how various common bivalves can be ordered in ability to adjust to high particle loads or to select against nonnutritious particles.

The entire bivalve compartment system may be able to respond in unison to changes in seston concentration. For example, an optimal ingestion model suggests that ingestion rate should increase with increased food quality (Taghon 1981). As food quality increases (nutrients available per particle), gut throughput should increase because more food will be exposed to digestive enzymes and will therefore be absorbed. On the other hand, the cost of digestion and the maximum rate of digestion might impose limits on gut throughput (Willows 1992). If there is a unified compartment system response, then increased food quality should result in shorter gut residence times and increased transport rates on the gill and palp compartments up to the point of diminishing returns owing to the cost of digestion.

Taghon (1981) demonstrated an increased gut throughput in a benthic deposit-feeder with increased particle quality. Similarly, we have found an increased gill dorsal tract particle transport rate with increased food quality in the oyster *Crassostrea gigas* (Levinton & Ward unpublished data), and Bayne et al. (1987, 1989) found increased gut throughput with increased food concentration, which might be a surrogate for increased food quality. Cockles slow gut throughput when there is a large fraction of indigestible particles and gut residence time is minimized when nutritious food particles are available (Ibarrola et al. 1998). It may be that in these cases digestive efficiency is not limiting.

Clearance rate may also vary with food quality, although particles may often enter the mantle cavity in direct proportion to their occurrence in the water column (Baker et al. 1998; Ward et al. 1998a,b). The intake of water into the mantle cavity in bivalves does not seem to be adaptable to particle rejection. Therefore, pumping rate is the only mechanism of adjusting for total particle intake. Subsequent to entry into the mantle cavity, retention of particles depends upon mechanisms of sorting and rejection of particles.

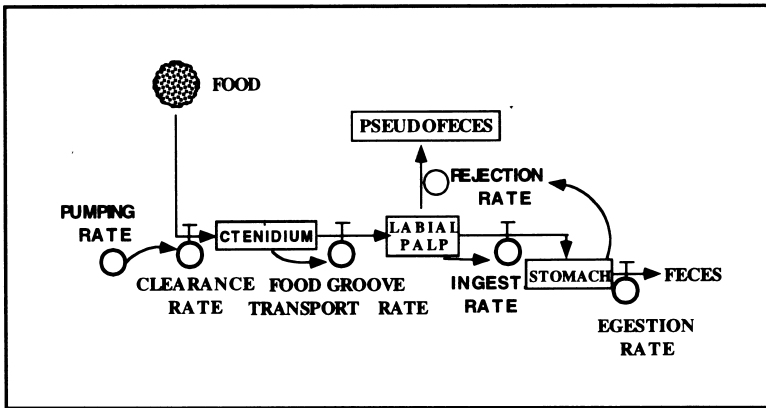


Fig. 2. The construction of a simple model of interactions in the bivalve compartment model, showing feedback loops that might affect the in between-compartment interactions.

On the other hand, changes in quantity and quality of the food supply might create imbalances among the compartments. For example, it may be relatively easy to move particles through the siphon, but handling toxic cells on the gill surfaces and ciliary tracts may be far more difficult, creating a rate-limiting step for particle processing. Similarly, retention of indigestible particles might slow digestive processes, even though these particles can be rapidly delivered to the mouth just as easily as digestible cells. Thus there is reason to believe that the variation in food quality and quantity seen in coastal waters, which minimally involves seasonal changes and strong spatial patchiness, might require adaptive responses beyond mere adjustments up and down of the entire compartmental system. This alternative model would argue that imbalances might be established that require feedback adjustments among the compartments. Thus pseudofeces rejection might work to allow a suitable throughput to the gut, but it is also possible that gut fullness or a maximum of digestive capacity provides a signal that causes the gill-palp system to reject particles as pseudofeces to differing degrees.

The transfer system inherent in bivalve compartments (Fig. 2) might be likened to a set of biochemical pathways, where threshold concentrations of a substrate may cause feedback and adjustments of the entire system (Levinton et al. 1996). Thus as the gut is overloaded, a feedback signal might be transferred to the gills and palps to reduce transfer rates. This might be accomplished by (a) shutting down incurrent or siphon activities; (b) reducing transport rates of particles collected on the gills; (c) rejecting more particles by gills and palps, so that they will not be ingested and saturate the gut. Bivalve pumping rate may change, but to a small degree, with changing particle concentration; a complete shutdown of siphon activities may occur, however, when there is no food or too high a particle concentration seems unlikely. That reductions in transport rates, in isolation from reduced pumping or increased rejection, are an option at high particle concentrations, if only because particles would accumulate on the gills and overload them. The reduced transport would only work if particles were rejected from the gills as pseudofeces. This mechanism could be employed without changing transport rates very much.

A final issue that must be taken into account is the large variation in anatomy of the compartments among bivalve species with differing gill, palp, and gut architectures. For example, gills range from organs that appear only to cleanse the mantle cavity (e.g., *Yoldia limatula*, Levinton

et al. 1996) to those that have elaborate variations in gill form, ciliary transport direction, and even direction of particle transport (e.g., oysters, Atkins 1937; Ward et al. 1994). Oysters have complex plicate gills, capable of collecting particles and transporting them in different directions. Particles may be transported in plical troughs to a basal ciliated tract where particles are then moved anteriorly in a slurry to the palp (Ward et al. 1994), or they may be transported ventrally along the plical crests, where they are moved anteriorly in a mucus-string, also to the palp. Ventrally transported particles may be rejected as pseudofeces or processed further and ingested. By contrast, *Mytilus* gills do not appear to have a sufficiently complex gill structure to have such flexibility in ctenidial particle transport, although strong selectivity is still possible on the palps (Ward et al. 1998b).

Methods

Video endoscopy was employed to make qualitative observations of particle collection and transport. For oysters and mussels, methods followed Ward et al. (1998a) and for zebra mussels methods followed Baker et al. (2000). Discrimination among particles was accomplished by means of flow cytometry (see Shumway et al. 1990). The video endoscope was employed to permit, by means of a micromanipulator, the placement of a micropipet that could withdraw particles from different locations in the mantle cavity. Methods are described in detail in Ward et al. (1998a). When detrital particles were prepared they were sieved to place them within the size range of phytoplankton cells that were fed to bivalves concurrently. We also performed depletion experiments at different particle concentrations by sequentially sampling the chamber over time (either with bivalves or control) and running the withdrawn sample through a flow cytometer or Coulter counter according to methods reported in Ward et al. (1998a,b). Using the flow cytometer, it was possible to make direct comparisons of selectivity of identical size classes, even when the range of detrital particles was found to be greater than phytoplankton cells.

Results and Discussion

AN INTERNAL CONSTRAINT WITHIN THE BIVALVE COMPARTMENT SYSTEM

As mentioned above, bivalves are exposed to changing concentrations of suspended particles, and to varying combinations of particles of differing quality. The question arises whether bivalves respond to changing particle concentrations by making adjustments within the feeding compartment system. Figure 3 demonstrates the response of the oyster *Crassostrea virginica* to prolonged feeding on *Rhodomonas lens* at concentrations of 10^4 and 10^5 particles per ml. At 10^4 particles ml^{-1} there is a slight increase in pseudofeces production over a period of 9 h. This suggests that, as a result of increasing gut fullness, the gut is signaling the gill-palp system to increase rejection of otherwise nutritious particles as pseudofeces. The response at 10^5 cells ml^{-1} demonstrates a far steeper slope with time of food exposure, suggesting that the gut is sending a signal for higher degrees of rejection.

While we mainly wish to point out the gut fullness phenomenon as an internal constraint, the bivalve response to high concentrations of cells can also have an impact on the ecosystem. If, when particle concentrations are high, more cells are rejected as pseudofeces, two ecosystem effects may occur. If bottom currents are sluggish, then rejected cells will be added to the sediment, thus enhancing biodeposition of nutrient-rich material to the benthic deposit-feeding community. Biodeposition is known to strongly affect benthic processes in fresh and salt water (Izvekova Lvova-Katchanova 1972; Tenore et al. 1982; Wisniewski 1990; Reusch et al. 1994). Alternatively, bottom

currents may be sufficient to resuspend biodeposits and restore them to the water column above (Rhoads & Young 1970). Zebra mussels, for example, efficiently remove all particles from the water column of the Hudson River nonselectively, but resuspension of biodeposits returns rejected and defecated material back to the water column above (Roditi et al. 1996; Baker et al. 1998).

AN ECOSYSTEM IMPACT UPON THE BIVALVE FEEDING-COMPARTMENT SYSTEM

Estuaries and back-bar lagoons of the eastern and southeastern United States are commonly bordered by marshes dominated by the cordgrass *Spartina alterniflora* (Redfield 1972), which develop especially well under conditions of rising sea level (Ranwell 1972). But little of the total production of *Spartina* is consumed by herbivores and most material enters detrital portions of the food web (Burkholder 1956; Odum & Smalley 1959). Salt marsh sediments often are composed of substantial amounts of detritus derived from *Spartina* (Levinton & Bianchi 1981; Levinton 1985; Lopez & Levinton 1987), suggesting that the combined processes of leaf decomposition, transport as suspended particles, and deposition dominate salt marsh systems. It follows, therefore, that both suspension and deposit feeders are exposed continually to a complex mixture of clays, living phytoplankton cells, and *Spartina* detrital particles. *Spartina* detritus is a particular challenge, because it is highly refractory for both deposit feeders and suspension feeders, as opposed to bacteria and many types of microalgae (Newell 1965; Lopez et al. 1977). While decomposing, *Spartina* detritus loses nitrogen much more rapidly than carbon, as opposed to phytoplankton detritus (Buchsbbaum et al. 1991). This material, dominated by cellulose, is nutritionally very poor. The oyster *Crassostrea virginica* can absorb only 3% of the carbon in this food; an estuary like the Choptank River (part of the Chesapeake Bay system) probably provides not more than 1% of total carbon through this route

(Crosby et al. 1989). Even the ribbed mussel, *Geukensia demissa*, which lives among salt marsh blades, can only absorb 9% of the carbon (Newell & Langdon 1990). It is not clear what proportion of particles in such an environment consist of phytoplankton cells or nonnutritive particles. This is further complicated by particles that derive from fresh and relatively digestible seaweed detritus (Levinton & McCartney 1991).

Thus, the *Spartina* estuarine and lagoonal ecosystems provide a food resource challenge to oysters, which are confronted with a large, but as of yet uncharacterized, proportion of refractory particles. This raises the question of whether oysters, which are often common in such estuarine environments, can actively select between particles that are nutritionally rich and poor. If they cannot, then all particles must enter the gut, posing a significantly different challenge. Pre-ingestive rejection involves perhaps additional investments of

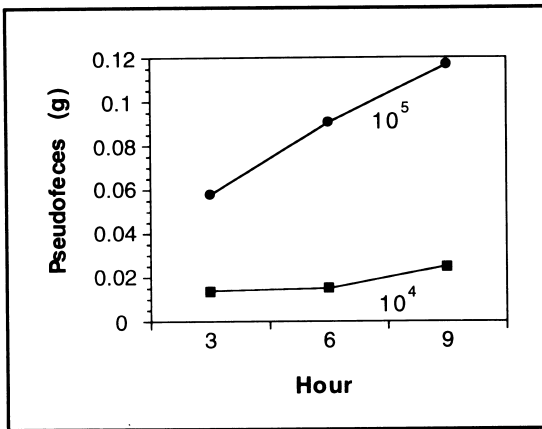


Fig. 3. Production of pseudofeces (g dry mass) by the oyster *Crassostrea virginica* after prolonged feeding at concentrations of 10^4 and 10^5 cells ml^{-1} . Note the increased slope with time at the higher food concentration. Number of replicate oysters for each treatment = 5. Data were analyzed with a repeated measures design. Pseudofecal production at 3 h was significantly different from production at 9 h ($p < 0.05$).

ciliary energy to separate and reject unsuitable *Spartina* particles, or losses of time in processing and sorting among particle types. Post-ingestive responses, however, might involve adjustments of gut transport rates, secretion of digestive enzymes, and degrees of sorting and diversion of particles into a digestive diverticulum. Previous work (Newell & Jordan 1983) demonstrates conclusively that pre-ingestive sorting can reduce the nutritive quality of the pseudofeces, in comparison with the food supply. But where does the sorting occur? Newell and Jordan suggested that the palps are the locus of sorting, which means that the gill could transport enormous quantities of material that would have to be handled by the next compartment.

To evaluate the nature of these responses, we examined the response of the oysters *Crassostrea virginica* from New York waters and *C. gigas*, cultured on rafts on San Juan Island, Washington. Both species have a plicated gill, with principal filaments that transport particles dorsally to a basal ciliated tract and ordinary filaments that transport particles either toward the basal (= dorsal) tract or ventrally toward a mucus-laden ventral tract (Fig. 4). We fed equal mixtures of aged *Spartina alterniflora* particles and cells of the red-colored flagellate *Rhodomonas lens* (Ward et al. 1998a,b). We sampled the water, basal tract, and ventral tract, and calculated an electivity index (Bayne et al. 1977), which represents the selection of *Rhodomonas* relative to *Spartina* (Fig. 4). *Rhodomonas* particles are sorted preferentially basally and are transported eventually to the mouth. *Spartina* particles by contrast are preferentially moved ventrally and are eventually moved toward the palp and are rejected as pseudofeces. The degree of selectivity was strong and suggests that sorting occurs efficiently on the gill. The palp did not participate in further sorting. These results suggest that adjustments are made before ingestion, which increases the quality of ingestive particles and increases the potential for digestive efficiency. Under other circumstances the palp may also play a role in selection. In this case, however, the gill did all of the work of selecting among particle types.

A BIVALVE FEEDING COMPARTMENT SYSTEM IMPACT UPON THE ECOSYSTEM

Presumably bivalves adjust filtration and ingestion rate, and select among different particle types to maximize nutrient uptake immediately and eventually to maximize fitness. Such behavioral adjustments, however, may affect the seston, given the intimate interaction between bivalves and shallow-water ecosystems (Dame 1993a,b). Oysters are dominant bivalves in estuaries and may have had an important effect on the seston of estuaries as large as Chesapeake Bay (Newell 1988). Unfortunately, most of our evidence concerning the controlling effect of benthic suspension-feeding bivalve grazing on nearshore ecosystems involve plausibility arguments, based upon reasonable models of grazing balanced against phytoplankton growth and mixing (Officer et al. 1982).

Combining such models with experimental introductions or removals of suspension-feeder populations would be more desirable, but this is obviously not practical, especially in the desirable form of replicate experiments in replicate estuaries. A surrogate might be so-called natural experiments, where an event has occurred in an ecosystem for which we have previously recorded survey data. For example, the introduction of the Asian clam, *Potamocorbula amurensis* (Carlton et al. 1990), caused major changes in the phytoplankton levels of San Francisco Bay. This invasion, however, was facilitated by a large reduction in salinity, which means that more than one factor might have been at work in affecting the phytoplankton. This problem often plagues such natural experiments.

The zebra mussel, *Dreissena polymorpha*, invaded North American fresh waters in the mid-1980s and formed dense benthic suspension-feeding populations with a high filtration capacity

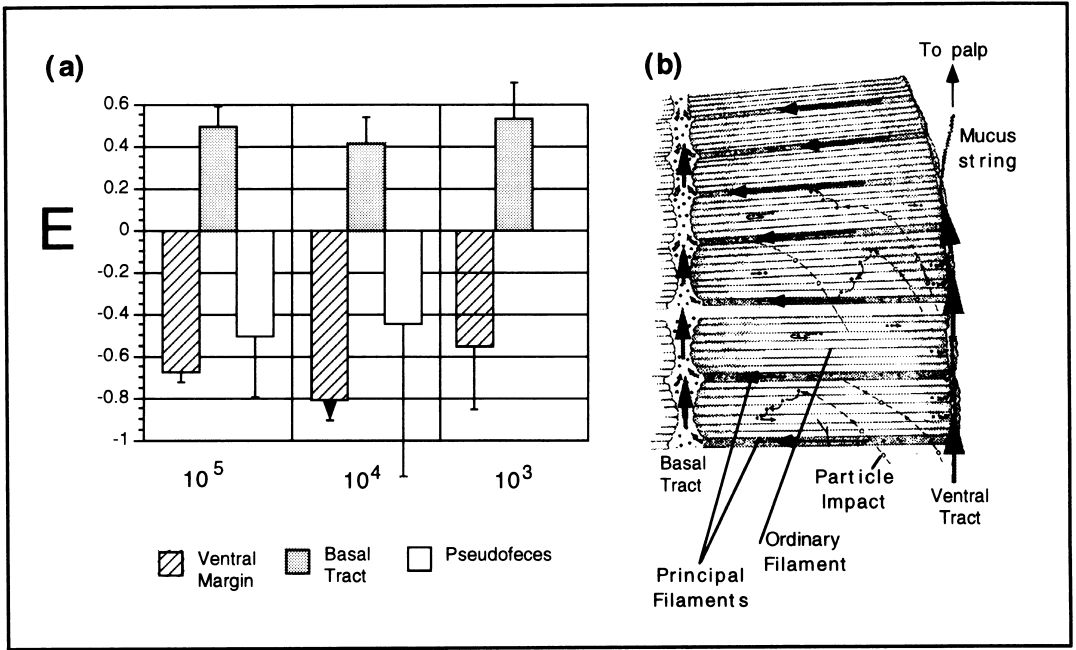


Fig. 4. Selectivity on the gills of the oyster *Crassostrea gigas*. (a) Electivity index, E , for the red-colored flagellate *Rhodomonas lens* at different cell concentrations ml^{-1} , relative to aged detritus of *Spartina alterniflora*, on the basal tract, ventral tract (= margin), and in pseudofeces, relative to food, in which the two particle types were presented in approximately equal numbers and concentrations. A positive value means that *R. lens* was enriched in the sample, relative to the food supplied (after Ward et al. 1998b). (b) Schematic of a gill lamella of *Crassostrea* with location of basal (= dorsal) and ventral marginal tract. Particles move basally mainly via slurries in the principal filaments. Ciliary movement on the ordinary filaments may be basal or ventral (after Ward et al. 1994).

(Reeders et al. 1989, 1993). Following their arrival, many water bodies experienced strong reductions in phytoplankton abundance (MacIsaac et al. 1992; Holland 1993; Leach 1993; Fahnenstiel et al. 1995).

The invasion of the Hudson River (Strayer & Smith 1993) is an interesting case, because work has been done both on the composition and abundance of the phytoplankton before and after the zebra mussel invasion in 1988 (Caraco et al. 1997). Despite the massive reduction in phytoplankton biomass in the Hudson River, water transparency increased by only 12%, owing to the persistence of nonliving particles, which dominated the seston (Caraco et al. 1997). Furthermore, dominance by cyanobacteria before the invasion has shifted to dominance by diatoms since the invasion. Thus there are a number of changes that might be related to bivalve behavior and to properties of the Hudson River ecosystem.

Baker et al. (1998, 2000) used endoscopy to examine the response of zebra mussels to exposure to mixtures of cyanobacteria (*Microcystis* sp.) formerly dominant in the Hudson River and nonliving vascular plant detritus, formed from grinding the cat-tail, *Typha*, and sieved to match the cyanobacterial cells in size. Particles were apparently trapped on the gills and transported ventrally to the gill margin. Near the margin, however, an obvious sorting occurred: *Microcystis* particles were

carried to the marginal groove, transported anteriorly to the palp and ingested, whereas *Typha* detritus was transported somewhat above the groove to the palp and rejected as pseudofeces. This would explain why nonliving vascular detrital material might not be removed from the system, especially since the vigorous bottom currents that characterize Hudson River zebra mussel habitats would resuspend the delicate pseudofeces back into the water column.

Baker et al. (1998) used flow cytometry to examine the potential for zebra mussels to select among a variety of particle types. Clearance rates were higher in the presence of *Microcystis*, which was also preferentially ingested relative to other particle types, including several diatoms and green algal species. Bastviken et al. (1998), using more traditional counting of cells, found a similar preference for *Microcystis* cells. Baker et al. (1998) found that diatoms were rejected as diffuse pseudofeces, which were readily resuspended even in still water. A combination of selective feeding and resuspension therefore explained the shift in phytoplankton composition with no accompanying change in turbidity. The relatively slower doubling time of *Microcystis* may also have contributed to their decline relative to the faster reproducing diatoms.

Is selectivity independent of the particular combinations of particle types to which the bivalves are exposed? If so, we might expect a bivalve to select a particular favored phytoplankton species relative to others, and always selectively eliminate it from the spectrum of particle types. On the other hand, selectivity might vary with the spectrum of particle type. For example, zebra mussels preferentially ingested the diatom *Cyclotella* species when paired with *Thalassiosira pseudonana* in combination with three different particle types, but there was no preferential ingestion when *Cyclotella* was paired with *Thalassiosira* only (Baker et al. 1998). This suggests that, depending upon the antecedent phytoplankton assemblage, the zebra mussel invasion might bring about different trajectories of phytoplankton community composition.

Conclusion

It is well known that dense populations of suspension feeders can affect the particle concentration of the water column, but somewhat less appreciated is that other properties, such as species composition of the phytoplankton, and routes of supply of organic matter to benthos or water column may also be affected by suspension-feeding processes. Of course suspension feeders remove particles from the water column and dense populations should draw down the seston if the water column is shallow and well mixed (e.g., Cloern et al. 1982). But responses such as rejection of particles of poor nutritive quality and the feedback effect of gut fullness on ingestion rate also apparently can have strong effects on the seston. These effects depend greatly on the character of particle rejection and the rate of resuspension of biodeposits to the water column.

The above considerations suggest that a model is required that connects individual limitations and feedbacks, as depicted by the bivalve feeding-compartment model, and their relationships to water column stability, phytoplankton reproduction, resuspension, and water retention time in the estuary. Only then will we be able to completely understand the cycling of seston in nearshore waters dominated by benthic suspension-feeding activities.

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