

Interactive effects of flow speed and particle concentration on growth rates of an active suspension feeder

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Abstract

Suspension-feeding organisms dominate subtidal habitats in the Gulf of Maine (GOM) at depths of 25–40 m. *Parasmittina jeffreysi* is an encrusting cheilostome bryozoan found in this zone throughout the GOM. Regional variation between coastal and offshore locations in both flow speed and particle concentration makes the GOM an ideal location to study the effect of these factors on the growth of *P. jeffreysi*. Particle flux measurements at two offshore and two coastal sites indicated that flow speeds were >3-fold greater offshore than at coastal sites. Chlorophyll *a* concentrations and particulate quantity and quality were greater at offshore sites, but sedimentation rates were greater in the coastal region. The growth rate of *P. jeffreysi* was measured at each of the sites using unobstructed colonies free from spatial competition and colonies that remained within their natural community.

Both unobstructed colonies and those in quadrats within the natural community displayed no regional difference in growth rates, despite higher particle flux in the offshore region. The interactive effects of flow speed and particle concentration are acting upon growth rates in opposite directions, resulting in the net effect of no regional differences in growth. Growth of unobstructed colonies at one of the coastal sites (Halfway Rock) was less than that at any of the other three sites and may have resulted from the combination of high sedimentation and extremely low flow at this site.

A comparison between unobstructed colonies and those in natural quadrats suggested that growth was limited by spatial competition in the natural community. A significant site interaction effect indicates that this response did not occur at all four sites and was absent at Halfway Rock because of poor growth of unobstructed colonies. Any differences in growth due strictly to differential food acquisition (e.g., unobstructed colonies) appear to be dampened by competitive interactions in the natural community.

Most sessile marine invertebrates are suspension-feeding organisms that obtain nutrition from particulate matter in the water column. The supply of particulate food, or food particle flux, to these organisms is a function of two factors: particle concentration and flow speed. Previous efforts to study the effect of flow speed and particle concentration on the feeding and growth of suspension-feeding organisms

have been similar in many ways. In most studies, investigators have concentrated their efforts on the effect of either flow speed or particle concentration in single-factor experiments over a range of values. The use of laboratory flow tanks (Vogel and LaBarbera 1978) has been instrumental in approximating field flow regimes in controlled laboratory settings, whereas short-term studies (trials on the order of minutes) examining feeding rates for these organisms have assumed that an increase in feeding translates into an increase in growth rate (but see Okamura 1992). In most studies in which the effects of differences in particle concentration on growth have been examined, food quality has been treated as a constant in nature, and the heterogeneity of particulates in the field has not been considered.

Each of the reductionist steps listed above help to isolate a specific aspect of the suspension-feeding process and allow for greater precision than would otherwise be possible in experiments conducted in the field. However, it is the performance of organisms in their natural community that is of ultimate interest to ecologists. Conducting field tests of lab results is the only way to determine whether or not a specific parameter can singularly predict the organism's performance in nature or whether, instead, it is the interaction of several variables that is most important. In this study, we took an integrated approach to investigate the growth of an encrusting bryozoan at four Gulf of Maine (GOM) sites by first measuring those factors previously determined to impact

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feeding and growth (e.g., flow speed and particle concentration) and then comparing growth rates at these sites to what would be predicted based on the results from previous studies.

Bryozoan suspension feeding—Bryozoans are active suspension feeders that use a ciliated tentacular organ, the lophophore, to generate a feeding current to enable them to capture particulate matter suspended in the water column. Although bryozoans experience decreased feeding success at flow speeds $>5 \text{ cm s}^{-1}$ (Okamura 1984, 1985, 1988, 1992), their growth rates have been shown to decrease in laboratory studies (Okamura 1992; Eckman and Duggins 1993) or to increase in field experiments (Keough 1986; Cancino and Hughes 1987). Okamura (1992) attributed the decrease in feeding success (and hence growth) with increased flow to an inhibition of particle flow into the lophophore. This inhibition occurs as increased flow speeds act to increase downstream movement of food particles, with the flow generated by the lophophore less able to overcome these inertial forces on food particles (Okamura 1992).

The increased growth rate in response to increased flow was reported for bryozoans in two field studies (Cancino and Hughes 1987; Hughes 1989) where colonies growing on petri dishes were exposed to different flow regimes by placing conical baffles over the petri dish. In these two cases, as in a third field study where growth was greater in regions of enhanced flow (Keough 1986), a reduction in sedimentation (related to increased flow) rather than an increase in feeding was cited as a probable cause.

Particle concentration can have as significant an effect as flow speed on rates of particle capture by suspension feeders. The feeding rate of a bryozoan increased in response to elevated particle concentrations up to a saturation level of suspended food particles (Best and Thorpe 1983). The level of peak feeding may be at particle concentrations where the filtering elements of the lophophore are saturated faster than excess particles can be rejected.

The word “particle” has been used previously to represent food items (i.e., those having nutritive value) that a suspension feeder may ingest. However, nonfood items (e.g., particulate inorganic matter) also are suspended in the water column and are available for suspension feeders to capture. Whether these particles are indiscriminately consumed or actively rejected by an animal, they may impose an energy cost on the suspension feeder because of either digestion or lost feeding time, respectively. For example, the hard clam *Mercenaria mercenaria* experiences a significant decline in both feeding success (Bricelj and Malouf 1984) and growth rate (Bricelj et al. 1984) in response to high levels of suspended sediments.

Another, more extreme effect of nonfood particles on suspension feeders is sedimentation (Rogers 1990), where these particulates settle out of the water column onto feeding structures of suspension feeders. Thayer (1979) suggested that the decline of articulate brachiopod fauna in the Mesozoic was due to sedimentation (via increased bioturbation), which fouled their lophophores (but see Richardson 1981). In a more geologically recent example, Rhoads and Young (1970) proposed that modern suspension feeders are exclud-

ed from habitats high in suspended sediments because of the clogging of their filtering devices, among other factors. Although Cook (1977) reported that the bryozoan *Lichenopora* sp. is capable of removing “a fine layer of mud” in a short time (10–15 min), the energetic cost associated with survival in an environment where a significant amount of time is spent clearing feeding structures may exceed metabolic intake.

The interactive effects of flow speed and particle concentration on bryozoan growth was illustrated by Keough (1986), who reported that field growth rates of a bryozoan on seagrass blades were greater in regions of enhanced flow (the tip or distal end of blades vs. the basal ends). The explanation for this result was that colonies receiving greater flow were exposed to less sedimentation, the rate of which is inversely related to flow speed. This relationship is known formally as Stoke’s Law, which states that for a given size and shape of particle, there is a critical upwardly directed component of the velocity below which that particle will settle out of the water column as the downward gravitation force exceeds the opposing lift force (Vogel 1981). Although flow speeds $>5 \text{ cm s}^{-1}$ result in reduced feeding success for bryozoans in laboratory experiments (Okamura 1984, 1985, 1988, 1992), there may be an indirect, beneficial effect of decreased sedimentation in field situations. In the two lab studies where the growth rate of bryozoans was greater at low flow velocities (Okamura 1992; Eckman and Duggins 1993), the influence of sedimentation on growth was not considered. Okamura (1992) removed any material that accumulated on colony surfaces by “gently brushing or rubbing colony surfaces” on a weekly basis, whereas Eckman and Duggins (1993) mounted bryozoans “normal to gravity . . . such that colonies were facing down.”

The effects of flow speed and particulate food concentration have been studied independently, but in very few cases have investigators manipulated both variables simultaneously. These few studies provide a multifactorial analysis of flow speed and particle concentration on the feeding success of crinoids (Leonard 1989) and on the growth rate of scallops (Cahalan et al. 1989) and oysters (Lenihan et al. 1996). Fr chet te et al. (1989) used field measurements over an intertidal mussel bed in a model detailing mussel consumption rate as a function of flow speed and phytoplankton concentrations. In each of these studies, investigators attempted to portray field conditions where the interactive effects between flow speed and particle concentration influenced the feeding ecology of suspension-feeding organisms.

The Gulf of Maine as a model system—Regional variation in both flow speed and particle concentration within the GOM make it an ideal location to examine the effects of these factors on the growth of suspension-feeding organisms that dominate the rocky subtidal habitats at depths of 25–40 m. Offshore regions within the GOM are thought to be lower in phytoplankton biomass than coastal regions (Yentsch et al. 1979; Yentsch and Garfield 1981); however, the influence of internal waves in supplying phytoplankton-rich water to the offshore benthos (Witman et al. 1993) suggests this may not be the case within the suspension-feeding zone (Genovese and Witman unpubl. data). Average flow speeds are

typically 3–8 times greater at offshore sites (15–25 cm s⁻¹) when compared to similar depths in coastal regions (3–5 cm⁻¹) in the southern GOM (Genovese 1996; Genovese and Witman 1997).

In this investigation, we examined the effect of flow speed and particle concentration on the growth of the cheilostome bryozoan *Parasmittina jeffreysi* in the GOM. *P. jeffreysi* has excellent overgrowth capabilities and appears to be a top-ranked competitor in deep-water (>25 m) suspension-feeding communities in the GOM (Genovese 1996) and in the northeast Atlantic Ocean (Ward and Thorpe 1989). Because it occurs throughout the GOM, *P. jeffreysi* can be considered a model active suspension feeder with which to study the interactive effect of natural differences in flow speed and particle concentration.

We addressed the following specific questions:

1. Are there regional differences in the ambient flow speed and particle concentration between offshore and coastal regions?
2. Are there regional differences in the growth of *P. jeffreysi*?
3. Is there evidence that competition for either space or food limits the growth of *P. jeffreysi*?
4. If competition limits the growth of *P. jeffreysi*, is this true across particle flux regimes?

Materials and Methods

Study sites—Four study sites in the Gulf of Maine where *P. jeffreysi* occurs were chosen 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. Two replicate coastal sites were established at Halfway Rock (42°30'09"N, 70°46'31"W) and Star Island (42°58'30"N, 70°36'54"W), which have been previously described by Sebens (1984) and Witman (1985), respectively. Two offshore sites were established at Ammen Rock Pinnacle (ARP) (42°51'25"N, 68°57'11"W), which is part of the Cashes Ledge formation located 105 km offshore in the central GOM (Witman et al. 1993). These sites, treated as replicates in this study, are located over 100 m apart at mean depths of 28 m and 33 m, respectively.

Given the study sites, the general model used to analyze data from the various experiments includes a location effect distinguishing between offshore and coastal regions and between two distinct particle flux regimes. The model also contains a site effect, corresponding to the two replicate sites within each region. Because each of the sites is unique to a specific location, the site variable is nested within the location variable.

Near-bottom oceanography—The magnitude and direction of the free-stream flow regime was quantified at each of the sites using an electromagnetic current meter (InterOcean® Model S4) fixed 0.5 m above the substratum. Flow speed was continuously sampled at 2 Hz and averaged in situ by the instrument every 10 s. Deployments lasting 3 d at each site provided flow data over several tidal cycles.

Phytoplankton <50 µm in size are the major food source for bryozoans (Winston 1977). Chlorophyll *a* (Chl *a*), the photosynthetic pigment common to all algal cells, is easily measured in situ at field sites with a fluorometer and can be used to represent phytoplankton abundance (Yentsch and Menzel 1963). A SeaBird® CTD equipped with a SeaTech® in situ fluorometer measured nearbed Chl *a* concentrations, temperature, and depth. As with the S4 current meter, this instrument package was deployed for 3 d at each site, sampled at 2 Hz, and stored 10-s average samples. Simultaneous records from the fluorometer and S4 current meter were averaged to 1-min intervals and used to calculate Chl *a* particle flux (µg Chl *a* 0.1 m⁻² s⁻¹), which was calculated as the product of Chl *a* concentration and flow speed.

Near-boundary flow speed measurements—To assay for bulk fluid transport closer to the bryozoan feeding structures, dissolution of rectangular alabaster slabs (CaSO₄·2 H₂O) was measured using methods previously employed in subtidal habitats (Eckman et al. 1989; Yund et al. 1991; Leichter and Witman 1996). Prior to deployment, each slab was spray painted on all but the top side with waterproof enamel. The slab was then weighed, and the exposed, unpainted surface area was measured. Three slabs (each 5 × 3 × 1.5 cm) were attached directly to both the rock walls where *P. jeffreysi* was found and the Plexiglas® plates used in the unobstructed growth experiment. To relate near-wall and growth experiment flow speeds to free-stream flow speed, three additional slabs were attached to a vane suspended in the water column at the same height off the bottom as the S4 current meter. The deployment and subsequent retrieval of these slabs coincided with that of the S4 current meter.

After retrieval, the slabs were rinsed with fresh water and dried to a constant weight. Because 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 h⁻¹. At each site, dissolution rates were compared among the three treatments (S4, wall, growth experiment plates) using an analysis of variance (ANOVA) after variances were first checked for homogeneity with an *F*-max test (*P* > 0.05). Planned pairwise comparisons were made among all three treatments using Fisher's least squares difference (LSD) method.

Particulate food quantity and quality—To determine the distribution of particle sizes and the percentage of particles containing Chl *a*, water samples from each of the sites were analyzed using flow cytometry. Water samples were collected <5 cm from the substrate using 500-ml Nalgene bottles. Divers were careful not to resuspend any sediments that might have settled on the rock walls. One 3-ml subsample from each bottle was fixed using 60 µl of 25% glutaraldehyde to yield a final glutaraldehyde concentration of 0.5% (v/v). Samples were then frozen in liquid nitrogen and stored at -40°C until processing. Flow cytometry was performed at the Bigelow Laboratory for Ocean Sciences using a Coulter Epics V flow cytometer (Cucci et al. 1985). Particles were grouped into size classes of 5–10, 10–20, and >20 µm, and particle quality was assessed by chlorophyll content. Following the practice of Lesser et al. (1992), those particles

containing chlorophyll were considered to be phytoplankton, whereas those that were nonfluorescing were assumed to be either detrital or inorganic matter. Three samples were collected for flow cytometry at each site during each of the 3-d summer deployments of the current meter and CTD fluorometer.

We examined the total number of chlorophyll-containing particles as a means of comparing food quantity, and the proportion of chlorophyll-containing particles (number of chlorophyll-containing particles divided by the total number of particles) was used to compare the quality of the food supply. Because of unequal variances among samples, we \log_{10} transformed the number of chlorophyll-containing particles and arcsine-square transformed the percentages of total particles containing chlorophyll (Sokal and Rohlf 1981).

Particles in the 1–5- μm range were not included in the statistical analysis because they comprise the highest density in these water samples (thus consuming the greatest amount of sorting time and computer memory) yet are too small to be used as food for bryozoans (Winston 1977; Riisgård and Manríquez 1997; Nielsen and Riisgård 1998). For completeness, a single sample from each site was analyzed for this size fraction to determine if the results agreed with those from the larger size fractions.

Sedimentation rates—Passively collecting sediment traps (45 cm height \times 5.5 cm diameter) were deployed for several weeks at each of the four sites to determine if sedimentation rates differed between locations and sites. An appropriate aspect ratio (>7) was chosen to minimize sampling biases due to differences in flow regimes between sites (Butman 1986). Ten tubes were deployed at each site, and subsequent to retrieval, samples were dried in a muffle furnace at 450°C for 6 h. The ash-free dry weight of the sediment was recorded for each tube, and the sedimentation rate was calculated as mg sediment d^{-1} . To correct for unequal variances between sites, data were \log_{10} transformed and compared using an *F*-max test ($P > 0.05$) prior to an ANOVA.

Field growth of P. jeffreysi—To examine growth rates of *P. jeffreysi* at each of the field sites in the absence of spatial competition, unobstructed growth experiments were conducted for a 1-yr period. We collected *P. jeffreysi* colonies from a given site by chipping colonies off the substrate with a paint scraper. We then photographed the colonies after they had been attached to 100-cm² Plexiglas[™] plates using marine epoxy (Pettit[®] polyoxy). Plates were then deployed on vertical rock walls for 1 yr at the site where colonies were collected, and upon retrieval the plates were rephotographed. The slides were projected to life size (1 : 1), and colony outlines were digitized and measured with a digital planimeter (Numonics Model 2400) to determine colony surface area at the beginning and end of the experiment.

To obtain data on the growth rate of a large number of individual *P. jeffreysi* colonies, several quadrats ($8 \leq n \leq 14$) containing this bryozoan in its natural community were haphazardly established on rock walls at each of the four study sites. Quadrats were photographed at the times of deployment and retrieval of the unobstructed growth experiments to yield growth rates of *P. jeffreysi* within the com-

munity that could be compared both among sites and with the corresponding unobstructed growth at each respective site. Only those colonies that increased in size and did not experience either overgrowth by other organisms or loss of surface area due to disturbance were used in this analysis.

Statistical analysis of growth experiments—Differences in colony growth rates after 1 yr were determined using analyses of covariance (ANCOVAs), with original size (surface area) as the covariate (*x*). Bartlett's test (Winer 1971) was used to check for homogeneity of variances in both the unobstructed and natural quadrat growth experiments because there were large differences in sample sizes among treatments (max : min ratio >3). \log_{10} transformation of growth rates and original size was necessary to stabilize the variance in all cases.

ANCOVAs were performed using SYSTAT (version 5.2). For each model tested, we first checked for any significant interaction between the covariate (original size) and the treatment; no interaction is equivalent to meeting the assumption of homogeneity of slopes as first required when performing an ANCOVA (Wilkinson et al. 1992). If nonsignificant, this interaction term was removed from the model and only the covariate and treatment were used as predictors. Post hoc testing for pairwise differences in growth rates between sites was accomplished using the conditional Tukey–Kramer test (Day and Quinn 1989).

Results

Near-bottom oceanography—We deployed the oceanographic instrument array at each of the four sites for 35 h and nearly three complete tidal cycles during the summer of 1993 and for over 70 h and almost six tidal cycles during the summer of 1994. Because the data are nearly identical between years, we only present the 1994 data set here (see Genovese and Witman 1997 for 1993 data).

Representative offshore and coastal time series data reveal a greater magnitude and variation in both flow speed and Chl *a* concentration at the offshore site (Fig. 1). Previous work (Witman et al. 1993) has indicated that high variability in offshore Chl *a* concentrations can be due to internal waves that displace the phytoplankton-rich Chl *a* maximum layer over these study sites. Plots of the cumulative distribution of individual flow speed measurements (1-min averages) at the four sites indicate that at each offshore site $\leq 30\%$ of the measured flow speeds were $<10 \text{ cm s}^{-1}$, whereas at the coastal sites $>90\%$ of all observations were $<10 \text{ cm s}^{-1}$ (Fig. 2). Given that both mean flow speed (Fig. 3A) and Chl *a* concentration (Fig. 3B) were higher at the offshore sites, the values for particle flux (calculated as the product of flow speed and food concentration) were over 5 times greater at offshore sites than at coastal sites (Fig. 3C). When comparing mean values for each of the three variables (flow speed, fluorescence, and particle flux) among sites, the sites can be ranked in the order ARP 28 m $>$ ARP 33 m \gg Star Island $>$ Halfway Rock.

Near-boundary flow speed measurements—At each site, there were significant differences (ANOVA $F > 6.65$, $P <$

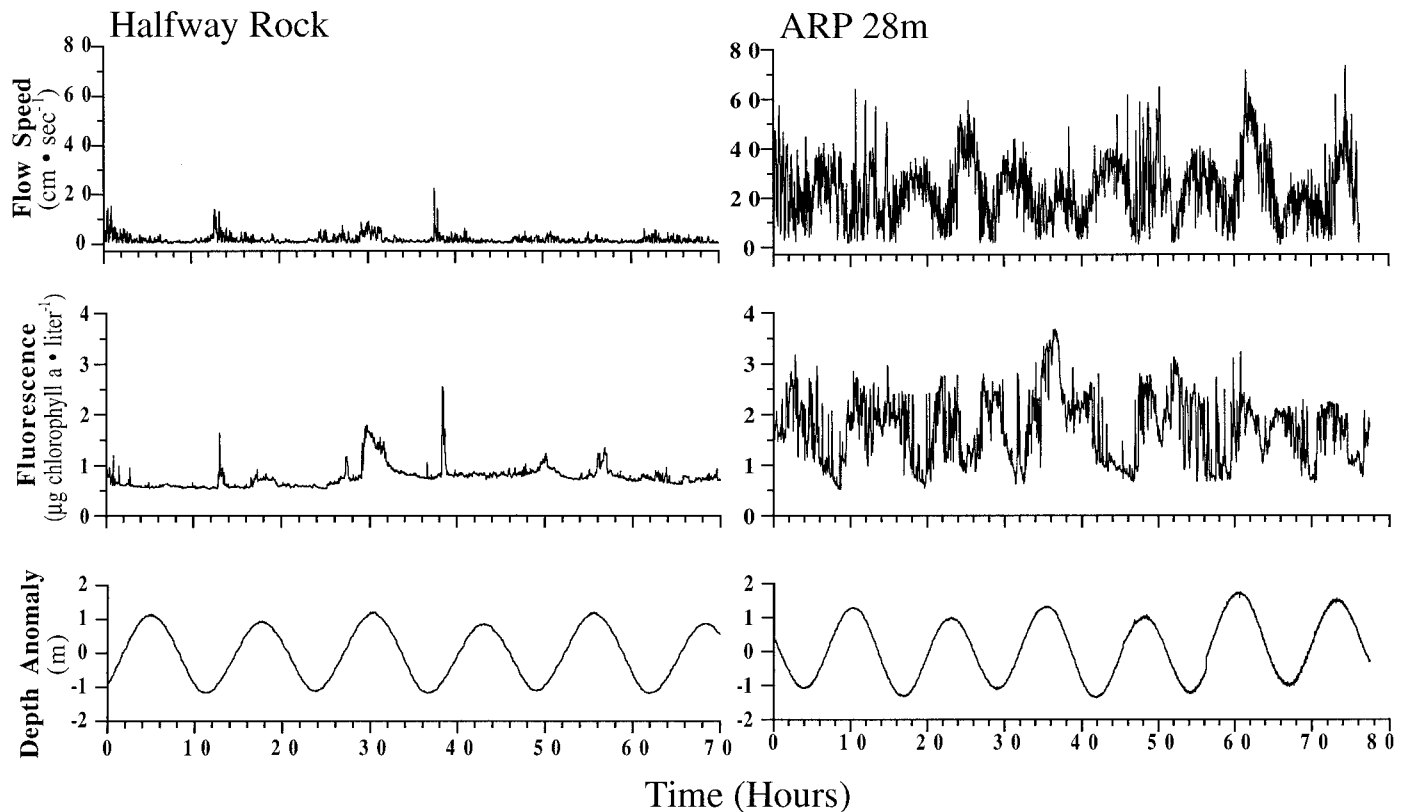


Fig. 1. Representative flow speed and fluorescence data from Halfway Rock (coastal) and ARP 28 m (offshore) in 1994. Records from each site are over 70 h in length and span several tidal cycles. Flow speed and fluorescence were sampled at 2 Hz, stored as 10-s averages, and subsequently converted to 1-min averages.

0.03, $df = 2,6$ for each site) in the dissolution rates among alabaster blocks level with the S4 current meter, on the walls where quadrats were established, and on the unobstructed growth plates (Fig. 4). With the exception of Halfway Rock,

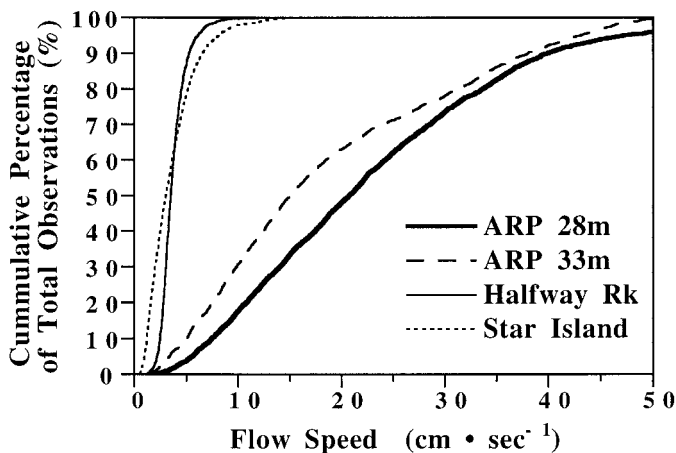


Fig. 2. Cumulative frequency distributions of free-stream flow speed (0.5 m above substrate) at each of the four sites (28–33 m depth), using data presented in Figure 1. At the offshore sites, $\leq 30\%$ of the total observations of flow speed were $< 10 \text{ cm s}^{-1}$, whereas at the coastal sites $> 90\%$ of the observations were $< 10 \text{ cm s}^{-1}$.

dissolution rates at each site were higher near the S4 current meter than on the wall or on the unobstructed growth plates, and dissolution rates between the latter two treatments were not significantly different. At Halfway Rock, dissolution rates were not different between the S4-level blocks and those on the wall, whereas dissolution for each of those treatments was greater than for blocks on the unobstructed growth plates.

Particulate food quantity and quality—Significant differences in the densities of chlorophyll-containing particles in the three size classes $> 5 \mu\text{m}$ were noted among particle size classes and sites (Table 1A), with the decrease in density from the small to the larger size fractions being most pronounced (Fig. 5A). For differences among sites, densities at ARP 28 m and ARP 33 m were both higher than at Halfway Rock (Scheffé test, $P < 0.03$). There was a significant location effect (Table 1B), with offshore sites having a greater percentage of chlorophyll-containing particles than coastal sites, even for the 1–5- μm fraction (Fig. 5A,B).

Sedimentation rates—Sedimentation rates were higher in the coastal region than in the offshore region (Table 1C, Fig. 6). The significant site effect was examined in greater detail with pairwise comparisons using Ryan's Q stepwise test with the Kramer modification for unequal sample size (Day and Quinn, 1989). Sedimentation rates at the two coastal sites

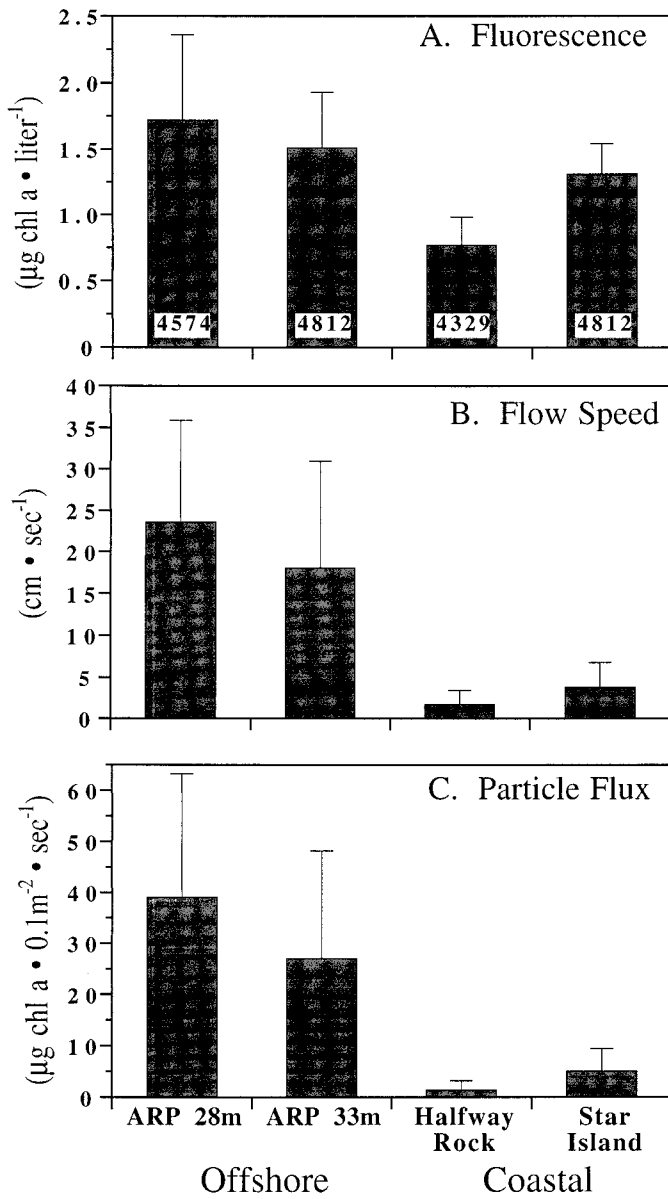


Fig. 3. Mean values of minute-averaged samples for (A) fluorescence, (B) flow speed, and (C) particle flux (calculated as product of 1-min-averaged values of flow speed and particle concentration) from 1994 deployments at each of the four study sites. Error bars represent standard deviations. Sample size was equal among variables within a given site and is listed with the fluorescence bar.

were not significantly different ($P > 0.05$), and both were greater than rates at either of the offshore sites. At the offshore sites, ARP 28 m had a higher rate of sedimentation than ARP 33 m ($P < 0.01$ in all cases).

Unobstructed growth experiments—We found homogeneity of slopes between treatments, thus were able to use ANCOVAs to test for site and location effects. There were differences in growth rates among sites but no significant difference in growth between offshore and coastal locations (Table 2A). Colonies of *P. jeffreysi* at ARP 28 m, ARP 33

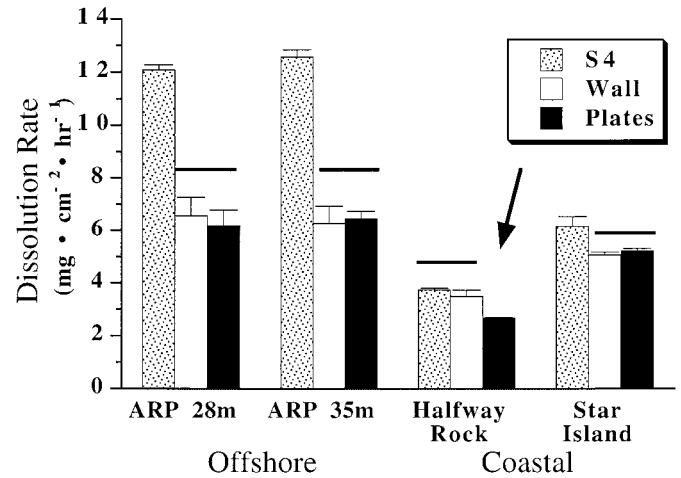


Fig. 4. Mean dissolution rates of alabaster slabs placed level with the S4 current meter, on rock walls where natural field quadrats were located, or on unobstructed growth experiment plates. After detecting a significant difference among treatments at each of the sites (one-way ANOVA, $F > 6.65$, $P < 0.03$, $df = 2,6$ for each site), planned post hoc comparisons with Fisher's protected LSD indicated that at three of the four sites, bulk flow was greatest near the S4 and not different between the wall and the unobstructed growth plates. At Halfway Rock, bulk flow was reduced near the unobstructed growth plates when compared with the S4-level and wall slabs. Unbroken horizontal bars indicate no significant difference for those treatments under a given bar; error bars represent standard errors.

m, and Star Island displayed higher growth rates ($P < 0.01$) than colonies at Halfway Rock (Fig. 7). By observing growth patterns of the unobstructed colonies over the course of the year, it was apparent that the period of maximum growth for *P. jeffreysi* occurs from late spring through the summer months.

Growth within natural communities—Differences in the field growth rate of *P. jeffreysi* among sites were examined in two ways. First, the entire range of original colony sizes for *P. jeffreysi* was used in an ANCOVA that showed no difference in slopes among treatments and no difference in growth rates between offshore and coastal locations or among the four sites (Table 2B, Fig. 8). Second, only those colonies whose original sizes fell within the range of original colony sizes from the transplant study were used in the ANCOVA. Once again, there were no differences in slopes among the treatments and no difference in growth rates between colonies from either location or any of the four sites (Table 2C, Fig. 9).

Unobstructed vs. quadrat growth—Growth of *P. jeffreysi* in the unobstructed growth experiment and in the natural community were compared by pooling data from the two experiments described above. Using the standard model with an added treatment variable to account for unobstructed vs. naturally occurring colonies, the slopes were indistinguishable (Table 2D), but further analysis revealed differences between treatments and among sites. The interaction term between treatment and site was also significant, indicating that

Table 1. Analysis of particulate data. (A) Results of two-way nested ANOVA on the log-transformed number of chlorophyll-containing particles per milliliter, based upon particle size (5–10 μm , >10–20 μm , >20 μm), location (offshore or coastal), and site (nested within location). (B) Results of two-way nested ANOVA on the arcsine-square root transformed percentage of chlorophyll-containing particles, based upon the criteria in A. (C) Results of one-way nested ANOVA on log-transformed sedimentation rates at two sites in both offshore and coastal locations.

Source	Sums of squares	df	Mean squares	F	P
A. Particulate food quantity: Density of particles containing Chl <i>a</i>					
Size	7.936	2	3.968	36.721	<0.001
Location	0.994	1	0.994	2.395	0.262
Site (location)	0.830	2	0.415	3.840	0.041
Size \times location	1.094	2	0.547	6.637	0.054
Size \times site (location)	0.330	4	0.082	0.763	0.563
Error	1.945	18	0.108		
Scheffé post hoc contrasts: ARP 28 m, ARP 33 m > Halfway Rock*					
B. Particulate food quality: Percentage of particles containing Chl <i>a</i>					
Size	18.691	2	9.345	0.361	0.702
Location	1859.428	1	1859.428	143.120	0.007†
Site (location)	25.984	2	12.992	0.502	0.613
Size \times location	145.509	2	72.755	11.978	0.021
Size \times site (location)	24.296	4	6.074	0.235	0.915
Error	465.514	18	25.862		
C. Sedimentation rate					
Location	122.265	1	122.265	219.113	0.005‡
Site (location)	1.117	2	0.558	5.737	0.007
Error	3.115	32	0.097		
Ryan's Q pairwise contrasts with Kramer modification for unequal sample size: Halfway Rock, Star Island \gg ARP 28 m > ARP 33 m*					

* Significance levels: > = 0.05, \gg = 0.01.

† Offshore > coastal.

‡ Coastal > offshore.

the difference between treatments was not independent of site.

The significant treatment effect demonstrated that unobstructed colonies experience higher growth rates than colonies within field quadrats (Fig. 9). Pairwise comparisons were made for the treatment \times site interaction, because the treatment effect was not independent of site. With the exception of Halfway Rock, the unobstructed bryozoan colonies had higher growth rates than did colonies in the natural community at each of the sites ($P < 0.01$).

Discussion

Regional variation in particle flux—There were striking differences between coastal and offshore regions of the GOM with respect to particle flux regime. The variation in both flow speed and particle concentration is even more noteworthy. Despite these physical differences, there was no difference in offshore and coastal growth rates of *P. jeffreysi*. Previous investigations examining the feeding and growth response of bryozoans to differences in flow speed and particle concentration can be used in conjunction with our results to predict the response of *P. jeffreysi* to the differences experienced between coastal and offshore GOM locations in this study.

Mean free-stream flow speeds were several times greater offshore, and the frequency distribution of flow speeds at the offshore location usually exceeded maximum coastal values. By comparing the alabaster dissolution data from the vicinity

of the S4 current meter with the two near-wall locations, free-stream flow speeds can be used to describe the flow regime experienced by bryozoan colonies on either the rock walls or the unobstructed growth plates. At the offshore sites, dissolution rates on the plates and wall were about half the values recorded at the level of the S4 meter. Therefore, the mean near-wall flow speed offshore would still be ca. 10 cm s^{-1} , which is more than twice free-stream values at the coastal location. Previous studies on bryozoans at similar flow speeds suggest this would lead to greater feeding success and growth in the coastal location (Okamura 1985, 1988, 1992; Eckman and Duggins 1993). This hypothesis is supported by video recordings of particle capture and water pumping by 15 species of bryozoans, in which the downward (toward the mouth) flow speeds generated by the lophophore ranged from 1.78 to 3.11 mm s^{-1} (Riisgård and Manríquez 1997). These flow speeds were too slow to overcome the inertial forces carrying food particles downstream. However, these flow speed data need to be evaluated in context with the particle concentration data.

Considering nonfood particles, the sedimentation rates were over an order of magnitude higher at the coastal sites than offshore. The low flow speeds at the coastal location may have resulted in greater feeding success for *P. jeffreysi*, but they also may have led to higher sedimentation, which is detrimental to this organism. Conversely, the sediment load was low at the offshore sites, so that the high flow speeds associated with this location may not have provided any beneficial relief from sediment deposition.

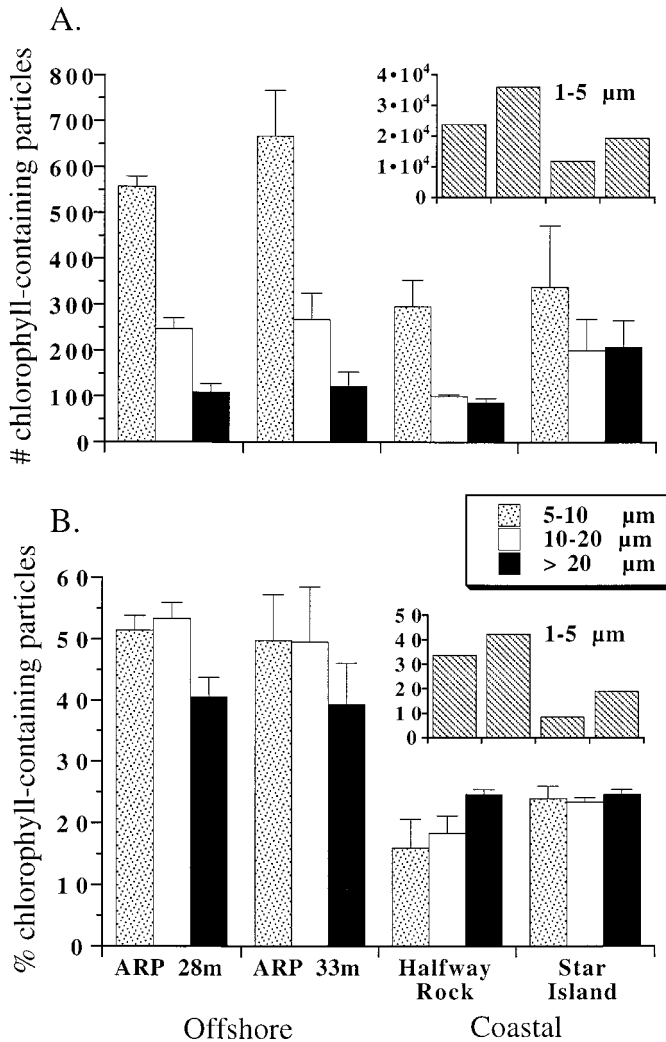


Fig. 5. Flow cytometry data from 1994, presented as (A) mean number and (B) mean percentage of chlorophyll-containing particles ml⁻¹ according to size class and site. Three samples were averaged at each site for the size fraction >5 μm, and a single sample was analyzed for the 1–5-μm fraction. Error bars represent standard errors.

Mean Chl *a* values at 30 m depth, and thus phytoplankton concentrations, were greater at offshore sites than along the coast during the summer. This finding is contrary to predictions for GOM surface waters (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 unpubl. data). Seasonal data collected from the coastal sites indicate that Chl *a* values fluctuate throughout the year in these habitats (Genovese 1996). CTD casts from April (Townsend et al. 1989) and October (Townsend and Corwin 1990) at ARP indicate that Chl *a* concentrations at 28–33 m are within the range of those reported for Halfway Rock and Star Island in October 1993 and April 1994 (Genovese 1996), suggesting there may be no difference in phytoplankton concentrations in offshore and coastal regions during the spring and fall. Because *P.*

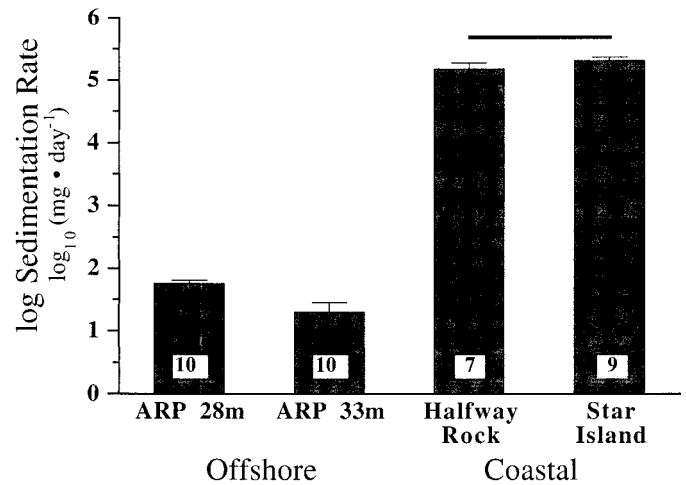


Fig. 6. Log₁₀-transformed values for mean sedimentation rates at each site indicate greater sedimentation at coastal sites. Horizontal bars indicate that the sites beneath do not have significantly different values. The number of sediment tubes retrieved from each site is listed within the data bar for that site; error bars represent standard errors.

jeffreysi growth occurs during the summer months, the summer values for Chl *a* concentration will be the most relevant. Similar patterns of seasonal growth have been reported for other temperate (Stebbing 1971) and polar (Barnes 1995; Barnes and Clarke 1998) bryozoans. Thus, the alternative hypothesis that similar growth rates observed for coastal and offshore locations are due to seasonal variation in relative food concentration between locations can be rejected.

If particle flux alone were important to *P. jeffreysi*, without any regard to the relative contributions of flow speed and particle concentration, then the offshore populations should have a clear growth advantage over coastal populations. Predictions from past studies on encrusting bryozoans (Okamura 1985, 1988, 1992) suggest that not only will the contribution of flow speed to particle flux provide no benefit to particle capture, it will act in a detrimental fashion. Thus, although particle flux values are much greater offshore than in the coastal zone, they should not be a good predictor of bryozoan feeding success or growth.

The two major questions 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 the animals. Likewise, at locations where there are high densities of food particles that are part of an overall poor-quality food pool (e.g., high 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 actively rejecting these particles. Consideration given to such questions has focused on commercially important bivalve species such as *Mytilus edulis* (Willows 1992; Bayne et al. 1993), *Placopecten ma-*

Table 2. Nested ANCOVA of growth experiments. (A) There was no location effect for unobstructed colonies, but growth was significantly lower at Halfway Rock. (B) There were no differences in growth rate among colonies growing in the field, based on either site or location. (C) Same as B except only for those colonies in the field whose original size encompasses the same size range as those bryozoans used in the unobstructed growth experiment. (D) Comparison of growth rates for unobstructed bryozoans vs. those in field quadrats.

Source	Sums of squares	df	Mean squares	F	P
A. Unobstructed colonies					
Slope: size × site (location)					0.075
Size	0.164	1	0.165	3.061	0.087
Location	0.244	1	0.244	0.216	0.688
Site (location)	2.261	2	1.131	20.985	<0.001
Error	2.586	48	0.054		
Conditional Tukey–Kramer post hoc tests: ARP 28 m, ARP 33 m, Star Island ≫ Halfway Rock*					
B. Field colonies over entire original size range					
Slope: size × site (location)					0.560
Size	10.502	1	10.502	37.697	<0.001
Location	0.002	1	0.002	0.029	0.879
Site (location)	0.139	2	0.069	0.250	0.779
Error	37.333	134	0.278		
C. Field colonies over original size range of unobstructed colonies					
Slope: size × site (location)					0.757
Size	1.253	1	1.253	6.255	0.015
Location	0.001	1	0.001	0.033	0.872
Site (location)	0.670	2	0.033	0.166	0.847
Error	13.419	67	0.200		
D. Unobstructed and field colonies over original size range of unobstructed colonies					
Slope: size × treatment × site (location)					0.649
Size	1.282	1	1.282	9.210	0.003
Location	0.163	1	0.163	0.325	0.626
Site (location)	1.004	2	0.502	3.607	0.030
Treatment	4.859	1	4.859	34.917	<0.001†
Treatment × location	0.128	1	0.128	0.120	0.762
Treatment × site (location)	2.126	2	1.063	7.639	<0.001
Error	16.141	116	0.139		

* Significance levels: ≫ = 0.01.

† Unobstructed growth > field growth.

gellanicus (Cranford 1995; MacDonald et al. 1998), and *Mya arenaria* (MacDonald et al. 1998), which show decreased absorption efficiency in response to increases in dietary inorganic content. The flow cytometry data indicate the superiority of the offshore region in terms of both food quantity (high Chl *a*) and quality (low sedimentation). In fact, the results of the flow cytometry analysis concur with those from the in situ fluorometer and the sediment traps.

Several investigators (Bullivant 1968; Winston 1977; Hunter and Hughes 1993) have been able to assess the feeding success and growth of bryozoans when placed in a variety of algal suspensions. The majority of algal species in each of these studies had average dimensions of 5–20 μm. Okamura (1984, 1985, 1988, 1990, 1992) used inert latex beads (diameters of 9–20 μm) to assess particle capture and feeding success for several species of encrusting and arborescent bryozoans. Recent studies (Riisgård and Manríquez 1997; Nielsen and Riisgård 1998) examining the particle capture mechanism and filter apparatus of 15 species of bryozoans indicate that particles >6 μm can be retained by the filtering apparatus whereas nearly all particles <5 μm will pass through the filter. This body of work suggests that

the two most relevant size classes in the flow cytometry analysis were 5–10 μm and 10–20 μm, but the possibility that bryozoans may be utilizing both smaller and larger size classes of particles cannot be overlooked. The flow cytometry data indicate a similar ranking of the quality and quantity of particulates among the sites for both smaller (1–5 μm) and larger (>20 μm) size classes.

Our work suggests that the negative effect of high flow speeds on feeding success offshore balances out the positive effect of a relatively superior food supply in comparison to the coastal location. There can also be significant metabolic costs associated with high flow speeds (Patterson and Sebens 1989; Patterson et al. 1991; Patterson 1992) that may act to decrease the growth of this organism, independent of any effect on feeding success. This decreased growth is due to the increased respiration that often accompanies higher flow speeds and results from greater passive gas exchange across the surface of many aquatic invertebrates (Patterson 1992).

Growth of P. jeffreysi—The main intent of this experiment was to elucidate any regional differences in the growth of *P. jeffreysi* within the GOM, given either conditions of un-

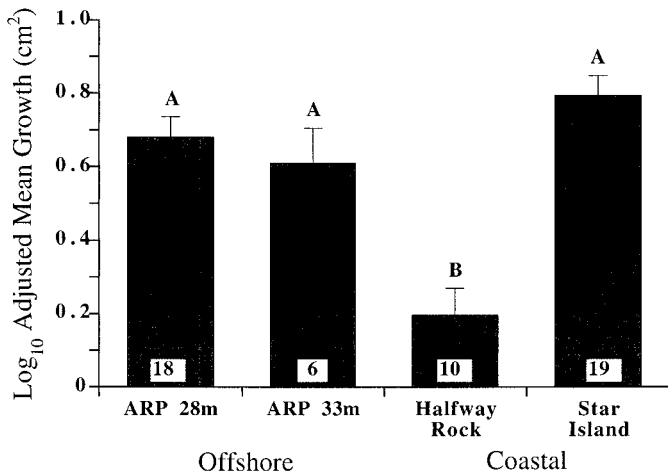


Fig. 7. *Parasmittina jeffreysi* growth results from unobstructed growth experiment. Log₁₀-adjusted mean growth (±SE) from an ANCOVA. The number of colonies in each treatment is indicated within the corresponding bar. Similar letters above error bars indicate no difference in adjusted means. Growth of unobstructed colonies was significantly lower at Halfway Rock ($P < 0.01$) when compared with growth at the other three sites.

obstructed growth or conditions within the local community (i.e., field quadrats). Within-site comparisons of these treatments were conducted to address competition for both space and food. Comparisons were made at both offshore and coastal locations, to determine whether or not responses were independent of changes in resource availability (i.e., across particle flux regimes). An alternative hypothesis for differences (or lack thereof) in growth rate could be that resources were differentially allocated towards reproduction and somatic growth across sites. As with many other species of bryozoans (e.g., Barnes and Clarke 1998), *P. jeffreysi* produces ovicells in late summer–early fall. In this study, we examined growth rates from late one summer to the middle of the next summer. Although we are unable to conclude whether there would have been differential reproductive efforts among locations had this experiment been continued, we are confident that up until the time when this experiment was terminated, most allocation was toward somatic growth, as indicated by the absence of ovicells in these colonies.

Given the absence of spatial competition in the unobstructed growth experiment, comparisons failed to reveal any significant regional effect, suggesting that the high flow speeds offshore probably negated any of the beneficial effects from the superior food supply. Bryozoans at the three other sites exhibited greater growth than did the colonies at Halfway Rock, where the lowest mean free-stream flow speeds were found. The interactive effect of high sedimentation in conjunction with low flow at Halfway Rock could account for the lower growth rates reported for these colonies.

Growth rates of *P. jeffreysi* in its natural community were not significantly different between locations or among sites during the same period that the unobstructed growth experiments were conducted, suggesting that any effect that may have been evident in the absence of spatial competition was

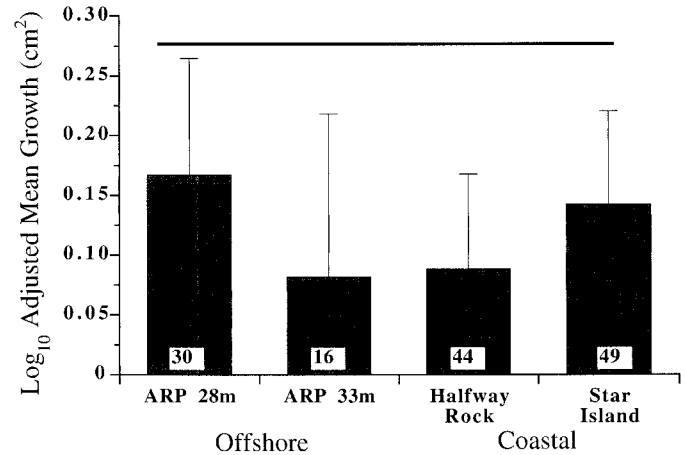


Fig. 8. Log₁₀-adjusted mean growth (±SE) from an ANCOVA on *P. jeffreysi* growth results from natural field quadrats over the entire range of original colony sizes. Growth was measured over the same period as the unobstructed growth experiments. The number of colonies in each treatment is indicated within the corresponding bar. There was no difference in adjusted mean growth among sites, as noted by the unbroken horizontal bar above the mean values.

no longer a factor. Flow speeds in the vicinity of the quadrats at Halfway Rock were greater than those near the unobstructed growth plates at this site (but less than those at the other sites), which may account for the improved performance of naturally growing colonies at Halfway Rock.

Comparisons can be made between growth of colonies from the unobstructed growth experiment with those of colonies from the field quadrats. The experimental protocol was

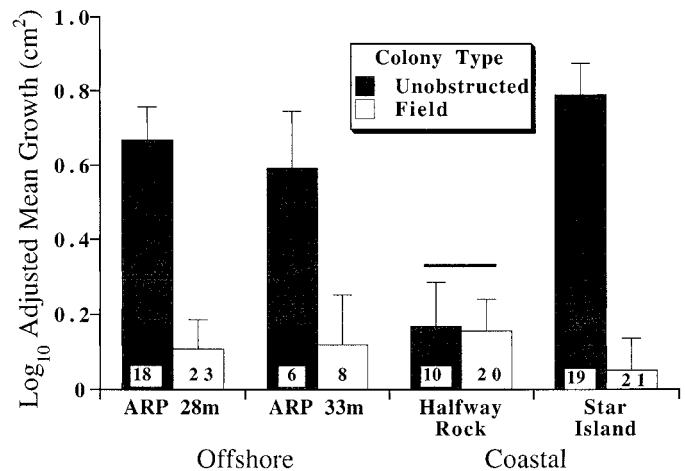


Fig. 9. Comparison of log₁₀-adjusted mean growth (±SE) between the unobstructed *P. jeffreysi* colonies and colonies from natural field quadrats whose original colony sizes overlap those from the unobstructed growth experiment. There was no difference in growth among sites for this subset of the natural field colonies (Table 2C). The number of colonies in each treatment is indicated within the corresponding bar; horizontal bars indicate no difference between treatments within a given site. Growth of unobstructed *P. jeffreysi* colonies was greater than that of colonies from the natural field quadrats at each site, with the exception of Halfway Rock.

quite different between experiments, but the influence of two factors on bryozoan growth can be examined: 1) in the absence of spatial competition (i.e., unobstructed colonies), the growth of *P. jeffreysi* should be higher than in cases where spatial competition is present (i.e., within the field quadrats), given similar conditions of flow speed and particle concentration; and 2) neighboring organisms in the field quadrats may either facilitate (Okamura 1985, 1988) or interfere with (Okamura 1984, 1992) feeding by bryozoans, resulting in a corresponding growth response (Okamura 1992).

A comparison of growth rates for *P. jeffreysi* colonies demonstrated that unobstructed colonies had higher growth than did those colonies in the field quadrats, suggesting that growth was higher in the absence of spatial competition and/or that feeding interference occurred in the field quadrats. Differences in growth between unobstructed and naturally occurring colonies were not independent of site; only at Halfway Rock were the adjusted mean growth rates of unobstructed colonies no different than those of colonies within the field quadrats. This lack of difference was due to the relatively low growth rate of unobstructed colonies at this site.

Despite particle flux regimes that were very different between offshore and coastal regions, there were no strong regional effects on the growth of *P. jeffreysi*. The interactive effects of flow speed and particle concentration probably were acting upon feeding success and growth in opposing directions at each location, resulting in the net effect of no difference. In a similar study using only a single offshore and coastal GOM site, Lesser et al. (1994) reported higher offshore growth for the sea anemone *Metridium senile* and higher coastal growth for the horse mussel *Modiolus modiolus*. Those findings, along with the results reported in this study, are a clear indication that despite experiencing similar particle flux regimes, growth rates will vary for suspension-feeding organisms employing different mechanisms of particle capture. Although *P. jeffreysi* displays excellent overgrowth capabilities, significantly higher growth was observed in the absence of spatial competition. It appears that any growth effect due strictly to bottom-up forces (sensu Menge 1992) will tend to be dampened by strong competitive interactions (Genovese and Witman unpubl. data), perhaps to the extent that these differences in growth are no longer evident when examined from within the suspension-feeding community.

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