# GRAZING OF NATURAL PARTICULATES BY BIVALVE MOLLUSCS: A SPATIAL AND TEMPORAL PERSPECTIVE

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## INTRODUCTION

The production of suspension feeders may be limited by processes ranging from cm to km scales, and time periods from seasonal changes in temperature to tidal cycle changes in the seston flux. Field observations have shown that the processing of phytoplankton, organic detritus and inorganic particulates by shellfish beds results in kilometer scale effects on particle concentration which can be simulated by computer modelling. A four-year study (1986-1990) (Newell 1991) at four commercial mussel bottom lease sites in Maine, USA, examined oceanographic and biological processes in a variety of field experiments. The data were used to build and test mussel production models for determination of carrying capacity and optimal seeding density. Seven key factors in the benthic-pelagic coupling were studied:

- Height of the mussel feeding zone
- Fine vertical gradients (0-50 cm) in the food supply
- Variations in mussel pumping rates over tidal cycles
- Differential feeding of mussels on phytoplankton and silt particles
- Clearance of different phytoplankton species and effects of food quality on growth.
- Density-dependent growth of mussels within patches
- Spatial variations in water volume flux, and benthic boundary layer particle flux, as determined with

NATO ASI Series, Vol. G 33
Bivalve Filter Feeders
in Estuarine and Coastal Ecosystem Processes
Edited by Richard F. Dame

physical flow models forced by tide, and influenced by local bathymetry and boundary layer roughness

In addition, studies on remote sensing (LANDSAT, airborne video at 400 m) along with sea-truthing transects in a Maine estuary system suggest the estuary-scale processes of tidally-supplied diatom blooms to be a major forcing function of production of benthic filter-feeders.

In shallow, nutrient-rich bays where the hydrodynamic residence time is on the order of the water recycling time of the benthic filter-feeding biomass (Officer et al 1982), an increasing quantity of literature has suggested that benthic filter-feeders play a major role in controlling eutrophication and stabilizing estuarine ecosystems (Herman and Scholten 1990). In regions of high shellfish biomass, [e.g. 100-1500 g ADW$\cdot m^{-2}$ in intertidal wild mussel populations (Smaal 1991); 450-1900 g ADW$\cdot m^{-2}$ in Maine bottom-cultured mussels (Newell, 1990); and 800-2200 g ADW$\cdot m^{-2}$ in the Netherlands (Prins and Smaal 1990)], filtration rates of over 50 mg chl a $m^{-2}$ $h^{-1}$ may be observed (Dame and Dankers 1988; Prins and Smaal 1990). Edible species of phytoplankton such as diatoms may be consumed at high rates during the spring bloom, and high assimilation provides for an efficient transfer of energy into shellfish biomass, with an upper limit defined by the horizontal and vertical flux of food (Fréchette et al 1989) and the shellfish density distribution (Newell 1991). In less nutrient-rich oligotrophic waters such as those in Maine, U.S.A., shellfish may maximize shell gape during certain periods of the tidal cycle to improve their energy gain when resources are most available (Newell and Gallagher 1992) . In relatively dilute waters (i.e. <2 $mm^3 \cdot l^{-1}$), increased filtration rates of algal vs non-algal particles may provide an important mechanism for grazing on energy-rich components of the seston.

An understanding of the factors which control the flux and consumption of particles in shallow waters may be useful in the management of aquacultural operations, as well as in improving our understanding of the role of shellfish populations in coastal ecosystems. Due to the site-specific nature of both biological (phytoplankton) and physical (vertical flux)

processes, they are best investigated *in situ* at sites of interest. A commercial lease site (Mud Cove, Stonington, Maine, U.S.A.) provided a shallow, subtidal environment (1-5m depth) with relatively constant bathymetry and bi-directional tidal currents in which to investigate rates of particle supply and demand at a variety of temporal and spatial scales. Following a review of food items of marine bivalves, the physical factors relating to supply (settling, advection, vertical transfer), physiological factors related to shellfish production, and the effects of food quality, we present data which show how a combined oceanographic and biological approach may be used to develop site-specific models of the production of benthic suspension-feeding bivalves.

## Food items

While many studies have appeared in the literature regarding the preferential ingestion of organic over inorganic material by filter-feeding bivalve molluscs (e.g. Martin 1925; Newell and Jordan 1983; Bayne et al 1987; Navarro et al 1992; Fegley et al 1992; Stenton-Dozey and Brown 1992), few studies have been made of the specific food items of these shellfish.

In one of the earliest studies of the food of filter-feeding shellfish, Dean (1887) determined that diatoms composed over 88% of the diet of oysters (*Crassostrea virginica*) and Lotsy (1896) believed diatoms to be the sole food source of this species. Moore (1907, 1910), Kellogg (1910) and Grave (1912) all confirmed the dominant role of diatoms in the diet of oysters. Field (1911) examined the digestive tracts of 50 individual mussels (*Mytilus edulis*) and identified 29 species of diatoms and 9 species of protozoa. He also noted the importance of detritus.

Conversely, Petersen (1908) and Petersen and Jensen (1911) concluded that the essential food all bottom-feeding, filter-feeding marine invertebrates was detritus. Blegvad (1914) examined the stomach and intestinal contents of some 45 species of bivalve molluscs representing an array of habitats and feeding mechanisms and concluded that all were "without

Table 1. Organisms identified in gut contents of the mussel, *Mytilus edulis*, from the Gulf of Maine (from Newell et al 1989)

| Species | Size (µm) | Habitat* | Occurrence |
|---|---|---|---|
| Bacillariophyceae | | | |
| *Achnanthes longipes* | 60 | B | occasional |
| *Amphipora* sp. | 80 | B | occasional |
| *Amphora* spp. | 40 | B | occasional |
| *Coscinodiscus* sp. | 85 | B/P | occasional |
| *Eucampia zoodiacus* | 100 (chain) | P | occasional |
| *Leptocylindrus* sp. | 30-45 | P | occasional |
| *Licmophora* sp. | 20-56 | B | common |
| *Melosira sulcata* | 30-40 (chain) | B | common |
| *Navicula* spp. | 24-250 | B | very common |
| *Nitzschia closterium* | 70-100 | B | common |
| *Nitzschia seriata* | 100 | B | occasional |
| *Nitzschia* spp. | 10-100 | B | very common |
| *Pleurosigma* sp. | 110 | B | common |
| *Skeletonema costatum* | 15-35 (chain) | P | occasional |
| *Surirella* sp. | 10-25 | B | common |
| *Thalassiosira* spp. | 15-25 | P | very common |
| *Thalassiosira gravida* | 20 | P | occasional |
| *Thalassiosira rotula* | 60-78 (chain) | P | common |
| *Thalassiothrix nitzschioides* | 40-70 | B | common |
| unidentified pennates | 20-50 | B | very common |
| Dinophyceae | | | |
| *Dinophysis* sp. | 30 | P | occasional |
| *Dinophysis acuminata* | 50-55 | P | occasional |
| *Dinophysis acuta* | 50-65 | P | occasional |
| *Dinophysis norvegica* | 50-65 | P | occasional |
| *Dinophysis rotundata* | 35-50 | P | occasional |
| *Gonyaulax spinifera* | 25 | P | occasional |
| *Heterocapsa* sp. | 30 | P | occasional |
| *Prorocentrum micans* | 55 | P | very common |
| *Protogonyaulax tamarensis* | 35 | P | common |
| heterotrophic dinoflagellate | 50 | P | common |
| autotrophic *Peridinium* | 30-35 | P | occasional |
| dinoflagellate cysts | 35-40 | B | occasional |
| Other | | | |
| silicoflagellate strew | | | common |
| *Dictyoca* | 10-15 | P | occasional |
| *Distephanus* | 30-45 | P | occasional |
| zooplankton strew | | | common |
| detritus | | | very common |
| bacteria | | | very common |
| motile flagellates | 3-15 | | occasional |
| motile ciliates | 75-110 | | common |

*B = Benthic; P = pelagic

exception true detritus eaters" and was of the opinion that in Danish waters lamellibranchs depend entirely on detritus as feed (see also Hunt 1925). He indicated that the shellfish were able to "sort through the detritus"; however, specifics of gut analyses were not presented.

Subsequent studies confirm earlier claims regarding the importance of diatoms and other algae as food items. Hunt (1925) examined the stomach contents of over 200 individual shellfish representing over a dozen species and questioned the importance of detritus, noting that in Plymouth waters the proportion of living organisms in the stomachs of bivalves was considerable and seasonal. He further noted that, while the amount of supposed detrital material could be significant at times, the material was undoubtedly the remains of small and delicate organisms taken alive but rendered unrecognizable by the digestive process. Naviculoid diatoms were noted to be the most frequent component and he concluded that living organisms, primarily diatoms, were the most important food organisms. Martin (1925) considered nannoplankton, especially small flagellates and peridines, to constitute the main food source of oysters but acknowledged that diatoms were also important. Nelson (1947) went so far as to call *Skeletonema* "the most valuable of diatoms in New Jersey waters". While pointing out the importance of various particulates as food sources, Galtsoff (1964) noted that "organisms found in the stomach of the oyster reflect the composition of plankton and nannoplankton present in the surrounding water."

Few authors have studied the specific contents of shellfish guts in recent years and our knowledge is still very much limited to the early studies on oysters and mussels. Hummel (1985) noted that during periods of submersion the algal species composition of stomachs of *Macoma balthica* closely resembled that of the overlying water. While there was a shift in species composition during emersion (periods of deposit feeding), the resemblance to water samples remained and Hummel concluded that *Macoma* depends upon food present in the water column for the majority of its energy requirements. Newell et al (1989) identified over 38 items in the guts of mussels

(*Mytilus edulis*) in Boothbay Harbor, Maine, U.S.A. and noted that over two-thirds of the algal species identified were benthic in origin (Table 1). It was also noted that large particles (>110μm) may form a significant portion of the diet of mussels. Studies on gut contents of two species, *Placopecten magellanicus* and *Spisula solidissima* (Shumway et al 1987; unpublished) demonstrated the presence of an array of particles ranging in size from 10-350μm including algae, pollen grains, ciliates, zooplankton tests and considerable detrital material and bacteria. Benthic and pelagic algal species were common and it was concluded that the gut contents generally reflected available organisms in the immediate habitat. In a study of near-bottom seston fluxes, Muschenheim and Newell (1992) found considerable uptake of benthic diatoms and detrital carbon from the bottom 5-10cm of the water column over a Maine mussel bed.

While some species of bivalve molluscs may differentiate between organic and inorganic particles during the ingestion process, and some may preferentially digest specific particle types, the bivalve species studied thus far appear to ingest the particulate matter available to them in the overlying waters.

The presence of poorly edible, noxious, or toxic phytoplankton may reduce filtration rates of shellfish and any subsequent control of the shellfish over algal blooms. Nutrient enrichment has been cited as one of the several factors known to enhance blooms of toxic algal species (Lindahl 1983; Holligan 1985; Smayda 1989, 1990;, Smayda and White 1990; Wyatt 1990). The impacts of these blooms on filter-feeding shellfish range from decreased feeding rates to mass mortalities (Tracey 1988; see Shumway 1990 for review); further, prolonged periods of toxicity result in losses to both wild and cultured shellfisheries operations. These blooms are not limited to any specific algal group, although dinoflagellates are still the most common offenders. Blooms of *Alexandrium* and related species responsible for worldwide outbreaks of paralytic shellfish poisoning also result in mass mortalities of shellfish. Other algal species (e.g. *Gyrodinium, Gymnodinium,*

*Aureococcus, Chrysochromulina*) are responsible for an array of responses in shellfish including reduced growth and feeding, reproductive and recruitment failure and mass mortalities. Responses recorded to date are species-specific and dependent upon the shellfish and algal species involved (for specific references, see Shumway 1990, 1992; Shumway et al 1990; Shumway and Cembella 1992 and references therein). While many of these blooms are perfectly natural events, there seems little doubt that their increased frequencies are at least partially explained by increased eutrophication. The impact of these blooms on ecosystems is then further exacerbated by reduced feeding/grazing by resident shellfish.

Settling and resuspension of particles.

Sinking and floating of phytoplankton has been considered in great detail by Bienfang (1981), Hutchinson (1967), Smayda (1970) and Walsby and Reynolds (1980). These works all make reference to the number of variables associated with phytoplankton buoyancy, including: hydrodynamics of the water column; size, shape and orientation of cells; ability to form chains and protruberences such as setae; cell density; concentration of silica; and water density. Bienfang (1981) reports sinking rates of heterogeneous, temperate phytoplankton populations to range from 0.3 to 1.7m·d$^{-1}$. Smayda and Boleyn (1965) recorded sinking rates of about 1m·d$^{-1}$ for chain forming centric diatoms such as *Skeletonema costatum*.

The coflocculation of algae and silt has recently been cited as an important mechanism for the vertical transport of seston. Riebesell (1991a, 1991b) observed particles 0.1 - 3.5mm diameter (dominant size class 200-600$\mu$m) during and after the spring bloom in the southern North Sea composed primarily of algae, detrital particles and bacteria. Aggregates, defined as agglomerations >100$\mu$m diameter as determined with *in situ* photography, have a much higher settling rate (velocity of about 40m·d$^{-1}$, Verhagen, pers. comm.), than their individual constituent particles . This may increase the vertical flux to suspension feeders by 25% or more.

## Physical Factors

Food supply is a complex relationship between the volume flow per square meter at a site (e.g. $m^3 \cdot m^{-2} \cdot day^{-1}$), the vertical flow of the water, indicated by U star ($U_*$), and the size, nature and settling velocity of the particles. Limits to mussel food supply include boundary conditions at the edge of the embayment, as well as modifications to the food supply due to spatial differences in current speed, water depth, bottom roughness, mussel biomass, and mussel density distribution (aggregation). Because physical flow characteristics are site-specific, a rapid method is given (Appendix 1) for estimating volume flux based on measurements made during half a tidal cycle.

## Vertical Mixing

Since mussels in bottom culture obtain their food from the overlying water column, their food supply is limited by: transport of food through the site (horizontal advection); mixing of the food to the bottom (vertical diffusion); rate (volume filtered, $m^3 \cdot h^{-1}$ or "filtration velocity" in units of $m^{-1} \cdot h^{-1} \cdot m^{-2}$ of mussel bed); water depth (H); and height above the mussel bed from which the mussels ingest food (Fréchette et al 1989; Sankar 1991). Settling of particles is also important, especially during slack tide (see below). In the previous section, we considered volume flow of seawater over the mussel lease site as a function of the tidal current speed, U, which is controlled by the M2 tide and the local bathymetry. While the volume flow is much greater than the mussels can filter completely, their food supply is limited to the amount available to the bottom. Vertical mixing, or eddy viscosity, A, of the water in unstratified (well mixed) flows depends on the relationship:

$$A = K U_* z(1 - z/H) \qquad (1)$$

where K = von Karmen's constant 0.4; z = height above the bottom, and where:

$$U_* = U(K)/(\ln(H/Z_o)) \qquad (2)$$

where $Z_o$ = bottom roughness, or approximately 1/30 x mussel

shell length. For a review of relevant boundary-layer physics, see Fréchette et al 1989; Monismith et al 1990, and the paper by Fréchette et al, in this volume.

Mussel filtration

To develop a carrying capacity model for mussel lease sites designed to optimize seed and harvest yields, mussel growth is considered as a mass balance problem bounded by the supply of food particles and mussel demand, or volume of water filtered. Since the mussels live on the bottom, supply is more complicated than in rope culture, since current speed decreases logarithmically near the bottom. Mussel filtration pressure on the total particle spectrum is a function of the volume of water filtered by the mussels, particle concentration, gill retention efficiency, and both horizontal and vertical components of current speed. As mussel density approaches the "carrying capacity" (defined in this case as density-dependent growth due to food depletion), particle densities for mussels downstream may be reduced as much as 50% of the supply to their upstream neighbors. For example, with filtration rates of $3 l \cdot h^{-1}$, particle volumes available to mussels may be reduced from $11.8 mm^3$ to $5.7 mm^3$ inside a patch of mussels with a biomass of 1 $kg \cdot m^{-2}$. Above the volume of particles needed for a mussel to maintain a maximum gut volume (i.e. a "full stomach"), mussels will produce pseudofeces, rejecting excess particles. At higher particle densities, they may even close the valves slightly to reduce filtration rate. If pseudofeces are produced, rates of ingestion (I) may then be corrected for total particles cleared by the mussels as:

I = Volume pumped x seston concentration x (1-P)

P = Wt pseudofeces/(Wt pseudofeces + feces)

where I is ingestion, P is percent pseudofeces

Since most areas studied in Maine rarely had particle concentrations above the pseudofeces threshold for mussels, (i.e., $2.0 \times 10^7$ particles $\cdot ml^{-1}$, Foster-Smith 1975), the product of clearance rates and food concentration could be used to determine mussel demand in relation to supply. Pseudofeces

production was observed on windy days at two sites, and more frequently at the Long Cove sites, where measurements of suspended particulate matter (SPM; GFC filtered seston dried at 85°C) were over 10 mg per liter and particle concentrations were above $2.0 \times 10^7$ particles $>3\mu m \cdot l^{-1}$. Most of the occurrences of high particle concentrations in the field were in the vicinity of mudflats, during and after storms, and during the spring bloom. During calm experimental days, the Maine mussels rarely produced pseudofeces under natural particle concentrations of $0.5\text{-}2 \times 10^7$ particles$\cdot l^{-1}$.

Below the pseudofeces threshold, mussels are thought to filter at a relatively constant maximum rate and to retain all particles above 4μm at close to 100% efficiency (Møhlenberg and Riisgård, 1978) and at about 50% for particles at 2μm. Thus, the limit of mussel's filtering ability is at the approximate size of inorganic particles, microflagellates, large cyanobacteria and particles of organic detritus with attached bacteria. Below 2μm, many clay particles and bacteria pass through the gills into the exhalent water. It is noteworthy to mention that the beat frequency of the laterofrontal cirri may also regulate the size at which 100% retention occurs (in the range of 3-14μm, Jørgensen et al, 1986), and these may play a role in feeding selectivity adaptations. Mussels might possibly increase gill "leakage" to numerous inorganic particles in the 3-5μm range when presented with algal particles of slightly higher diameters (Bayne et al 1977), and gill leakage has also been noted during spawning (Newell and Thompson 1984). Variable retention efficiency in the 2-5 μm range may be an important aspect of mussel/particle interactions in the coastal zone.

In very dilute suspensions, e.g. $5 \times 10^6$ particles$\cdot l^{-1}$ $>3\mu m$ diameter, (at low tide on the 11/8/90 experiments at Mud Cove, see results) food availability was below the mussels' ability to obtain positive energy gain by active feeding at maximal shell gape, and the mussels may close for several hours, periodically sampling the water to see if conditions have improved. A few authors have mentioned a lower concentration threshold at which mussels pump actively (Thompson and Bayne

1972), but this has not been investigated thoroughly in the field. Thus, during the typical "summer crash" in food concentration in Maine, periods of the tidal cycle may be spent with prolonged shell closure. Mussels fed actively at high tide and through the ebb, until food concentrations fell, after which they closed up for 3-4 hours (see video experiments, below). Low respiration rates were also observed during periods of shell closure.

Most previously published studies on mussel feeding have used Coulter Counters which count particles within a given size range (e.g. >3$\mu$m) regardless of particle type. By comparing particle uptake rates of mussels in flow-through feeding chambers to control chambers with no mussels (i.e. Fréchette and Bourget 1985), the difference in particle concentration is multiplied by water flow rate to get rates of particle consumption. Feeding and oxygen consumption of benthic filter feeders are best investigated at the sites of interest using water pumped off the bottom (e.g. 0.5m) through experimental chambers. In a flow-through system, after Fréchette and Bourget (1985), with flow rates >250ml·min$^{-1}$ to prevent recirculation (Møhlenberg and Riisgård 1979):

Consumption (mg·h$^{-1}$) =

flow rate (l·h$^{-1}$) x (conc.$_{control}$ - conc.$_{mussel}$) (mg·l$^{-1}$)

Filtration rate (l·h$^{-1}$) = Consumption (mg·h$^{-1}$)/conc.$_{control}$(mg·l$^{-1}$)

In a flow-through efflux chamber with a stir-bar such as used in the Mud Cove field experiments, one considers $C_m$, the concentration of particles around the mussel, $C_i$, the concentration in the incoming water, and $C_o$, the concentration of the outgoing water (Hildreth and Crisp 1976). Then filtration rate is:

$$\text{Filtration rate} = \text{flow rate} \times (C_i - C_o/C_m)$$

If there is a stir bar, $C_m$ is approximately equal to $C_o$, such that filtration rate is:

$$\text{Filtration rate} = \text{flow rate} \times (C_i - C_o/C_o)$$

Determining pumping rates using the particle tracer method as described above correlates well with more direct measurements using microscopic current probes in the exhalent

siphon and laser-beam techniques (Famme et al 1986) above critical flow rates (in the 200-400 ml·min$^{-1}$ range per 45 mm mussel).

Inherent in the use of electronic particle counters (Coulter$_{TM}$) in measuring filtration rates are the assumptions:

- A 100% efficiency in clearance above a given particle size, i.e. 3µm.
- Equal clearance rates on all particles above 3µm, regardless of particle type (e.g. sediment vs algal cell).

In the absence of pseudofeces production, food consumption rates are usually determined by multiplying pumping rate by food concentration (e.g. Chl a, algal cells, SPM, POM, PON, POC, energy (joules), particle volume):

Consumption rate = filtration rate x particle concentration

Particle consumption can also be studied in closed systems, where the exponential decline in particle numbers in a well-mixed chamber is followed over time and the filtration rate is calculated according to the Coughlan (1969) method:

$$m = \frac{M \times \log_e (C_o/C_t)}{n \times t}$$

where m = filtration rate, M = volume of suspension, n = number of mussels, $C_o$ = initial concentration, $C_t$ = concentration at time, t.

Williams (1982) cautions that when filtration efficiency is less than 100%, i.e. under 5µm particle diameter for mussels, the use of the above equation will underestimate filtration rate. Particle production by mussels may also bias these types of experiments and should be investigated further. The Coughlan method was used in all the flow cytometry experiments described below.

To obtain near-natural conditions for measurements of physiological rates, techniques have been developed to enclose an area of the shellfish bed in a benthic ecosystem tunnel, BEST (Dame et al 1984; Dame and Dankers 1988; Prins and Smaal 1990), or in a flume with vertical walls (Asmus and Asmus 1991). For the tunnel,

Particle flux (mg·h$^{-1}$) = flow rate x ($C_i$ - $C_o$)

where $C_i$ = tunnel inlet; $C_o$ = tunnel outlet.

Results are easily converted to a-square meter basis by dividing volume flow ($m^3 \cdot s^{-1}$) by area ($m^2$) enclosed by the tunnel or flume, and converted into individual rates based on mussel density and biomass within the tunnel. Non-invasive techniques include the time-lapse benthic video monitor (TLBVM, Newell and Gallagher, 1992) which give an indication of pumping rates which are proportional to shell gape (Jørgensen et al 1988; Kramer et al 1989). These are useful for observing tidal variations in feeding in relation to short-time food supply dynamics, but are not as good as direct methods of particle consumption by the mussels.

Food particle (=seston) ingestion rates, forming a size-specific maximum when the mussel gut is full, may be modelled (Hawkins et al 1990) in relation to individual gut volume (indicated by gut content (GC), and gut passage time (GPT):

Ingestion rate ($mg \cdot h^{-1}$) = GC (mg)/GPT (h)

where $GC = 0.08\ X^{0.68}$; $GPT = 1.30\ X^{0.34}$; X = dry tissue weight (mg)

Thus for a bed of given biomass, the vertical flux of particles required for the mussels to maintain a maximum ingestion rate is related to the seston concentration as in Fig 1. Ingestion rate may also be modelled according to Bayne et al, (1989) as a function of particle concentration:

Ingestion rate = $IR_{max} * (1-e^{-aC})$

where $IR_{max}$ = maximum rate based on body size

a = rate at which maximum IR is approached

C = particle concentration

In the Brylinsky model (Brylinsky and Septhon 1991), ingestion rate is modelled as the lesser of the size specific maximum ingestion rate ($IR_{max}$) and the rate accounted for by somatic body size and temperature. Increases in pumping rates with temperature are due to decreased kinematic viscosity of seawater over the range of 0 - 20°C (Jørgensen et al 1990).

Due to high frequency variability in mussel feeding rates, frequent samples are needed to obtain a reasonable picture of rates at a give time, e.g. stage of the tide (Fréchette and Newell 1988, unpublished). In the Maine field feeding experiments, filtration rate was based on Coulter Counter samples (>100 can be processed per day) or extracts of

chlorophyll a (>100 can also be processed). In a few cases, direct uptake of particle volume, particle concentration, POC, PON, phytoplankton cells, POM, and SPM were determined. In the 10 flow cytometric experiments in the lab, the Coughlan method was used to determine filtration rates on chlorophyll and non-chlorophyll particles. In the September (1990) drogue experiment, the flow cytometer was also used to analyze surface and bottom water samples upstream and over a commercially seeded mussel farm (Mud Cove).

Scope for growth

Scope for growth is a useful method of obtaining an instantaneous value of a mussel's energy budget with a simplified balance, in energy equivalent terms:

Scope for growth (SFG) (cal $h^{-1}$) = (Cp x E x AE) - R

where:

Cp = particulate food ingested

E = energy content of food

AE = assimilation efficiency of food

R = respiration.

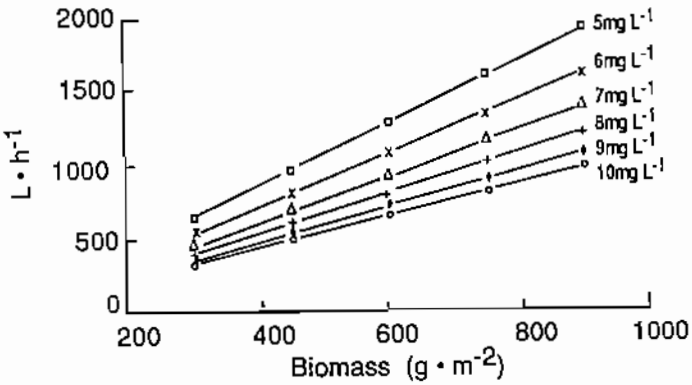


Figure 1. Volume of water required to the mussel feeding zone per square meter for maximum ingestion (Hawkins et al 1990) at ranges of shellfish biomass for varying seston concentrations.

Other terms in the mussel energy budget, such as energy lost due to excretion, are minor and are not considered here. However, since energy available for growth may also be diverted into reproductive products, scope for growth may be different from actual growth, especially in relation to meat size after spawning has taken place.

The scope for growth = zero at the minimum food required to keep the mussel alive but not growing, the so-called "maintenance ration". A reported value for mussels (Bayne et al 1989 and Widdows and Hawkins 1989) has been 4.7 joules$\cdot g^{-1} \cdot d^{-1}$ It is common for mussels to achieve 0 or negative scope for growth and actually lose meat yield during certain times of the year in the absence of spawning. This happened in Mud Cove with low food and no phytoplankton bloom in fall and winter of 1990.

Even during one tidal cycle, conditions for mussel scope for growth may change dramatically:

- At low particle concentrations mussels reduce shell gape and pumping rate causing values of particulate food ingested (Cp) to decline rapidly.
- Reduced shell gape and accompanying reduced water flow decrease oxygen diffusion and reduce mussel respiration to a fraction of the value at maximum pumping rate.

To predict average conditions for growth at any site, daily scope for growth becomes a composite of the values at all tidal cycles. Thus, for annual cycles in mussel scope for growth, the range in food available during a tidal cycle on a single day may equal the range in that parameter over an annual cycle. Similarly, wide ranges in mussel size, age, particle concentration and food quality within a lease site may result in unequal growth rates and reduced yields. Factors important in scope for growth calculations also include mussel size, mussel age, and water temperature.

A measure of a mussel's ability to grow at a given time is called the net growth efficiency, which accounts for the fact that mussels have a higher respiration rate while actively growing: Net growth efficiency = G/G+R; R = mussel respiration which reaches a maximum of about 75% during the

productive time of the year (Riisgård and Poulsen 1981) and varies with phytoplankton concentration, i.e. 19% at 3 x $10^6$ cells·$l^{-1}$ vs 61% at 26 x $10^6$ cells·$l^{-1}$ (Riisgård and Randlov 1981).

Assimilation of organic matter ingested by the mussels is most commonly investigated by the ash tracer, or Conover (1966) method. This is based on periodic collection of ambient water samples and fecal pellets during an experiment (typically 1 tidal cycle), obtaining dry weight, ash weight, and weight of organic matter by the difference. Since suspended particles may have weight of structural water in clays, as part of the dry weight (Billen 1978), there is some uncertainty in the organic weight value which is typically determined at 90°C (Bayne and Widdows 1978) and ash weight determined after 3 hours at 450°C. Comparison of lab samples at 80° and 92°C yielded no significant differences in organic weight, and ashing at 450° vs 500°C would account for only about 5% additional weight loss (Mook and Hoskin 1982), but filters become brittle close to 500°C.

Extensive studies on mussel assimilation efficiency in relation to the relative food quality (i.e. % organic matter) of the diet (Bayne and Hawkins, 1990) have shown that gross and net food absorption efficiencies improve with increasing organic content of the diet. Mussels are adapted to long-term changes in the food supply by varying gut passage time and the secretion of digestive enzymes. Bayne et al (1989) reported a regression of absorbed ration (= food ingested x assimilation efficiency) to food quality as:

$$\text{Absorbed ration (joules}\cdot h^{-1}) = 22\ (1 - e^{-2.55\ \text{POM}})$$

A maximum efficiency was obtained at POM levels of 1.9 mg $l^{-1}$.

Mussel respiration is measured in a similar way to feeding, by comparing chambers with and without mussels at known flow rates, although flow rates are reduced to about 100 ml $min^{-1}$ to see differences:

$$\text{Respiration (ml } O_2\cdot h^{-1}) = \text{flow rate x } (C_c - C_m)$$

where $C_c$ = concentration $O_2$ control chamber (ml·$l^{-1}$); $C_m$ = concentration $O_2$ mussel chamber (ml·$l^{-1}$)

In the tunnel, differences between inlet and outlet are calculated, yielding total mussel bed respiration.

Effects of body size and age

The dry tissue weight, to which most physiological functions are scaled, changes over time. As animals grow larger, rates of essential physiological processes such as feeding, oxygen consumption and assimilation, change in relation to body size, with varying exponents. Since the exponent for respiration is higher than that for feeding, smaller mussels have an energetic advantage during periods of low food supply. Mussel filtration rate per gram tissue weight increases with dry tissue weight (Møhlenberg and Riisgård 1979) as:

$$\text{Filtration rate } (l \cdot h^{-1} \cdot g^{-1}) = 7.45X^{0.66}$$

Mussel oxygen consumption is related to body size W in mg (Riisgård and Randlov 1981) as:

$$\text{Respiration rate: } (\mu l\ O_2 \cdot h^{-1}) = 1.83W^{0.75}$$

Metabolic fecal losses, or the energy required to digest the food, increase with body size W in mg, forming a significant energy drain of as much as 15% of the ingested food (Hawkins et al 1990): Metabolic fecal loss $(\mu g \cdot h^{-1}) = 1.33W^{0.64}$

Metabolic fecal loss per unit ingestion:

$$\mu g \text{ fecal loss per mg ingestion} = 21.6W^{-3}$$

where W = dry tissue weight (mg).

Dependency of the size of particles ingested by mussels on mussel size has not been investigated to this date, however large benthic diatoms and ciliated protozoa of over 100$\mu$m long were common in 30 - 60 mm mussel digestive glands (Newell et al, 1989, also Table 4).

Spawning output also increases with mussel size, such that in typical studies (e.g. Griffiths 1981; Bayne 1976), mussel reproductive output rose from about 10% of the net energy gain for 20 mm mussels to over 90% for large 70-80mm mussels. Bayne (1976) reported dry weight of gamete production related to body size as:

$$\text{Fecundity} = 73.5W^{2.79}$$

Mussel net growth efficiency decreases with mussel age due

to reduced efficiency of protein metabolism in the cells as they age (Hawkins 1991). Rates of protein turnover causing higher energy expenditure add to the reduced net energy gain in older, larger spawning adults. Similar differences in protein turnover rates may be found in mussels of different genotype (Koehn and Bayne 1989).

Effects of temperature

Because mussels are poikilotherms, chemical reactions are based on seawater temperatures and metabolic rates increase with temperature such that oxygen consumption may be modelled as (Page and Ricard 1990) as a summary of published works by Thompson (1984); Widdows et al (1979) and Widdows (1978) as:

$VO_2 = aW^b$

where: $VO_2$ = volume of oxygen consumed e.g. ml $h^{-1}$

$b = 0.782$; $a = 0.117 \times 10^{0.044T}$

W = tissue weight (g)

Similarly, temperature has been modelled in assimilation rate (Bayne 1976) as: $AE = AE(T=0) - 0.007 \times T$

AE = percent absorption efficiency

T = temperature (°C)

Shell size can be modelled both as a function of temperature controlling rates of inorganic deposition of the shell, (Almada-Villela et al 1982) and modelled by Brylinksky and Septhon (1991) as $Q_{10}$ shell = 0.1386; and whether or not there is positive scope- for-growth allowing for growth of the organic portion of the shell, e.g. in Brylinsky and Septhon (1991):

Growth Shell inorganic matter = ROI * GRSHO * QSI

where GRSHO = growth of shell organic matter

ROI = ratio organic/inorganic shell input

QSI = $Q_{10}$ shell inorganic deposition rate

Food quality

For a given volume of particulate food ingested, mussel energy gain is due to the food quality, or percent organic matter of the diet. This can be expressed as the weight of organic matter per particle volume (mg POM·$mm^{-3}$) (Bayne et al

1989), the POM/SPM ratio, the chlorophyll *a* to SPM ratio, the carbon to nitrogen ratio (C:N), or the phytoplankton carbon to total carbon at the site. These indicators of food quality reflect the proximate (protein, carbohydrate, lipid) content of the diet, and the relative dilution by inorganic sediment. In areas of high turbidity and low food quality, mussels reduce filtration rates and increase gut passage time to obtain acceptably high rates of assimilation from the generally nutritionally poor resuspended bottom sediments, and growth is reduced. The proximate composition of phytoplankton has been shown to be closely matched with bivalve tissue, and less so with detrital food sources. The importance of food quality on assimilation is discussed above.

Mussel density

The effects of mussel density, or crowding within a patch, may indirectly reduce scope for growth due to "neighbor interference" beyond the seston depletion, or food competition effects. The ability of mussels to achieve full shell gape, and pump at maximum rates, may be reduced by lateral pressure within a mussel patch, which may overcome the opening moment of the valve ligament. Workers have found a significant correlation between pumping rate and shell gape (Jørgensen et al 1988). Underwater video observations (Newell and Gallagher 1992) indicate active movements of the mussel valves over time scales of 10 minutes which illustrate competition for space within patches. Mussel mantle extension, even at reduced gape, may help to increase filtration rates by increasing the siphon area and elongating the gill axis (Jørgensen 1990). Nonetheless, density- dependent growth of mussels in bottom patches over 1 m diameter is significantly affected by conditions of local mussel density (Newell 1990). The degree to which growth interference is based on local competition for food or crowding, in relation to model results, indicates that food competition may account for most of the reduced growth observed at the lease sites in patches of over 500 mussels$\cdot m^{-2}$. The observation that beds of mussels reaches a constant biomass

(i.e. the carrying capacity) at a given site (Hosomi 1985; Newell 1990) suggests that site-specific seston flux limits production in shellfish populations.

## Field and laboratory experiments

A five year study (1986-1991) of commercial mussel bottom lease sites in Maine, U.S.A., investigated the sensitivity of mussel growth and seed to harvest yields to conditions controlled by the mussel farmer, namely:

- Seeding density (both mean density and density distribution (aggregation).
- Site selection, including current speed, seston concentration and seston quality.

Also investigated were rates of particle clearance by mussels, respiration, assimilation and growth from commercial lots of 3,000 metric tons of mussels seeded at a variety of sites during the study. A mussel growth model (Newell and Campbell 1992) was produced which predicted growth of Maine mussel populations for each lease section (~3 hectares). Optimal seeding densities, based on meat yield, varied from 300 mussels$\cdot m^{-2}$ to over 1000$\cdot m^{-2}$ at some highly productive sites. Preliminary data from this study (Newell 1991) are presented here, along with a discussion of factors on both spatial (kilometer to centimeter) and temporal (hours to annual cycles) scales.

Over 1500 water samples were taken using a horizonal alpha bottle (Grizzle 1988) of 2.2 l capacity to which a 243$\mu$m filter was added to the outlet hose to remove zooplankton. Both bottom (2-12cm off the bed) and surface (1 m below surface) samples were taken. Typical water depths were 2-4 meters during the study. Samples were taken for chlorophyll *a* fluorescence (Phinney and Yentsch 1985), weight of seston (POM, SPM, POC, PON), phytoplankton species and biovolume, particle concentration and particle volume. For phytoplankton and particle counts, only particles above 3$\mu$m were counted. Using flow cytometric analysis (see Newell et al 1989), particle sizes and types (chlorophyll vs non-chlorophyll) were

determined.

The physical and oceanographic characteristics of the site were determined by surveyor, navigational charts, and at 30m grid intervals in a 2-dimensional flow model (DUCHESS), validated with tide gauges and an electromagnetic S4 current meter moored 0.5m off the bottom or profiling. Tidal range varied from about 3m on neap tides to 4m on spring tides. All sites studied were shallow and subtidal (= 1 - 5m depth at low tide). Bottom roughness was identified with side-scan sonar and direct observations by diver. Boundary layer measurements of current speed above mussels in a flume were used to check theoretical estimates of $z_o$ and U..

Sampling for mussel filtration rate was performed using either flow-through chambers (as in Fréchette and Bourget 1985), in a so-called efflux apparatus (consists of a head tank, a multi-channel peristaltic pump and 10 individual chambers with stir bars), in a benthic ecosystem tunnel, BEST (Dame et al 1984), using a device called the benthic organic seston sampler, BOSS (Muschenheim and Newell 1992), and sampling surface and bottom waters following a drogue over a 20 hectare seeded mussel lease site (Mud Cove).

## RESULTS

### Physical factors

Boundary layer characteristics above a mussel bed were investigated in 1987 flume experiments (Geyer and Newell 1987, unpubl.), in a 17m long, 20cm deep CRL flume at Woods Hole, MA (Trowbridge et al 1989) to which a 2-meter patch of 60mm mussels was added. Laser-doppler velocimeter (LDV) profiles were made in triplicate at 6 positions along the flume upstream, over and downstream of the mussel bed. Values for U. and $Z_o$ were measured for 5 and 15 $cm \cdot s^{-1}$ flows (Table 2). Note that with a mussel shell length of approximately 60mm, a theoretical value for bottom roughness of $Z_o$ of 6/30 = 0.2cm is reasonably close to the flume run.

U. is directly proportional to current speed, U, and

decreases slightly with increasing depth. In the flume runs, a 20 cm water depth was used where the boundary layer actually extends close to the surface. At mussel grow-out sites, in 1 - 5m water depths, lower $U_*$ values are expected in relation to U. Since it is difficult to get good $U_*$ measurements in the field, some approximations must be made to get realistic values for equation (1)(see p._). While field roughness is probably higher than that determined on the basis of shell length, and mussel patch form drag would contribute to greater roughness, as a matter of course, $U_*$ can be approximated as U/16 for field mussel grow-out sites in Maine (R. Geyer, pers. commun). See Appendix 2 for a discussion of field profiles (Table I) vs estimated values of $U_*$ (Table II) at subtidal mussel farm sites in Maine.

Once $U_*$ and $z_o$ have been determined for the site, the food supply to the mussels at the bottom, e.g. a feeding zone of the bottom 2-5cm, is the result of a balance between the rates of horizontal and vertical fluxes over the entire water column. Since the vertical flux is the result of a concentration gradient above the bed, the eddy diffusivity A (equation 1 above) can be solved using a finite difference model (Fréchette et al 1989; Sankar, 1991), where A is determined by a computer and combined with values of U at a series of specified depths (assuming a logarithmic velocity profile) to balance the uptake at the bottom layer by the mussels with a decrease in the food concentration further up in the water column. Food changes on horizontal and vertical scales can be investigated as a function of two major parameters: $U_*$, as U/16, in $cm \cdot s^{-1}$, and mussel filtration velocity, $W_{flt}$, $m \cdot h^{-1}$, equivalent to $m^3$ filtered by the mussels per square meter per hour.

Table 2. Values of $U^*$ and $Z^0$ obtained from verticle profiles in a flume over a 2.0m mussel bed (Geyer and Newell, unpublished)

| RUN ($cm \cdot s^{-1}$) | $U_*$ ($cm \cdot s^{-1}$) | $Z_o$ (cm) | $r^2$ | DISTANCE FROM EDGE (m) |
|---|---|---|---|---|
| 5 | 0.75 | 0.01 | 1.00 | 0.2 |
| 5 | 0.73 | 0.18 | 0.99 | 0.8 |
| 5 | 0.66 | 0.17 | 0.99 | 1.6 |
| 15 | 1.78 | 0.16 | 0.93 | 0.2 |
| 15 | 1.61 | 0.105 | 0.99 | 0.8 |
| 15 | 1.50 | 0.134 | 0.97 | 2.2 |

As the water moves downstream, the output of the model is food concentration as a percentage of the initial concentration with a decrease in the downstream direction, and with a vertical gradient in food concentration. Site-specific model runs of food depletion (Fig.2) give direct estimates of flux to the mussel bed in which the balance between ingestion rate required for mussel growth and particle supply can be investigated. The dimensionless parameter, $W_{fil}/U_*$ can be examined at varying depths for a given shellfish biomass to find the near-bed food concentration (Figs.3,26). These model runs can then be used to determine different management scenarios on the effects of mussel seeding density on food supply at the given lease site, under a range of environmental conditions. For example, if we determine that a 50% decrease in food availability over a 200m seeded bed is the maximum allowable for a given lease site, the seeding density of mussels may be adjusted to obtain the desired results. For Mud Cove, measured values of $W_{fil}/U_*$ at 550 mussels$\cdot m^{-2}$ increased from less than 0.1 at seeding to over 0.2 after 1 growing season, to over 0.4 after two seasons (Newell 1991).

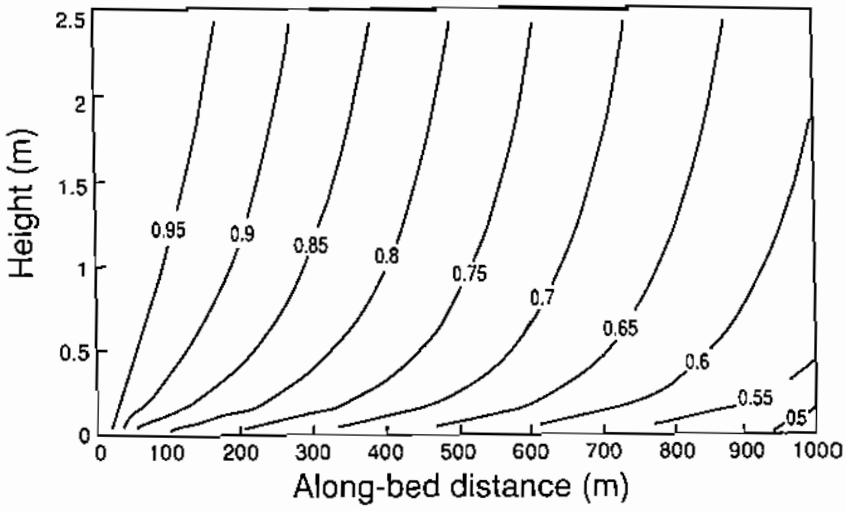


Figure 2. Output of particle contours $W_{fix}$ 1.5 m $h^{-1}$, bulk current velocity 30 cm $s^{-1}$, $z_o$ = .0025m, ingestion height = 4 cm. From Sankar, 1991 for Mud Cove simulation (Newell, 1991).

Characterization of site-specific hydrodynamics and food supply to the boundary layer

To obtain spatial resolution of food supply to a given mussel bed, the results of physical oceanographic models may be useful on length scales of 25-100 meters. By using the DUCHESS 2-dimensional current simulation model (Richardson et al 1992) for Mud Cove (Fig.4) output of volume flow and current speed agree well with the rapid method described in Appendix 1.

Placement of tidal gauges and current meter moorings, along with precision bathymetry provide sufficient data to run models for each site. Because of the strong dependence of eddy diffusivity on U. as discussed above, current speed at the particular lease section is more critical to mussel growth than volume flux per se. For example, the following comparisons were made at Mud Cove for 960 $m^2$ grid points within lease sites B, C and D taking into account local water depth and land boundaries:

Table 3. Volume flow, tidal exchange and mean current speed for three stations in Mud Cove, Stonington, Maine

| | Spring Tide | | | Neap Tide | | |
|---|---|---|---|---|---|---|
| Station | Flow ($m^3\ s^{-1}$) | Exchange | Current ($cm\ s^{-1}$) | Flow ($m^3 \cdot s^{-1}$) | Exchange | Current ($cm \cdot s^{-1}$) |
| B | 10.8 | 73% | 11.6 | 7.0 | 62% | 7.8 |
| C | 13.8 | 78% | 15.3 | 8.5 | 64% | 10.2 |
| D | 8.0 | 74% | 7.8 | 4.4 | 62% | 5.2 |

Tidal exchange, was calculated as (Dyer 1973):

$$\text{Exchange} = \frac{\text{Volume high tide} - \text{Volume low tide}}{\text{Volume high tide}}$$

Thus at station C, mussel food supply would be almost twice as great as at D, while tidal exchange only varies by 2-4% and volume flow by 25-35%. The vertical flux, proportional to U. as current divided by 16 varies from 0.95 cm $s^{-1}$ at station C at spring tides to 0.33 $cm \cdot s^{-1}$ at station D during the neap tide. In a study by Carver and Mallet (1990), supply vs demand of POM at a Nova Scotia mussel farm was based on such a tidal exchange. In areas which are not enclosed basins, however, a "flush" type of exchange is more appropriate. Following drogues in Mud Cove revealed flushing rates several times that predicted by tidal exchange. Thus, the use of current speed as an indicator of both horizontal and vertical flux of food is warranted at that site.

Once current speed is determined for the area of interest, a logarithmic profile of speed vs depth (equation 2 above) can be used to predict vertical variations in current speed. Diver observations of $z_o$ ranged from 0.3cm to 0.6cm in mussel hummocks (Newell, 1991). The effects of increased roughness (ranges $z_o$ = 0.001 - 0.003cm investigated) or ingestion height of mussels (1.5 to 5cm investigated) on near bed food concentration were, however, small in model simulations relative to differences in water depth, mussel filtration velocity, or current speed.

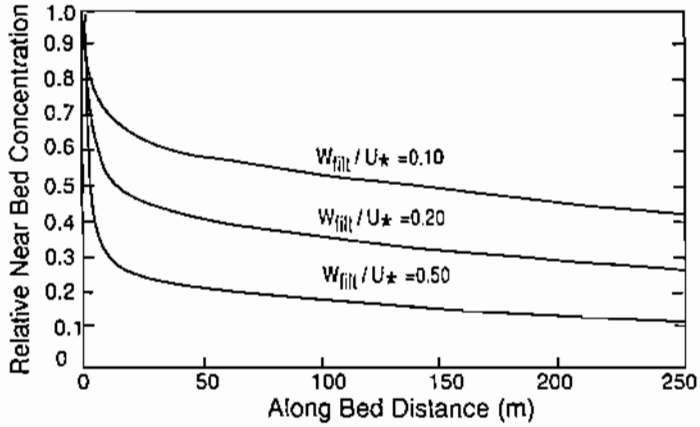


Figure 3. Relative near-bed food concentration in water depth of 2 meters in relation to dimensionless parameter, $W_{fall}/U^*$. (Sankar 1991).

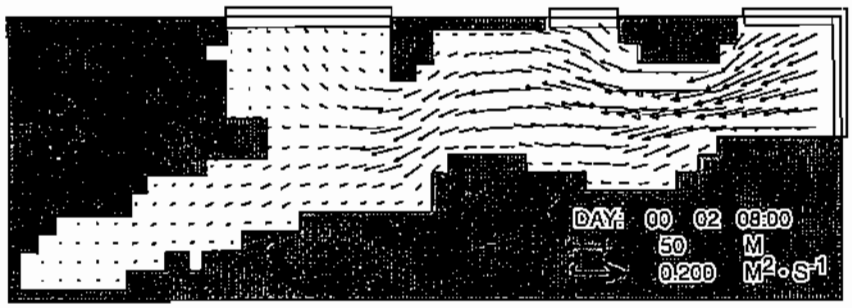


Figure 4. Output of DUCHESS current simulation model for 35 m grid in Mud Cove lease area on the flood tide. Grid mesh size is 31 meters. (Newell and Richardson, in preparation)

Settling and resuspension

Flocs from 0.1 to 2mm diameter were observed frequently at high tide at the Mud Cove site during the video experiments (see below) and near the peak of the spring phytoplankton bloom, but were not present in pre-filtered coulter counter

samples. Whether the flocs break up upon entry into the mussel mantle cavity is unknown at this time. Settling rates on the order of 10 - 20 $m \cdot d^{-1}$ are considered realistic, and indicate the importance of flocs in vertical supply of food during certain times of the year. Thus, algae advected into a lease site 3m off the bottom at high tide would be able to settle to the bottom between high water and mid-ebb tide. Settling of particles is more important at low-current sites, such as Webb Cove and Roque Island, Maine with low U. values of about 0.15 $cm \cdot s^{-1}$.

Due to the high abundance of benthic diatoms and associated high values of chlorophyll *a* in the sediments adjacent to mussel patches (Table 6), any resuspension could result in delivery of nutritionally significant benthic diatom biomass and detrital carbon to the mussel bed. In a study in Nova Scotia (Grant et al 1986) with comparable U. values to Mud Cove, sediments exported 0.12 mg chl $a \cdot h^{-1} \cdot m^2$. It was necessary to include resuspension in a mussel production model (Newell and Campbell 1992) to match observed growth with food supply. In a field investigation of seston consumption by a continuous wild bed of mussels (Muschenheim and Newell 1992), high rates of uptake were noted of benthic diatoms (*Nitzschia* and *Pleurosigma*) from the bottom 5 to 10cm of the water column. Investigations of the current or waves required for the resuspension of phytobenthos might shed some light on the availability of this nearby food resource. The "phytobenthos garden" in the vicinity of shellfish biodeposits may be an important factor in the carrying capacity of embayments for shellfish culture.

Table 3. Characteristics of surface sediment in vicinity of mussel patches at Mud Cove, Stonington. Surface sediment (1-2 cm) sampled by diver.

| DATE | N | CHLOROPHYLL ($\mu g \cdot cm^{-2}$) | CARBON ($\mu g \cdot cm^{-2}$) | NITROGEN ($\mu g \cdot cm^{-2}$) | PHYTOPLANKTON ($cells \cdot cm^{-2}$) |
|---|---|---|---|---|---|
| 3/22/91 | 6 | 9.9 | 2927 | 399 | - |
| 11/9/90 | 2 | - | 1917 | 272 | 238,840 |

Kilometer scale studies of seston availability

In a study of the use of aerial and satellite remote sensing for assessing bivalve shellfish aquaculture sites (Campbell et al 1991), a transect was made in September, 1989 in an estuary in Maine, U.S.A. (Frenchman's Bay, Hancock County), Fig.5, while a Landsat photograph, and aerial videos were taken at 3,000, 1,600 and 900m during high and low tide.

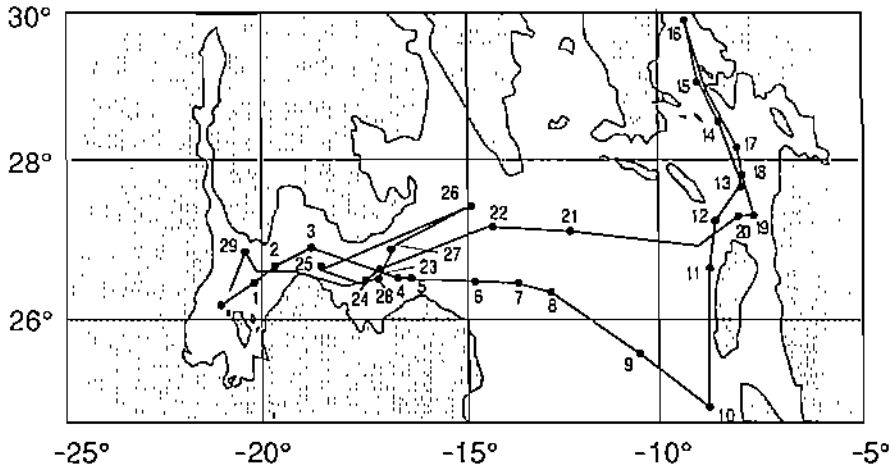


Figure 5. Map of study area, Frenchman's Bay, Maine showing boat's track and location of the sampling stations.

*In-vivo* fluorescence, temperature, and surface (-1.0m) water samples were taken along an ocean transect (Fig.6).

Results indicate higher chlorophyll in the mouth of the estuary than in the shallow bay at low tide. The phytoplankton are advected into shallow water on the flood tide (compare outgoing transect at low tide, solid line, to incoming transect, dashed line, at high tide, Fig.6). At low tide, phytoplankton cell counts increased dramatically toward the mouth of the estuary (Fig.7), and at the end of the low tide transect into Flander's Bay cell numbers declined in shallow water (Fig.7). The transect data indicate that at about 14-18'N, 68'W a bloom of *Rhizosolenia delicatula* at the mouth of Mt. Desert Narrows and Flander's Bay was a source area of phytoplankton for the nearby embayments, associated with probable upwelling at Googin's Ledge and Half-tide ledge. Refinement of air-borne video sensors holds great promise in tracking these blooms in shallow coastal areas. With the hypothesis of tidal transport of seston into coastal embayments, the effects of shellfish beds on food availability in the boundary layer were studied *in-situ* with the drogue experiments.

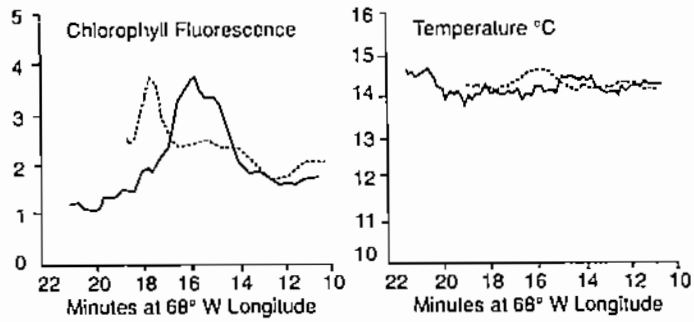


Figure 6. Outgoing (solid) and incoming (dashed) transects of chlorophyll fluorescence and temperature on September 6, 1989. Outgoing was at low tide and incoming was at high tide.

Within embayments: drogue experiments

To examine depletion of seston above mussel beds, it is important to follow the same water mass across an area of known

mussel density to reduce error associated with short term (i.e. 15 minute) variability in seston concentration. A weighted drogue at approximately mid-depth with a high cross-sectional area and surface buoy were followed at various positions along the site of interest. At Mud Cove, where 1,000mt of mussels were seeded at an average density of about 500·$m^{-2}$, the drogue was followed over the seeded beds, and water grab samples were taken (Fig. 8) relative to stations along the seeded mussel plots.

Stations were determined as: Upstream (at flood tide, upstream of station B, at ebb tide upstream of station E); stations B to C (350m); stations C to D (200m); stations D to E (275m); surface (1 m below top of water); and bottom (horizontal alpha bottle, effectively the bottom 2-12cm).

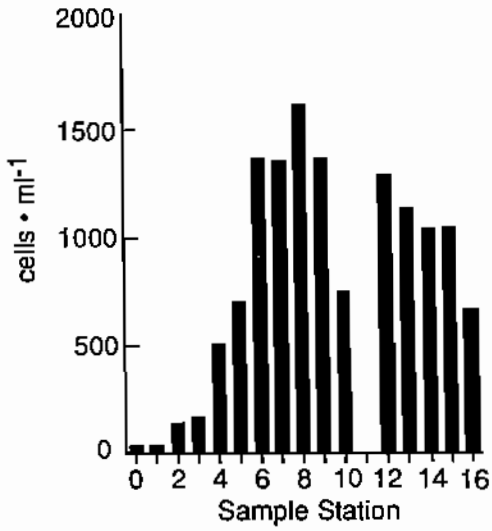


Figure 7. Concentrations of *Rhizosolenia delicatula* (cells $ml^{-1}$) surface waters along cruise out of Mt. Desert Narrows (stations 1-10) and into Flander's Bay (stations 12-16) on September 6, 1989. Outgoing transect (stations 1-16) was made at low tide and incoming transect was made around high tide.

Drogue experiments were performed during June, July, August and September, 1990, when mean mussel biomass at Mud Cove was 200-500 g dry wt·$m^{-2}$. Drogue positions were compared with current speed and direction data. Since the S4 current meter was 0.5 m off the bottom, it underestimated bulk current speeds. On August 8, 1990, measured speed by the drogue was 15cm·$s^{-1}$ vs 10.25 measured by the S4. In most vertical profiles at the site in water depth of 2-4m, current speed at 0.5m depth x 1.2 = bulk current. Drogues could only be used on relatively calm days, for a 2-layered flow was observed with strong NW winds on the floodtide. Since the water was partially stratified during the summer, (in some cases, surface water was 2°C warmer than water at 3m depth) comparisons of surface vs bottom concentrations should be made with caution.

The concentration of seston was measured in surface and bottom waters alongside a moving drogue over tidal cycles (in July, August and September, 1990). The decline in POM concentration across the lease is striking on both the flood and the ebb tides (Figs.9 and 10).

Over a tidal cycle, at station D, POM concentration at surface and bottom waters suggests tidally transported POM imported to the lease in the surface waters at high tide, which settles and reaches the bottom at ebb tide (Fig.11). These results go along with conclusions reached with the video experiments, which show maximal shell gape and feeding activity during high and ebb tides at Mud Cove (Newell and Gallagher 1992).

On September 24, 1990, samples were also taken for phytoplankton carbon from settled biovolumes of phytoplankton, and flow cytometric (FCM) characterization of particle size and type (chlorophyll vs non-chlorophyll). Since the FCM samples had to be prefiltered at 80μm, the results on the larger phytoplankton chains should be viewed with caution. Chlorophyll a on grab samples declined from 2.1 to 1.4μg $l^{-1}$ from Stations B -D on the flood tide. Phytoplankton carbon declined from 79.3μg at station B to 27.9μg at station D, a 283% decline (Fig.12). Diatom cell counts dropped the greatest in bottom water samples, while surface phytoplankton were relatively unchanged (Fig.13).

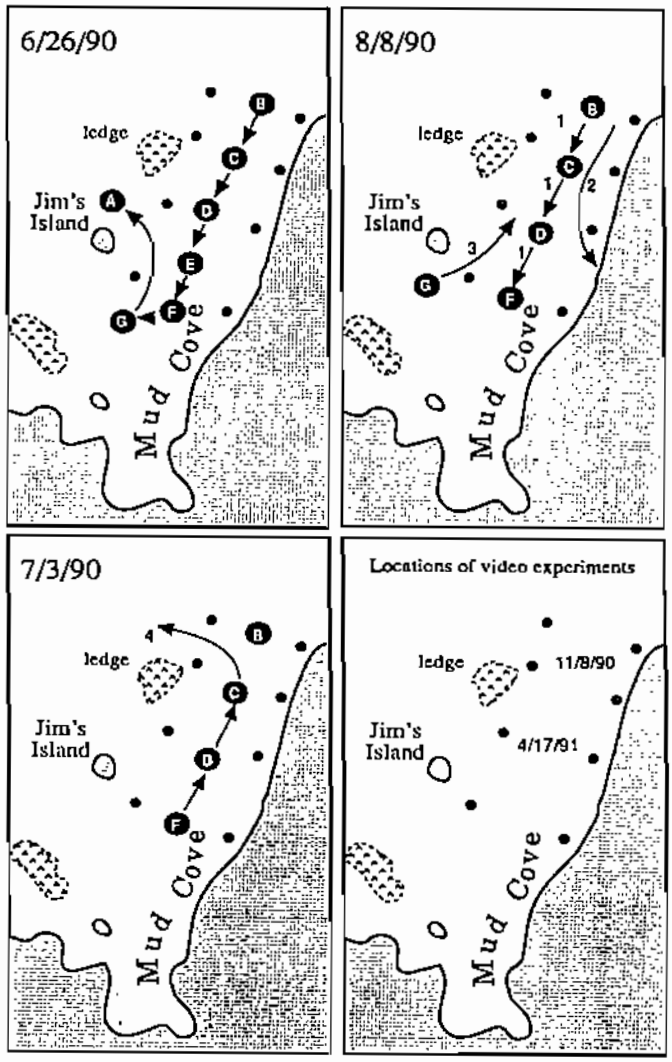


Figure 8. Location of drogue paths at Mud Cove mussel lease site on four sampling dates (see also Fig. 3) and location of underwater video experiments. Black dots are seafarm corner buoys. Water depth is approximately 1m at low tide with a 3m average tide.

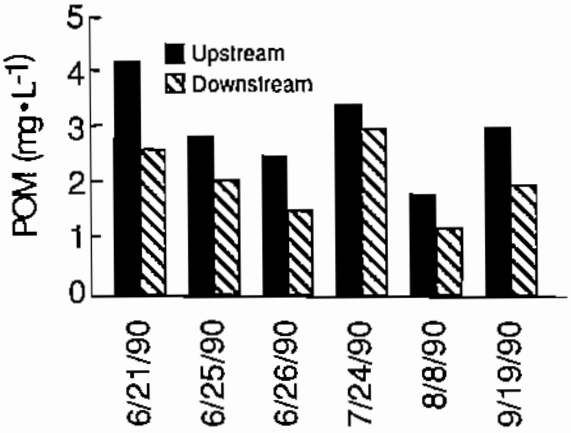


Figure 9. Change in POM across Mud Cove mussel lease on flood tides from grab samples obtained while following a drogue. Bottom water samples.

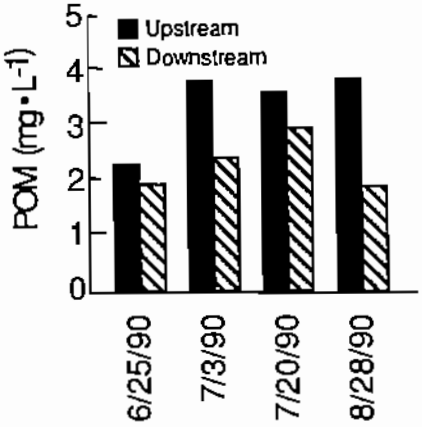


Figure 10. Change in POM across Mud Cove mussel lease on ebb tides from grab samples obtained while following a drogue. Bottom water samples.

The flow cytometer counts of particle concentration and particle type (non-fluorescent, silt particle vs fluorescent

algal cell) from surface and bottom samples (Figs.14 and 15) indicate mussels cleared 30-50% of both algal and silt particles in the 5-17μm particle size range from bottom waters, but clearance was lower in the 3-5μm range (under 10%). Other workers have noted mussel gill "leakage" to particles under 5μm (see Review Section). The ratio of upstream to downstream particle concentrations in relation to particle size and type (Fig.15) supports this hypothesis. Unfiltered samples (for phytoplankton direct counts) showed more dramatic declines in total phytoplankton cells than the flow cytometer counts due to prefiltering prior to analysis (removing larger plankton chains, e.g. *Chaetoceros sociale*).

Small-scale (cm) vertical gradients in the food supply

Problems in vertical flux may be investigated by examining the fine vertical gradients of suspended food near the bottom of mussel growing areas. It is difficult to sample natural

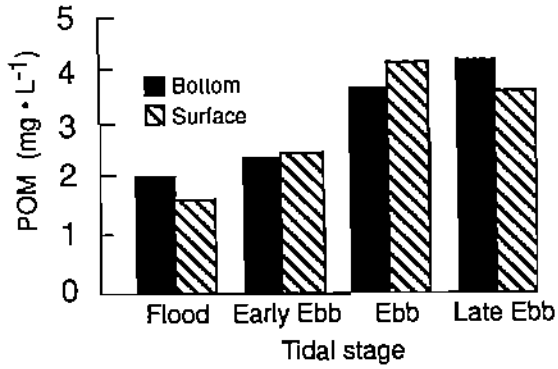


Figure 11. POM at station D, Mud Cove monitored over a tidal cycle 9/24/90.

gradients without a special device, such as the Benthic Organic Seston Sampler (BOSS), which gives duplicate water samples at heights 5-50cm off the bottom at 5 cm intervals (Muschenheim and Newell 1992). A continuous, single-layered mussel bed in Frenchman's Bay, Maine was investigated by BOSS sampling at 2

locations. Upstream of the site, about 20 meters before the mussel bed and over the mussel bed 22 meters from the upstream edge of the bed.

The current was monitored continuously with the S4, and was nearly continuous in speed (9.8 cm·s$^{-1}$) and direction during

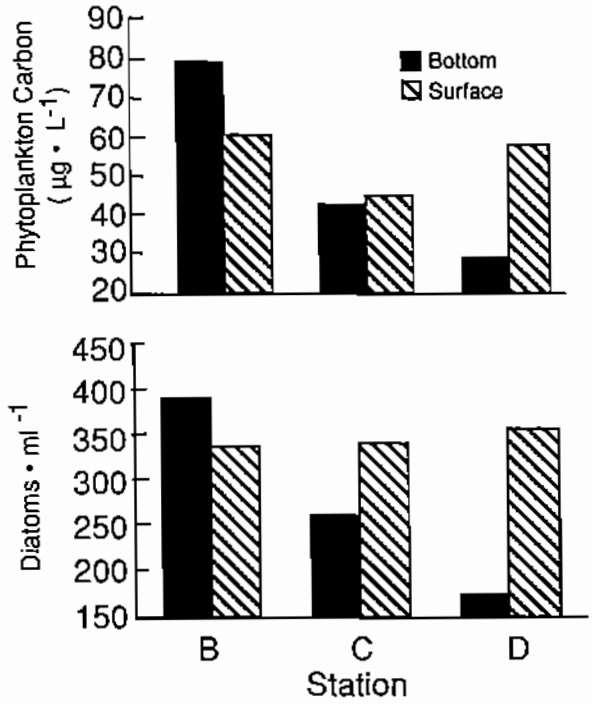


Figure 12. Phytoplankton carbon from grab samples following a drogue in Mud Cove on the flood tide, 9/24/90. Values obtained from direct measurements of phytoplankton cell volume and carbon to biovolume conversions in the literature.

Figure 13. Reduction in numbers of diatoms along drogue path in Mud Cove for bottom and surface samples, flood tide, 9/24/90.

the BOSS deployments. Water density between surface (-0.5m) and bottom (4m) varied less than 0.41%. The upstream samples acted as controls for the effects of mussels on particle concentration in the near-bottom waters. Simultaneous measurements of current speed and mussel pumping rates were used to investigate the feeding zone and filtration capabilities of a productive, high biomass mussel bed. Observations of predicted vs observed organic carbon were also compared with a finite difference model (Fréchette et al 1989; Geyer, pers. commun).

The results show that upstream of the mussel bed, bottom (0-5cm) waters are enriched in benthic diatoms and organic detritus, forming an enhanced food supply to mussels living "on the edge" (Fig.16). Mussels downstream from the edge of the bed rely on surface water for a quantitatively and qualitatively different diet, the flux rate of which limits mussel biomass. Depletion of nearly 50% of the phytoplankton in the mussel feeding zone was noted in the field experiments, indicating a significant refiltering of the water close to the bottom. Calculation of volume flux of water, $Q_f$ relative to the pumping capability of the mussel bed, $Q_m$:

$$Q_m \cdot m^{-2} \; / \; Q_f \cdot m^{-2} \; = \; 1$$

resulted in calculations of the feeding zone of mussels (Fig.17).

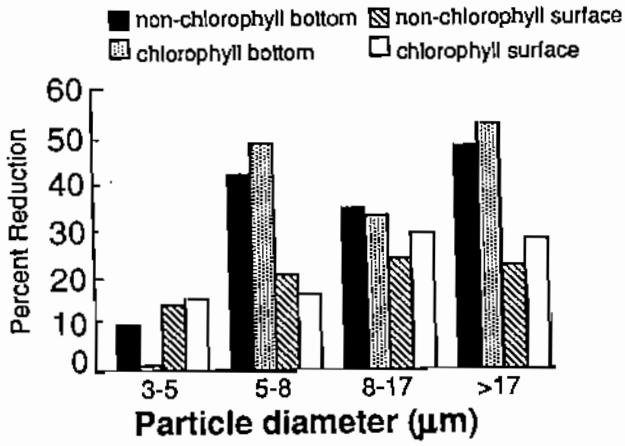


Figure 14. Percent reduction of particles (station B to D) along drogue path 9/24/90 in Mud Cove.

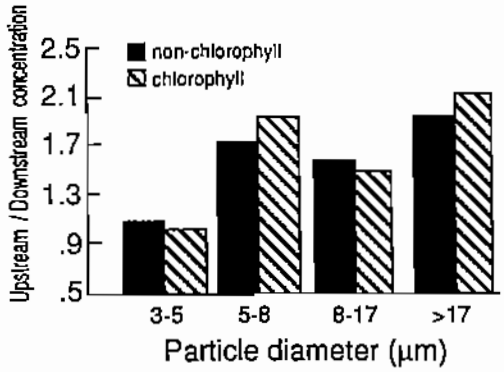


Figure 15. Mud Cove flood tide drogue station B to D 9/24/90, relative concentration of chlorophyll and non-chlorophyll particles by particle size as determined by flow cytometry.

Due to difficulties in obtaining detailed velocity profiles in the field concurrent with measurements in fine vertical gradients in the food supply, sampling with the BOSS has its limitations. Further work is needed in extrapolating fine vertical current gradients obtained from laboratory studies in depth-limited flumes to representative field environments at water depths of several meters.

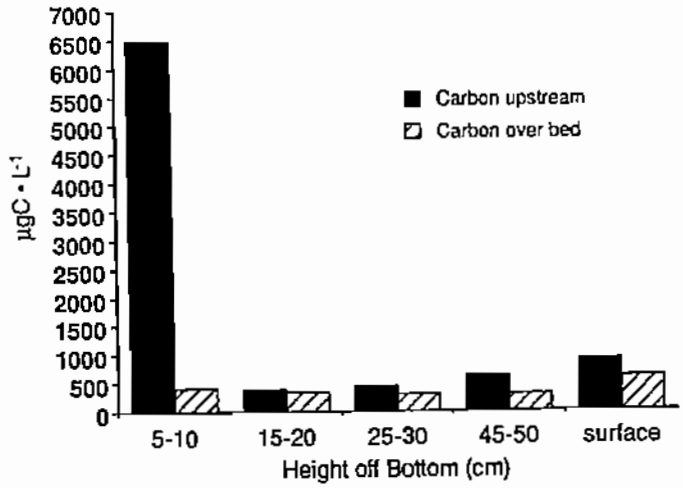


Figure 16. Particulate organic carbon from upstream and above a continuous 22 m mussel bed in 9/89 (Muschenheim and Newell 1992).

The importance of particle selection below the pseudofeces threshold: flow cytometry experiments

In 1987, mussel feeding on natural particulates at lease sites at Ray Point, Camp Island and Webb Cove was investigated using a flow cytometer (see Cucci et al 1989), a device which can measure both particle size and the nature (chlorophyll vs non-chlorophyll) of particles mussels upon which mussels are feeding (e.g. over 3μm diameter). At the study sites in June, 1987, about 15-30% of the particles were fluorescent (chlorophyll-containing). Mussel feeding studies at natural seston levels (1-2 x $10^4$ particles·$ml^{-1}$) indicated approximately 40% higher clearance rates of phytoplankton cells than silt particles at 5 of the 6 sites (Newell et al 1989). From 1989-

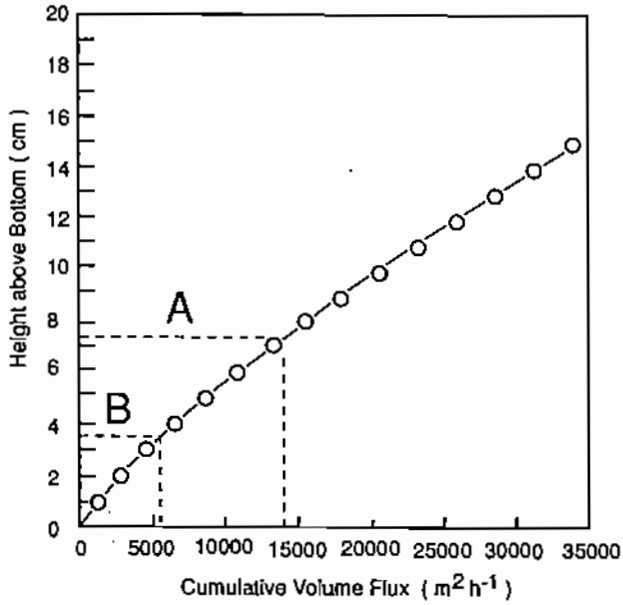


Figure 17. Hourly volume equivalent pumped by the mussels (Region A) and hourly volume equivalent filtered if significant refiltration occurs (Region B) (Muschenheim and Newell 1992).

1991, the effects of particle concentration and food quality (% particles phyto-plankton) were further investigated in two similar experiments using 1 x $10^4$ and 2 x $10^4$ particles·$ml^{-1}$ with varying food quality (Newell and Shumway 1991). Finally, an

experiment was performed sampling water from the mussel excurrent siphon to examine possible bias in the data due to particle production by mussels.

The experiments using field water samples are reported in Newell et al. (1989), and data from June 2 and June 9, 1987, are included in the results presented here. Experiments performed in 1989-1991 used Boothbay Harbor water to which ashed mudflat silt, 0.45μm filtered seawater, or cultured algae were added to obtain the following conditions (Fig.18):

| Dates | Particle concentration (number·ml$^{-1}$) | % Phytoplankton |
|---|---|---|
| 11/28 - 12/1/89 | 8-10,000 | 18-35% |
| 9/25 - 9/28/90 | 20,000 | 10-25% |

The 11/28/89 - 12/1/89 experiments at approximately particle concentrations of 1 x $10^4$ particles·ml$^{-1}$ and the 9/24/90 - 9/28/90 experiments at concentrations of 2 x $10^4$ particles·ml$^{-1}$ (Fig.18)
showed that mussels feed at higher rates on algal particles at

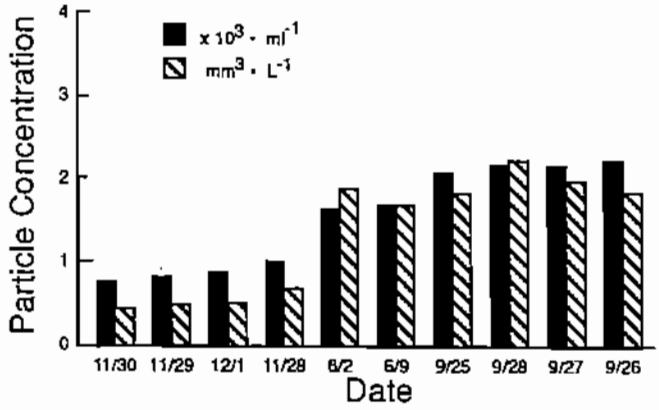


Figure 18. Control particle concentrations (particles ml$^{-1}$ x $10^3$ or mm$^3$ l$^{-1}$) for flow cytometry experiments.

low concentrations (10,000 particles·ml$^{-1}$) but lose their ability to remove phytoplankton selectively from silt particles at higher concentrations (20,000 particles·ml$^{-1}$), at about the pseudofeces threshold where sorting occurs on the labial palps. Differences in filtration rate on chlorophyll and non-chlorophyll particles (Fig.19), along with t-tests of differences in clearance rate due to particle type (Table 5) indicate the importance of selection in relatively clear, non-turbid waters. If selection is occurring, preferential consumption of algae is not indicated using a standard Coulter Counter unless a particular bloom can be identified by its particle size. For example, with 75% silt par-ticles and 25% algal cells at cell concentrations of 1 x $10^8$ l$^{-1}$, mussels may be seen to filter 2 l·h$^{-1}$ while they are actually feeding at a rate of 4 l·h$^{-1}$ on algal cells and 1.5 l·h$^{-1}$ on the silt particles (see Newell et al 1989). In the feeding experiments, 40% higher feeding rates on algal cells have been noted with particle concentrations at 10-20 x $10^6$ particles·l$^{-1}$.Thus, energy gain estimated with the Coulter Counter would be 30-40% less than observed due to selection. These experiments demonstrate a possibly significant factor controlling ingestion of food particles. The results indicate that at normal food levels, 1-2 x $10^7$ particles·l$^{-1}$, the mussels pump at a maximum rate and ingestion rate is determined by food concentration and quality (Newell et al 1989). Higher clearance rates on identically-sized glass coated beads treated with and without algal extracts (Ward and Targett 1989) suggest a chemical cue involved in particle selection prior to ingestion below the pseudofeces threshold. If mussels selectively retain algal particles and leave sediment particles of the same size in suspension, ingestion of organic-rich food particles is greater than expected by a model of mussel particle retention which is independent of food concentration below the pseudofeces threshold. Above the pseudofeces threshold, mussels may also select algal over inorganic particles on the labial palps, rejecting a proportionately higher percent of silt in the pseudofeces (Kiørboe and Møhlenberg, 1981). This results in a model of particle selection for mussels (Table 5) which is

maximum between particle concentrations required the initiation

Table 4. Significance of differences in filtration rate (chlorophyll - non-chlorophyll) for each feeding trial.

| Date | Significance level (t-test) |
|---|---|
| 11/28/89 | 0.02 |
| 11/29/89 | 0.01 |
| 11/30/89 | 0.005 |
| 12/01/89 | 0.05 |
| 06/02/87 | 0.05 |
| 06/09/87 | NS |
| 09/25/90 | NS |
| 09/26/90 | NS |
| 09/27/90 | NS |
| 09/28/90 | NS |

of feeding to the pseudofeces threshold. The mechanism behind the differential retention of algal particles over silt should be investigated further. This has a significant effect on the ability of mussels to obtain high quality food in relatively clear waters, but also results in greater competition for food quality at the lease site. The results also explain the ability of mussels to sustain high energy gain in clear waters.

Table 5. Conceptual view of algal selection by *Mytilus edulis* in relation to ambient seston levels.

| Particle Conc.x $10^6 l^{-1}$ | Filtration | Selection of Algae |
|---|---|---|
| <5 | low | some |
| 8-20 | maximum | 20-50% |
| >20 | reducing | on palps |

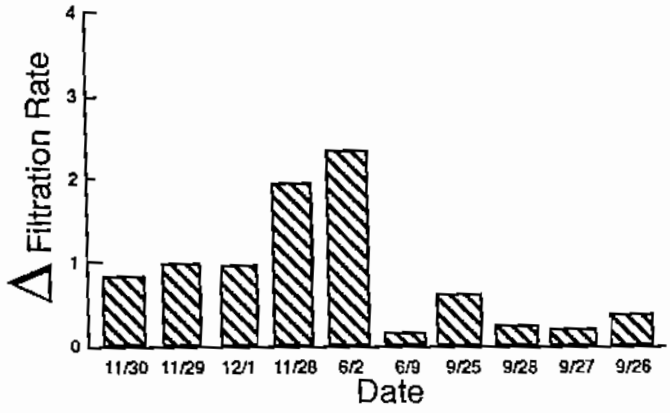


Figure 19. Filtration rate differences: filtration rate on chlorophyll - filtration rate non-chlorophyll particles.

Future models of shellfish control over eutrophication should consider mussel feeding rates not as a simple product of non-selective particle clearance and food concentration, but as modified by enhanced filtration of algal cells in relatively non-turbid waters (0.5-1.5 x $10^7$ particles$\cdot l^{-1}$, particle volume 0.5 - 1.5 $mm^3 \cdot l^{-1}$).

Tunnel experiments

The role of filter-feeders in removing suspended particles (seston), and effects on chemical fluxes (especially oxygen and ammonia) is best investigated *in situ*, preferably in an undisturbed bed composed of the shellfish and associated flora and fauna. A benthic ecosystem tunnel (BEST) was developed by Richard Dame et al (1984), which utilizes a 10m long Plexiglass tunnel which is installed over the bed of filter-feeders parallel to tidal flow. The tunnel has been used by workers in the Netherlands to investigate the role of mussel beds in their ecosystem (Prins and Smaal 1990; Dame and Dankers 1988), and is currently being used in France to study uptake rates of bottom cultured oysters. In this study (see Fig.20), a total of seven 1.2 meter sections (8.4 m long) of the original BEST were

obtained from Dr. Richard Dame of Coastal Carolina College, South

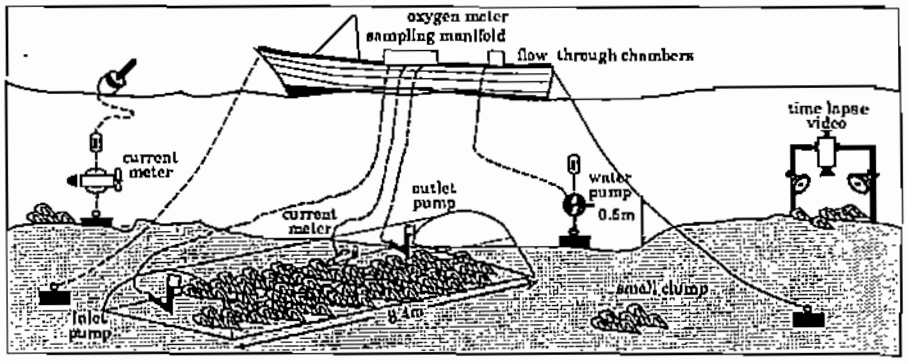


Figure 20. Experimental set-up for April 17, 1991 tunnel experiments in conjunction with underwater video at Mud Cove.

Carolina. A Marsh-McBirney flow meter was attached to the center of the chamber to measure water flow ($cm \cdot s^{-1}$) at mid-depth and two battery driven centrifugal Rule pumps were used to pump water samples from 0.5m in from the inlet, and 0.5m in from the outlet of the tunnel, respectively. Since comparisons between inlet and outlet water can be made only when the tide is running, the tunnel was installed by diver at low tide, samples were made on the flood and ebb tide, and the tunnel was removed at the second low tide. After removal of the tunnel, 8 x 0.61 $m^2$ cores were made by diver, and mussel biomass, density and mean size were determined. Since a high density mussel bed was needed for tunnel experiments, samples were also taken of lower density mussel patches from the same seed cohort near the tunnel site.

Particle flux was calculated as:

Flux ($mg \cdot h^{-1}$) = Flow rate ($l \cdot h^{-1}$) * ($mg \cdot l^{-1}$ (inlet-outlet))

Results may be presented on a square meter basis by dividing volume flow ($m^3 \cdot s^{-1}$) by area ($m^2$) enclosed by the tunnel between the inlet and outlet pumps. Mussel biomass (g dry tissue $\cdot m^{-2}$) and density (number of mussels $\cdot m^{-2}$) can be used to calculate rates of particle removal per individual mussel, and size to

weight exponents adjusted accordingly. For the April 17,1991 run at the Mud Cove lease site in Maine (see Fig.20), the specifications listed for the tunnel experiments are given in Appendix 3. At sampling times during the April 17, 1991 experiment, volume fluxes over the mussels in the tunnel (Appendix 3) were about 10-13 $m^3 \cdot h^{-1}$. Simultaneous with the tunnel experiment, a time-lapse benthic video monitor recorded shell gape of 37 mussels at 2 second intervals every ten minutes over 1.5 tidal cycles (Newell and Gallagher, in preparation). Mussels were also placed in flow-though efflux chambers on the moored vessel and were monitored for particle clearance rates using water pumped from 0.5m of the bottom.

Mussels from a cohort of 38 mm (0.2 g dry tissue weight) mussel seed at a seeding date of May 15, 1990 at Station C, Mud Cove were monitored for tissue and shell growth over an eleven month period, to a sample date of April 17, 1991 (Fig.21). Growth (both shell volume and meat size) was over 4.5 times faster in the small clumps (600 $m^{-2}$) than in the adjacent heavily-seeded patch of mussels (600 per square meter vs 1800) in small clumps. However, the biomass of the low and high density mussel aggregates (patches) was similar (669 vs 595 g dry tissue weight$\cdot$ $m^{-2}$). Thus, at the time of the experiment the carrying capacity of the lease section studied was about 600-650 g dry tissue weight$\cdot m^{-2}$. Particle clearance per individual mussel (mean dry weight 0.36 g) is presented in Table 7. Water samples were taken during flood and ebb tides, and phytoplankton carbon biomass calculated from measured cell volumes was compared for flood (Fig.22) and ebb (Fig.23) tides. The consumption of about half of the blooming diatom (*Chaetocerus sociale*) by the mussel bed (representing the bottom 0.5 m of the water column) within the tunnel was evident in the water samples. With a particle consumption of 3.88 $mm^3 \cdot h^{-1}$ per mussel, a square meter of bottom would require 7073 $mm^3 \cdot h^{-1}$ or at a seston level of 4 $mm^3 \cdot l^{-1}$, a vertical flux of about 1768 $l \cdot h^{-1}$.

Table 6. Mean particle clearance per mussel as measured in tunnel experiments 4/17/92

| | |
|---|---|
| POC ($\mu g \cdot h^{-1}$) | 376 |
| Particles ($\times 10^6 \cdot h^{-1}$) | 10.3 |
| Phytoplankton ($cells \cdot h^{-1}$) | 7762 |
| Particle volume ($mm^3 \cdot h^{-1}$) | 3.88 |
| Chl *a* ($\mu g \cdot h^{-1}$) | 3.93 |

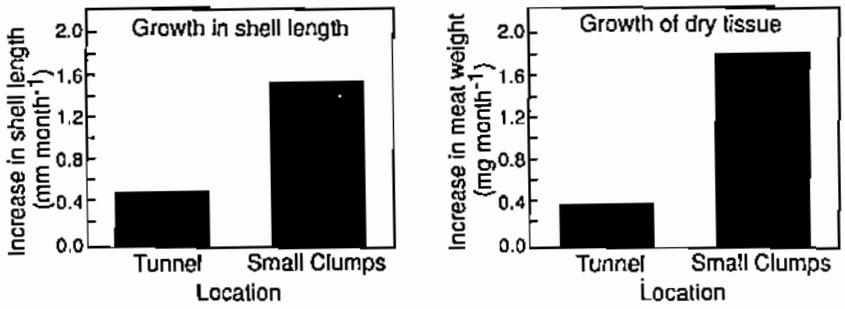


Figure 21. Mussel growth rates over an 11-month period in relation to seeding density for small clumps (595 $m^{-2}$) and over a continuous patch of mussels in the tunnel (1823 $m^{-2}$).

A comparison of mean filtration rate and oxygen consumption estimated with the tunnel and the flow-through chambers is presented below:

| | Tunnel | Chambers |
|---|---|---|
| Filtration rate ($l \cdot h^{-1} \cdot g^{-1}$) | 3.24 | 2.67 |
| Respiration ($ml\ O_2 \cdot h^{-1} \cdot g^{-1}$) | 0.30 | 0.30 |

Tidal cycle variations in shell gape: video experiments

An instrument was developed to measure, *in situ*, the effects of particle concentration on feeding activity in undisturbed mussels. The tripod-mounted instrument (Time-Lapse Video Benthic Monitoring, TLBM) uses time-lapse video technology to monitor shell gape of mussels for periods exceeding two weeks. Video tapes, analyzed field by field,

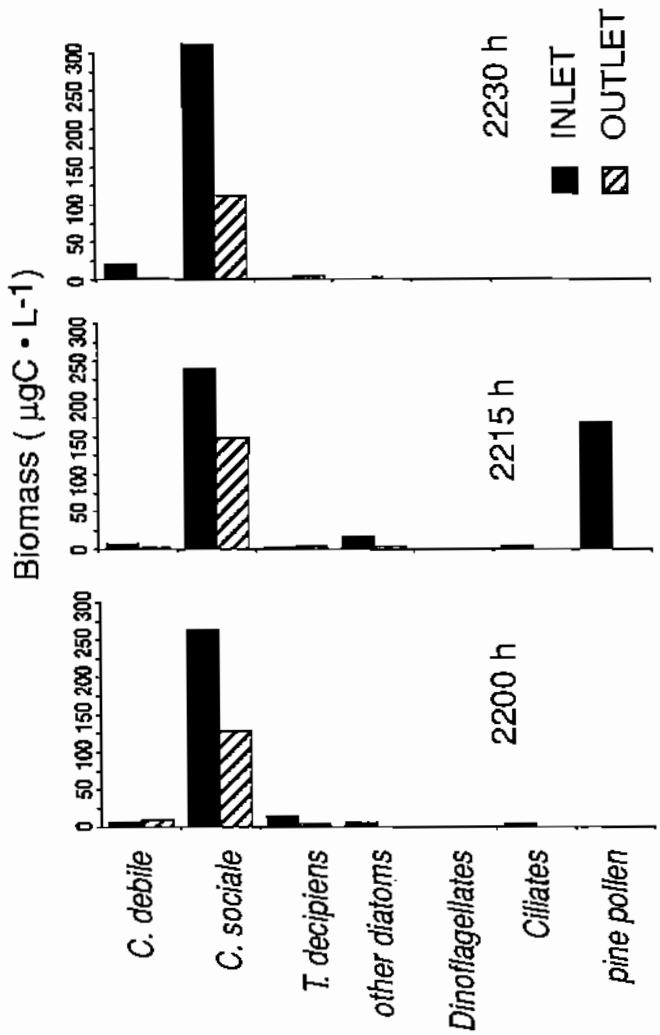


Figure 22. Flood tide differences in phytoplankton biomass taken from inlet and outlet of benthic ecosystem tunnel.

allowed measurements of shell gape of up to 30 mussels at intervals of 1 minute (Newell and Gallagher 1992). Results indicate a positive correlation between mussel shell gape and concentrations of POM and chlorophyll *a*, and a potential particle concentration threshold for the initiation of active feeding by mussels (Newell and Gallagher, in preparation). The results are briefly summarized below.

In the laboratory, mussel shell gape was calibrated to filtration rate by measuring the decrease in chlorophyll with time following pulsed additions of cultured algae to filtered seawater in a running flume.

Clearance rate was measured over a tidal cycle in a flow-through, efflux apparatus using ambient seawater and 10 efflux chambers with stir-bars (Fig.24) in fall (11/8/90), and in a benthic ecosystem tunnel (see section above) while time-lapse video recorded shell gape of over 30 mussels in undisturbed bottom patches from known seeded cohorts of mussels. Mussel filtration rates and shell gape were monitored *in situ* during high food (April, 1991) and low food (November, 1990) conditions. A sine wave pattern of shell gape (Newell and Gallagher, in preparation) indicates a coupling of bivalve pumping rates with mechanisms of particle supply with both tidal (e.g. Stenton-Dozey et al 1992) and seasonal components. During the fall, periods of shell closure were associated with a low seston concentration (under $8 \times 10^4$ particles$\cdot l^{-1}$, Fig.24). Low filtration rates and low oxygen consumption (25% of levels during active feeding) were observed around the period of low tide. A time-series of measurements of scope for growth over 4 tidal cycles in October (Newell and Davis, unpublished) in the efflux apparatus resulted in similar results during periods of low seston concentration.

In April, a 20-fold increase in food concentration resulted in higher shell gape during the tidal cycle, with greatest gape on the ebb. While the shapes of the shell gape curves were similar in both cases, the response to flood tide in November

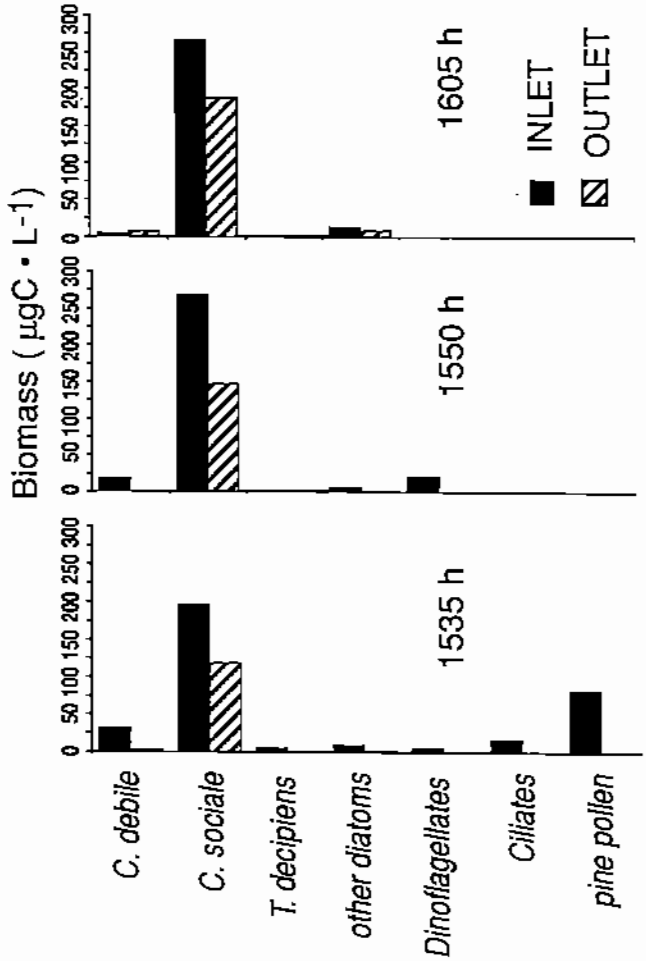


Figure 23. Ebb tide differences in phytoplankton biomass taken from inlet and outlet of benthic ecosystem tunnel 4/17/91.

near station B (edge of lease) and ebb tide in April near station D (about 250m from the edge) was probably due to site-specific effects of mussels on the population's food supply. In November, the lack of competition at station B (see Figs.8 and 9) on the edge of the lease resulted in rapid food supply to the mussels.

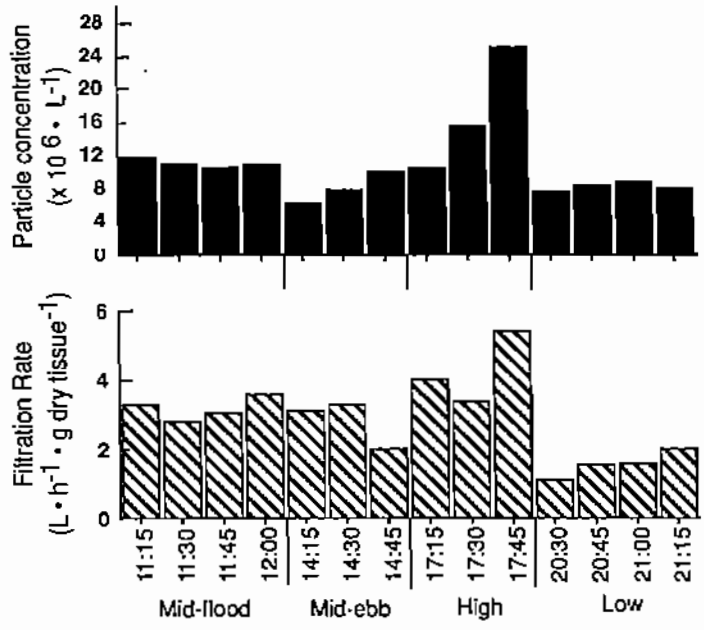


Figure 24. Mussel filtration rates (B) in efflux apparatus in relation to control particle concentration (A) on 11/8/92 at Station B, Mud Cove.

In April, depletion contours would develop in the bottom waters of the middle of the seeded mussel lease on the flood tide, (stations B to C, Fig.8) with settling increasing the supply of food-rich particles by high water/ebb tide (see Fig.11).

Future investigations of the shell gape assay for filtration rate of undisturbed shellfish beds should include more simultaneous measurements of shell gape and filtration rate, and studies of the limitations due to variable gill retention efficiencies.

Seasonal changes in food quality

Seston quantity and quality parameters at the Mud Cove lease site are given in Table 8. Bottom and surface concentrations were similar with the exception of phytoplankton carbon, which was higher in surface waters at all study sites, a combined result of mussel feeding and summer stratification. Both total and detrital C/N ratios were slightly higher in

bottom waters, indicating the role of settling of detritus. Carbon to chlorophyll ratio (C:Chl) averaged about 200:1, with low values during the spring bloom in February and March, 1990

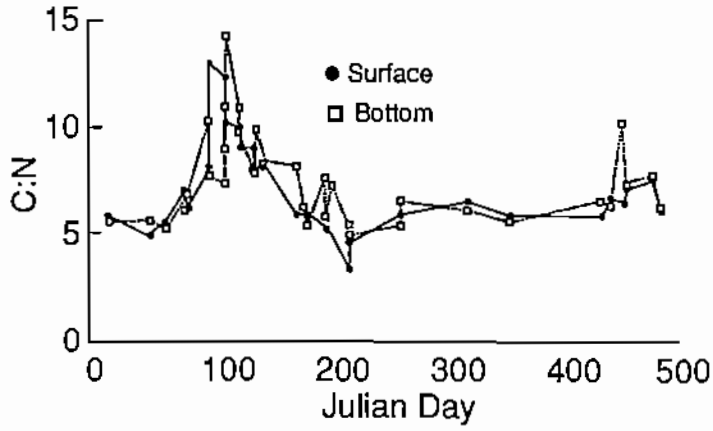


Figure 25. C/N ratio of GFC filtered seston from January, 1990 to June, 1991, bottom and surface samples, at Mud Cove.

and April, 1991 at Mud Cove. A distinct seasonal pattern in seston C/N ratio was observed (Fig. 25) rising from 5 to 10 after the spring bloom, providing mussels with an important source of detrital carbon in late spring and early summer. This food source provides additional energy for the rapid growth obtained by the mussels during this time. Data from all Maine sites show the same trend, with values over 10 during and after the spring bloom, falling to about 5 in the summer. The fraction of POM/SPM changed relatively little during the study, making it a poor indicator of food quality. Phytoplankton nitrogen/ total nitrogen ratio increased during the spring bloom and was lowest during late fall and winter at Mud Cove. Detrital nitrogen lagged behind the phytoplankton bloom by several weeks and was highest during the early summer, following the peak in detrital carbon.

Table 7. Mean values of various indicators of food quality at Mud Cove, Maine from January, 1990 - June, 1991

| Seston attribute | units | bottom | surface |
|---|---|---|---|
| SPM (total weight) | $mg \cdot l^{-1}$ | 8.09 | 7.52 |
| POM (weight organic matter) | $mg \cdot l^{-1}$ | 2.84 | 2.70 |
| Chlorophyll *a* | $\mu g \cdot l^{-1}$ | 3.09 | 3.04 |
| Particulate organic carbon | $\mu g \cdot l^{-1}$ | 396.44 | 390.31 |
| Phytoplankton carbon | $\mu g \cdot l^{-1}$ | 88.29 | 130.40 |
| Detrital carbon | $\mu g \cdot l^{-1}$ | 368.54 | 352.04 |
| Particulate organic nitrogen | $\mu g \cdot l^{-1}$ | 54.38 | 58.40 |
| Phytoplankton nitrogen | $\mu g \cdot l^{-1}$ | 9.62 | 13.07 |
| Detrital nitrogen | $\mu g \cdot l^{-1}$ | 49.54 | 53.39 |
| Particle concentration | no. $l^{-1} \times 10^6$ | 15.15 | 13.31 |
| Particle volume | $mm^3 \cdot l^{-1}$ | 0.93 | 1.66 |
| Organic weight/volume | $mg/mm^3$ | 1.72 | 1.41 |
| POM/SPM | mg/mg | 0.36 | 0.36 |
| Chl a/SPM | $\mu g/mg$ | 0.38 | 0.38 |
| Total POC/PON | $\mu g/\mu g$ | 7.40 | 6.90 |
| Detrital C/N | $\mu g/\mu g$ | 6.67 | 6.25 |
| Phyto C/Total C | $\mu g/\mu g$ | 0.15 | 0.18 |
| Phyto N/Total N | $\mu g/\mu g$ | 0.15 | 0.19 |
| C/Chl *a* | $\mu g/\mu g$ | 211.00 | 218.30 |
| Detrital N/C | $\mu g/\mu g$ | 0.15 | 0.16 |

Phytoplankton carbon reached a maximum of about 50% of total carbon during the spring bloom and was very low at Mud Cove during the summer period. The detrital N/C ratio increased just after the phytoplankton bloom, and rose again during the summer.

Due to the relative insensitivity of POM measured to changes in food quality, use of POM/particle volume was a relatively poor indicator of food quality over a seasonal cycle in contrast to the laboratory studies of Bayne et al (1989). For different field sites, phytoplankton and total carbon were

good indices of food quality during and after the spring bloom, while detrital nitrogen was a better indicator later in the year.

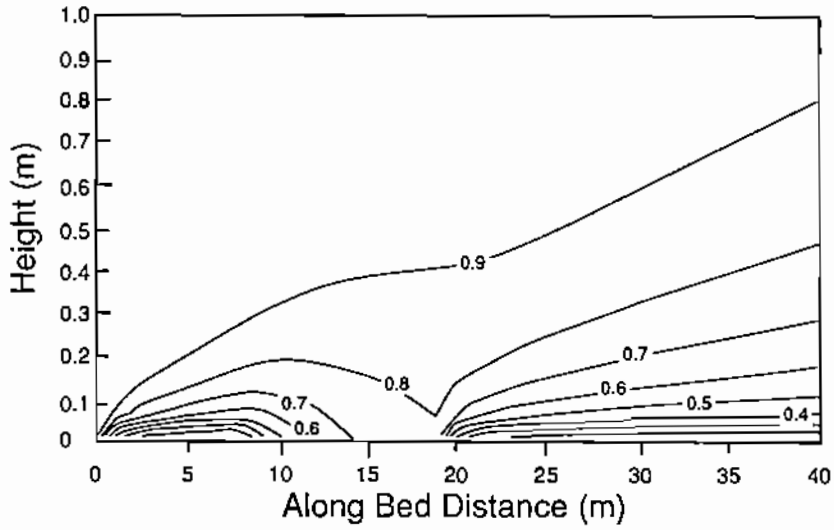


Figure 26. Concentration contours of phytoplankton in areas with no mussels between 9 and 19 meters (from Sankar 1991).

## CONCLUSIONS

A review of the literature and recent experiments in Maine have resulted in a dynamic view of mussel/particle interactions from cm to km scales, over periods ranging from tidal cycles to seasonal changes in food quality. Future investigations using natural particulates and relatively undisturbed beds of shellfish of high biomass in the field will elucidate the true role of these organisms in coastal ecosystems. It is recommended that the following approaches be used to investigate the grazing of natural particulates by shellfish:

| Problem | Approach | Tool |
|---|---|---|
| Current speed and volume flux | Hydrographic flow model | DUCHESS |
| Particle concentration | Seston profiles | BOSS |
| Scope for growth | Flow-through chambers | EFFLUX |
| Tidal variation in pumping | Shell gape assay | TLBVM |
| Meso-scale processes | Drogue experiments | ALPHA<br>BOTTLE |
| Population grazing | *In-situ* tunnels | BEST |
| Boundary layer processes | Flow profiling | FLUMES |
| Selective feeding | Feeding experiments | FLOW<br><br>CYTOMETER |

Our studies indicate the following attributes on a variety of spatial and temporal scales which exert a major control on shellfish and seston interactions:

| Attribute | Spatial Scale | Temporal Scale |
|---|---|---|
| Tidal supply of seston | km | hours |
| Vertical supply of seston | cm | hours |
| Algal biomass | km | weeks |
| Seston quality | km | days |
| Current speed | dm | hours |
| Shellfish size | cm | months |
| Temperature | km | weeks |
| Shellfish density | m | days |

Further limits to our knowledge of particle flux include: long-term patterns of shell gape and filtration activity; the role and mechanism of higher algal retention efficiency on the gills; effects of particle flocculation on vertical transfer rates; the relationships among nutrient concentrations and the

type of algae present; and resuspension of bottom detritus and benthic algal mats. Combined oceanographic and ecophysiological studies will become more important as we attempt to model shellfish and seston interactions. As we attempt to manage shellfish populations, both for aquaculture production and to maintain control over algal blooms, computer modelling will become an increasingly useful tool for simulations and "what if" scenarios. Studies of current and food gradients in the benthic boundary layer in both field and laboratory flumes will do a great deal to test and validate current models of seston transfer (Fréchette et al 1989; Monismith et al 1990). A computer simulation of depletion contours above a seeded mussel bed (Fig. 26) is an illustration of how mussel farmers may benefit from current computer models by placing spaces between seeded plots to allow greater food supply to the benthic boundary layer.

## ACKNOWLEDGMENTS

This research was supported by National Science Foundation SBIR Awards ISI8660201 and ISI8809760 to Great Eastern Mussel Farms. Thanks are due to Deb Murphy and Terri Ainaire (laboratory assistants); Dr. Scott Gallagher (video experiments); Dr. Richard Dame (tunnel experiments); Dr. Rockwell Geyer (flume experiments) and summer support for Sam Sankar; Dr. Cheryl Ann Butman (flume experiments); Dr. Dan Campbell (mussel model); Dr. Charles Gregory (phytoplankton analyses); Joth Davis (efflux apparatus); Dr. Vijay Panchang and John Richardson (hydrographic model); Dr. Janet Campbell and Roger Greene (Remote Sensing Experiments); Dr. Kee Muschenheim (BOSS experiments); Drs. Ray Grizzle, Marcel Fréchette and David Wildish for helpful discussions, and captain Hubba Bradford for help with the commercial seeding experiments. The authors are grateful to Drs. H. and R. Asmus, Dr. Richard Dame and one anonymous reviewer for helpful comments on the manuscript.

## Appendix 1. Rapid method for volume flux calcuation at a lease site

If we consider a tide gauge measurement of water depth, H, and a current meter measurement of water velocity, V, to be representative of a region $\Delta$ x, $\Delta$ y and H, then the flow entering an area with dimensions $\Delta$ x times H is q ($m^3 \cdot s^{-1}$). Assuming velocity varies in time as a sin curve:

$V = V_o \sin(\omega t)$ where $V_o$ = maximum velocity, $\omega$ = frequency, and water depth varies in time as a sin curve:

$H = H_m + \sin(\omega t + a)$ where $H_m$ = mean water depth and $a = \pi/2 = 90°$ and $\omega = 2\pi/12.4$

(i.e. velocity and water depth are out of phase by 90° or 3.1 hours), so $H = Hm + \cos \omega t$.

To find the volume, V, entering the area between times 1 and 2, the integral of $qdt$ from $t_1$ to $t_2$, with integration and substitution:

$$V = 2 H_m V_o \Delta x/\omega$$

Over a period of 6.2 hours, the flow through this vertical plane, $q = (2 H_m V_o \Delta x)/\pi$ ($m^3 \cdot s^{-1}$)

This average flow goes over a lease area, e.g. 1 square meter, at the rate:

$$2 H_m V_o/\pi \quad (m \cdot s^{-1})$$

Appendix 2. Estimation of $U_*$ at field sites.

One can calculate values of $U_*$ based on velocity profiles made in the field, from the slope of the velocity vs the natural logarithm of depth (U vs ln(z)) curve, by the equation:

$$U_* = K/b \quad \text{where } x = U,\ y = \ln(z) \text{ and } y = ax + b \qquad (3)$$

Very high $r^2$ values are needed for obtaining $U_*$ from velocity profiles, especially if less than five heights are used. Field data of velocity profiles using the S4 current meter and the Marsh-McBirney probe resulted in the following values of $U_*$ using the profile method (Table I). Because field profile $r^2$ values are less that 0.99, field values of $U_*$ values are suspect and must be extrapolated from the flume experiments.

Using the equation above, and representative values of U and H at the Mud Cove lease site, a range in values of $U_*$ may be calculated using a value of 0.16 for $z_o$, and compared with the simple equation $U_* = U/16$ (Table 4).

Table I $U_*$ calculated from velocity profiles at mussel culture sites.

| Location | U ($cm \cdot s^{-1}$) | $U_*$ ($cm \cdot s^{-1}$) | $r^2$ | H (cm) |
|---|---|---|---|---|
| Mud Cove (Stn B seeded) | | | | |
| 1a | 26 | 3.10 | 0.93 | 300 |
| 1b | 26 | 2.71 | 0.88 | 310 |
| 1c | 30 | 1.74 | 0.68 | 300 |
| 1d | 27 | 2.22 | 0.82 | 300 |
| 2a | 5 | 1.74 | 0.29 | 410 |
| 2b | 4.5 | 1.10 | 0.34 | 414 |
| Lamoine Lease (not seeded) | 15 | 1.05 | 0.96 | 300 |
| Schieffelein Cove (seeded) | | | | |
| 4 | 5.2 | 0.80 | 0.84 | 500 |
| 6 | 4.5 | 1.14 | 0.30 | 350 |

Table II. Expected values of U. from Mud Cove

| U ($cm \cdot s^{-1}$) | $z_o$ cm | H (cm) | U. | U. as U/16 |
|---|---|---|---|---|
| 5 | 0.16 | 125 | 0.30 | 0.31 |
| 5 | 0.16 | 250 | 0.27 | |
| 5 | 0.16 | 375 | 0.26 | |
| 5 | 0.16 | 500 | 0.248 | |
| 10 | 0.16 | 125 | 0.601 | 0.63 |
| 10 | 0.16 | 250 | 0.544 | |
| 10 | 0.16 | 375 | 0.515 | |
| 10 | 0.16 | 500 | 0.497 | |
| 15 | 0.16 | 125 | 0.901 | 0.94 |
| 15 | 0.16 | 250 | 0.816 | |
| 15 | 0.16 | 375 | 0.773 | |
| 15 | 0.16 | 500 | 0.746 | |
| 20 | 0.16 | 125 | 1.201 | 1.25 |
| 20 | 0.16 | 250 | 1.088 | |
| 20 | 0.16 | 375 | 1.031 | |
| 20 | 0.16 | 500 | 0.994 | |
| 25 | 0.16 | 125 | 1.501 | 1.56 |
| 25 | 0.16 | 250 | 1.360 | |
| 25 | 0.16 | 375 | 1.289 | |
| 25 | 0.16 | 500 | 1.243 | |
| 30 | 0.16 | 125 | 1.801 | 1.87 |
| 30 | 0.16 | 250 | 1.632 | |
| 30 | 0.16 | 375 | 1.546 | |
| 30 | 0.16 | 500 | 1.491 | |

Appendix 3. Benthic ecosystem tunnel characteristics, April, 1991 field experiment.

- Tunnel length (8.9 m)
- Tunnel width (0.9 m)
- Distance between pumps (6.7 m)
- Effective area enclosed by the tunnel (6 $m^2$)
- Mussel density within tunnel (1823·$m^{-2}$)
- Mussel mean individual dry weight (0.357 g, n = 240)
- Mussel mean shell length (43.6 mm, n = 239, s.dev.= 6.5)
- Mussel biomass (669 g·$m^{-2}$)
- Cross-sectional area tunnel (0.225 $m^2$)
- Velocity correction factor (0.84, R. Dame pers. commun.)
- Mussel density small clumps (595 $m^{-2}$, n=4, s. dev. = 164)
- Mussel mean dry meat wt small clumps (0.96 grams, n = 120)
- Mussel mean shell length small clumps (54.5 mm)
- Mussel biomass small clumps (571 g·$m^{-2}$)

For seven sections of the tunnel, volume flow is calculated as a result of current speed, e.g.:

3 cm $s^{-1}$ x 0.225 $m^2$ x 0.84 = .000567 $m^3 \cdot s^{-1}$

Over the 6 square meter mussel bed studied, at 3 cm $s^{-1}$, volume flux was 0.0034 $m^3 \cdot s^{-1}$ (= instantaneous net flux).

Table III. Current speed and volume flux through a Benthic Ecosystem enclosing 10,938 mussels on flood and ebb tides at Mud Cove on April 17, 1991.

| EBB | U ($cm \cdot s^{-1}$) | Flow ($m^3 \cdot h^{-1}$) | normalized flow·$m^{-2}$ ($m \cdot h^{-1}$) |
|---|---|---|---|
| 15:35 | 3.0 | 12.2 | 2.0 |
| 15:50 | 3.0 | 12.2 | 2.0 |
| 16:05 | 3.0 | 12.2 | 2.0 |
| 16:20 | 2.5 | 10.3 | 1.7 |
| FLOOD | | | |
| 22:00 | 3.2 | 13.0 | 2.2 |
| 22:15 | 3.2 | 13.0 | 2.2 |
| 22:30 | 2.9 | 11.9 | 2.0 |
| 22:45 | 2.4 | 9.8 | 1.6 |

REFERENCES


Almada-Villela PC, Davenport J, and Gruffydd LD (1982) The effects of temperature on the shell growth of young *Mytilus edulis* L. J Exp Mar Biol Ecol 59: 275-288

Bayne BL, Widdows J and Newell RIE (1977) Physiological measurements on estuarine bivalve molluscs in the field. In:Biology of Benthic Organisms eds. Keegan, O'Ceidigh and Boaden, Pergamon Press Oxford p. 57-68

Bayne BL, and Widdows J (1978) The physiological ecology of two populations of *Mytilus edulis* L. Oecologia 37:137-162

Bayne BL, Widdows J, and Thompson RJ (1976) Physiological integrations, p.261-291. In Bayne BL, (ed.), Marine mussels: their ecology and physiology. IBP 10. Cambridge University Press. 506 pp

Bayne BL, Hawkins AJS, Navarro E, and Iglesias IP (1989) Effects of seston concentration on feeding, digestion and growth in the mussel *Mytilus edulis*. Mar Ecol Prog Ser 55:47-54

Bayne BL and Hawkins AJS (1990) Filter-feeding in bivalve molluscs: controls on energy balance. Comparative physiology Animal nutrition and transport processes. Comp Physiol 5:70-93.

Bayne BL, Hawkins AJS, and Navarro E (1987) Feeding and digestion by the mussel *Mytilus edulis* L. (Bivalvia: Mollusca) in mixtures of silt and algal cells at low concentrations. J Exp Mar Biol Ecol 111:1-22

Bienfang PK (1981) Sinking rates of heterogeneous, temperate phytoplankton populations. J Plank Res 3:235-252

Billen G (1978) A budget of nitrogen recycling in North Sea sediments off the Belgian Coast. Estuar Coast Mar Sci 7:127-146

Blegvad H (1914) Food and conditions of nourishment among the communities of invertebrate animals found on the sea bottom in Danish waters. Rep Danish Biol Sta 1914 pp. 45-78

Brylinsky M, and Sephton TW (1991) Development of a computer simulation model of a cultured blue mussel (*Mytilus edulis*) population. Can Tech Rep Fish Aquat Sci 1805.vii+81p

Campbell JW, Garside JC, Greene RH and Newell CR (1991) Use of high resolution aerial and satellite remote sensing for assessing bivalve shellfish aquaculture sites. Maine Aquaculture Innovation Center, Orono, Me. Tech Rep 1991 47 pp

Carver CEA and Mallet AL (1990) Estimating the carrying capacity of a coastal inlet for mussel culture. Aquaculture 88:39-53

Conover RJ (1966) Assimilation of organic matter by zooplankton. Limnol Oceanogr 11:338-354

Coughlan J (1969) The estimation of filtering rate from the clearance of suspensions. Mar Biol 2:356-358

Cucci TL, Shumway SE, Brown WS, and Newell CR (1989) Using phytoplankton and flow cytometry to analyze grazing by marine organisms. Cytometry 10:659-669

Dame RF, Zingmark RG, and Haskin E (1984) Oyster reefs as processors of estuarine materials. J Exp Mar Biol Ecol 83:239-247.

Dame RF and Dankers N (1988) Uptake and release of materials by a Wadden Sea mussel bed. J Exp Mar Biol Ecol 118:207-216
Dyer KR (1973) Estuaries:A Physical Introduction. Wiley and Sons Toronto Ont. pp 109-110
Dean B (1887) The food of the oyster, its conditions and variations. Suppl. to 2nd Rept., Oyster Investigations, State of New York pp. 49-78
Famme P, Riisgard HU, Jørgensen CB (1986) On direct measurements of pumping rates of the mussel *Mytilus edulis*. Mar Biol 92:323-327
Fegley SR, MacDonald BA and Jacobsen TR (1992) Short-term variation in the quantity and quality of seston available to benthic suspension feeders. Estuar Coast Shelf Sci 34: 393-412
Field IA (1911) The food value of sea mussels. Bull US Bur Fish 29:85-128
Foster-Smith RL (1975) The effect of concentration of suspension on the filtering rates and pseudofecal production for *Mytilus edulis* L., *Cerastoderma edule* L. and *Venerupis pullastra* Montagu. J Exp Mar Biol Ecol 17:1-22
Fréchette M and Bourget E (1985) Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. Can J Fish Aquat Sci 42:1158-1165
Fréchette M, Butman CA, and Geyer WR (1989) The importance of boundary-layer flows in supplying phytoplankton to the benthic suspension feeder *Mytilus edulis* L. Limnol Oceanogr 34:19-36
Galtsoff PS (1964) The American oyster. Fishery Bulletin 64:1-480
Grant J, Mills EL, and Hopper CM (1986) A chlorophyll budget of the sediment-water interface and the effect of stabilizing biofilms on particle fluxes. Ophelia 26:207-219
Grave C (1912) A manual of oyster culture in Maryland. 4th Report of the Board of Shellfish Commissioners of Maryland, Baltimore. 376pp
Griffiths RJ (1981). Production and energy flow in relation to age and shore level in the bivalve *Choromytilus meridionalis* (Kr.). Estuar Coast Shelf Sci 13:477-493
Grizzle RE (1988) The relative effects of tidal currents, seston and bottom sediments on individual growth of *Mercenaria* (Linne): Feeding ecology and aquacultural implications. Ph.D. Thesis, Rutgers University 293 pp
Hawkins AJS (1991) Protein turnover: a functional appraisal. Func Ecol 5:222-233
Hawkins AJS, Navarro E, and Iglesias JIP (1990) Comparative allometries of gut-passage time, gut content and metabolic faecal loss in *Mytilus edulis* and *Cerastoderma edule*. Mar Biol 105:197-204
Herman PMJ, and Scholten H (1990) Can suspension-feeders stabilise estuarine ecosystems? In: M. Barnes and R.N. Gibson (eds.) Trophic relationships in the marine environment. Aberdeen University Press, Aberdeen. pp. 104-116
Hildreth DI and Crisp DJ (1976) A corrected formula for calculation of filtration rate of bivalve molluscs in an

experimental flowing system. J Mar Biol Ass UK 56:111-120
Holligan PM (1985) Marine dinoflagellate blooms - growth strategies and environmental exploitation. pp. 133-139 in: Anderson, White and Baden (eds.) Toxic Dinoflagellates. Elsevier Science Publishers New York/Amsterdam.
Hosomi A (1985) On the persistent trend of constant biomass and the constant total occupation area of the mussel *Mytilus galloprovincialis* (Lamark). Venus Jpn J Malacol 44:33-38
Hutchinson GE (1967) A treatise on Limnology Vol. 2. Introduction to lake biology and the limnoplankton. Wiley New York.
Hummel H (1985) Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. Neth J Sea Res 19:52-76
Hunt OD (1925) The food of the bottom fauna of the Plymouth fishing grounds. J Mar Biol Assoc UK 13:560-599
Jørgensen CB, Larsen PS, Møhlenberg F, and Riisgård HU (19B8) The bivalve pump:properties and modelling. Mar Ecol Prog Ser 45:205-216
Jørgensen CB, Larsen PS, and Riisgård HU (1990) Effects of temperature on the mussel pump. Mar Ecol Prog Ser 64:89-97
Jørgensen CB (1990) Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology. Olsen and Olsen, Denmark. 140 p
Jørgensen CB, Famme P, Kristensen HS, Larsen PS, Møhlenberg F, and Riisgård HU (1986) The bivalve pump. Mar Ecol Prog Ser 34:69-77
Kellogg JL (1910) Shellfish industries. Holt and Co. New York 361pp.
Kiørboe T and Møhlenberg F (1987) Particle selection in suspension-feeding bivalves. Mar Ecol Prog Ser 5:291-296
Koehn RK and Bayne BL (1989) Towards a physiological and energetic understanding of the energetics of the stress response. Biol J Linnean Soc 37:157-171
Kramer KJM, Jenner HA, and de Zwart D (1989) The valve movement response of mussels: a tool in biological monitoring. Hydrobiologia 188/189: 433-443. In: Munawar M, Dixon G, Mayfield CI, Reynoldson T, and Sadar MH(eds). Environmental Bioassay Techniques and Their Application. Kluwer Academic Publishers Belgium
Lindahl O (1983) On the development of a *Gyrodinium aureolum* occurrence on the Swedish west coast in 1982. Mar Biol 77: 143-150
Lotsy JP (1896) The food of the oyster, clam and ribbed mussel. Rept U.S. Comm Fish and Fisheries for 1893: 375-386
Martin GW (1925) Food of the oyster. Botanical Gazette 75(2):143-169
Møhlenberg F and Riisgård HU (1979) Filtration rate, using a new indirect technique, in thirteen species of suspension-feeding bivalves. Mar Biol 54:143-147
Møhlenberg F and H.U. Riisgård (1978) Efficiency of particle retention in 13 species of suspension-feeding bivalves. Ophelia 17:239-246
Mook DH and Hoskin CM (1982) Organic determinations by ignition: caution advised. Estaur Coast Shelf Sci 15:697-699

Moore HF (1907) Survey of oyster bottoms in Matagorda Bay, Texas. Document 610, Bureau of Fisheries

Moore HF (1910) Volumetric studies of the food and feeding of oysters. Bulletin of the U.S. Bureau of Fisheries 28:1295-1308

Muschenheim DK and Newell CR (1992) Utilization of seston flux over a mussel bed. Mar Ecol Prog Ser 85:131-136

Navarro E, Iglesias JIP and Ortega MM (1992) Natural sediment as a food source for the cockle *Cerastoderma edule* (L.): effect of variable particle concentration on feeding, digestion and the scope for growth. J Exp Mar Biol Ecol 156:69-87

Nelson TC (1947) Some contributions from the land in determining conditions of life in the sea. Ecological Monographs 17:337-346

Newell CR (1990) The effects of mussel (*Mytilus edulis* L. 1758) position in seeded bottom patches on growth at subtidal lease sites in Maine. J Shellfish Res 9:113-118

Newell CR (1991) Development of a model to seed mussel bottom leases to their carrying capacity. Phase II Report. NSF SBIR ISI8809760. 800 pp

Newell CR, Shumway SE, Cucci TL and Selvin R (1989) The effects of natural seston particle size and type on feeding rates, feeding selectivity and food resource availability for the mussel *Mytilus edulis* L. at bottom culture sites in Maine. J Shellfish Res 8:187-196

Newell CR and Campbell D (1992) Output of a model to seed mussel bottom leases to their carrying capacity: calibration, validation and sensitivity analysis. J Shellfish Res 11:203

Newell CR and Gallagher SM (1992) Short-term variability in seston flux and physiological responses of bottom-cultured mussels: (*Mytilus edulis*) in Maine. J Shellfish Res 11:203

Newell CR and Shumway SE (1991) Mussel feeding selectivity below the pseudofeces threshold: the importance of particle concentration. J Shellfish Res 10.

Newell RIE and Jordan SJ (1983) Preferential ingestion of organic material by the American oyster *Crassostrea virginica*. Mar Ecol Prog Ser 13:47-53

Newell RIE and Thompson RJ (1984) Reduced clearance associated with spawning in the mussel *Mytilus edulis* L.(Bivalvia, Mytilidae). Mar Biol Lett 5:21-33

Officer CB, Smayda TJ and Mann R (1982) Benthic filter feeding: a natural eutrophication control. Mar Ecol Prog Ser 9: 203-210

Page HM and Ricard YO (1990) Food availability as a limiting factor to mussel *Mytilus edulis* growth in California coastal waters. Fish Bull 88:677-686

Petersen CGJ (1908) First report on the oysters and oyster fisheries in the Lim Fjord. Rept Danish Biol Station 15:1-42

Petersen CGJ and Jensen PB (1911) Valuation of the sea. I. Animal life of the sea-bottom, its food and quantity. Rept Danish Biol Station 20:1-78

Phinney DA and Yentsch CS (1985) A novel phytoplankton chlorophyll technique: toward automated analysis. J Plankton

Res 7:633-642
Platt T and B Irwin (1973) Caloric content of phytoplankton. Limnol Oceanogr 18:306-310
Prins TC and Smaal AC (1990) Benthic-pelagic coupling: the release of inorganic nutrients by an intertidal bed of *Mytilus edulis*. Trophic relationships in the Marine Environment pp. 89-103. Proc 24th Europ Mar Biol Symp. Barnes and Gibson (eds.) Aberdeen University Press
Richardson J, Newell CR and Panchang V (1992) Estimation of mussel seeding densities by hydrographic mathematical modeling. J Shellfish Res 11:205
Riebesell U (1991a) Particle aggregation during a diatom bloom.I. Physical aspects. Mar Ecol Prog Ser 69:273-280
Riebesell U (1991b) Particle aggregation during a diatom bloom. II. Biological aspects. Mar Ecol Prog Ser 69:281-291
Riisgård HU and Randlov A (1981) Energy budgets, growth and filtration rates in *Mytilus edulis* at different algal concentrations. Mar Biol 61:227-234
Riisgård HU and Poulsen E (1981) Growth of *Mytilus edulis* in net bags transferred to different localities in a eutrophicated Danish fjord. Mar Pollut Bull 12:272-276
Sankar SN (1991) Modeling plankton depletion over mussel beds: why it's good to live on the edge. Woods Hole Oceanographic Instituion Woods Hole Mass. Summer student fellow under Dr. Rockwell Geyer, final report
Savage RE (1925) The food of the oyster. Fishery Invest. (II)8: 2-50
Shumway SE (1990) A review of the effects of algal blooms on shellfish and aquaculture. J World Aqua Soc 21:65-104
Shumway SE (1992) Mussels and Public Health. Chapter 11 (pp. 511-542) In: The Mussel, *Mytilus* (Gosling EM ed) Elsevier Science Publishers BV Amsterdam
Shumway SE, Selvin R and Schick DF (1987) Food resources related to habitat in the scallop *Placopecten magellanicus* (Gmelin, 1791): A qualitative study. J Shellfish Res 6:89-95
Shumway SE, Barter J and Sherman-Caswell S (1990) Auditing the impact of toxic algal blooms on oysters. Environ Auditor 2:41-56
Shumway SE and Cembella AD (1993) The impact of toxic algae on scallop culture and fisheries. Reviews in Fisheries Science. In press
Small AC (1991) The ecology and cultivation of mussels: new advances. Aquaculture 94:245-262
Smayda TJ (1970) The suspension and sinking of phytoplankton in the sea. Oceanogr Mar Biol Ann Rev 8:353-414
Smayda TJ and Boleyn BJ (1965) Limnol Oceanogr 10:499-509
Smayda TJ (1989) Primary production and the global epidemic of phytoplankton blooms in the sea: a linkage? pp. 449-483 in: Cosper EM, Bricelj VM and Carpenter EJ (eds) Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms. Springer-Verlag New York
Smayda TJ (1990) Novel and nuisance phytoplankton blooms in the sea: evidence for a global epidemic. pp. 29-40 in: Granéli E et al (eds) Toxic Marine Phytoplankton. Elsevier Science Publishers New York/Amsterdam

Smayda TJ and White A (1990) Has there been a global expansion of algal blooms? If so, is there a connection with human activities? pp. 516-517 in: Granéli E et *al* (eds) Toxic Marine Phytoplankton. Elsevier Science Publishers New York/Amsterdam

Stenton-Dozey JM and Brown AC (1992) Clearance and retention efficiency of natural suspended particles by the rock-pool bivalve *Venerupis corrugatus* in relation to tidal availability. Mar Ecol Prog Ser 82:175-186

Thompson RJ and Bayne BL (1972) Active metabolism associated with feeding in the mussel *Mytilus edulis* L. J Exp Mar Biol Ecol 9:111-124

Thompson RJ (1984) The reproductive cycle and physiological ecology of the mussel *Mytilus edulis* in a subartic, non-estuarine environment. Mar Biol 79:277-288

Tracey GA (1988) Feeding reduction, reproductive failure, and mortality in *Mytilus edulis* during the 1985 "brown tide" in Narragansett Bay, Rhode Island. Mar Ecol Prog Ser 50:73-81

Trowbridge JH, Geyer WR, Butman CA, and Chapman RJ (1989) The 17m flume at the Coastal Research Laboratory. Part 2. Flow characteristics. Woods Hole Oceanogr Inst Tech Rep WHOI-89-11

Walsby AE and Reynolds CS (1980) Sinking and floating. In: The physiological ecology of the phytoplankton. I. Morris (ed), U. California Press

Ward JE and Targett NM (1989) Influence of marine microalgal exudates on the feeding behavior of the blue mussel *Mytilus edulis*. Mar Biol 101:313-321

Widdows J (1978) Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. J Mar Biol Assoc UK 58:125-142

Widdows J, Fieth P and Worrall CM (1979) Relationships between seston, avaiable food and feeding activity in the common mussel *Mytilus edulis*. Mar Biol 85:217-232

Widdows J and Hawkins AJS (1989) Partitioning of rate of heat dissipation by *Mytilus edulis* into maintenance, feeding and growth components. Physiol Zool 62:764-784

Williams LG (1982) Mathematical analysis of the effects of particle retention efficiency on determination of filtration rate. Mar Biol 66:171-177

Wyatt T (1990) Do algal blooms play homeostatic roles? pp. 249-252 in: Granéli et *al* (eds). Toxic Marine Phytoplankton. Elseviers Science Publishers New York/Amsterdam.