Particle Flux Measurement in Deep (25-40m) Suspension-feeding Communities in the Gulf of Maine

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Throughout the Gulf of Maine (GOM), sessile suspension-feeding organisms dominate rocky subtidal habitats at depths of 25-40m. At many locations the percent cover of these organisms approaches 100%, suggesting there may be intense spatial competition in these communities. Because direct overgrowth of other organisms requires the allocation of resources (i.e. food) to the production of somatic tissue, the ability of an organism to obtain these resources will determine its competitive ability. Therefore, variation in food supply among sites can indirectly affect the magnitude or direction of competitive interactions between species at these sites. In this paper we present a protocol for the measurement of particle flux over a time period encompassing several tidal cycles, using a mixture of both high technology instrumentation and low technology "off the shelf" methodology. When this protocol is repeated seasonally, it can document within- and among-site variation in those factors important for growth and competitive ability of these organisms on an annual basis.

INTRODUCTION

Throughout the Gulf of Maine (GOM), sessile suspension-feeding organisms dominate rocky subtidal habitats at depths of 25-40m. These organisms include several species of sea anemones and octocorals, bivalves, ascidians, bryozoans, and sponges (Witman and Sebens, 1990; Leichter and Witman, 1996), all of which obtain nutrition from particulate matter in the water column. This particulate matter is composed of an assortment of possible food items, including particulate organic matter, bacteria, detritus, and phytoplankton.

At many locations the percent cover of these organisms approaches 100%, suggesting there may be intense spatial competition in these communities. Direct overgrowth of one organism by another provides indisputable evidence of spatial competition (Buss, 1990). Investigators working in the GOM have taken advantage of this fact to study overgrowth interactions among the species found on its subtidal rock walls (Sebens, 1986; Genovese, 1996). Because direct overgrowth of other organisms requires the allocation of resources (i.e. food) to the production of somatic tissue, the ability of an organism to obtain these resources will determine its competitive ability. Particulate food can be an additional limiting resource for suspension feeding organisms competing for space (Buss, 1979, Buss and Jackson, 1981; Best and Thorpe, 1986), such that direct overgrowth (interference competition) may be mediated in part by acquisition of the ambient food supply (exploitative competition). Therefore, variation in food supply among sites can indirectly affect the magnitude or direction of competitive interactions between two species at these sites.

The supply of particulate food to a suspension feeding organism per unit time (= food particle flux) is the product of two factors: particle concentration and flow speed. An estimate of particle flux alone is not sufficient to describe the hydrodynamic environment of a suspension feeder. While a given species found in two discrete habitats may experience similar levels of particle flux, the flow speed and food concentration may differ between habitats. It is the interaction between these two factors that may result in differential particle capture and growth rates for this organism between habitats. Similarly, two species found in the same habitat may also experience differing rates of particle capture and growth due to the performance of each species under ambient conditions. Therefore for a complete understanding of the physical and biological factors determining the distribution and abundance of sessile suspension-feeding animals, it is essential to measure both particle concentration and flow speed.

The challenge to subtidal ecologists attempting to conduct research at these depths (25-40m) has been obtaining sufficient bottom time to complete measurements and experiments comparable to those of our terrestrial and intertidal counterparts. Although the implementation of technological advances such as Nitrox breathing mixtures within the scientific diving community has proved invaluable in our ability to conduct rigorous studies (Mastro and Dinsmore, 1990), we continue to operate at a comparative disadvantage with respect to ecologists working in other environments. Given the logistical constraints imposed by our environment, we must employ techniques and instrumentation which will maximize data collection.

In this paper we present a protocol for the measurement of particle flux over a time period encompassing several tidal cycles, using a mixture of both high technology instrumentation and low technology methods. The instrument package employed provides high frequency sampling of the particle flux regime in these habitats, allowing us to quantify the variation in these parameters. These instruments are complemented by simple, inexpensive techniques to provide additional information about the particle flux regime encountered by suspension feeding members of these communities. The principal limitation of these methods is that they integrate measurements over the entire sampling period. However, we feel a combination of these techniques provides some of the most detailed characterizations of particle flux regimes in subtidal environments.

MATERIALS AND METHODS

Study sites

The four Gulf of Maine study sites (Figure 1) where measurements for this study were conducted were chosen due to the diversity and spatial coverage of the suspension feeding community, as well as to provide differences in flow speed and particle concentration. The depth range at which this work was conducted was held constant among sites at 28-33 m, to minimize any effect of depth on environmental variation. The two replicate coastal sites established at Halfway Rock (42°30'09"N, 70°46'31"W) and Star Island (42°58'30"N, 70°36'54"W), have been previously described by Sebens (1984) and Witman (1985) respectively. Halfway Rock is located approximately 5 km off the coast of Marblehead, Massachusetts, while Star Island is located 10 km offshore of Portsmouth, New Hampshire. The distance between these sites is 70 km.

Two offshore sites were established at Ammen Rock Pinnacle (ARP) (42°51'25"N, 68°57'11"W) part of the Cashes Ledge formation, 105 km offshore in the central GOM (Witman *et. al.*, 1993). These sites are located over 100m apart, at mean depths of 28 m and 33 m.

Freestream particle flux measurement

The freestream flow regime was quantified at each of the sites using an electromagnetic current meter (InterOcean® Model S4) moored 0.5 m above the substratum, to measure the direction and magnitude of the freestream current. Flow speed was continuously sampled at 2 Hz (i.e., one sample every half-second), and averaged *in-situ* by the instrument every 10 seconds. This method provided the best frequency of sampling given the instrument's limited internal memory. The three day deployment was sufficient to provide flow data over several tidal cycles.

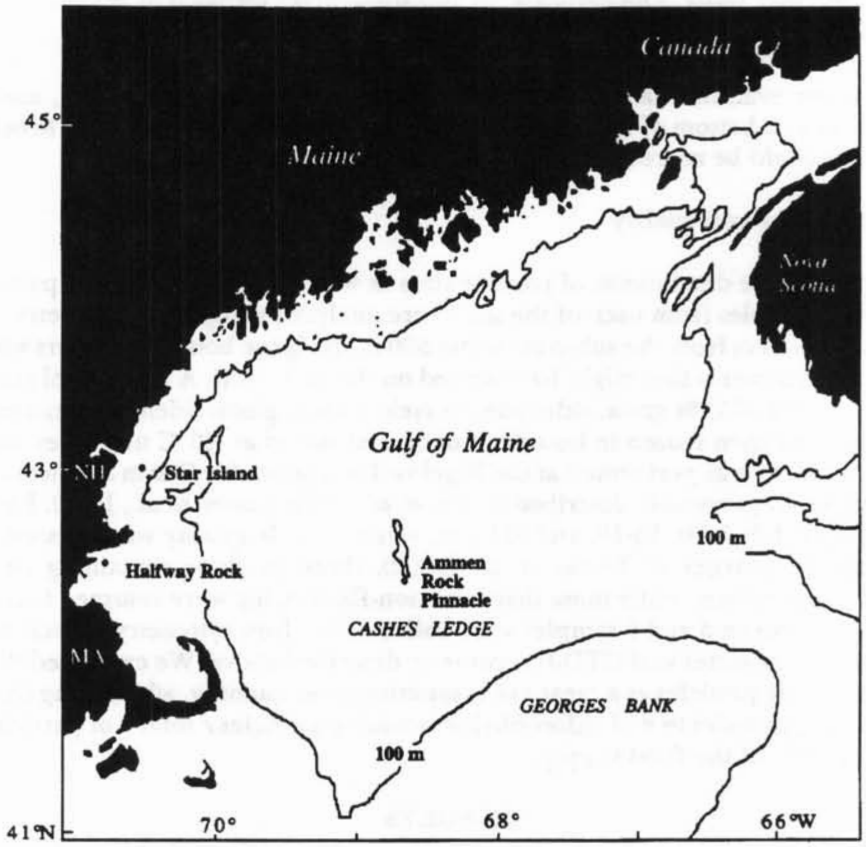

Figure 1. Map of study sites in the Gulf of Maine. Coastal sites are located at Halfway Rock and Star Island, both of which are within the 100 m isobath. The two offshore sites, ARP 28m and ARP 33m, are located at Ammen Rock Pinnacle on Cashes Ledge, and are located approximately 100 m apart.

Phytoplankton under 50 μm in size are the major food source of bryozoans (Winston, 1977). Chlorophyll *a*, the photosynthetic pigment common to all algal cells, is easily measured at field sites with a fluorometer and can be used to represent phytoplankton abundance (Yentsch and Menzel, 1963). A SeaBird® CTD (Conductivity, Temperature, Depth) equipped with a SeaTech® *in situ* fluorometer measured chlorophyll *a* concentrations, temperature, and depth at each of study sites during 3 day moored deployments (Witman *et. al.*, 1993). As with the S4 current meter, this instrument package sampled at 2 Hz, and stored 10 second average samples. Simultaneous records from the fluorometer and S4 current meter were used to calculate chlorophyll *a* particle flux (μg chlorophyll $a \cdot 0.1 m^{-2} \cdot sec^{-1}$), which is simply the product of chlorophyll *a* concentration and flow speed, as measured by these instruments.

Near-boundary flow speed measurements

To assay for bulk fluid transport closer to the suspension feeding organisms in which we are interested, dissolution of rectangular alabaster slabs ($CaSO_4 \cdot 2H2O$) was measured using methods previously employed on subtidal rock walls (Eckman *et. al.*, 1989). Prior to deployment each slab was spray painted on all but the top side with waterproof enamel. The slab was then weighed, and the projected (unpainted) surface area was measured with a Numonics™ 2400 digitizer. Three slabs (each roughly 5 x 3 x 1.5 cm) were attached directly to the rock walls using bolts epoxied into the rock wall. To relate near-wall flow speeds to freestream flow speed recorded by the S4 current meter, 3 additional slabs were attached to a vane suspended in the water column at the level of the S4 current meter, for comparison with those mounted to the rock walls. The deployment and subsequent retrieval of these slabs coincided with that of the S4 current meter.

Subsequent to retrieval, the slabs were rinsed with fresh water, allowed to dry, and weighed once again. Since the sides and bottom of these slabs had been painted to allow dissolution to occur only on the top face, dissolution could be represented in units of mg • cm^{-2} • hr^{-1}.

Particulate food quantity and quality

To gain insight into the distribution of particle sizes as well as the percentage of particles containing chlorophyll *a* , water samples from each of the sites were analyzed using flow cytometry. Water samples were collected less than 5 cm from the substrate using 500 ml Nalgene bottles, by divers who were careful not to resuspend any sediments that might have settled on the rock walls. A single 3 ml sample from each bottle was fixed using 60 μl 25% glutaraldehyde, to yield a final glutaraldehyde concentration of 0.5% (v/v). The samples were then frozen in liquid nitrogen and stored at -40°C until they were ready to be processed. Flow cytometry was performed at the Bigelow Laboratory for Ocean Sciences using a Coulter Epics V flow cytometer as previously described (Cucci *et. al.*, 1985; Lesser *et. al.*, 1992). Particle sizes were grouped in the ranges, 1-5, 5-10, 10-15, and >15 μm, while particle quality was assessed by chlorophyll content. Following the practice of Lesser *et. al.* (1992), those particles containing chlorophyll were considered to be phytoplankton, while those that were non-fluorescing were assumed to be either detrital or inorganic matter. Between 3 and 6 samples were collected for flow cytometry at each site during each deployment of the current meter and CTD-fluorometer described above. We examined the total number of chlorophyll-containing particles as a means of comparing food quantity, while using the proportion of chlorophyll-containing particles (= # of chlorophyll-containing particles / total # of particles) as a method of comparing the quality of the food supply.

RESULTS

Freestream particle flux measurement

During the summer of 1993, the instruments were deployed for at least 35 hours and nearly 3 complete tidal cycles at each of the offshore and coastal sites (Figures 2 and 3, respectively). At the two offshore sites, ARP 28m and ARP 33m, mean flow speeds were more than three times greater than at the coastal sites (Figure 4A). In addition, offshore flow speeds are highly variable and appear to peak during ebb and flood tides (compare A and C in Figure 2). At the coastal sites, Halfway Rock and Star Island, flow speeds are less variable, and again appear to peak during ebb and flood tides (compare A and C in Figure 3).

The cumulative distribution of individual flow speed measurements (one minute averages) at each of the sites is plotted in Figure 5. At each offshore site no more than 30% of the measured flow speeds are less than 10 cm • sec^{-1}, while at the coastal sites over 90% of all observations are less than 10 cm • sec^{-1}. In addition, at the offshore sites less than 50% of all observations are below 20 cm • sec^{-1} and less than 80% are below 30 cm • sec^{-1}.

Mean values of chlorophyll *a* concentration are greater at the offshore sites than at the coastal sites (Figure 4B). Also note the heteroscedastic nature of this response, with an increase in standard deviation along with the increase in the mean value. Time series plots of chlorophyll *a* concentration reveal that values at offshore sites were consistently more variable than at coastal sites (Figures 2B, 3B). Previous work (Witman *et. al.*, 1993) has indicated that this variation is due to internal waves which displace both the thermocline and the phytoplankton-rich chlorophyll *a* maximum layer over these study sites.

Because both flow speed and chlorophyll *a* concentration are higher at the offshore sites, it then follows that particle flux values will also be greater at offshore sites than at coastal sites. Mean values of

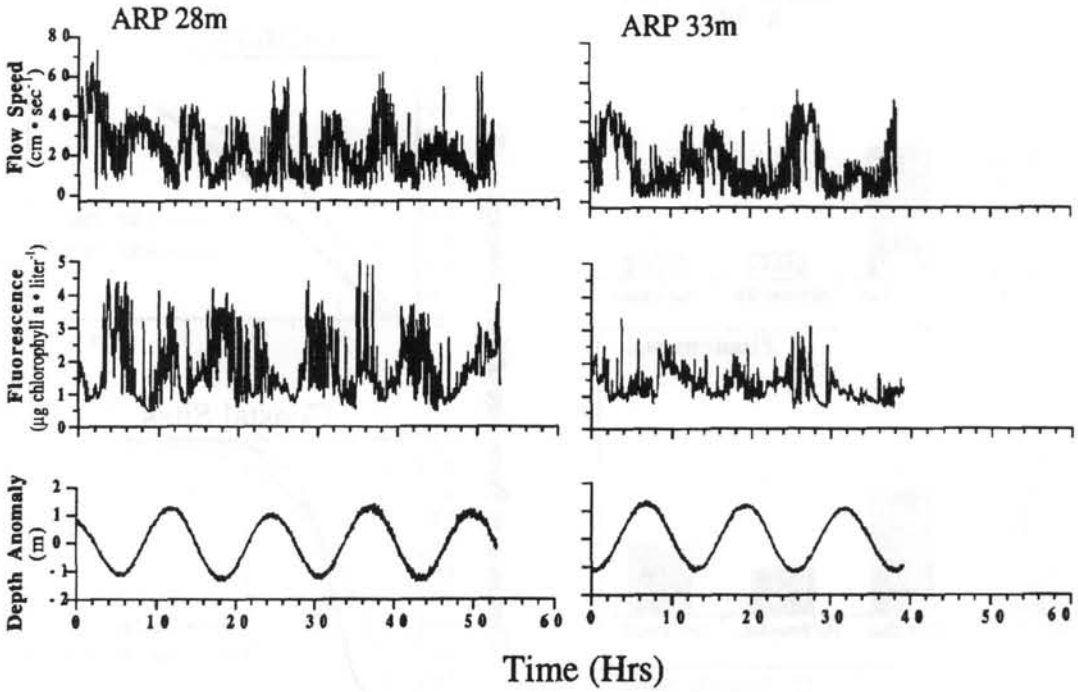

Figure 2. A) Flow speed and B) fluorescence data from the offshore sites ARP 28m amd ARP 33m in 1993. Records from each site are each over 40 hrs in length, and span several tidal cycles, as noted from the depth plot (C). Flow speed was measured with an InterOcean S4 current meter, fluorescence was measured with a SeaTech *in situ* fluorometer attached to a SeaBird CTD, which was used for the depth plot. The instruments sampled at 2 Hz and stored 10 second averages which were subsequently converted to minute averages.

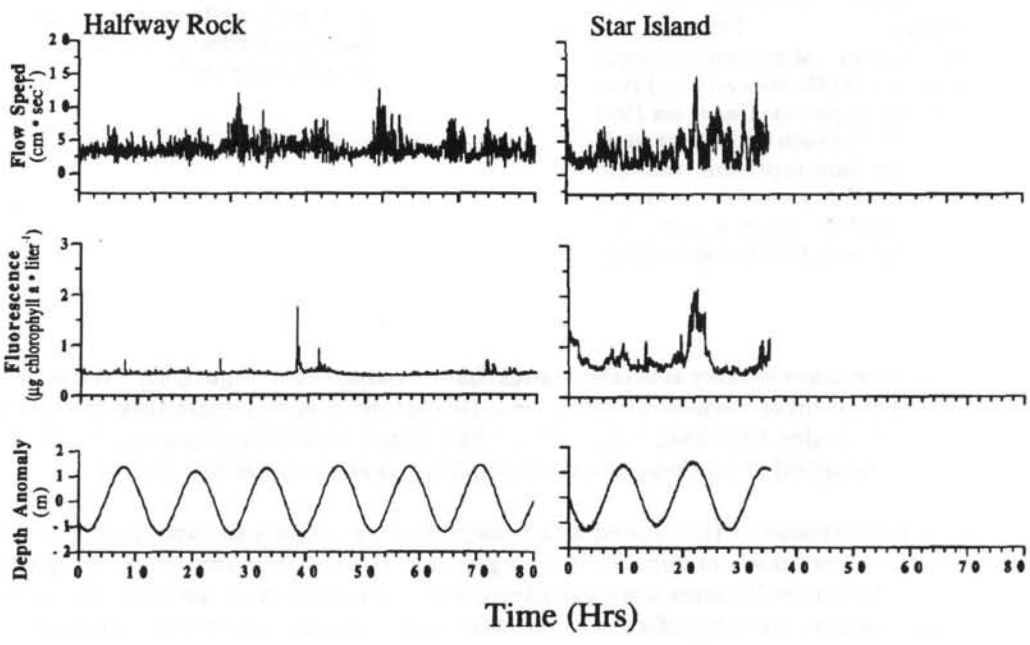

Figure 3. A) Flow speed and B) fluorescence data from the coastal sites Halfway Rock and Star Island in 1993. Records from each site are each over 30 hrs in length, and span several tidal cycles, as noted from the depth plot (C). Physical variables were recorded as described in the Figure 2 caption.

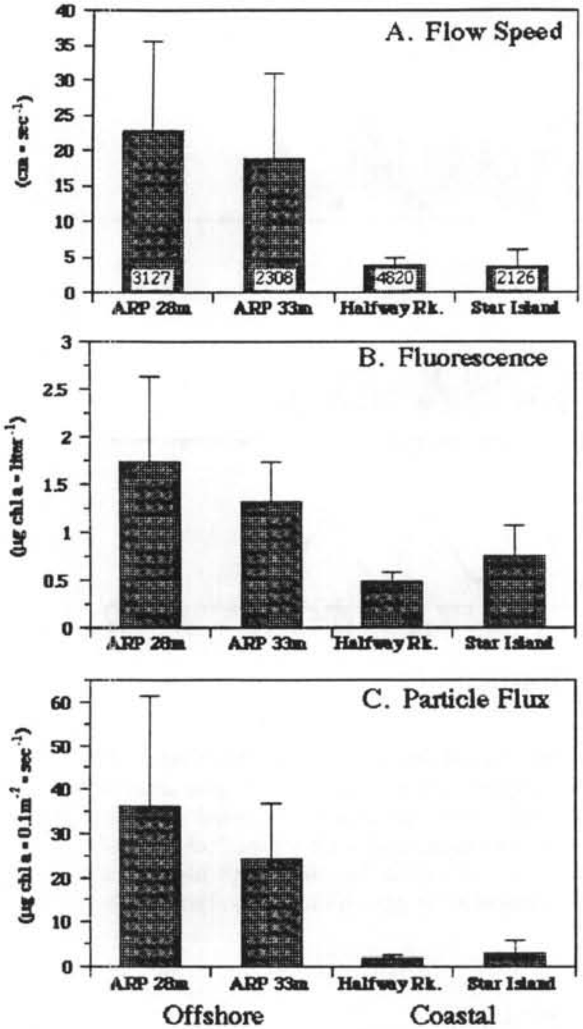

Figure 4. Mean values of minute-averaged samples for A) fluorescence, B) flow speed, and C) particle flux from 1993 deployments at each of the four study sites. Error bars represent standard deviations. Sample size is equal among variables within a given site, and is listed with the flow speed bar.

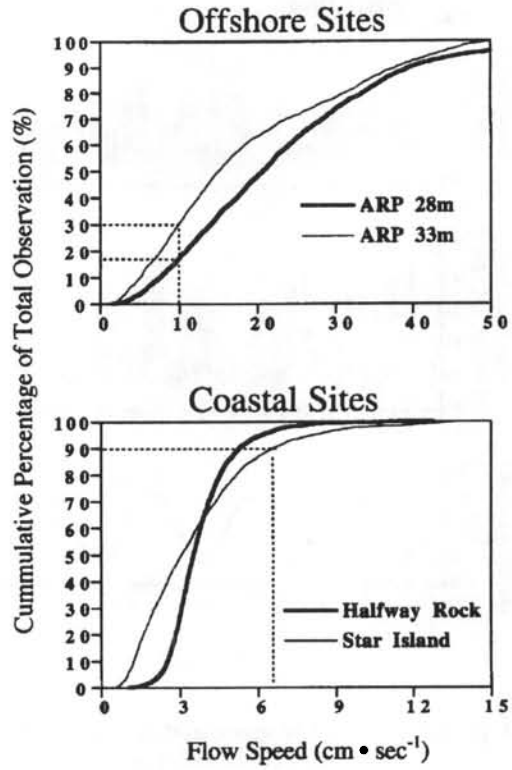

Figure 5. Cumulative frequency distributions of flow speed at each of the four sites, using data from 1993 as presented in Figures 2 and 3. At the offshore sites, no more than 30% of the total observations of flow speed are < 10 cm • sec^{-1}, while at the coastal sites, more than 90% of the observations are < 10 cm • sec^{-1}.

particle flux are over five times greater at offshore sites than at coastal sites (Figure 4C). When comparing the mean values of each of three variables (flow speed, fluorescence and particle flux) among sites, the sites can be ranked in the order ARP 28m > ARP 33m > Star Island > Halfway Rock in each case with the exception that mean flow speed at Halfway Rock was slightly greater than at Star Island.

To determine if fluctuations in flow speed and fluorescence at a given site are correlated with each other, and also to determine which of the two have a greater effect on the variability in particle flux, Spearman's rank correlation coefficients were calculated for combinations of the three variables (Table 1). All correlation coefficients were significant at $P < 0.001$, with the exception of the correlation between flow speed and fluorescence at Star Island ($P > 0.05$). Flow speed and fluorescence were negatively correlated each site except Star Island. Flow speed has a greater effect on particle flux than fluorescence, as at each site the correlation between flow speed and particle flux was greater than the correlation between fluorescence and particle flux. This difference was significant when compared using correlation coefficients from all site deployments with a paired t-test ($t = 4.090$, 3 df, $P < 0.05$).

Offshore

ARP 28m

(n=3127)	Flow Speed	Fluorescence
Fluorescence	-0.278	
Particle Flux	0.701	0.452

ARP 33m

(n=2308)	Flow Speed	Fluorescence
Fluorescence	-0.054	
Particle Flux	0.926	0.300

Coastal

Halfway Rock

(n=4812)	Flow Speed	Fluorescence
Fluorescence	-0.159	
Particle Flux	0.828	0.291

Star Island

(n=2126)	Flow Speed	Fluorescence
Fluorescence	0.017 **ns**	
Particle Flux	0.901	0.403

Table 1. Matrices of Spearman's correlation coefficients comparing flow speed, fluorescence, and particle flux at each of the four study sites in 1993. Each variable was simultaneously sampled and compared as one-minute averages. All correlations are significant at $P < 0.001$ except where noted by **ns.**

Near-boundary flow speed measurements

At each site there were significant differences between the dissolution rates of alabaster blocks level with the S4 current meter and those on the walls inhabited by suspension-feeding organisms (Figure 6). Dissolution rates at each site were higher near the S4 current meter than on the wall (Mann-Whitney U test, $P < 0.05$). From the difference in dissolution rates between blocks near the S4 current meter and those on the wall, it is possible to estimate the reduction in flow speed when working in or near a boundary layer. At the offshore sites, ARP 28m and ARP 33m, that reduction is a significant 51% and 37% of freestream values, respectively. At the coastal sites the reduction in flow speed is modest, with near wall flow speeds 87% of freestream values at Halfway Rock and 80% of freestream values at Star Island.

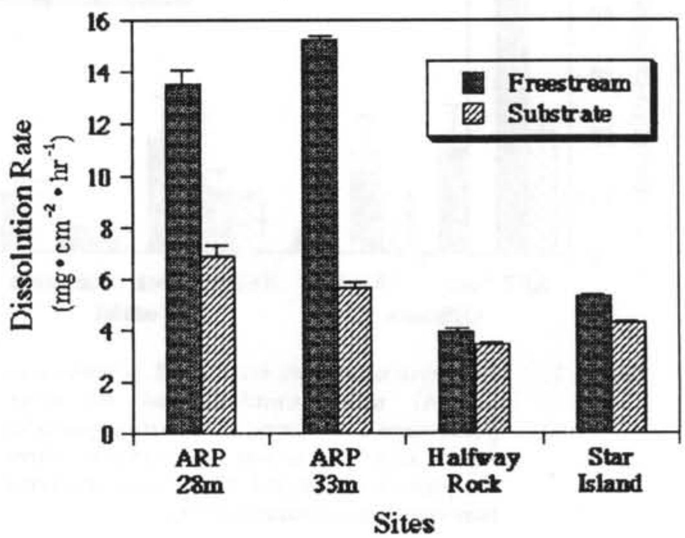

Figure 6. Mean dissolution rates of alabaster slabs placed either level with the S4 current meter or on rock walls where suspension-feeding organisms were located. Error bars represent standard errors.

Particulate food quantity and quality

The most obvious feature of the data is the large number of chlorophyll-containing particles in the smallest (1-5 μm) size fraction (Figure 7A). In addition to the expected significant size effect, ANOVA on log-transformed data of the number of chlorophyll-containing particles also indicate differences among sites (F= 28.17, df= 2, 63, P< 0.001). For the number of chlorophyll-containing particles , ARP 28m > ARP 33m and Star Island, and also Halfway Rock > ARP 33m (Scheffé Test, P< 0.01). As for food quality (Figure 7B), ANOVA on arcsine-square root transformed values revealed the same significant effects as those for food quantity (F= 27.27, df= 2, 63, P< 0.001). In this case samples from ARP 28m had higher food quality than the other three sites (Scheffé Test, P< 0.001).

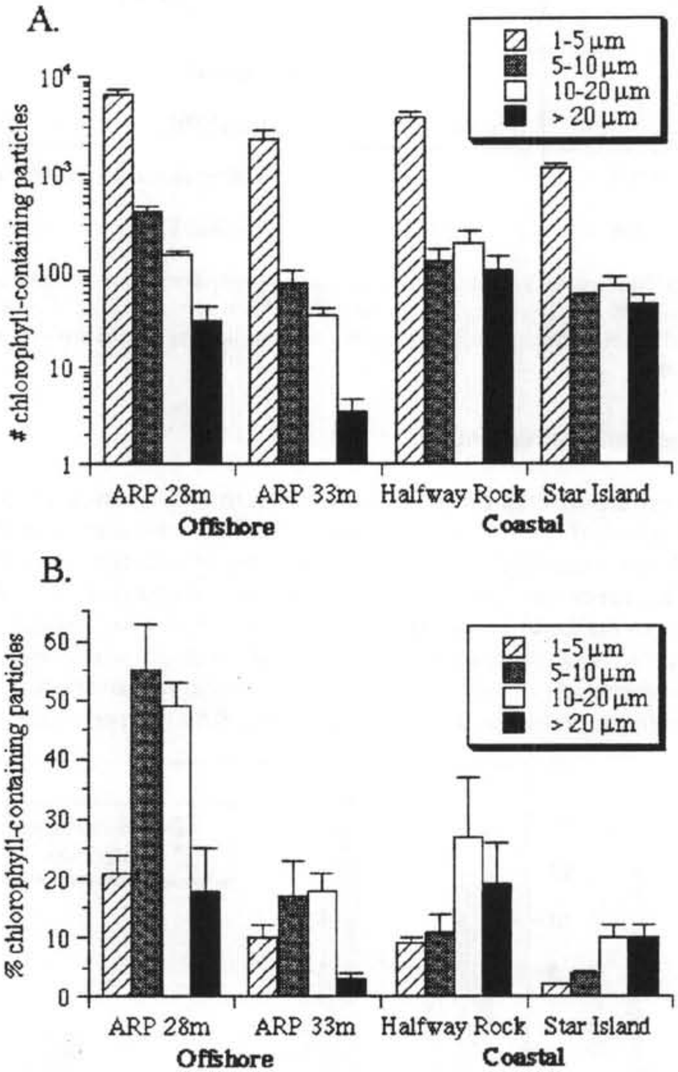

Figure 7. Flow cytometry data from 1993, presented as the A) mean number, and B) mean percentage, of chlorophyll-containing particles • ml^{-1}, according to size class and site. Three samples were averaged in each case, and error bars represent standard errors.

DISCUSSION

Regional variation in particle flux

The physical data presented within this study indicate that there are striking differences between coastal and offshore regions of the Gulf of Maine with respect to particle flux regime. Mean freestream flow speeds are several times greater at the offshore location, and the frequency distribution of flow speeds at the offshore location suggests that flow speeds are usually in excess of maximum coastal values. Using the alabaster dissolution data, these values can be adjusted downward to describe the flow regime experienced by suspension feeding organisms on the rock walls. At the offshore sites, dissolution rates on the natural substrate were roughly half that experienced at the level of the S4 current meter. Therefore the mean near-wall flow speed offshore is still approximately 10 cm • sec^{-1}, which is more than twice the freestream values at the coastal location.

Mean chlorophyll *a* values, and thus phytoplankton concentrations, were greater at offshore sites than along the coast. This is contrary to predictions from the oceanographic literature (Yentsch *et. al.*, 1979; Yentsch and Garfield, 1981), but this phenomenon may be restricted to within the subtidal (25-40 m) suspension feeding zone (Genovese and Witman, 1995). If it is particle flux alone which is most important to the growth rates of community members, without any regard to the relative contributions of flow speed and particle concentration to the overall value, then offshore suspension feeding organisms would have a clear growth advantage over coastal populations. However, results from past studies on the horse mussel, *Modiolus modiolus* (Lesser *et. al.*, 1994), and an encrusting bryozoan (Genovese, 1996) suggest that this may not be the case for active suspension feeders (those animals which generate their own feeding currents). Thus while particle flux values are much greater offshore than in the coastal zone, they should not be expected to be a good predictor of feeding success or growth for all members of these communities.

The interactive effect of particle concentration and flow speed on feeding success denotes the importance of comparing the fluctuation in these variables through time at each of the sites. Spearman's rank correlation coefficients indicate a significant negative association between chlorophyll *a* concentration and flow speed at both offshore sites. This situation is most beneficial for the feeding success of organisms negatively impacted by an increase in flow speeds, because the high levels of chlorophyll *a* are accompanied by relatively lower flow speeds. At the coastal sites there is either no significant correlation (Star Island) or a negative correlation (Halfway Rock). However the lack of large variation in both coastal flow speeds and fluorescence over the deployment period suggests that feeding success is constant over the tidal cycle.

The two major questions that the flow cytometry analysis was designed to address involved the quantity and quality of food particles at each of the locations. Either aspect of the food supply considered alone would not provide a complete understanding. One location may provide suspension feeding organisms with a high quality food supply, but the overall densities of these food particles may be too low to meet the nutritional needs of community members. Likewise, at locations where high densities of food particles are part of an overall poor quality particulate pool (e.g. much higher densities of non-food particles), suspension feeding organisms would either pay the metabolic cost of indiscriminately digesting a large percentage of particles with no nutritional values, or lose a significant amount of feeding time by instead actively rejecting these particles. Most consideration given to such questions has focused on commercially important bivalve species such as *Mytilus edulis* (Willows, 1992; Bayne *et. al.*, 1993) and *Placopecten magellanicus* (Cranford, 1995) which show decreased absorption efficiency in response to increases in dietary inorganic content.

It is evident that ARP 28m is a superior site in terms of both food quantity and quality, while Halfway Rock has an edge over ARP 33m in the quantity of food particles in the first sampling period. With the exception that the samples from ARP 33m are relatively low in food quantity and quality, the results of the flow cytometry analysis concur with those from the *in situ* fluorometer.

Other Methodological Issues

There are several materials which can be used to measure dissolution as an indicator of bulk transport, or flow speed. In this study we employed rectangular slabs of alabaster or soapstone, which can be obtained in large pieces from art supply stores. The large blocks can be subsequently cut into smaller pieces on a table saw with a combination blade. Due to the soft nature of this material a rock or masonry blade is not necessary. You should be sure to cut this material outdoors or in a very well ventilated area, due to excessive dispersion of dust. While alabaster has been previously used in this manner (Eckman *et. al.*, 1989; Leichter and Witman, 1996), other similar materials have also been used in subtidal studies, including plaster of paris (Graham and Sebens, 1996) or dental chalk (Yund *et. al.*, 1989). With each of these materials it is useful to have real-time calibration of dissolution rates (as opposed to previous or post calibration in laboratory flow tanks) because in addition to differences in fluid transport, dissolution rates can vary due to differences in a host of physical variables, most prominently temperature and salinity (Jokiel and Morrissey, 1993; Thompson and Glenn, 1994), that may also differ among sites and within a given deployment (Genovese, 1996).

Although our measurements of chlorophyll *a* concentrations were recorded with a SeaTech® *in situ* fluorometer, another alternative recently available to scientists is Wet Labs WetStar miniature fluorometer, which is a relatively low cost (< $4K), low power instrument easily integrated with SeaBird CTDs. This product may provide an inexpensive means to add chlorophyll *a* measurement capability to existing CTDs. For measurement of freestream flow speeds, we have used S4 current meters throughout the Gulf of Maine for nearly a decade, and have found them to be extremely reliable and robust to the often harsh treatment encountered during deployment and retrieval. This seems to outweigh any disadvantage of not being able to record flow speeds less than 50 cm from the substrate, due to the physical size of the instrument.

CONCLUSIONS

Despite logistical constraints faced when conducting subtidal research, we have presented a protocol for detailed measurement of the particle flux regime encountered by sessile suspension-feeding organisms in the Gulf of Maine for a period of several tidal cycles. This protocol can be effective in other subtidal habitats (e.g. coral reefs), and when repeated seasonally, can document within- and among-site variation in those factors important for growth and competitive ability of these organisms on an annual basis.

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