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Variable retention of diatoms on screens during size separations

Abstract—Particles smaller than filter mesh pores can collide and stick to mesh fibers, biasing size separations based only on pore diameter. The removal of flocculating diatoms (*Chaetoceros gracilis, Nitzschia angularis*) was greater than removal of a nonfloc-forming species (*Thalassiosira weissflogii*) even after including the effects of cell size. Over a 5-d period an average of 1.4% of cells of *N. angularis* were removed by 230-μm pore-diameter screens; on day 6, 7.5% of cells were removed as cells began to flocculate. The percentage of *C. gracilis* removed continually increased from 0.4 to 28% during the same period, while the removal of *T. weissflogii* was constant at 0.19% over a 10-d period. Prior to the onset of flocculation, sticking coefficients (rate of cell attachment to mesh fibers/rate striking fibers) were 0.05 for *T. weissflogii*, 0.26 for *N. angularis*, and 0.73 for *C. gracilis*. Size separations will therefore tend to concentrate more flocculent species of phytoplankton into size fractions much larger than cell diameters.

Phytoplankton, biomass, and chlorophyll are often separated into different size fractions before analysis. Separations performed with screens or mesh cannot be accomplished solely by particle straining because particles smaller than the mesh pores can strike the mesh and be removed. This retention of smaller particles increases the mass of particles retained on the mesh and overestimates the composition of the larger size fraction (Sheldon and Sutcliffe 1969; Malone et al. 1979; Logan 1993). A failure to measure differences in composition between retained and filtered size fractions could, therefore, be due to excessive retention of smaller particles on the mesh and a failure to accomplish a sharp size separation.

Research on particle removal by small pore-diameter depth filters and polycarbonate filters has demonstrated substantial alteration in size distributions due to filter clogging, variation in filtration rate, and coagulation (Sheldon and Sutcliffe 1969; Sheldon 1972; Buffle et al. 1992). The alteration of particle size distributions by screens and mesh was recently modeled with a capillary pore model (Logan et al. 1993). It was shown that for a particle size distribution separated into 31 size classes (from 0.1 to 100 μm), as much as 50% of the total particle mass (8% of the particle numbers) could be retained on a 210-μm pore-diameter filter, even though all particles were <100 μm. The importance and extent of particle removal was a function of the sticking coefficient—a measure of the efficiency of adhesion of particles to the mesh.

The purpose of this study was to measure the extent of adhesion of individual species of

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Table 1. Characteristics of phytoplankton.

Characteristic	*Thalassiosira weissflogii*	*Chaetoceros gracilis**	*Nitzschia angularis*
Size (μm)			
Max†	14 (12–17)	10 (6–14)	43 (42–45)
Min†	7 (6–9)	3 (2–4)	5 (4–10)
Avg diam (n = 20)	13	7	17
Shape	Disk	Box (with spines)	Spindle
Flocculation potential‡	FP−	FP+; cells produce large amounts of exopolymer and form loose flocs in roller bottle during late exponential growth phase	FP+; cells produce little exopolymer and form dense flocs in roller bottle at all times

* Length of spines (~50 μm) is neglected in calculations.
† Numbers in parentheses indicate ranges in size measured for these cultures.
‡ FP+ and FP− indicate presence or absence of aggregates in flocculation potential experiment with rolling cylinders.

phytoplankton to polycarbonate screens. A second set of objectives was to use the pore model to calculate sticking coefficients of phytoplankton and to examine whether these coefficients were a function of culture age. The adhesion of marine organisms to surfaces is important in particle capture by filter feeders, colonization of suspended particles on fixed surfaces, cell–cell attachment during coagulation and formation of marine snow, and biofouling of ship hulls (Rubenstein and Koehl 1977; Jackson 1990; Characklis and Marshall 1990). Screen fibers and other surfaces in seawater quickly become coated with dissolved organic molecules. We therefore pretreated the mesh with filtered seawater to provide surfaces more representative of those exposed to seawater.

Three different species of diatoms were chosen based on size and flocculation characteristics. The typical ranges in minimum and maximum sizes are shown in Table 1. Flocculation characteristics were established by monitoring the flocculation potential (FP) of batch cultures with a rolling table device (Shanks and Edmondson 1989). Each day a constant number of cells was removed from the culture, placed in a 250-ml polycarbonate bottle (6-cm diam), and coagulated at 2 rpm for up to 24 h. The formation of aggregates was qualitatively established by visually checking the contents of the roller bottle for the presence (FP+) or absence (FP−) of >1-mm aggregates (Table 1). The FP of *Chaetoceros gracilis,* a small (3 × 10 μm) diatom with curved setae (~50 μm), changed with the age of the culture. At a concentration of 5.6×10^5 cell ml^{-1}, no flocs formed in the roller bottle during the early exponential stage of the culture, but tiny (~0.5 mm) flocs formed (within 24 h) on days 3 and 4 during late exponential and stationary growth phases. Thereafter, *C. gracilis* flocculated within 1 h after transfer into the roller bottle into large, highly tenuous aggregates containing large amounts of exopolymeric material. The pennate diatom *Nitzschia angularis* (5 × 43 μm) aggregated even during the early exponential growth phase (day 1, 8.4×10^4 cells ml^{-1}) but formed denser flocs that contained little polymeric material. The disk-shaped diatom *Thalassiosira weissflogii* did not aggregate even during senescence at maximal cell concentrations (4.5×10^5 cells ml^{-1}).

The retention of these three diatoms during size separation was examined with polycarbonate screens (Spectramesh) composed of overlapping fibers 210 μm in diameter forming rectangular pores 230 μm wide. Polycarbonate screens were used because they were available in many different sizes of defined geometry and for comparison of results to previous studies (Logan 1993). Circular pieces of screens (2.4-cm diam) were cut from large sheets and placed in a 10-place vacuum manifold box containing stainless steel funnels and bases and Teflon valves (Hoefer Scientific). The screen was covered by a rubber gasket held in place by the heavy funnel to prevent leakage around the edges of the screen. All screens were soaked in filtered (0.4 μm, Nuclepore) seawater for 2 h before use. Phytoplankton were grown in f/2 media with silica (Guillard 1975) at 12°C and an irradiance of 100 μmol quanta m^{-2} s^{-1}. A

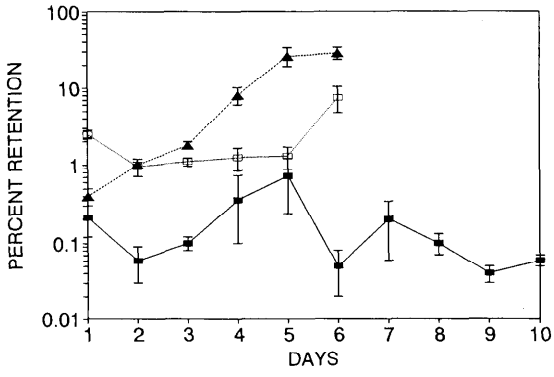

Fig. 1. Retention of three diatom species on 230-μm pore-diameter screens (■—*Thalassiosira weissflogii*; ▲—*Chaetoceros gracilis*; □—*Nitzschia angularis*). Error bars denote SD of each mean.

10-ml aliquot of culture was transferred by pipette into the funnel and gravity filtered through the screens at velocities (20 ml min^{-1}) necessary to produce laminar flow through the mesh. Laminar flow was required for the hydraulic equations used to calculate sticking coefficients (*see below*). All measurements were made in triplicate with the same culture.

The number of particles retained on the mesh was determined by measuring the fraction of chlorophyll retained on the screen. Total chlorophyll was measured by passing 2–5 ml of the sample through 25-mm glass-fiber filters (Whatman GF/F). Controls for adsorption of dissolved chlorophyll were measured with particle-free media prepared by filtration (0.4 μm). All chlorophyll concentrations were determined fluorometrically with standard methods (Parsons et al. 1984).

The relative adhesion of the different phytoplankton to the mesh was evaluated with a sticking coefficient, α, defined as the rate particles stick to a fiber to the rate they strike the fiber. For the mesh and cell sizes used in these experiments, nonaggregated particles should only be removed by interception with the fibers of the screen (Logan et al. 1993). The sticking coefficient for flow through screens can be calculated with

$$\alpha = \frac{P}{100(2R - R^2)^{3/2}}. \quad (1)$$

P is the percent of particles retained on the screen and R the pore interception number, defined as the ratio of the particle diameter to the pore diameter. The average diameter of a cell was calculated from the projected surface area for *C. gracilis* and *N. angularis* (Table 1). The arithmetic average of the two different projected surface areas (circle and cylinder) was used for *T. weissflogii*.

If cells became attached to the mesh based solely on the average sizes, Eq. 1 implies that attachment would follow the order *N. angularis* > *T. weissflogii* > *C. gracilis*. However, there was a consistently smaller percentage of *T. weissflogii* than the other two diatoms retained on the 230-μm pore-diameter mesh (Fig. 1). Over a 10-d period, an average of 0.19% of *T. weissflogii* cells were retained (range 0.04–0.72%). The low concentrations of chlorophyll measured for this species contributed to the relatively wide range of values indicated by error bars in Fig. 1.

The retention of *N. angularis* averaged 1.4% (range 0.95–2.5%) until day 6 when it increased to 7.5%. The higher retention on this final day was due to flocculation of cells. Flocculation produced larger particle sizes and therefore increased collisions of cells with the mesh fibers during filtration.

The percentage of *C. gracilis* retained on the mesh continually increased over the 6-d period from 0.4% on the first day to 28% on the sixth day. Flocs became visible in these cultures on the last 2 d. Sonication in a water bath (Ultrasonic dismembrator, model 150, Artek Corp.) decreased retention from 28 to 19%, but we were unsuccessful in completely dispersing the aggregates (data not shown). Other work with this diatom has shown that the polymeric material produced by *C. gracilis* forms stable transparent exopolymer particles (TEP) that serve to coagulate the cells (Alldredge et al. 1993). Since this material is nearly transparent, it is difficult to determine the fraction of aggregated cells without staining TEP with carbohydrate-specific stains.

The sticking coefficient reflects the relative adhesion of a particle for a surface. It is corrected (with Eq. 1) for cell size by quantifying the probability of attachment of a particle striking the mesh fiber. Two of the diatoms (*C. gracilis* and *N. angularis*) formed aggregates during the latter stages of growth in our cultures, and therefore we calculated sticking coefficients only for those days when aggregates were not initially present. *C. gracilis* had

the highest adhesion to the screen mesh of the three species based on sticking coefficients using the average cell size (Table 2). During the first 3 d, α = 0.73 (range, 0.27–1.2) for *C. gracilis*. The sticking coefficient during the first 5 d (before any noticeable flocculation) for *N. angularis* was 0.26 (range, 0.18–0.46). *T. weissflogii* never aggregated in culture over the 10-d period and also had the smallest average sticking coefficient of 0.07 (0.05–0.13).

The choice of the cell size affected the magnitude of the sticking coefficient. In Fig. 2 the sticking coefficients are shown as functions of the maximum, minimum, and average sizes of the cells listed in Table 1. The pennate diatom *N. angularis* had the widest range in sticking coefficients each day due to the largest variation in size. The basic trend in attachment is not altered as a function of the size characteristic used and *C. gracilis* consistently had the largest sticking coefficient (Table 2).

The species of diatoms that had high sticking coefficients were the same species that produced aggregates and were rated as flocculant (FP+) in the rolling cylinder tests. The most flocculent species (*C. gracilis*) had the largest sticking coefficient, and the least flocculent species (*T. weissflogii*) had the smallest sticking coefficient. The similarity in patterns between calculated α and flocculation potential suggests that the cell surface properties that are responsible for coagulation of cells to each other also contribute to attachment to surfaces. Kiørboe et al. (1990) measured an increase in coagulation-derived α from ~0.001 to 0.1 during the aging of a batch culture of *Thalassiosira pseudonana*, whereas the sticking coefficient of *Skeletonema costatum* was much less variable (α > 0.05–0.1). Although the absolute values of α estimated by different methods may not be directly comparable, our study gives further evidence that the stickiness of a diatom and its pattern of change during growth are highly species-specific.

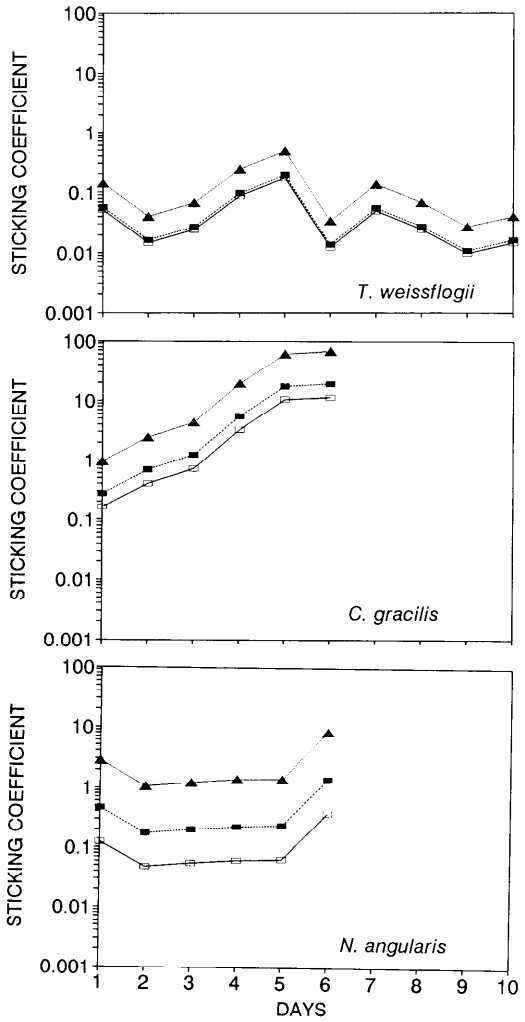

Fig. 2. Retention of *Thalassiosira weissflogii, Chaetoceros gracilis,* and *Nitzschia angularis* as a function of different cell sizes (□—maximum; ■—average; ▲—minimum).

These results have several implications for fractionating phytoplankton with screens. First, size separations cannot be performed with 100% efficiency by straining because a certain

Table 2. Sticking coefficients (average and range) of phytoplankton with maximum, minimum, and average cell dimensions.

	Days	Sticking coefficient (α)		
		Max size	Min size	Avg size
Thalassiosira weissflogii	1–10	0.05 (0.01–0.18)	0.13 (0.027–0.49)	0.05 (0.011–0.20)
Chaetoceros gracilis	1–3	0.43 (0.16–0.73)	2.6 (1.0–4.3)	0.73 (0.27–1.2)
Nitzschia angularis	1–5	0.07 (0.05–0.13)	1.6 (1.1–2.8)	0.26 (0.18–0.46)

percentage of cells from the smaller size fraction will be removed by collisions with mesh fibers. Second, cell retention on mesh will not necessarily be in proportion to cell size because similar-sized species can have different sticking coefficients. Third, size separations will tend to concentrate flocculant and chain-forming species because these species have high sticking coefficients and can aggregate into particles larger than their individual cell size. For example, the aggregation of *C. gracilis* cells in culture on day 5 resulted in the retention of 28% of cells on the 230-μm mesh even though individual cells of this diatom were the smallest of the three species chosen.

Although we could not calculate sticking coefficients after aggregation of *C. gracilis* began, sticking coefficients prior to aggregation were the highest of the three species examined. It cannot be conclusively stated that the spines on this species did not play an important role in attachment because the spines could extend 50 μm from the end of the cell. However, we think a more important factor was large amounts of TEP produced in the older cultures. TEP particles can reach several hundred microns in length in laboratory cultures and have been observed to capture and coagulate cells (Alldredge et al. 1993). TEP is not visible under brightfield illumination, so we would not have observed what percentage of cells was attached to TEP.

All experiments on diatom retention by screens were conducted at low fluid velocities to produce laminar conditions and to minimize cell breakage. Higher fluid velocities could have reduced cell attachment to filters by lowering collision frequencies with the mesh. In addition, the higher shear rates produced at the mesh surfaces by higher fluid velocities could have removed particles that had collided with the fibers but were not firmly attached, decreasing the total number of particles removed by the mesh. We did not investigate the effect of higher fluid velocities because laminar conditions were required for the fluid mechanical model used to calculate sticking coefficients.

Size separations using mesh will probably be most accurate with nonaggregating species. Mesh should be selected that has much larger pore sizes than the size of particles that are intended to pass through the mesh. Separation of different species of phytoplankton with screens will be difficult to achieve if those species are close in size or if smaller species have higher sticking coefficients than the larger species. Since screening efficiency is a function of particle stickiness, and since stickiness can vary with cell growth phase, size separations performed with mesh may reflect changes in cell properties in the absence of changes in cell sizes. The interpretation of size fractionation studies should therefore include consideration of both particle size and particle attachment to mesh surfaces.

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The size ratio between planktonic predators and their prey

Abstract—Size selectivity spectra of 28 planktonic predators from 18 studies in the literature are compared. The linear size ratio between predators and their optimal prey is 1 : 1 for a dinoflagellate, 3 : 1 for other flagellates, 8 : 1 for ciliates, 18 : 1 for rotifers and copepods, and ~50 : 1 for cladocerans and meroplankton larvae. These size ratios seem consistent within groups, and their validity is supported by quantitative information from the literature. However, a difference between filter feeders and raptorial-interception feeders, preferring relatively smaller and larger prey respectively, is evident across the taxonomic groups. A classification of planktonic predators into functional groups is therefore crucial for the construction of models of pelagic food webs.

The pathways for flow of organic matter in pelagic food webs are to a wide extent determined by the food selectivity of the pelagic predators. Several criteria may be involved in food selection, including prey size, motility, surface characteristics, biochemical composition, electrostatic forces, etc. (e.g. Poulet and Marsot 1978; Robinson 1983; Gilbert and Bogdan 1984; Van Alstyne 1986). Among these criteria, prey size is generally believed to play a major role, and usually a fixed size ratio of 10 between predator and prey is assumed (Sheldon et al. 1977; Conover and Huntley 1980; Azam et al. 1983). This assumption is in accord with the classification of plankton into logarithmic size fractions (pico, nano, micro, meso, and macro, sensu Sieburth et al. 1978), and it has facilitated integrative trophodynamic studies of pelagic environments above the population level. This assumption has also been instrumental in the formulation of models of pelagic ecosystems for theoretical and steady state considerations (e.g. Kerr 1974; Azam et al. 1983) as well as for the formulation of carbon budgets and dynamic simulation (e.g. Riemann et al. 1990; Maloney and Field 1991). Longhurst (1990) asked whether there is a generalized prey : predator ratio within protists, invertebrates, fish, and cetaceans and found a standard deviation of 2.5 times the mean predator : prey ratio. He concluded that including more data only increases scatter around the regression line, and therefore that it is difficult to generalize ratios even within groups that appear to be relatively homogeneous.

In this note we re-evaluate the assumption of a fixed size ratio between pelagic predators and their prey on the basis of data now available in the literature. Data were selected from laboratory studies where size selectivity has been assessed with one prey size at a time at a constant initial volume fraction and from in situ studies with tracer particles added to the natural prey composition. In some of these studies selectivity was expressed as an Ivlev electivity index (Ivlev 1955). The studies cover pelagic predators of 5–1,000 μm (nano-, micro-, and mesozooplankton) from freshwater as well as marine environments.

Size selectivity is usually expressed as a ratio of ingestion rates of two or more size classes

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