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Impact of fouling organisms on mussel rope culture: interspecific competition for food among suspension-feeding invertebrates

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Abstract: The clearance rate of natural planktonic assemblages was measured for the blue mussel *Mytilus edulis* (L.) and a co-occurring fouling community from mussel rope cultures using flow cytometry. Blue mussels had significantly higher clearance rates for all particle types and size classes. In addition, blue mussels showed selective feeding in favor of small phytoplankton (3–5 μm), whereas the solitary ascidian *Ciona intestinalis* (L.) and the suspension-feeding gastropod *Crepidula fornicata* (L.) showed preferential selection for large phytoplankton (> 16 μm). Clearance rates for large phytoplankton by these members of the fouling community were, however, always lower than blue mussels. Under conditions where food is not a limiting factor, interspecific competition for food by the associated fouling community should not significantly limit the yield of mussels.

Key words: *Botryllus*; *Ciona*; Competition; *Crepidula*; Filter-feeding; Flow cytometry; Mussel; *Mytilus*; Tunicate

INTRODUCTION

Competition for space is often viewed as the major limiting resource for sessile suspension-feeding invertebrates (Connell, 1961; Dayton, 1971; Harger, 1972). Experimental studies have documented significant changes in the density-dependent growth rate of suspension-feeding bivalves (Peterson, 1982; Okamura, 1986; Peterson & Black, 1987), but distinguishing whether space and/or food was the limiting factor is difficult. Experimental models to discriminate between space and food limitation, based on self-thinning, have recently been described (Fr chet te & Lefavre, 1990), and work by Buss (1979), Buss & Jackson (1981), and Okamura (1984, 1985) have demonstrated competition for food among encrusting and arborescent bryozoans. There is additional evidence of food limitation among suspension-feeders in coral reef flats (Glynn, 1973), cryptic reef habitats (Buss & Jackson, 1981), and in large mussels beds (Wildish &

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Kristmanson, 1984, Fréchette & Bourget, 1985). Large-scale field experiments conducted by Peterson & Black (1987) suggested that those bivalves on tidal flats that are immersed first on the flood tide will deplete suspended particulate food in incoming water. Fréchette et al. (1989) found a significant reduction in phytoplankton concentration in the boundary layer close to intertidal beds of blue mussels *Mytilus edulis* (L.), while Wildish & Kristmanson (1984) found similar results for both blue mussels and northern horse mussels *Modiolus modiolus*. They hypothesized that depletion of food in water overlying extremely dense mussel aggregations could constrain the areal extent and shape of the beds in relation to oncoming flow. In agreement with this hypothesis, Newell (1990) recently demonstrated that growth rates of *M. edulis* were significantly higher at the edge than the middle of mussel beds of > 20 m in diameter. These studies address exploitative competition from an ecological perspective; however, competitive interactions related to space or food will also be of interest to those aquaculturists who depend upon natural seston to supply food to fast-growing post-metamorphic bivalves. Energetic costs are high during this period of growth and competition for food by fouling communities could have a significant impact on commercial yields. For those aquaculturists who practice mussel rope culture, effects of food limitation may be eliminated by having mussels in the water column above any food depleted zone; however, if the stocking density of mussels is high enough, food limitation could still occur (Fréchette & Lefaivre, 1990). Additionally, food limitation in mussel rope cultures is not directly supported by a report of mussel rope culture yield an order of magnitude higher than wild mussels (Rodhouse et al., 1985).

Mussel and oyster rope cultures are constantly submerged and become fouled by solitary and colonial ascidians, barnacles, hydroids, bryozoans, filter-feeding gastropods, and several species of seaweed or kelp (Arakawa, 1990; Figueras, 1990; pers. obs.). In Maine, common members of the rope culture fouling community include the ascidians *Botrylloides aureum*, *Botryllus schlosseri* (Pallas), and *Ciona intestinalis* (L.), the barnacle *Semibalanus balanoides* (L.); the bryozoans *Electra pilosa*, *Membranipora unicornis*, and *Bugula turrita*; and the common Atlantic slipper snail *Crepidula fornicata* (L.). These sessile suspension-feeders intercept or filter particles from the water column and food acquisition is strongly dependent upon the nature and magnitude of particle transport (Jørgensen, 1966; LaBarbera, 1984).

Particle selection by suspension-feeding bivalves based on particle size (Shumway et al., 1985; Newell et al., 1989; Lesser et al., 1991), particle type (Newell et al., 1989), and the presence or absence of algal metabolites (Ward & Targett, 1989) has been demonstrated. Any assessment of exploitative competition among suspension-feeders must consider the availability, character, and size of particulate food resources since resource partitioning in these communities may limit the intensity of these competitive interactions (Schoener, 1974). In a study on the uptake of suspended particles by a fouling community, Mook (1981) found that a large range of particles (1–40 μm) could be utilized, but the use of size alone may not be sufficient to assess adequately resource partitioning by a suspension-feeding community. Recent work by Newell et al. (1989)

utilized flow cytometry to assess the effects of detritus, phytoplankton, and particle size on particle selection and feeding rates in *M. edulis*. Mussel rope cultures experience the full spectrum of food resources due to tidally driven resuspension of particulate matter from the benthos, and in this paper we utilize flow cytometry to examine resource partitioning and the potential for interspecific competition among blue mussels and the associated fouling community of rope cultures.

MATERIALS AND METHODS

Specimens of the ascidians *B. schlosseri* and *C. intestinalis*, the barnacle *S. balanoides*, the gastropod *C. formicata*, and the mussel *M. edulis* were collected from rope cultures growing at Abandoned Farms, Walpole, Maine, USA, in September 1990. All samples represented sizes typical of those found on an 1-yr-old rope culture or seeded bottom area (Rodhouse et al., 1985; E. Myers, pers. comm.). Measurements of clearance rates were performed on individual animals ($n = 5-6$), except in the case of *B. schlosseri* where five 1-cm² pieces of this colonial ascidian were used (a piece of this size includes a rosette of zooids with their common exhalent siphon). Animals were cleaned of all epizoic organisms and maintained in unfiltered running seawater from Boothbay Harbor, Maine, USA, prior to use in experiments. Animals were not fed any supplementary food. Prior to feeding experiments, all animals were allowed to purge themselves in filtered seawater (0.4- μ m Gelman glass filter) for 24 h. Feeding experiments were carried out at 10 °C (ambient temperature of seawater at the time of the experiments) within 1 wk of collection. Natural seawater from Boothbay Harbor was collected and characterized by flow cytometry (see below) the day of the experiment. Individual specimens were placed in beakers with seawater and gently aerated to maintain a homogeneous mixture of particles. Control beakers, without animals, were run simultaneously to correct for any algal cell division during the experiment. Experiments lasted from 30 min to 3 h depending upon the species, with samples taken from experimental and control beakers at the end of the experimental period.

The composition of particles in the water samples was analysed by flow cytometry based on the differences in fluorescence patterns from their respective photosynthetic pigments and/or particle size from forward angle light scatter as described previously (Shumway et al., 1985; Cucci et al., 1985). Briefly, we used a Coulter Epics V flow cytometer with a single Argon ion 5-W laser having an excitation wavelength of 514 nm and 1000 mW of power. Fluorescence derived from each particle is split by a 590 nm dichroic mirror and is received by two photomultiplier tubes located at 90° to the intersection of the laser beam and sample stream. One photomultiplier tube receives a wavelength spectral region of > 630 nm such as would result from chlorophyll emission, and the other receives shorter wavelengths (530–560 nm) such as would result from phycoerythrin and phycocyanin emission. Using this technique, we could discriminate particle type based on cell size (3–5, 5–8, 8–16 and > 16 μ m) and relative chlorophyll content. Particles containing chlorophyll were presumably phytoplankton,

while nonfluorescent particles were considered to be detrital particles. Clearance rates were calculated by the method of Coughlan (1969), and presented as clearance rates per individual ($\text{particles} \cdot \text{ml}^{-1} \cdot \text{h}^{-1} \cdot \text{ind}^{-1}$) rather than on a weight-specific basis. The question asked in this study is what is the effect of the total number of commonly found fouling organisms on food acquisition by mussels? We are interested in the total number of particles obtained over time by any individual, thus normalizing these rates to mass is not related to the practical application of this study. For instance, on a weight-specific basis, barnacles exhibit the highest rates of feeding, but that does not provide information about their actual impact on seston depletion and mussel feeding as a population. Since there is excellent uniformity of mass within species and large differences in mass between species, we believe that comparing weight-specific clearance rates between species would be misleading since we could not account for any allometric effects of size on feeding rates within any species.

STATISTICAL ANALYSES

Clearance rates of natural assemblages for all species were compared with a two-way ANOVA at a significance level of 5% (Sokal & Rohlf, 1981). No unequal variances were detected using the F_{\max} test for the ANOVA (Sokal & Rohlf, 1981), and where significant treatment effects occurred, the Student–Newman–Keuls (SNK) multiple comparison test was applied at the 5% significance level to identify individual differences among the data sets.

RESULTS

A description, by particle type and size range, of a typical natural seston assemblage used for these feeding experiments is given in Table I. As particle size increases the total particle count decreases, and the percentage of phytoplankton particles increases. During a typical experiment, 27–65% of all particles were cleared. The incubation times were varied to insure that particle concentration did not drop below a critical point where feeding rates would change in response to decreased particle concentration. Also,

TABLE I

Description of a typical natural assemblage of particles used in these feeding experiments by size class and particle type.

Size (μm)	Total particles	Nonchlorophyll particles (%)	Chlorophyll particles (%)
3–5	18 719	17 097 (91)	1 622 (9)
5–8	1 820	1 476 (79)	375 (21)
8–16	720	303 (42)	418 (58)
> 16	224	47 (20)	178 (80)
Total	21 483	18 973 (88)	2 593 (12)

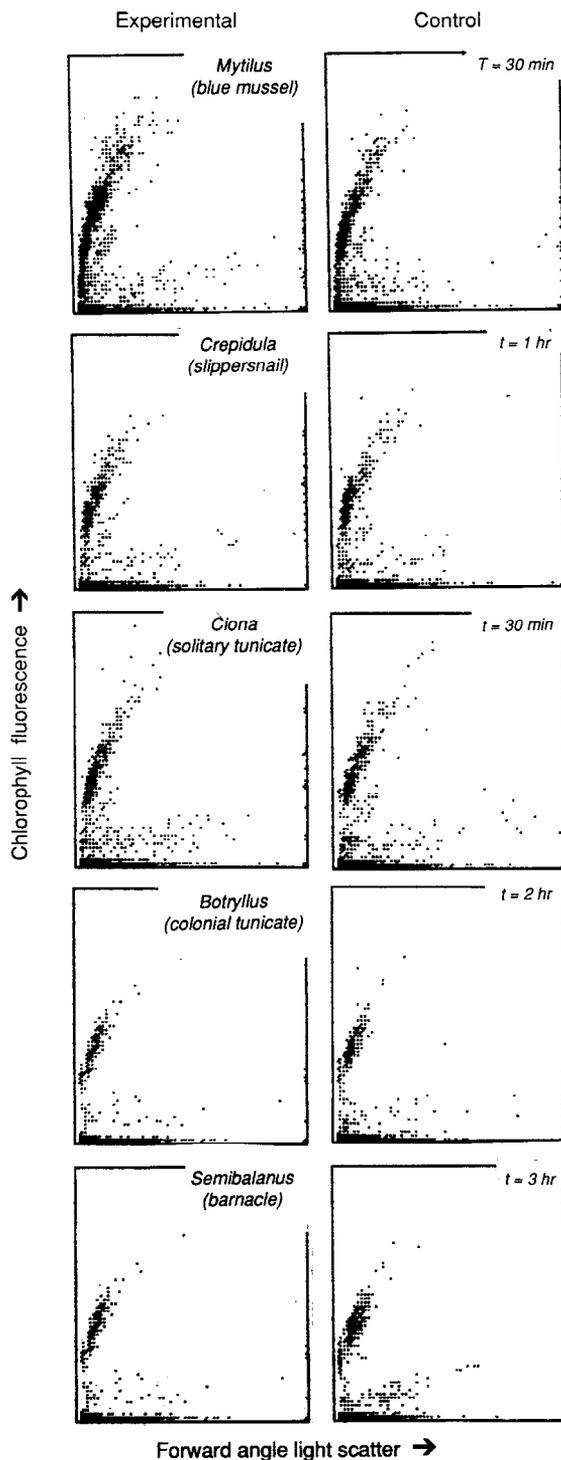


Fig. 1. Bivariate plots showing relative changes in particulate numbers within natural assemblages of particulates due to clearance by suspension-feeding invertebrates. Each dot represents a particle. Chlorophyll fluorescence is on ordinate scale and forward angle light scatter, or size, is on abscissa. Plots on left-hand side represent particle concentration at beginning of experiment, while plots on right-hand side represent particle concentration after a period of feeding.

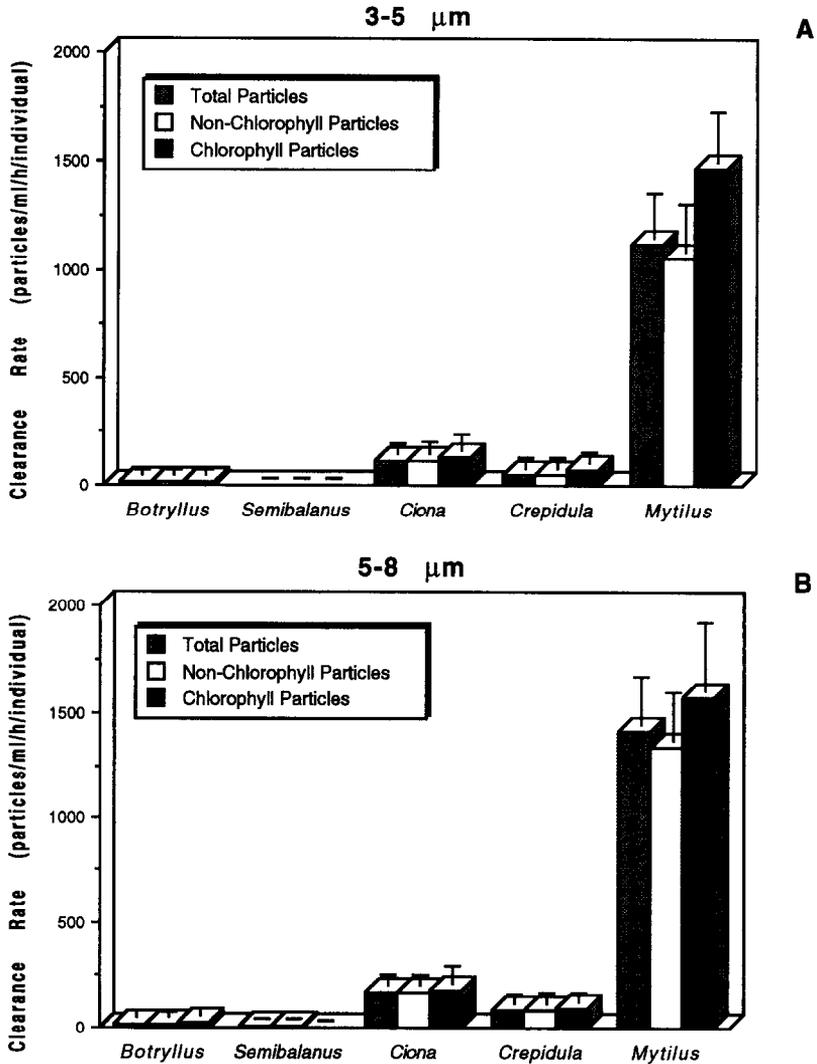


Fig. 2. Histograms of clearance rates (particles \cdot ml⁻¹ \cdot h⁻¹ \cdot ind⁻¹) for all experimental species $\bar{x} \pm$ SD): A, 3–5; B, 5–8; C, 8–16 and D, > 16 μm .

experiments in still water do not account for any changes in feeding rate due to direct effects of flow on feeding (e.g., flow-induced back pressure), or the indirect effects of water flow on particle delivery. Changes in the flow regime and subsequent particle availability would likely occur on a rope culture as a result of the complex flow patterns generated by the influence of neighbors (Johnson, 1986; Okamura, 1988).

Typical results for all species tested are presented in Fig. 1. In all cases there was a decrease in particles exhibiting autofluorescence (phytoplankton) and in those that

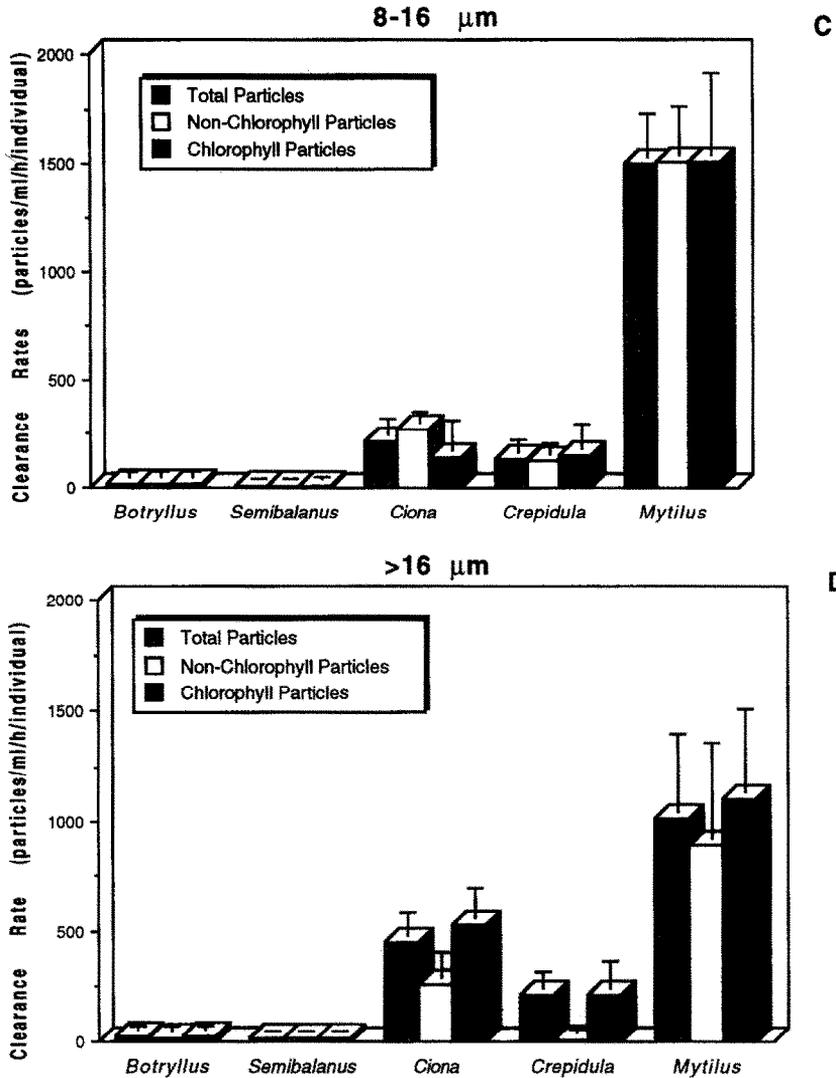


Fig. 2. For legend, see p. 96.

were nonfluorescent but recognized by their forward angle light scatter signal (detritus and nonorganic particles). Note the apparent increase in particle concentration for *S. balanoides* and *B. schlosseri* (Fig. 1), particle clearance for these organisms is slower than the division rates of the phytoplankton communities. Correcting the treatment vial using the control allowed us to calculate clearance rates for these species. For clearance rates of total particles and nonchlorophyll particles, the effects of species, size range of particles, and the interaction of these two variables were all significant in the

two-way ANOVA, while for chlorophyll-containing particles, only species and the interactive effects exhibited significant differences (Table II). The interactive results for the clearance of chlorophyll-containing particles shows that the size of chlorophyll particles influences clearance rates in some or all of the species tested despite the absence of an independent effect of chlorophyll particle size on clearance rate (Table II). Multiple comparison testing and the interactive incidence tables from the two-way ANOVA show that *M. edulis* exhibits significantly higher rates of clearance across all size classes and particle types, especially chlorophyll particles (SNK: $P < 0.05$, Fig. 1). *B. schlosseri* and *S. balanoides* exhibit significantly lower rates of clearance for all particle types and sizes tested in these experiments (SNK: $P < 0.05$, Fig. 2), and *C. fornicata* and *C. intestinalis* have intermediate clearance rates that are significantly higher than both *B. schlosseri* and *S. balanoides*, lower than *M. edulis*, and significantly different from one another in all size classes (all comparisons, SNK: $P < 0.05$). Although *M. edulis* feeds on all particle types, the preferred size range from the interaction tables is 5–16 μm and particles sizes above or below result in lower feeding rates (Fig. 2), except for chlorophyll particles where high rates are also observed in the smallest size class (3–5 μm). *S. balanoides*, *C. intestinalis* and *C. fornicata* show a steady increase in feeding rates on all particle types as size increases (Fig. 2) except with particles of

TABLE II

Results of two-way ANOVA for clearance rate (particles·ml⁻¹·h⁻¹·ind⁻¹) of total, nonchlorophyll, and chlorophyll particles based on species and cell size (3–5, 5–8, 8–16, and > 16 μm).

Total particles	df	F value	P value
Species (A)	4	413	0.0001
Size range (B)	3	4.05	0.0095
Interaction (A * B)	12	6.34	0.0001
Residual	92	NA	NA
Nonchlorophyll particles (detritus and inorganic particles)			
	df	F value	P value
Species (A)	4	323	0.0001
Size range (B)	3	7.17	0.0002
Interaction (A * B)	12	4.71	0.0001
Residual	92	NA	NA
Chlorophyll particles (phytoplankton)			
	df	F value	P value
Species (A)	4	330	0.0001
Size range (B)	3	0.32	0.8147
Interaction (A * B)	12	4.99	0.0001
Residual	92	NA	NA

df, degrees of freedom; NA, not applicable.

> 16 μm where there is a decrease in the clearance rate of *C. intestinalis* and *C. fornicata* on nonchlorophyll particles (Fig. 2d).

DISCUSSION

Exploitative competition and resource partitioning of food amongst suspension-feeders are important deterministic processes that affect the community structure of suspension-feeding communities (Buss, 1979; Stuart & Klumpp, 1984). The successful procurement of food can influence the outcome of direct (interference) competition, such as overgrowth, that occurs within encrusting invertebrate communities (Sebens, 1986). Similarly, acquisition and competition for food will affect the commercial yield of mussel rope culture. These feeding experiments, with natural particulate assemblages, show that *M. edulis* has higher feeding rates, for all particle types and sizes, than its major competitors on rope cultures. These rates are typical for blue mussels and, in the absence of food limitation, mussels should be able to sustain high feeding rates and high yields on rope cultures. Mussels maintain high feeding rates on phytoplankton within the lowest size class (3–5 μm); however, phytoplankton average $\approx 9\%$ of all particles in that size class, and only 12% for all size classes combined. Although feeding rates are reduced in the > 16- μm size class, the high proportion of large phytoplankton particles is probably important in the nutrition of these mussels as suggested in a previous study on mussels in bottom cultures (Newell et al., 1989).

The colonial ascidian *B. schlosseri* and the barnacle *S. balanoides* are not significant competitors for food with mussels. Colonial ascidians can filter particles as small as 1 μm , and particles 2–3 μm in size are retained with high efficiency (Jørgensen, 1966; Newell, 1979; Riisgård, 1988). The clearance rates of all size classes of particles tested were low, and a more significant effect on mussels comes from interference competition as colonial ascidians can easily overgrow mussels to the point where opening of the valves, and therefore feeding, is compromised (pers. obs.). Active clearance of particles in all size classes by barnacles was the lowest observed. Barnacles can clear a wide range of particles down to 2 μm (Jørgensen, 1966); however, in our experiments barnacles performed poorly in the 3–5- μm class relative to the other particulate size classes. It would take ≈ 500 barnacles, at the clearance rates measured for total particles in these experiments, to match the capacity of one mussel. Barnacles are generally regarded as nonselective feeders, although positive selection for phytoplankton has been reported (Jørgensen, 1966). Under ambient conditions, i.e., with water flow, barnacles can also feed passively and with higher fluxes of particles would be expected to exhibit higher clearance rates of phytoplankton. Clearance rates of total particles by *C. fornicata* in this study are very similar to those reported by Newell & Kofoed (1977). The slipper snail also feeds on a wide range of particles by trapping large particles on a mucus filter covering the incurrent aperture, and filtering medium- and small-particles with the gill (Jørgensen, 1966; Newell, 1979). There does appear to be some active selection against large (> 16 μm) nonchlorophyll particles in this

study, and Jørgensen (1966) has described a mechanism of particle rejection for large particles in *C. fornicata*. Comparing the clearance rates of mussels and slipper snails shows that it would take approximately four slipper snails (mean dry weight = 0.018 g) to equal the clearance rate of one mussel (mean dry weight = 0.83 g). *C. intestinalis* is known as a continuous feeder that can regulate its clearance rates (Robbins, 1984), maintain 100% filtering efficiencies at high particulate concentrations (Randløv & Riisgård, 1979; Robbins, 1984), and filter particles from $\geq 2 \mu\text{m}$ (Jørgensen, 1966; Newell, 1979). *C. intestinalis* exhibited the highest clearance rates of the fouling organisms examined, and showed some selection against large ($> 16 \mu\text{m}$), nonchlorophyll particles as did the slipper snail. Following the examples above, it takes approximately three *C. intestinalis* (mean dry weight = 0.22 g) to match the clearance rates of one mussel. This solitary ascidian can contribute a significant amount of dry biomass, as much as 25%, in a single rope culture (unpubl. data), and in terms of numbers and feeding capacity, represents the most significant competitor for a common resource which might become important in food-limited situations.

The results presented here do support resource partitioning in the larger size classes of phytoplankton among the species used in this study; however, *M. edulis* selects positively for phytoplankton and maintains the highest clearance rates in all size classes. Although the fine scale resource partitioning does not appear to be a significant component of the overall competition for food resources, it was only through the use of flow cytometry that we were able to detect these differences. For mussel rope culture, it appears that in the absence of significant food limitation, mussels should always do better in regard to feeding. If food becomes limiting, the initial impacts would manifest itself within the fouling community rather than the cultured mussels due to the tremendous biomass of mussels on any rope culture. As for any aquaculture endeavor, site selection becomes a critical issue. Choosing highly productive and energetic sites should theoretically provide sufficient food to support high yields.

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