Journal of Shellfish Research, Vol. 8, No. 1, 187–196, 1989.

THE EFFECTS OF NATURAL SESTON PARTICLE SIZE AND TYPE ON FEEDING RATES, FEEDING SELECTIVITY AND FOOD RESOURCE AVAILABILITY FOR THE MUSSEL *MYTILUS EDULIS* LINNAEUS, 1758 AT BOTTOM CULTURE SITES IN MAINE

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ABSTRACT Particle selection, both as a function of size and organic content, by the mussel (*Mytilus edulis*) was investigated using flow cytometric techniques. Feeding of mussels from several discrete locations was monitored using natural particle assemblages from the respective areas as food sources. Particles were analyzed for their fluorescing intensities as well as particle size (spherical diameter) and samples were preserved for bacterial counts. Results indicated that clearance rates by mussels were approximately 40% higher on phytoplankton (particles with chlorophyll fluorescence) than on nonfluorescent particles on 5 of the 6 days sampled. On day 6 there was evidence that high levels of nonfluorescent particles inhibited the ability of mussels to feed selectively. The implications of a feeding selectivity threshold on mussel energy acquisition are discussed.

Results are compared to water samples taken directly above a commercial lease site in which food quality was lower directly over the mussel bed than that measured higher in the water column.

Prefiltering the water for analysis on a single aperture resulted in the reduction of microscopic counts by as much as 75% and much less when smaller diatoms were dominant. The presence of chain-forming phytoplankton species resulted in an underestimation of cell numbers when counted using the flow cytometer. Over two-thirds of the algal species identified from gut contents were benthic in origin. Analyses of gut contents indicate that large particles (up to 110 μm) may form a significant portion of the diet of *M. edulis*.

KEY WORDS: mussels, *Mytilus edulis*, particle selection, diet, feeding

INTRODUCTION

The feeding behavior of mussels (*Mytilus edulis*) in response to natural particle assemblages (seston) is of interest for the selection of mussel farm sites and in the calculation of carrying capacities for bottom culture sites. Variations in the concentration of phytoplankton cells and silt particles may be correlated with position in the estuary, tidal stage, storm events or location at the mussel farm site. Responses both in the initiation of feeding at low particle concentration and the behavior of a feeding selectivity response have important implications for the feeding and growth of seeded mussels.

The effects of food (seston) quantity and quality on the physiology and growth of suspension-feeding bivalve molluscs have been the subject of numerous investigations (see Bayne and Newell 1983, Winter 1978, Bayne et al. 1987 for reviews), but few have measured feeding rates using natural particle suspensions (Bayne and Widdows 1978, Thompson 1984, Widdows et al. 1984, Lucas et al. 1987). While the quality and quantity of sestonic food has been shown to affect growth (Stromgren and Cary 1984) and feeding physiology (Kiorboe et al. 1980, Widdows et al. 1979, Bayne et al. 1987) of *M. edulis*, experiments have analyzed feeding behavior in response to particle size and concentration using a Coulter Counter, in which particles are distinguished only in terms of spherical equivalence in size. Only recently have experiments considered particle type using flow cytometric techniques (Shumway et al. 1985, Cucci et al. 1985). While these experiments have indicated selective feeding by some species using mixed algal suspensions, none have used natural suspensions consisting of algal cells and inorganic particles.

Investigations of selective feeding by bivalves in mixtures of algae and silt have demonstrated feeding selectivity at food concentrations above the pseudofeces threshold (Kiorboe et al. 1980; Kiorboe et al., 1981; Kiorboe and Mohlenberg, 1981; Newell and Jordan, 1983), but none have examined whether *M. edulis* can enhance its energy gain below the pseudofeces threshold at low concentrations of seston (under 4–5 mg/l, Widdows et al. 1979) by feeding selectively on algal cells.

Reported here are experiments which examine mussel feeding behavior (clearance rate) as a function of particle type (fluorescing particles, phytoplankton vs. non-fluorescing particles) and particle size using flow cytometry and seawater pumped from above three mussel cultivation sites. Data are compared with field measurements of seston quality at a commercial lease site, and the results of the flow cytometry experiments are compared with settling chamber counts of phytoplankton in filtered and unfiltered samples.

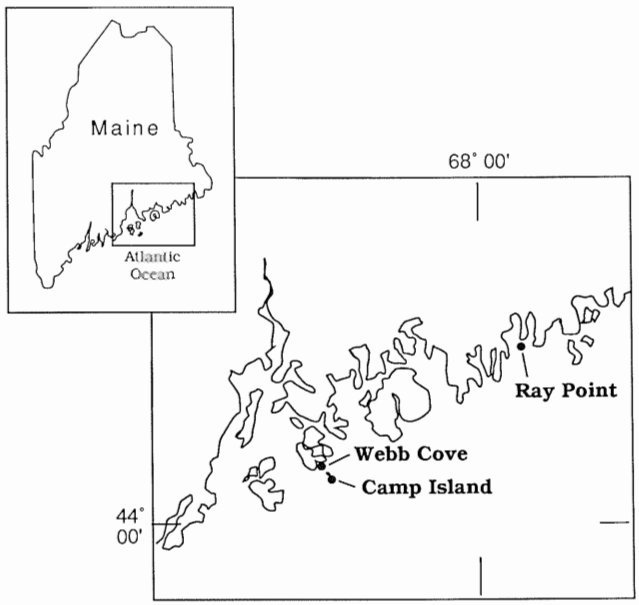

Figure 1. Sampling locations for mussels and water used in feeding experiments. All sites are commercial mussel bottom culture leases.

METHODS

A series of laboratory feeding experiments were designed to assess possible particle selection in the mussel *M. edulis*. The first set of experiments used mussels that were collected from coastal Maine waters (seeded bottom culture leases) at Webb Cove, Camp Island Cove and Ray Point (Fig. 1) one day prior to their use in the experiments and held in filtered seawater (0.7 μm) at ambient temperatures (14–15°C). This allowed the animals to purge previously ingested material from their guts. On the day of each experiment, water samples were pumped from 0.5 m off the bottom at each respective site, using a Rule 450 GPH centrifugal pump and 15 m of 13 mm interior diameter Tygon tubing. The water was prefiltered through 53 μm Nitex screening, kept refrigerated in the dark in large carboys and flown to the laboratory facilities in Boothbay Harbor, Maine. For each lease site, duplicate experiments were performed using 6 animals/experiment. Outer sites were located in deeper water near the seaward portions of the lease sites, and inner sites were closer to shore. Individual mussels were placed in gently aerated beakers containing 2l of seawater from their respective collection sites. Control vessels were left without animals to correct for changes in cell concentrations during the experiment. Experiments lasted 1 hr after which water samples were collected for flow cytometric analyses.

Horizontal variability in food availability over a subtidal mussel bed was assessed over a 600 m transect into Webb Cove. Stations 1, 3, 5, 7, 9 and 11 were pumped from 0.5 m below the surface while stations 2, 4, 6, 8, and 10 were pumped 0.5 m above the bottom (Fig. 2). Water samples were again refrigerated in the dark and flown immediately to the laboratory at Boothbay Harbor and analyzed for particle size, concentration and chlorophyll fluorescence using the FACS analyzer (see below).

Flow Cytometry (FCM)

Water samples were analyzed using a FACS Analyzer flow cytometer (Becton Dickinson, Mountainview, CA). The instrument was set up to analyze for chlorophyll a fluorescence (>665 nm) having an excitation light source of 426 (±20 nm) from a mercury arc lamp. The analyzer is able to simultaneously measure cell volume (equivocal spherical diameter, Coulter Counter principle) and chlorophyll fluorescence. As a result, the phytoplankton component can be easily distinguished from the total particulates of seawater. A total of 10,000 particles were analyzed for

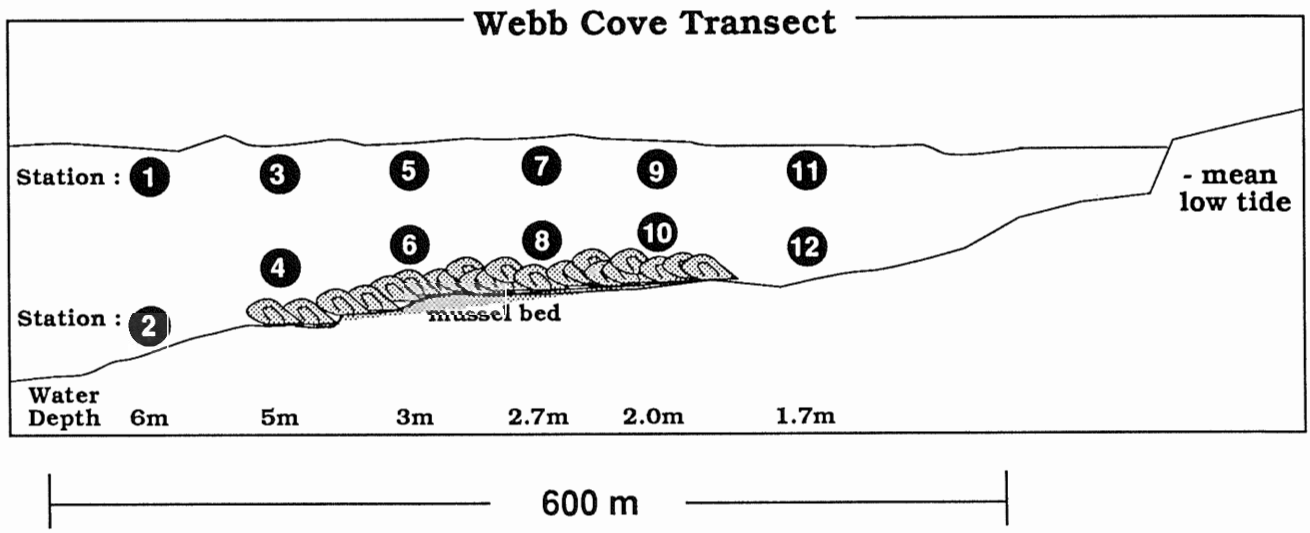

Figure 2. Transect on flood tide over seeded mussel lease area. Mussel density averaged 20–20 L m^{-2} with approximately 30% of the bottom covered with seed. Odd numbered stations were 0.5 m below the surface, even numbered stations were 0.5 m off the bottom.

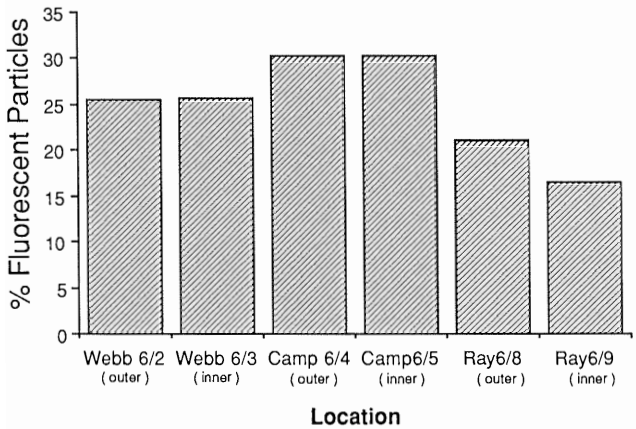

Figure 3. Food quality (% of particles with chlorophyll fluorescence) in control samples. Values are means of triplicate samples for all dates except June 2 where there was only one control.

each sample within the size range of 2.5–35 μm in diameter (using a 75 μm orifice and a current of 0.71 mA). Particles over 35 μm in diameter but under 53 μm were analyzed as fluorescing and non-fluorescing but were off scale for actual volume determination. The volume of sample analyzed was determined gravimetrically whereby the difference in weight (mg) of the sample from pre- and post-analysis was the total volume analyzed in ml. Particle densities were subsequently calculated.

Flow cytometric analyses were done on the water in each of the control and experimental vessels before the addition of the animals to the vessels (time 0 and after 60 min. Clearance rates were calculated based on the number of cells removed from suspension during the experiments using the Coughlan method (Coughlan 1969). The data were converted to clearance rates of a standard animal of 1 g dry flesh weight, using the equation:

$$\text{feeding rate} = ax^b \quad \text{where } b = 0.66$$

(Møhlenberg and Riisgard 1979)

Data were collected for total number of particles (both chlorophyll and non-chlorophyll), size fractionation of the particles present at each location and those cleared by the individual mussels. In addition, initial bacterial concentrations were determined. Settling chamber counts of cells and cell identifications were also made on filtered subsamples and unfiltered water from each of the sampling stations.

Gut Content Analysis

Mussels were collected from cages held subtidally at the laboratory in order to determine the types of particles ingested by the mussels. Gut content analyses were made immediately after collection as described previously (Shumway et al. 1987). Mussels from the collection sites used in the feeding experiments could not be used for gut content studies due to the time involved in returning the samples to the laboratory. Preliminary attempts to use these animals indicated that digestion was too rapid and after only 1 hr very few cells were identifiable from the guts.

RESULTS

The flow cytometer (FACS analyzer) allowed for the simultaneous analysis of both the size (particle volume) and fluorescence characteristics of prefiltered natural particle assemblages from 3 different lease sites on 6 separate occassions. Food quality, as percent of particles with chlorophyll fluorescence in control beakers, are presented in Fig. 3 and Table 1. Mean concentration of non-fluorescent particles reached a high of 14,200 ml-1 on June 9, and had a low of 7,139 ml-1 on June 4. Concentration of fluorescent particles (phytoplankton) had a maximum value of 4,639 ml-1 on June 2 and a low of 2,392 ml-1 on June 8. Food quality, as percent fluorescent particles, was highest at Camp Island (over 33%) on June 4 and 5 and lowest at Ray Point on June 9 (16.4%).

The effects of prefiltering water (53 μm mesh) on the numbers of phytoplankton cells were examined on 4 occasions. Settling chamber counts indicate a total reduction of cell numbers by prefiltering as high as 54.1% (Ray Point, 6/9/87) and a greater reduction (up to 74.4%) for larger cells than for total cells (Table 2). The experimental diets therefore underestimated true food resource availability at the mussel farm sites. The data also indicate that for studies of natural seston using the flow cytometer, prefiltering water samples should be done with caution. When smaller diatoms were dominant (e.g., *Chaetoceros gracilis*), there

TABLE 1.

Initial particle concentrations and food quality of experimental treatments. All samples are means of 3 controls except Webb Outer, 6/2/89, and are in numbers/ml.

Location	Date	Total Particles	Fluorescent Particles	Non-fluorescent Particles	Quality % Fluorescent
Webb Outer	6/2/87	16292	4639	11653	28.5
Webb Inner	6/3/87	10279	2830	7449	27.5
Camp Outer	6/4/87	10769	3630	7139	33.7
Camp Inner	6/5/87	10821	3629	7192	33.5
Ray Outer	6/8/87	11429	2392	9038	20.9
Ray Inner	6/9/87	16982	2782	14200	16.4

TABLE 2.

Effects of prefiltering water (53 μm mesh) on cell concentration in natural seston samples for flow cytometric analysis. Concentration is in million cells · l^{-1}.

Date	Total Cells			Cells over 15 μm		
	Unfiltered	Filtered	% Less	Unfiltered	Filtered	% Less
6/9 SFC	14.588	13.014	10.8	10.256	26.280	74.4
6/9 BOT	26.562	12.183	54.1	1.218	0.522	57.2
6/5 BOT	14.385	14.417	0	2.345	1.824	22.3
6/4 BOT	14.382	11.348	21.1	2.108	1.011	49.9

were less pronounced effects of prefiltering. Further, gut content analyses indicate that large particles (up to 110 μm) form a significant portion of the diet.

The cell concentrations estimated by the flow cytometer were compared with settling chamber counts and it was found that cell concentrations were generally underestimated by an average of 17.7% (Table 3). This is probably due to the fact that phytoplankton chains would be counted as one particle and heterotrophic flagellates would not be counted as fluorescent particles by the flow cytometer.

Particle counts from the flow cytometer allowed for separate determinations of clearance rates by the mussels as a function of:

1. Total particles (comparable to a standard Coulter Counter).
2. Fluorescent particles (phytoplankton).
3. Non-fluorescent particles (sediment particles, microheterotrophs).

Examination of the data suggests certain trends in feeding rates when examined with respect to particle type. Clearance rates for animals of 1 g standard weight were about 40% higher on the fluorescent particles (phytoplankton) than on the non-fluorescent particles on five of the six days (Table 4, Fig. 4). Clearance rates based on total cells, however, did not reveal large differences between groups.

On June 2, total particle concentration was similar to June 9 (about 16,000 · ml^{-1}) but higher food quality on June 2 (28.5% fluorescing cells) resulted in enhanced filtration rates on phytoplankton vs. non-fluorescent particles (4.45 vs. 2.2 $l \cdot h^{-1}$). On June 9, lower food quality (16.4% fluorescing cells) resulted in lower filtration rates and no evidence of particle selection for phytoplankton cells vs. non-chlorophyll particles (1.69 vs. 1.76 $l \cdot h^{-1}$).

In order to determine whether particle selection was size specific, water samples of control beakers and mussel beakers were examined for the percent of particles cleared in each size group (3–5 μm, 5–8 μm, 8–10 μm, 10–15 μm) for each of the experiments (Fig. 5). Data are not presented for particles of larger diameter due to their low frequency of occurrence in the samples. Mussels cleared higher percentages of fluorescent particles than non-fluorescing particles regardless of cell size except on June 9. It therefore appears that at least in the size range studied, feeding selectivity is not size specific.

ANOVA RESULTS

Analyses of variance were performed on clearance rates with day, lease area (Webb Cove, Camp Island and Ray Point) and location (inner lease or outer lease) as classes. Clearance rates of total particles were significantly affected by lease area ($P < 0.02$), with rates significantly higher at Webb Cove than at Camp Island or Ray Point (3.08, 2.16 and 1.99 $l \cdot h^{-1}$, respectively. However, rates on total particles were not significantly different by day or location. Clearance rates on fluorescent particles varied significantly with day with rates on June 3 higher than those on June 9 ($P < 0.0001$). Rates on fluorescent particles also varied with lease, with rates significantly higher at Webb Cove than at Camp Island or Ray Point ($P < .0001$). Clearance rates on non-fluorescent particles did not significantly vary with day. Therefore, it is concluded that higher clearance rates on total particles observed by the mussels at Webb Cove were due to their enhanced rates on phytoplankton rather than changes in their feeding rates on non-fluorescent particles.

The ratio of feeding rates on phytoplankton to rates on non-fluorescent particles (selectivity coefficient) was the lowest on June 9, correlated with the lowest clearance rates of all the experiments (1.69 $l \cdot h^{-1} \cdot g^{-1}$).

TABLE 3.

Comparison between flow cytometer (FCM) and settling chamber counts of phytoplankton cells. All samples taken 6/10/87 along field transect into Webb Cove, and were prefiltered with a 53 μm plankton net.

FCM Cells ml-l	Settling Chamber Cells ml	Percent Difference
3508	5210	−32.7
3853	5303	−27.3
4228	4095	+3.2
3328	5518	−39.7
2499	3029	−17.5
2515	2839	−11.4
1293	1275	+1.4
	Mean	+17.7%

TABLE 4.

Clearance rates of mussels with respect to particle type for each day. Values are means with standard deviations in parentheses.

Date	Location	N	Dry Wt. (g)	Total Particles $l\ h^{-1}\ g^{-1}$	Fluorescent Particles $l\ h^{-1}\ g^{-1}$	Non-fluorescent Particles $l\ h^{-1}\ g^{-1}$
6/2/87	Webb Cv. Outer	4	0.65 (.07)	2.70 (.88)	4.45 (.11)	2.20 (.77)
6/3/87	Webb Cv. Inner	6	0.41 (.09)	3.33 (.79)	5.09 (.90)	2.96 (.79)
6/4/87	Camp Is. Outer	6	0.54 (.08)	2.19 (.87)	3.13 (1.22)	1.83 (.83)
6/5/87	Camp Is. Inner	5	0.47 (.10)	2.14 (1.01)	3.06 (1.38)	1.96 (.92)
6/8/87	Ray Pt. Outer	5	0.73 (.12)	2.34 (1.05)	3.34 (0.72)	2.14 (1.10)
6/9/87	Ray Pt. Inner	6	1.07 (.26)	1.69 (.93)	1.76 (1.09)	1.66 (.93)

In order to determine on which days clearance rates were significantly enhanced on phytoplankton vs. non-fluorescent particles, paired sample one-tailed t-tests were performed for each experiment. Clearance rates were significantly higher on phytoplankton on June 2 and 3 (Webb Cove) and June 8 (Ray Point) ($P < 0.05$). On June 4 and 5 (Camp Island), low clearance rates in one individual on each day (0.63 $l \cdot h^{-1}$, June 4 and 0.76 $l \cdot h^{-1}$, June 5) contributed to high variance and non-significance in the t-tests on those two days.

A transect of water samples pumped along a water depth gradient into a commercial lease site (even numbers 0.5 m off the bottom, odd numbers 0.5 m from the surface, Fig. 2) revealed a trend toward reduced numbers of fluorescent particles (phytoplankton) on the lease, especially in the bottom waters (stations 8, 10 and 12, Table 5, Fig. 6). Food quality decreased in bottom waters (19–23% fluorescent particles) vs. surface waters (24–27% fluorescent particles) at all farm stations except the inner one (under 2 m depth) in which food quality was consistently low (16% fluorescent particles). The effects of mussels on food availability at selected sites (5 m depth and 2 m depth) are summarized in Table 6. A reduction of about ⅓ of food available to the mussels was observed along a horizontal gradient into the lease. However, the possibilities of stratification and other factors known to influence phytoplankton gradients should be considered in the interpretation of this data.

In the only other study on the food habits in *M. edulis* Field (1911) examined the digestive tracts of 50 individuals. He identified 29 species of diatoms and 9 species of protozoa. His results are presented in Table 7 with minor corrections and species sizes added. His analyses actually included 29 diatoms, 6 dinoflagellates, 1 silicoflagellate and 2 tintinnids. With only 3 exceptions (noted on Table 7) all scientific names are still valid. He also noted that detritus made up the bulk of gut contents. In the present study, detritus and bacteria also formed a major portion of the gut contents along with unidentified pennate diatoms. This is not surprising as the role of detritus as a major food source for bottom dwelling invertebrates has long been recognized. Blegvad (1914) listed all lamellibranchs as 'true detritus eaters' (see also Field 1922).

Analysis of gut contents is difficult and the loss of the more fragile cells and quickly digested species makes a complete analysis almost impossible. The variety of intact and identifiable cells found in the gut does, however, suggest that the technique is useful. Our results and those of Field (1911) (Table 7 and 8) indicate that *M. edulis* feeds commonly on large particles. This result may be misleading in that the smaller cells are more readily digested and not identifiable in the guts. In a laboratory experiment, mussels were fed on a pure culture of the cryptomonad *Chroomonas salina* (Wislouch Butcher clone 3C) and the gut contents examined immediately afterwards and at short intervals for the presence of whole cells. After only one hour, no cryptomonads were resolvable under microscopic examination. It is likely that other easily digested species including those which serve as prime food sources are overlooked through gut analyses. Examination of the algal species present in the water column at the time of samplings indicate that the mussels were feeding on all particle

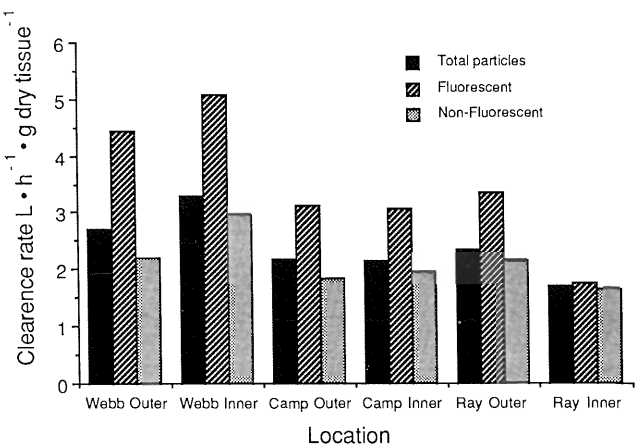

Figure 4. Clearance rates of mussels (L h^{-1}) with respect to particle type (total particles, fluorescent particles, nonfluorescent particles) for each sample location. Sample dates (1987) are the same as in Fig. 3.

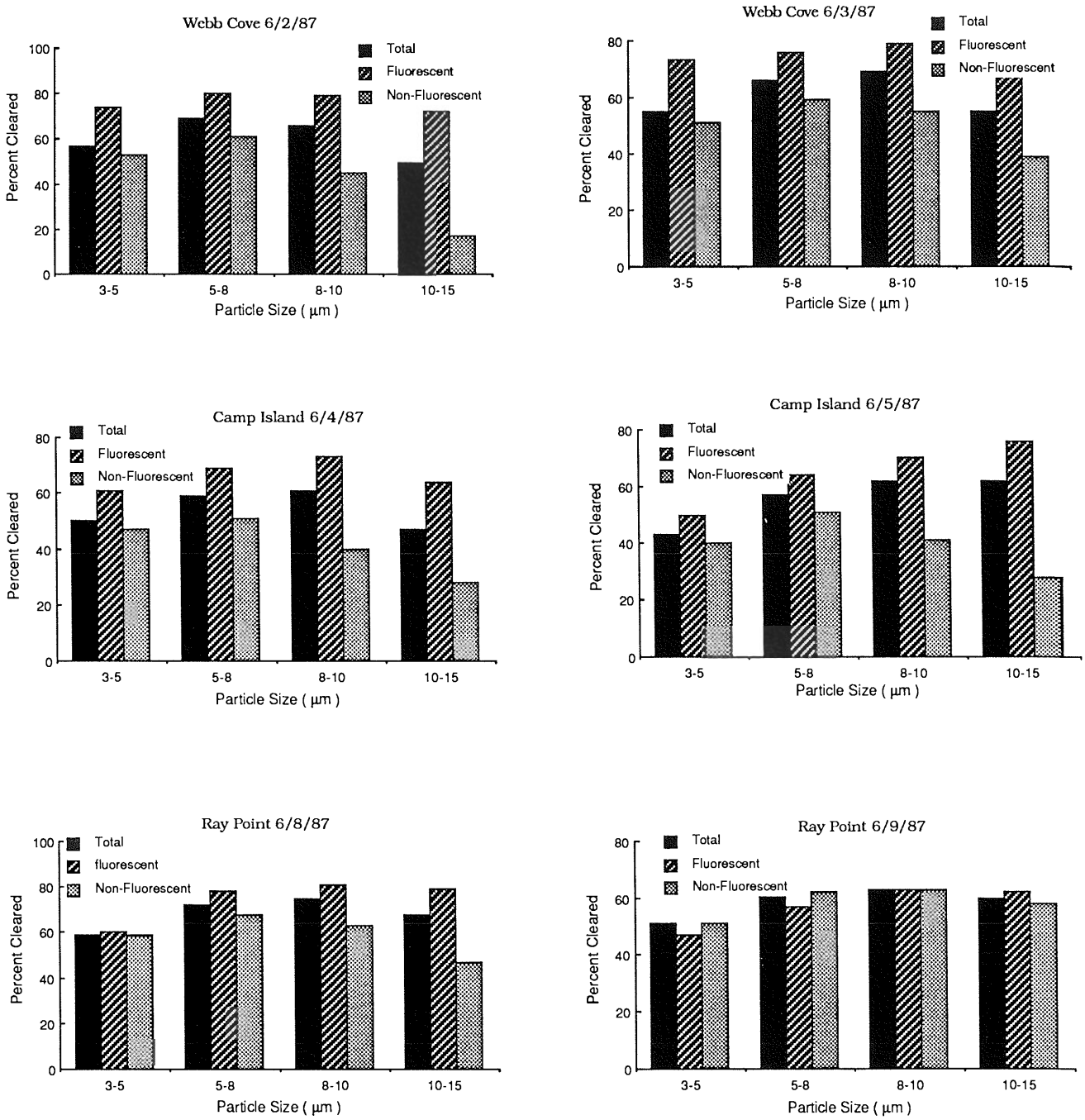

Figure 5. Percent of particles cleared during 1 hr feeding experiments with respect to particle type and size (equivalent spherical diameter). Values are means of 6 replicates except June 5, 8 (5 replicates) and June 2 (4 replicates).

types present. There was no obvious seasonal variation in food items present with the exception of *Dinophysis* spp. which were generally absent during winter months (November–March). While the mussels obviously take advantage of the phytoplankton in the water column, it is evident that they also depend, to a large extent, on resuspended bottom sediment rich in detrital matter and benthic algal species. Over ⅔ of the algal species identified by Field and in the present study are benthic in nature.

DISCUSSION

The use of the flow cytometer has allowed us to examine mussel feeding behavior with respect to particle type, and has revealed significant differences in mussel clearance

TABLE 5.

Large-scale horizontal variability in food availability along a 600 m transect into a seeded mussel lease, June 10, 1987. All water samples prefiltered with a 53 μm mesh. Concentration is particles ml^{-1}.

Station	Water Depth (m)	Total Particles	Fluorescent Particles	Non-fluorescent Particles	% Fluorescent	Bacteria $\times 10^6 l^{-1}$
1	6	11330	3113	8217	27	1256
2	6	13550	3634	9916	27	1518
3	5	13154	3508	9646	27	1523
4	5	17283	3853	13430	22	1468
5	3	15962	4228	11734	26	1548
6	3	15595	3614	11981	23	1654
7	2.7	13727	3328	10399	24	1841
8	2.7	12473	2645	9828	21	1806
9	2	9690	2499	7191	26	1957
10	2	13482	2515	10967	19	1619
11	1.7	7910	1293	6617	16	1897
12	1.7	8303	1352	6951	16	1443

rates on phytoplankton vs non-fluorescent particles, independent of particle size. Other workers (Lucas et al. 1987) found that mussels clear particles at similar rates in size ranges of 3–30 μm, but due to instrument limitations, feeding rates could not be distinguished with respect to particle type. They found a maximum resource yield, estimated by the C/N ratio, in natural particles in the size range of 5–25 μm diameter.

Our data indicates that a threshold for feeding selectivity occurs: when food quality estimated as percent fluorescent particles decreased below 20% (June 9), the mussels lost their ability to selectively filter out phytoplankton from mixed particle assemblages. Selective feeding would have the net result of leaving in suspension non-fluorescent inorganic particles with a decrease in food quality over the mussel bed. The field transect supports the results of the feeding experiments, with reduced food quality above the mussel bed at the commercial lease site. The consequences of feeding selectivity, and a possible threshold for this to occur, are that mussels on the outer edge of a lease site may have a higher food resource and higher feeding rate than those further inside the lease. Reductions in food quality may lead to a depression of feeding rates, a loss of the ability to select algae from silt particles, and slower growth of seeded mussels at inner lease sites.

Other workers (Famme and Kofoed 1983, Newell and Thompson 1985, Bayne and Widdows 1978) observed reduced feeding rates and particle retention in mussels during the spawning period, possibly due to a "shunt flow" of water bypassing the filaments of the gill demibranches. Since the experiments were performed in June, which is the normal spawning period for Maine mussels, it is possible that low clearance rates and the absence of a feeding selectivity response on June 9 were correlated with spawning condition in those mussels. Mussel mean dry flesh weight was 1.07 g on June 9 vs. 0.41 g on June 3, the days which were significantly different in clearance rates on fluorescent particles. Since mussel reproductive effort increases with mussel size (Bayne 1976), there is a chance that mussels on June 9 were reproductively active. No release of gametes

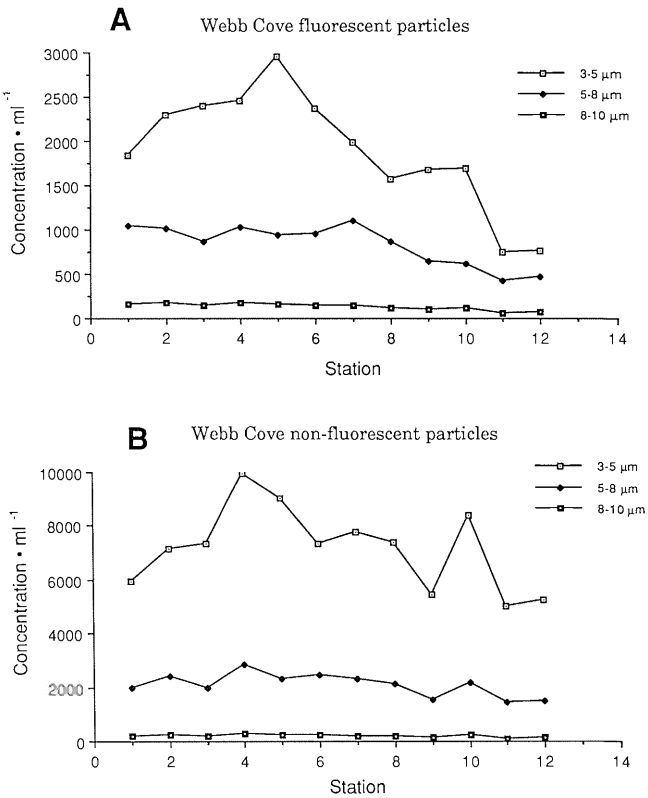

Figure 6. Large-scale horizontal variability in food availability along a 600 m transect into a seeded lease area, June 10, 1987. See text, Fig. 2 and Table 5 for details. Concentration of particles with respect to particle size for phytoplankton (A) and nonfluorescent particles (B).

TABLE 6.

Outer vs. inner cove sites: effects of mussels on food availability. Sample stations are the same as Fig. 1, all samples taken on June 10, 1987.

Station	Quality (% Fluorescent)	FCM No. Cells ml^{-1}	Mean	Settling Chamber (cells ml^{-1})	Mean	$\mu g\ Cl^{-1}$	Mean	$\mu gN1^{-1}$	Mean
3	27	3508	3681	5210	5257	462	445	57.3	57.0
4	22	3853		5303		428		56.7	
9	26	2499	2507	3029	2934	296	302	26.7	32.4
10	19	2515		2839		307		38.1	
Percent Difference			31.9		44.2		32.2		21.5

TABLE 7.

Organisms identified in gut contents of the mussel, *Mytilus edulis*, by Field (1911).

Species	Size (μm)	Habitat	Occurrence
Bacillariophyceae			
Actinoptychus undulatus	20–86	B	common
Amphipora lepidoptera	(240–280) × (32–36)	B	very common
Amphora proteus	40–60	B	frequent
Biddulphia favus	86–100; pervalver axis 40–50	P	frequent
Coscinodiscus excentricus	40–140; mostly 100	P	frequent
Grammatophora marina	60–70 × (10–12)	B	frequent
Hyaladoiscus subtilis	40–115	B	very common
Melosira sculpa	chain	B	very common
Navicula didyma	(50–90) × (17–36)	B	common
Navicula lyra	(70–120) × (27–40)	B	occasional
Navicula lanceolata	36–44	B	frequent
Navicula splendida var. *puella*	(70–160) × (24–40)	B	occasional
Nitzschia sigma	(200–240) × (10–12)	B	common
Nitzschia sigma var. *rigida*	(120–180) × (7–8)	B	common
Nitzschia sigma var. *sigmatella*	450 μ long	B	common
Pleurosigma affine	(140–220) × (28–36)	B	frequent
Pleurosigma angulatum	(128–280) × (32–36)	B	frequent
Pleurosigma balticum	(236–500) × (28–32)	B	common
Pleurosigma decorum	(220–260) × (24–28)	B	common
Pleurosigma elongatum	(130–380) × (24–30)	B	common
Pleurosigma naviculaceum	(80–100) × (15–20)	B	very common
Rhabdonema adriaticum	(40–100) × (10–15)	B	frequent
Rhabdonema arcuatum	(30–70) × (12–15) axis (50–250)	B	frequent
Rhizoselenia setigera	(8–25) length up to 300	P	very common
Stephanopyxis appendiculata varturris	40–90 μ long	P	occasional
Surirella ovalis var. ovata[1]	length 45–80	B	common
Synedra gallionii	(165–300) × (10–13)	B	very common
Tabellaria fenestrata	17–21	B	frequent
Dinophyceae			
Distephanus speculum	20–60	P	common
Exuviaella lima[2]	(32–50) × (20–28)	P	very common
Exuviaella marina[2]	(32–50) × (20–28)	P	common
Glenodinium compressa	24–64	P	common
Peridinium[3] *divergens*	(80–84) × 56	P	common
Prorocentrum micans	(35–70) × (20–50)	P	very common
OTHER			
Ceratium fusus	(200–300) × (15–30)		frequent
Tintinnopsis beroidea			very common
Tintinnopsis davidoffi			common

[1] now considered two species
[2] genus now *Prorocentrum*
[3] genus now *Protoperidinum*

TABLE 8.

Organisms identified in gut contents of the mussel, *Mytilus edulis*.

Species	Size (μm)	Habitat[a]	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

[a] B = Benthic; P = pelagic

was observed during the feeding experiments. Mussel tissues were not examined histologically.

By prefiltering the water, a small aperture could be used on the flow cytometer providing resolution of clearance rates at small size scales. Problems with prefiltering include the removal of large diatoms and for this reason, the field transect data should be interpreted with caution. Since the flow cytometer counted heterotrophic flagellates as non-fluorescent particles, the experiments underestimated feeding rates on other potentially nutritious particles. However, settling chamber counts made on sub-samples of water from each experiment revealed a dominance by autotrophic diatoms, especially *Chaetoceros debile, Skeletonema costatum, Nitzschia pungens, Leptocylindrus minimus, C. compressus, Thalassiosira decipiens, C. perpusillus, C. gracilis,* and *Dinobryum* sp. common. In all samples, diatoms were an order of magnitude more abundant than *Cryptomonas* sp. and micro-flagellates for cells under 15 μm when examined at low power (560×). These data are in general agreement with the gut analyses which indicated a preponderance of diatoms.

At low concentrations of total seston, Bayne et al.

(1987) found that the quality of a mussel's diet is best expressed as organic matter/unit volume of particles, and that scope for growth was a function of dietary quality over the short term. Our data supports those conclusions, with an additional mechanism, the selective feeding on phytoplankton over non-flourescent particles, operating to maximize energy gain during periods of relatively high food quality at low seston concentrations. At low food quality, mussels may compensate for the absence of feeding selectivity by increasing gut fullness and absorption efficiency (Bayne et al. 1987).

It is unclear how the mussels can select algal cells over inorganic particles of equivalent spherical diameter, in the absence of pseudofeces production. Previous workers have concentrated on the role of the labial palps in this regard (Kiorboe et al. 1980, Kiorboe and Mohlenberg 1981, Newell and Jordan 1983). If selection is taking place on the gills, it may be correlated with factors such as cell shape, electrical charge, or chemical cues such as algal ectocrines (Ward and Targett 1988). If chemical cues are involved, the absence of feeding selectivity at low food quality may be due to the dilution of chemical cues below a certain threshold for a feeding selectivity response. The threshold for feeding selectivity will be examined in future experiments.

The present study clearly shows a feeding selectivity response in *M. edulis,* and a threshold at which this occurs. Siting of mussel bottom culture leases should therefore consider both the quantity and quality of sestonic food available to the mussels. Sites adjacent to intertidal mudflats subject to wind wave-induced resuspension of inorganic particles may be suboptimal for mussel feeding and growth. Sites with high proportions of algal cells (over 20% fluorescent particles as estimated with the flow cytometer) appear to be the most promising. The role of larger phytoplankton cells in the nutrition of mussels should also be considered in future experiments.

ACKNOWLEDGMENTS

This research was supported by the National Science Foundation SBIR Award ISI8660201. Thanks are due to Dick Larrabee, Bruce Davis and Jack Hamblem for field support at their mussel farm sites. We also thank R. F. H. Freeman and V. M. Bricelj for comments on the manuscript.

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