

Living where the flow is right: How flow affects feeding in bryozoans

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Synopsis Bryozoans are suspension feeding colonial animals that remain attached to the substratum or other surfaces. How well a bryozoan can feed in a particular flow regime could help determine the distribution and abundance of that bryozoan. I tested how velocity of flow affects feeding rate in four species of bryozoans in the laboratory and how these species perform in different flow regimes in the field. I found that one species, *Membranipora membranacea*, had a higher ingestion rate than did the other three species at all velocities of flow tested. *Membranipora* also had a higher rate of ingestion at intermediate velocities, while velocity did not have as strong an effect on ingestion rate in the other three species. As predicted from the feeding experiments, all four species generally had greater abundance, attained a larger size, grew faster, and survived longer in flow regimes in which feeding is higher. Also as predicted, *Membranipora* had greater abundance, attained a larger size, grew faster, and survived longer than did the other three species both in slower and faster flow regimes in the field. Understanding how flow affects feeding can help predict the distribution and abundance of bryozoans in the field. Because especially efficient filterers like *Membranipora* can grow faster and have higher survival under a wide range of conditions of flow, this species may be able to outcompete many other species or take advantage of ephemeral habitats, thereby becoming a potentially effective invasive species as has been seen in the Gulf of Maine.

Introduction

The vast majority of colonial animals such as corals, hydrozoans, ascidians, and bryozoans are benthic suspension feeders that depend on currents of water to supply nutrients, eliminate wastes, and disperse gametes and larvae. The effect of velocity of flow on the capture of food is especially important because acquisition of energy is essential to perform most other life processes, and therefore, feeding performance may be a good proxy for fitness. In this study, I focus on how water flow affects feeding in bryozoans.

A bryozoan colony is made of individual units called zooids that are replicated by asexual budding. A zooid consists of a protective housing, or zoecium, that encloses and protects the living tissues. Bryozoans actively generate their own feeding currents with a crown of ciliated tentacles called a lophophore. Not all zooids are capable of feeding, but the ones that do feed have a movable part, or polypide, that contains the digestive system and bears the lophophore. Zooids arranged in different ways create different colony shapes, and zooids within the colony can coordinate their feeding currents. The feeding currents of the colony depend on the arrangement of lophophores within the colony and the shape of the colony as a whole (Cook 1977; Winston 1978, 1979; Lidgard 1981; Okamura 1984, 1985; McKinney 1990).

Many studies have investigated the feeding of bryozoans; however, many unresolved issues and methodological problems remain. The majority of studies were conducted in still water (Cook 1977; Winston 1978, 1979; Riisgård and Goldson 1997; Nielsen and Riisgård 1998), yet bryozoans probably experience still water rarely, if ever. A few studies have investigated bryozoan feeding in flowing water, but, with one exception (Okamura 1992), these do not relate feeding to distribution and abundance. The influence of velocity on feeding in an erect, tree-shaped colony, *Bugula stolonifera* (Okamura 1984), and an encrusting sheet-shaped colony, *Conopeum reticulum* (Okamura 1985), was variable, appearing to depend on both shape and size of the colony. However, a generic problem with all previous studies is the assessment of feeding in only a small number of ambient velocities of flow and the assumption that the relationship between feeding and flow is linear. Clearly, if the capture of food is a nonlinear function of velocity, then feeding must be measured over a wider range of velocities.

Many factors can influence capture of particles by bryozoans, including characteristics of the food (e.g. type, size, concentration); shape and size of the colony; size, shape, number, location, and level of activity of zooids; and environmental conditions

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(e.g. temperature, water velocity, salinity, competition from neighbors). While a number of studies look at the effect of one or more of these factors on bryozoan feeding (see McKinney 1990 for a review) and interactions among them may be important, no studies hold all of these other factors constant and examine how feeding success varies under a relatively wide range of velocities and in multiple species of different colony shapes. Whether water velocity has a consistent effect on success of capturing particles, and whether the relationship between water velocity and that success has an effect on the abundance and distribution of bryozoans remain unclear.

I measured how feeding varies over a broad range of flows for bryozoans of different colony shape, and how flow affects abundance, growth, and survival in the field. I had three predictions: (1) feeding changes as a unimodal function of velocity, (2) bryozoans will have higher abundance, growth, and survival in flows where feeding is high, and (3) colonies in the form of encrusting sheets will perform better in high-flow velocities than those in the form of erect trees.

The first prediction, that feeding will show a unimodal function of velocity, is based on theory as well as on previous experiments with other suspension feeders. According to Wildish and Kristmanson (1997), the rate of capture of food particles by suspension feeders generally follows a “continuous unimodal function” with a peak in rate of capture of food at intermediate freestream velocities. If the concentration of particles is held constant, the continuous-unimodal-function theory suggests that the rate of capture of particles at first increases with increased velocity, most likely due to an increase in the rate at which particles are encountered. Eventually, a maximum is reached beyond which the rate at which particles are captured is unaffected by further increase in velocity. This maximum particle-capture rate may be determined by such things as the size of the filtration surface or limits on the rate of transport of particles to the mouth. At yet higher velocities, flow begins to suppress capture of particles because the particles pass by too quickly to be diverted into the feeding structure or the feeding structure itself is deformed by the high flow and is less effective at capturing particles. At very high velocities, capture of particles may stop altogether, either because no food can be captured or the animal ceases feeding. The filtration rates of most suspension feeders that have so far been adequately examined fit the unimodal-function theory and Wildish and Kristmanson (1997) claimed this to be a general principle of suspension feeding. Examples of animals

that fit the unimodal-function theory include: cnidarians such as the sea pen *Ptilosarcus gurneyi* (Best 1988), the gorgonian corals *Pseudopterogorgia acerosa*, and *P. americana* (Sponaugle and Labarbera 1991), an alcyonacean soft coral (McFadden 1986), an annelid terebellid polychaete *Lanice conchilega* (Denis et al. 2007) and 10–12 species of marine and freshwater molluscan bivalves (Ackerman 1999), including the bay scallop *Argopecten irradians* (Kirby-Smith 1972; Wildish et al. 1987). Bryozoans have been inadequately studied for evaluating how feeding varies as a function of velocity, so it is unclear if the unimodal-function theory holds for all phyla that have suspension feeders.

The unimodal-function theory implies there is a velocity, or range of velocities, at which filtration rate is maximal. Does this help determine which habitats are most suitable for an organism? The second prediction is simply based on the idea that bryozoans should grow faster and survive longer and thus have greater abundance in environments in which there is greater capture of food. A few studies have related feeding success to the distribution and abundance of suspension feeders in the context of their flow environment. These include investigations of sea pens (Best 1988), octocorals (Sebens 1984; Patterson 1991a, 1991b), and sea anemones (Koehl 1977; Shick et al. 1979; Sebens 1981). One study on bryozoans showed that both feeding success and growth decreased with increasing velocity for an encrusting species, *Electra pilosa* (Okamura 1992). That study provided evidence that feeding patterns are reflected in growth, but more research is needed to see if this pattern is general.

While there may be a velocity at which feeding is optimized that accordingly predicts the most suitable habitats for bryozoans, encrusting colonies may be able to live in a wider range of flows. Erect colonies may be less successful in environments with high ambient velocities because of a higher risk of dislodgment or damage (Cheetham and Thomsen 1981; Cheetham 1986) and because high drag can cause deformation of the filtering surface and reduce the efficiency of filtration (Best 1988). Encrusting colonies are exposed to slower flows in the velocity gradient close to the substratum. Since an encrusting colony would experience slower local flow and has a much wider area attached to the substratum than does an erect colony, the encrusting colony would need less support to prevent dislodgement and would still be able to feed without the colony being deformed by the flow. This advantage of the encrusting form explains the third prediction that encrusting sheets should

have higher ingestion rates than do erect trees at high ambient velocities of flow.

Methods

Feeding as a function of velocity

Collection and preparation of colonies

Ingestion rate was measured for four species of bryozoans: *Membranipora membranacea*, *Celleporella hyalina*, *Bugula pacifica*, and *Schizoporella varians*. *Membranipora* and *Celleporella* are encrusting sheets, while *Bugula* and *Schizoporella* are erect trees (Fig. 1). Small colonies of each species were collected from the floating docks at the Friday Harbor Laboratories in Friday Harbor, WA, USA. Colonies of the two erect species were each glued with cyanoacrylate gel onto a Plexiglas plate (5 cm×5 cm). Because the glue only touched a very small part of the colony, where no feeding zooids were located, and the colonies were given plenty of time to recover after gluing (generally weeks), it was assumed that the glue had no effect on bryozoans' feeding rates. Colonies of the two encrusting species were carefully peeled from a red alga (*Mazzealla splendens*) and then placed on a glass slide (3 cm×1 cm) in a dish of seawater. The encrusting colonies were allowed to grow onto the slides until they were firmly attached (usually 1–2 days). Once colonies were firmly attached, the plates and slides were placed in racks and hung from the floating docks so the bryozoans could feed until needed for experiments. No difference in morphology was observed between colonies naturally growing in the field and colonies transferred and grown for experimentation.

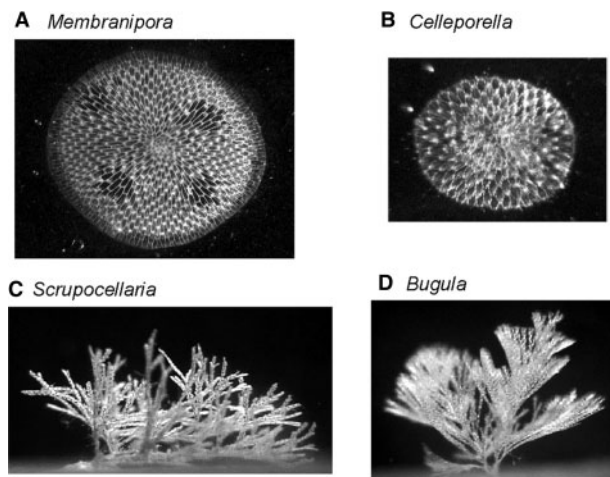


Fig. 1 Photographs of the four bryozoan species used in this study. (A) *M. membranacea*, (B) *C. hyalina*, (C) *S. varians*, and (D) *B. pacifica*.

Protocols for measuring ingestion rate

Feeding experiments were conducted in a recirculating flow-tank with a working section of 70 cm×10.2 cm×13 cm (Vogel and LaBarbera 1978). The flow-tank was filled with 0.45 µm filtered seawater and kept in a cold room at 12°C to maintain temperature similar to that of the bryozoans' natural habitat. Blue-dyed polystyrene beads (mean diameter = 10.3 µm, SD = 0.94 µm, density = 1050 kg/m³) at a concentration of 1000 beads/ml were used as food particles. Bead concentrations were measured using a nanoplankton counting meter. Sizes and concentrations of particles were chosen to coincide with those encountered in the field, as in other studies (Okamura 1984, 1985). Polystyrene beads have been used in many studies of suspension feeders (Nygaard et al. 1988; Shimeta and Koehl 1997), including bryozoans (Okamura 1984, 1985; Pratt 2005), and bryozoans have been shown to ingest them in large quantities (Okamura 1984, 1985). None of the species in the present study were ever observed to reject beads. Polystyrene beads are particularly convenient because they are not digested. Colonies can therefore be preserved and feeding rates determined later by counting the number of beads ingested.

A plate or slide containing a single colony was positioned flush with the bottom of the flow-tank so only the bryozoan protruded into the flow. After feeding for 20 min, the colony was removed, fixed in formalin, rinsed in 70% EtOH, and cleared in 50% glycerol. Feeding rate was measured for 3–5 colonies of each species at each velocity. Colonies used were close to 1 cm in length (*Bugula*: 0.98 ± 0.16 cm, *Celleporella*: 0.84 ± 0.19 cm, *Membranipora*: 0.88 ± 0.19 cm, *Scrupocellaria*: 1.43 ± 0.23 cm).

Rate of ingestion was measured in five freestream velocities: 0, 0.4, 2.3, 4.3, and 7.0 cm/s (Table 1). Velocities were measured by tracking particles in video recordings over known distances, using a laser light sheet to illuminate a 2D view. Near the substratum, the velocity (U , cm/s) showed a linear relationship with height above the bottom (z , cm). The slope of this relationship (dU/dz) allowed calculation of the shear velocity (U^*)

$$U = \left(\nu \frac{dU}{dz} \right)^{1/2}, \quad (1)$$

(Vogel 1994), where ν is the kinematic viscosity (in this case $\nu = 0.0128 \text{ cm}^2/\text{s}$). Estimates of U^* on the most exposed blades in a kelp bed range between 0.22 and 0.60 cm/s (Koehl and Alberte 1988); thus, the velocities used in this study (U^* between 0–0.37 cm/s) are likely to be within the lower range

Table 1 Characteristics of the five velocities of flow used in the feeding experiments

Freestream ^a (cm s ⁻¹)	Linear Relationship ^b			
	Range (cm)	Slope	R ²	U* ^c
0	NA	NA	NA	NA
0.4 ± 0.01	0–1	0.29	0.94	0.061
2.3 ± 0.05	0–0.8	2.5	0.96	0.18
4.3 ± 0.31	0–0.5	6.1	0.90	0.28
7.0 ± 0.74	0–0.35	10.7	0.86	0.37

^aValues of freestream velocity are the means ± SD of velocities measured between 2.5 and 5 cm above the bottom.

^bThere was a linear relationship between velocity (U) and height above the bottom (z). Range: range in heights above the bottom where the linear relationship was found. Slope: slope of the linear relationship (dU/dz). R^2 : coefficient of determination.

^cU*: calculated shear velocity.

of velocities experienced by bryozoans living on kelps in the field.

The total number of zooids and the number of beads ingested by each zooid in the colony were counted using a compound microscope at 100×. Only autozooids (with or without polypides) were counted for each species. Autozooids have a polypide in them at some point and are capable of feeding. Some autozooids will lose their polypides and serve another purpose, such as support, in an erect-tree colony or in an excurrent space in an encrusting colony. *Membranipora* only has autozooids but the other three species also have heterozooids with other functions. Mature *Bugula* colonies have reproductive ovicells and defensive avicularia, *Scrupocellaria* have defensive vibracula, and *Celleporella* have small, nonfeeding male zooids. However, autozooids are substantially larger than these heterozooids and thus make up most of the area of the colonies. Therefore, only autozooids are considered in this study and the terms autozooid and zooid are used synonymously.

Zooid ingestion rate is defined here as the number of beads eaten by a zooid divided by the time spent eating them (beads/min). Only the zooids that ate one or more beads were included in calculating mean zooid ingestion rates. Despite removing the large number of zeros by only including the zooids that ate, the data was still skewed and could not be transformed to conform to a normal distribution. Therefore, zooid ingestion rates were analyzed with a generalized, linear, mixed model using a negative binomial distribution (Proc GLIMMIX, SAS 9.1, SAS Institute 2006) with species (*Bugula*, *Celleporella*, *Membranipora*, *Scrupocellaria*) and velocity (0, 0.4, 2.3, 4.3, and 7.0 cm/s) as fixed effects and colony (3–5 colonies per treatment) as a random blocking effect.

While zooid ingestion rate can be used to compare the average feeding success of zooids that ate, comparing feeding success at the colony level is also important. Colony ingestion rate is defined here as the number of beads eaten by an entire colony divided by the total number of zooids in the colony and the time they spent eating (beads/zooid/min). Colony ingestion rates were normally distributed so an ANOVA model was used (Proc GLM, SAS 9.1, Freund et al. 1986) with species and velocity as fixed effects. Not all of the zooids were capable of eating since they all did not contain polypides. To be able to better interpret colony ingestion rates, it is useful to know how many zooids had polypides as well as how many of those polypides actually fed. Thus, I compared the percent of polypides that fed (number of polypides that fed divided by the total number of polypides times 100) and the percent of zooids that fed (number of polypides that fed divided by the total number of zooids times 100) using a two-way ANOVA model with species and velocity as fixed effects.

Interactions were compared *a priori* as simple effects using the Tukey–Kramer adjustment for multiple comparisons (or T-method as in Hayter 1989). This approach allowed comparison of each velocity within a species and each species within a velocity. I also performed *a priori* orthogonal polynomial tests for linear, quadratic, and cubic trends in velocity.

Sizes of zooids and colonies

Because feeding can be influenced by the size of zooids and of colonies and because these can vary among species, I measured several aspects of the morphology of zooids and colonies. To compare zooid size among species, I determined the area of the zooid, the volume of the lophophore, the height of the zooid, and the number of tentacles per zooid. The area of the zooid was calculated by multiplying the zooid's maximum length times its width. The volume of the lophophore was calculated by:

$$V = \frac{\pi h}{12}(D_1^2 + D_1 D_2 + D_2^2), \quad (2)$$

in which V = volume of the lophophore, h = the height of the lophophore, D_1 = the diameter of the base of the lophophore, and D_2 = the diameter of the top of the lophophore. I calculated zooid height by adding the height of the introvert to the height of the lophophore.

Size of a colony was estimated by measuring the diameter (encrusting sheets) or height (erect trees) of the colony as well as the area. To measure the area,

the outline of the colony was traced onto an acetate sheet. For encrusting sheets, the perimeter of the colony was easy to trace since they are essentially 2D sheets. For erect trees, the best nondestructive way to get a colony outline was to lay the colony on its side and trace it in side-view. Traced outlines were scanned into a computer and the area digitized using Scion Image. I also counted the number of branches in colonies of the two erect bryozoans by counting the number of tips of branches.

Analysis of covariance (ANCOVA) was used to compare how different variables scale among species (Proc GLM). First, the slopes were compared and if they were not significantly different (i.e. if $P > 0.05$), a common slope was used and the intercepts compared. All data for ANCOVA were transformed by natural logarithm.

Field experiments

Velocities at field sites

The two sides of the floating docks at the Friday Harbor Laboratories provided sites exposed to contrasting flow regimes. The “protected” site faced the shore, while the “exposed” site faced the harbor. Both sides of the dock have abundant sessile organisms that live on the tires or the abundant macroalgae that hang from the sides of the dock. Ambient flow was measured at each site by two methods. In the first, an electromagnetic current meter (Marsh–McBirney Model 511) measured free-stream velocity of the water. Maximum and minimum velocities were measured 15 cm from the dock and 30 cm below the surface of the water for each side of the dock over 1-min periods every 4 h over 24 h. The second method used solid-state dissolution modules (Pep-O-Mint Life Savers) to measure the relative ambient velocity near the substratum by using a substance that dissolves in water at a rate proportional to water velocity. Dissolution rate is measured by weighing the substance before and after a specified time. Blocks of gypsum have often been used for this purpose (Muus 1968; Doty 1971; but see Porter et al. 2000), but Pep-O-Mint Life Savers are also well suited for these measurements (Koehl and Alberte 1988). Ten replicate Life Savers were weighed, sewn onto kelp blades or tires, allowed to dissolve for 10 min, removed, and weighed again. Dissolution rate was calculated as the difference in weight before and after deployment, divided by the time deployed in the water (10 min).

One-tailed *t*-tests were used to compare the mean maximum and mean minimum velocity measured at the exposed site versus the protected site. A two-way

fixed ANOVA model was used to compare the effect of site (exposed, protected), substrate (algae, tire), and the site-by-substrate interaction on the dissolution rate of Life Savers (Proc GLM).

Observations of abundance and size

Abundance was assessed by estimating by eye the percent cover of each bryozoan species in 5 cm × 5 cm quadrats. Three quadrats were sampled on each of three substrata (tires, red algae, and brown algae) in five replicated blocks (tires) in each site. Blocks, substrata, and locations of quadrat sample were chosen at random. In addition to the measurements of percent cover, the length (diameter or height) of the two largest colonies of each species (if present) was measured in each block in each site. Abundance and size were measured four times over the course of late spring through the summer (5/25, 6/18, 7/29, 8/24) in the year 2000.

A four-way ANOVA model of percent cover with exposure, species, substratum, and time as fixed factors would not converge because of too many zero values. Therefore, I used a series of other models to make the comparisons of most interest. For the first model, I compared percent cover for each species separately with a three-way interaction of exposure (protected or exposed), substratum (tires, red algae, or brown algae), and time (0, 24, 65, or 91 days) as fixed effects and block as a random effect. I then compared the maximum percent cover over time for each species with a two-way interaction between exposure and substratum as fixed effects and block as a random effect. Finally, I found the maximum percent cover for each substratum-by-time interaction and then compared these values with a two-way interaction between exposure and species (*Bugula*, *Celleporella*, *Membranipora*, *Scrupocellaria*) as fixed effects and block as a random effect.

A three-way ANOVA model of maximum colony length with exposure, species, and time as fixed factors similarly would not converge because of too many zero values. Therefore, I compared the length of the largest colony for each species separately with exposure and time as fixed effects and block as a random effect. Then I compared the length of the largest colony for each time separately with exposure and species as fixed effects and block as a random effect.

Proc GLIMMIX with the assumption of a normal distribution was used for all the analyses of percent cover and colony length. The interactions were all compared *a priori* as simple effects using the Tukey–Kramer adjustment for multiple comparisons.

I also performed *a priori* orthogonal polynomial tests for linear, quadratic, and cubic trends in time.

Experiments on survival and growth

Growth and survival of three of the species (*Membranipora*, *Bugula*, and *Scrupocellaria*) were measured over 1 month at the two sites. *Celleporella* was not included because there were not enough colonies available for analysis. Single colonies of each species were allowed to settle or were glued (using cyanoacrylate gel) onto 16 replicate Plexiglas plates (11 cm×7 cm) that were attached vertically to PVC racks suspended on each side of the dock. Each rack held eight plates of each species. Colonies of each species were randomly assigned to location. Growth and survival of *Membranipora* and *Bugula* colonies were measured in the summer of 2000, while *Scrupocellaria* was measured in the summer of 2001. Measurements were taken four times regularly over approximately 40 days. During measurements, plates were cleaned of everything except the one colony of interest so as to minimize competition. Survivorship of each colony was noted, and measurements of area were made as already described.

Survival rate was calculated by:

$$l = \frac{N(t)}{N(t_0)}, \quad (3)$$

where l = the proportion of the original cohort surviving to day t , $N(t)$ = number of colonies at time t , t = time (in days), $N(t_0)$ = the number of colonies at t_0 , and t_0 = time zero. Relative growth rate was calculated by:

$$RGR = \left(\frac{A_t - A_{t_0}}{t * A_{t_0}} \right), \quad (4)$$

where RGR = relative growth rate, A_t = area after 12 days, A_{t_0} = initial area, t = 12 days. Even though area was measured four times over about 40 days, growth was calculated over 12 days because this period represents the longest time for which a relatively large sample size was available (many of the colonies did not survive to the next date of measurement).

Survival was analyzed using a Cox regression proportional-hazards model, and ties were handled using the exact method (Proc PHREG, SAS 9.1, Allison 1995). The covariates used in the full model were (1) two dummy variables for the different species (*Bugula* and *Scrupocellaria* with *Membranipora* as the withheld group), (2) a dummy variable for site (with the exposed site as the dummy variable and the protected site as the withheld group), and

(3) initial area. Relative growth rate was compared with a two-way ANOVA model with species (*Bugula*, *Membranipora*, or *Scrupocellaria*) and exposure (protected or exposed) as fixed effects (Proc GLM). Interactions were compared *a priori* as simple effects using the Tukey–Kramer adjustment for multiple comparisons.

Results

Feeding as a function of velocity

Ingestion rates

Zooid ingestion rates were significantly different among species ($P_{3,56} < 0.0001$): *Membranipora* had greater zooid ingestion rates than did *Bugula* and *Scrupocellaria* ($P < 0.0001$) and these three species had more frequent zooid ingestion than did *Celleporella* ($P \leq 0.001$) (Fig. 2). The random colony effect added significant variation to the data ($P < 0.0001$) but the velocity main effect and species-by-velocity interaction were not significant (velocity: $P_{4,74} > 0.05$, species×velocity: $P_{12,55} > 0.05$). All four species together had a significant quadratic trend in velocity ($P < 0.05$) but when each species was

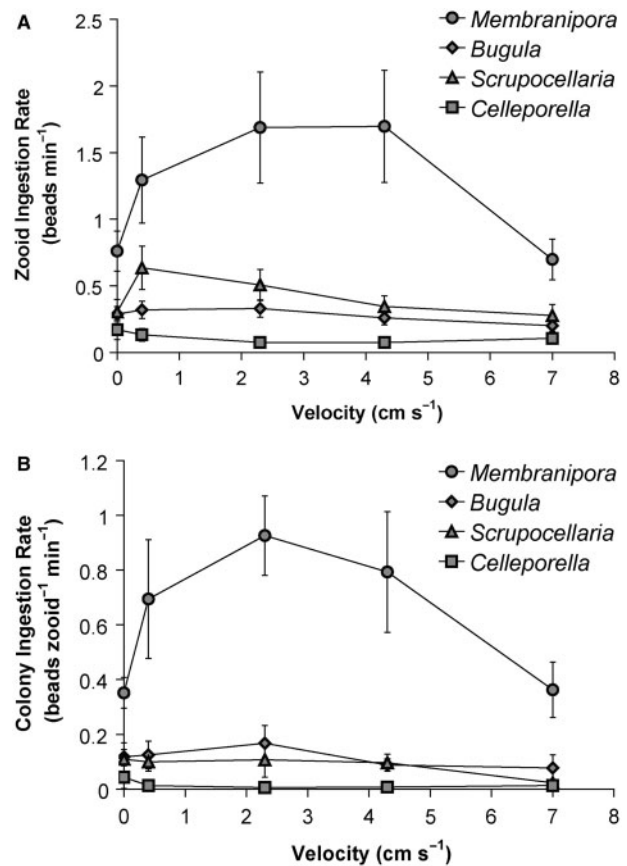


Fig. 2 Zooid (A) and colony (B) ingestion rates as a function of water velocity for four bryozoan species. Values are means ± SEM.

tested separately only *Membranipora* ($P=0.001$) and *Scrupocellaria* ($P<0.05$) had significant quadratic trends in velocity.

Colony ingestion rates were also significantly different among species ($P_{3,54}<0.0001$): *Membranipora* had greater ingestion rates than did the other three species ($P<0.0001$). The interaction between species and velocity was also significant ($P_{12,54}<0.01$) in which *Membranipora* had significantly greater colony ingestion rates than did the other three species from 0.4 to 7 cm/s ($P<0.01$) and no species differed at 0 cm/s (all $P>0.05$). Velocity had an overall effect ($P_{4,54}<0.05$): colony ingestion rates were higher for all species at 2.3 cm/s than at 7 cm/s ($P<0.05$) and showed a quadratic trend ($P<0.001$). When the simple interactive effects were compared, only *Membranipora* showed any significant effect among velocities; colony ingestion rate was greater at intermediate velocities (0.4, 2.3, and 4.3 cm/s >0 and 7 cm/s; all $P<0.05$) and there was a significant quadratic trend ($P<0.0001$).

The overall main effect of velocity on percent feeding was not significant (percent of polypides: $P_{4,54}>0.05$, percent of zooids: $P_{4,54}>0.05$). However, there was a small, but significant, linear decrease in the percentage that fed as a function of velocity (percent of polypides: $P<0.05$, percent of zooids: $P<0.05$). The interaction between species and velocity was not significant (percent of polypides: $P_{12,54}>0.05$, percent of zooids: $P_{12,54}>0.05$). The percent of polypides and zooids that fed differed significantly among species (both $P_{3,54}<0.0001$) (Fig. 3). *Membranipora* had a significantly greater percent of polypides and zooids that fed than did each of the three of the other species (each $P<0.01$), and *Bugula* had significantly greater percent of polypides and zooids that fed than did *Celleporella* and *Scrupocellaria* (each $P<0.05$).

Size of zooids and colonies

Membranipora zooids are generally larger in area and height and have greater volume of the lophophore than do the other three species (Table 2). *Scrupocellaria* zooids have the second largest lophophore volume and *Celleporella* has the smallest.

Bugula, *Celleporella*, and *Scrupocellaria* had similar zooid areas.

The slopes of the equations comparing the number of polypides as a function of the number of zooids were significantly different among species ($P<0.05$, Table 3); *Membranipora* had a significantly greater slope than did *Bugula* and *Celleporella* ($P<0.05$). At a value of 250 zooids, *Bugula* and *Membranipora* had a greater number of polypides than did *Celleporella* ($P<0.05$). At a value of 500 zooids, *Bugula* and *Membranipora* had a greater number of polypides than did *Scrupocellaria* and *Celleporella* ($P<0.05$), and *Scrupocellaria* had more polypides than did *Celleporella* ($P<0.001$). At a value of 1000 zooids, *Celleporella* had significantly fewer polypides than did the other three species ($P<0.01$).

Bugula had a significantly greater slope than did *Scrupocellaria* when the number of colony branches was compared as a function of the number of zooids ($P<0.05$; Table 3). Within the range of the data (from ~250 to 1000 zooids), *Bugula* always had a significantly greater number of branches for a given number of zooids ($P<0.0001$), meaning that *Bugula* colonies are bushier than are those of *Scrupocellaria*.

The slopes of the equations comparing the number of zooids as a function of the colony area were significantly different among species ($P=0.05$, Table 3). *Bugula* and *Celleporella* had significantly

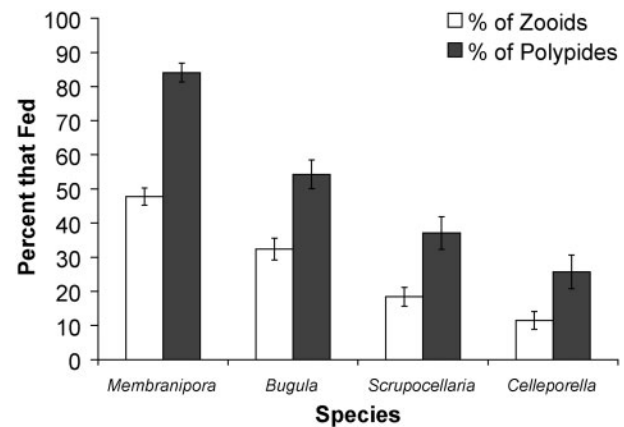


Fig. 3 The percent of polypides and zooids that fed for each of the four bryozoan species. Values are means \pm SEM.

Table 2 Mean (\pm one standard error of the mean) zooid area, zooid height, number of tentacles, and volume contained by the lophophore for four species of bryozoan zooids

Species	Zooid area (mm ²)	Zooid height (mm)	No of tentacles	Lophophore volume (mm ³)
<i>Celleporella</i>	0.1456 \pm 0.0001	0.1294 \pm 0.0002	13.0 \pm 0.0	283.2 \pm 0.004 $\times 10^{-4}$
<i>Bugula</i>	0.1232 \pm 0.0005	0.0550 \pm 0.0015	15.2 \pm 0.2	419.7 \pm 0.061 $\times 10^{-4}$
<i>Scrupocellaria</i>	0.1080 \pm 0.0006	0.1023 \pm 0.0007	16.0 \pm 0.0	711.9 \pm 0.149 $\times 10^{-4}$
<i>Membranipora</i>	0.2622 \pm 0.0016	0.2419 \pm 0.0053	16.7 \pm 0.4	842.2 \pm 0.547 $\times 10^{-4}$

Table 3 Results of the ANCOVA tests to compare morphological scaling in four species of bryozoans

Species	P versus Z		Br versus Z		Z versus A		Z versus L	
	Slope	Intercept	Slope	Intercept	Slope	Intercept	Slope	Intercept
<i>Celleporella</i>	0.70	0.85			0.89	2.42	1.45	2.76
<i>Bugula</i>	0.84	0.45	0.85	-1.19	1.00	2.69	1.45	1.70
<i>Scrupocellaria</i>	0.90	-0.14	0.69	-0.77	0.78	2.96	1.45	2.64
<i>Membranipora</i>	1.19	-1.68			0.66	3.09	1.45	2.53

A: total colony area (mm²); Br: total number of branches in the colony; L: length (mm); P: total number of zooids with polypides; Z: total number of zooids. Values are from equations in the general form $\ln Y = \alpha \ln X + \beta$ where α is the slope estimate and β is the intercept estimate. If slopes were not found to be significantly different in the full model, then common slopes were used and intercepts compared (see text for details).

greater slopes than did *Membranipora* ($P < 0.05$), and *Bugula* also had a significantly greater slope than did *Scrupocellaria* ($P < 0.05$). At an area of 25 mm², *Bugula* had a significantly greater number of zooids than did the other three species ($P < 0.001$) and *Scrupocellaria* had a greater number of zooids than did *Membranipora* ($P < 0.05$). At areas in the range of 50 to 100 mm², *Bugula* had a significantly greater number of zooids than did *Celleporella* ($P < 0.001$), and *Scrupocellaria* had a greater number of zooids than did *Membranipora* ($P < 0.001$).

The slopes of the equations comparing the number of zooids as a function of the length of the colony were not significantly different among species ($P > 0.05$), so they were set equal and the intercepts compared (Table 3). For a given length of colony, *Bugula* had a significantly greater number of zooids than did each of the three other species ($P < 0.0001$) and *Celleporella* had a significantly greater number of zooids than did *Membranipora* ($P < 0.01$).

Field experiments

Velocities at field sites

The mean maximum velocity at the exposed site (23.6 ± 6.6 cm/s) was significantly greater than at the protected site (8.6 ± 1.9 cm/s) ($P_{12} < 0.05$). The mean minimum velocity was also significantly greater at the exposed site (3.3 ± 0.5 cm/s) than at the protected site (1.3 ± 0.5 cm/s) ($P_{12} < 0.01$). Dissolution rates were similar between substrates within a site (protected, algae: 0.0024 ± 0.0001 g/s; protected, tires: 0.0024 ± 0.0001 g/s; exposed, algae: 0.0036 ± 0.0002 g/s; exposed, tires: 0.0036 ± 0.0001 g/s), but dissolution was significantly greater on the exposed side than on the protected side (site: $P_{1,32} < 0.0001$; substrate: $P_{1,32} > 0.05$; site \times substrate: $P_{1,32} > 0.05$).

Observations of abundance and size

Membranipora and *Celleporella* were found on both sides of the dock, while *Bugula* was rarely and

Scrupocellaria was never found on the exposed side. *Scrupocellaria* only occurred on tires, *Bugula* grew on tires and sometimes on brown algae, *Celleporella* grew on red algae and occasionally on brown algae, and *Membranipora* grew on red and brown algae. Percent cover increased as a linear function of time for *Bugula* (protected side, brown algae $P < 0.05$; protected side, tires $P < 0.0001$) and *Membranipora* (exposed side, brown algae $P < 0.05$; protected side, brown algae $P < 0.0001$; protected side, red algae $P < 0.0001$; but not exposed side, red algae where $P > 0.05$), but not for *Celleporella* (protected side, red algae $P > 0.05$) or *Scrupocellaria* (protected side, tires $P > 0.05$) (Fig. 4). The block random factor added significant variation to the percent cover of *Bugula* ($P < 0.01$) but not for any other species (each $P > 0.05$). When comparing the time with the maximum percent cover for each species, percent cover on the protected side was greater than on the exposed side of the dock (*Bugula* on tires $P < 0.01$; *Membranipora* on red algae $P < 0.05$; *Scrupocellaria* on tires $P < 0.01$), but there was no difference in some cases (*Bugula* on brown algae $P > 0.05$; *Celleporella* on red algae $P > 0.05$ and on brown algae $P > 0.05$; *Membranipora* on brown algae $P > 0.05$). In all cases where the comparison could be made, *Membranipora* had greater percent cover than did the other species (each $P < 0.001$).

Maximum length of the colony increased linearly with time on the protected side of the dock for all four species (each $P < 0.05$) (Fig. 5). It also increased linearly with time on the exposed side of the dock for *Membranipora* ($P < 0.0001$) but not for *Celleporella* ($P > 0.05$). *Membranipora* attained larger maximum size on the protected side than it did on the exposed side of the dock on days 24 and 65 ($P < 0.0001$), but *Celleporella* did not differ in maximum size between sides of the dock at any time ($P < 0.05$) and *Bugula* and *Scrupocellaria* were not found on the exposed side. *Membranipora* attained a larger maximum length than did any of the other species during days

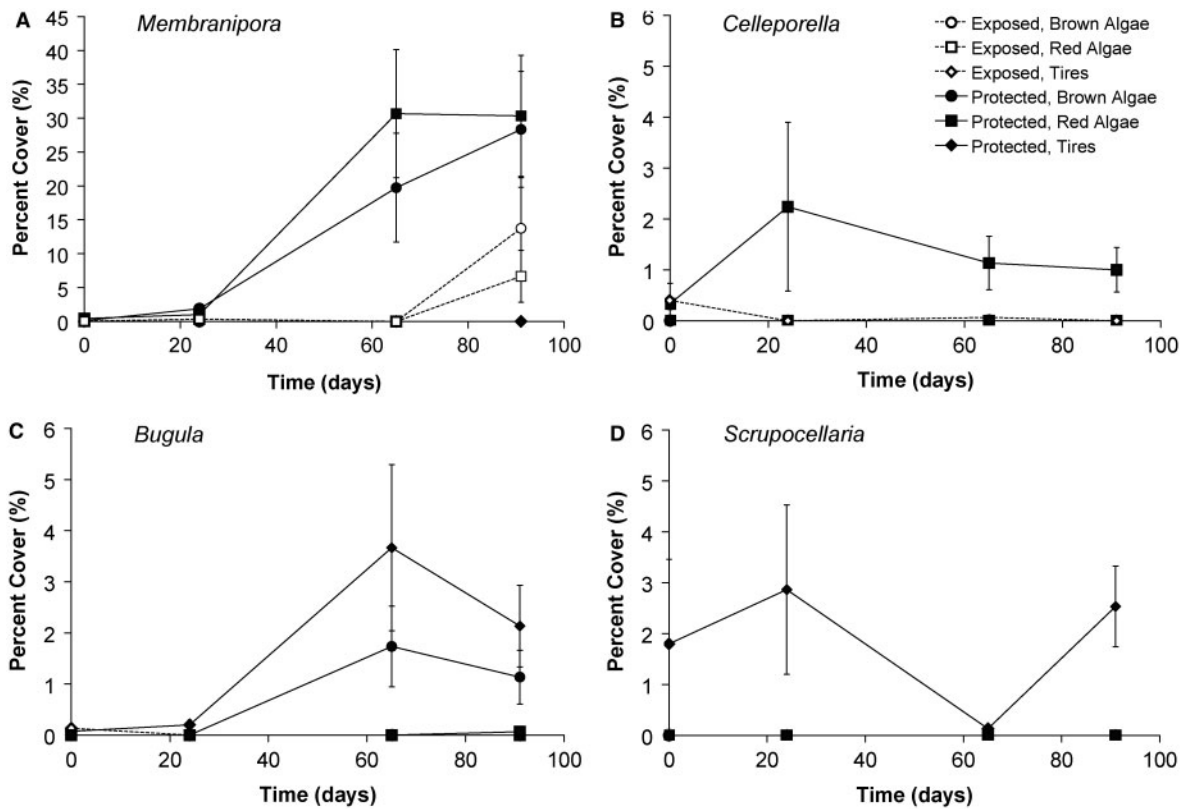


Fig. 4 Percent cover as a function of time on three different substrata (brown algae, red algae, tires) and two flow environments (exposed or protected side of the docks at the Friday Harbor Laboratories) for four species of bryozoans: (A) *M. membranacea*, (B) *C. hyalina*, (C) *B. pacifica*, and (D) *S. varians*. Values are means \pm SEM. Note that the scale is different for (A) but (B–D) have the same scale.

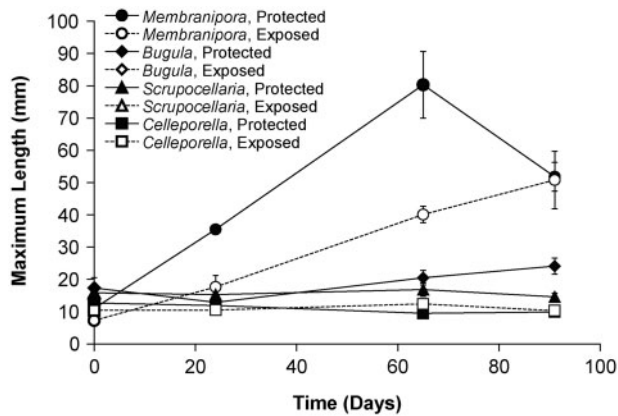


Fig. 5 Maximum length of colonies (diameter for encrusting colonies and height for erect colonies) as a function of time for four species of bryozoans in two flow environments (exposed or protected side of the docks at the Friday Harbor Laboratories). Values are means \pm SEM.

24–91 (each $P < 0.01$), *Bugula* and *Scrupocellaria* had larger maximum lengths than did *Celleporella* on days 65 and 91 (each $P < 0.001$), and *Bugula* had a larger maximum length than did *Scrupocellaria* on day 91 ($P < 0.001$). The block random factor added

significant variation to the percent cover of all species (each $P < 0.05$) except *Celleporella* ($P > 0.05$).

Experiments on survival and growth

Survival of none of the three species of bryozoans was affected by the initial area of the colony ($P > 0.05$). *Membranipora* had a significantly greater survival rate than did *Bugula* or *Scrupocellaria* overall as well as in each flow environment ($P < 0.05$): *Membranipora* was more than six times more likely to survive than was either *Bugula* or *Scrupocellaria* on the protected side and more than three times more likely to survive than either species on the exposed side of the dock (Fig. 6). *Bugula* and *Scrupocellaria* did not have significantly different survival rates ($P > 0.50$). Overall, all three species had significantly greater survival on the protected side than on the exposed side of the dock ($P < 0.001$). When comparing each species separately, *Membranipora* and *Scrupocellaria* both had greater survival on the protected side (each $P < 0.05$), while *Bugula* did not show a difference in survival between the protected and exposed sides of the dock ($P > 0.05$). Both *Membranipora* and *Scrupocellaria*

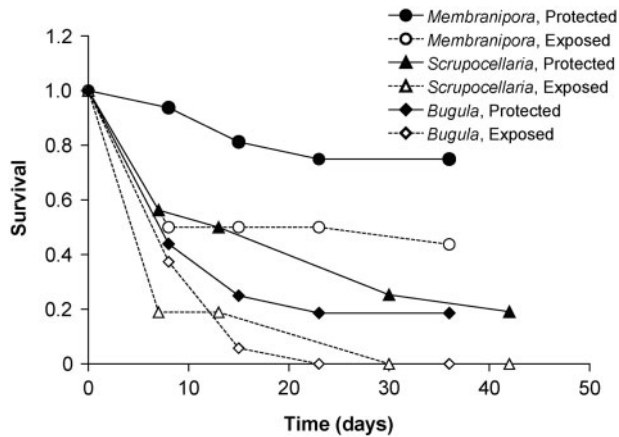


Fig. 6 Survival as a function of time for three species of bryozoans in two flow environments (exposed or protected side of the docks at the Friday Harbor Laboratories).

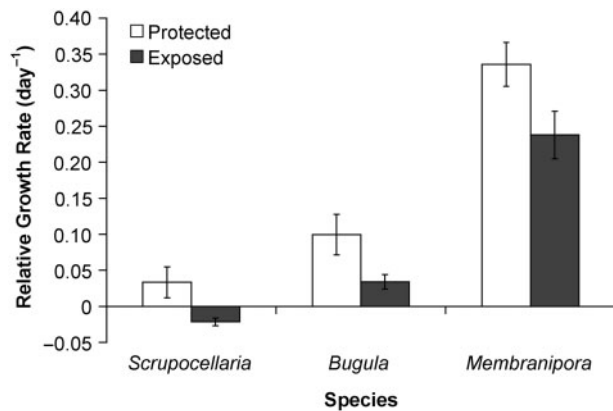


Fig. 7 Relative growth rate for three species of bryozoans in two flow environments (exposed or protected side of the docks at the Friday Harbor Laboratories). Values are means \pm SEM.

were three times more likely to survive on the protected side of the dock than was *Bugula*.

Consistent with the data on survival, *Membranipora* had a significantly greater relative growth rate than did *Bugula* or *Scrupocellaria* overall as well as in each flow environment ($P < 0.0001$), but *Bugula* and *Scrupocellaria* did not have significantly different relative growth rates from each other ($P > 0.05$) (Fig. 7). Overall, relative growth rates were greater on the protected side of the dock ($P < 0.01$). When comparing each species separately *Membranipora* had a greater relative growth rate on the protected side ($P < 0.01$), but neither *Bugula* nor *Scrupocellaria* showed a difference in relative growth rate between the protected and exposed sides of the dock ($P > 0.05$).

Discussion

Feeding as a function of velocity

The zooid ingestion rates of *Membranipora* and *Scrupocellaria* as well as the colony ingestion rate of

Membranipora followed a quadratic trend as a function of velocity as predicted; however, a quadratic trend was not found for the other species. The lack of this trend for the other two species, *Celleporella hyalina* and *Bugula pacifica*, suggests that the unimodal theory of Wildish and Kristmanson (1997) does not hold true for all suspension feeders. As found for some of the bryozoans in this study, studies on other suspension feeders also provide support for the unimodal function theory (Kirby-Smith 1972; McFadden 1986; Wildish et al. 1987; Best 1988; Sponaugle and Labarbera 1991; Wildish and Saulnier 1993). However, previous data on how water velocity affects the rates at which bryozoans feed generally show that feeding rate is either not affected by velocity or decreases with increased velocity (Okamura 1984, 1985, 1990, 1992). Such inconsistencies may be explained by measuring feeding in too narrow a range of velocities (Eckman and Duggins 1993) or not using the optimal type or concentration of particles (Okamura 1987b, 1990).

Feeding as a function of morphology

The general shape of the colony (encrusting versus erect) did not have a consistent effect on feeding. I expected that at higher velocities encrusting sheet colonies would have higher ingestion rates than would erect tree colonies. However, one encrusting species, *Membranipora*, had a higher feeding rate than did the erect species at all velocities while the other encrusting species, *Celleporella*, had the lowest feeding rate. This result suggests that the overall form of the colony is not the most important factor determining feeding success and few generalizations can be made. To properly assess the effect of colony form on feeding success, species differences need to be controlled. For example, it is important to take size of the colony into account since size does affect feeding in bryozoans (Pratt 2005). However, what measure of colony size to use in comparisons is not easy to determine because differences among species make it difficult to truly compare like with like. For example, only autozooids were considered in this study, while some species also produced heterozooids. Thus, total zooid numbers for *Membranipora* truly consider all the zooids in the colony since it only produces autozooids, but not for *Bugula*, *Scrupocellaria*, or *Celleporella* because, in addition, they produce some heterozooids. While area of a colony may be a useful measure of overall size, one species may have more zooids per unit area and more polypides as a function of zooid number, thereby giving a higher feeding capacity per unit area. *Bugula* had more zooids as a function of area, more

zooids per unit length, more branches as a function of total number of zooids, and smaller zooids than did *Scrupocellaria*. The ingestion rates of zooids and of colonies of these two species were similar and yet *Bugula* had a higher percentage of polypides and zooids that fed. *Membranipora* had fewer zooids as a function of area and fewer per unit length than did the other species, but this is because it had larger zooids. Not only did *Membranipora* have more polypides as a function of the total number of zooids, but it had the greatest percentage of polypides and zooids that fed, as well as the greatest ingestion rates by zooids and colonies. Whether *Membranipora*'s greater feeding rates are caused by having larger zooids, its encrusting shape, some other unmeasured factor, or a combination of morphology and/or behaviors is unclear.

Not only do morphological differences among the species make comparing them difficult, but differences among species cannot be effectively taken into account when using comparative methods to establish phylogenetic relationships (Harvey and Pagel 1991) because we currently lack an adequate hypothesis of phylogenetic relationships among bryozoan taxa. A previous study was able to avoid this problem by artificially creating an erect tree form of *Membranipora*. This erect form had a higher feeding rate than did the encrusting form at a moderate free-stream flow of 3 cm/s (Pratt 2005). Whether the erect shape continues to have higher feeding than the encrusting shape in flows of higher velocities is unknown.

While the effect of colony form on feeding success remains unclear, differences other than in the morphology of zooids or colonies can influence feeding. Different species may show increased efficiencies of retention or have preferences for particles of different sizes (Shumway et al. 1985; Okamura 1987a; Riisgård 1988; Newell et al. 1989; Riisgård and Manríquez 1997; Lisbjerg and Petersen 2001), and capture of particles of different sizes may be differentially affected by the magnitude of the ambient velocity of water (Okamura 1990; Shimeta 1996; Shimeta and Koehl 1997). Species also may vary in their preference for food of specific quality or surface chemistry ("taste") (Labarbera 1978; Rassoulzadegan et al. 1984; Sierszen and Frost 1992; Pedrotti 1995). More research is needed to determine if any of these factors can help explain the differences in feeding found among the species in this study.

The relatively high-feeding rate of *Membranipora* may result from larger zooids with greater

water-pumping capacity. Larger lophophores have been shown to have faster incurrent water velocities (Best and Thorpe 1986), which should increase particle flux and therefore ingestion rate. However, zooid size cannot be the only factor that determines feeding success because the larger *Scrupocellaria* zooids have greater water pumping capacity than do *Bugula* zooids, yet *Scrupocellaria* did not always have greater feeding success than *Bugula*.

A further explanation for the high-feeding success of *Membranipora* relates to the arrangement of the zooids within its colonies. *Membranipora* zooids are packed closely together in a sheet and this increases the capture of food with that of single zooids or of zooids that are more widely spaced (Eckman and Okamura 1998; Pratt 2004). Additionally, the results of the current study showed that *Membranipora* had a higher percent of polypides or zooids that captured food compared with the other three species, which supports the idea that *Membranipora* is especially good at filtering. If the heterozooids of the other species were taken into consideration, they would have an even lower percentage of zooids that fed, which suggests that *Membranipora* invests heavily in having a high-feeding capacity, and the higher percent of polypides that fed suggests that the polypides that are there are very effective at capturing food. Other unmeasured factors may also contribute to the high-feeding rate of *Membranipora*. For example, it is possible that *Membranipora* is especially efficient at filtering particles that are 10 μ in size. The effect of particle size on feeding in these four bryozoan species would have to be measured to test this hypothesis.

Performance in the field

Since the velocities measured on the protected side of the floating docks were in the range at which bryozoan feeding was high, all the species were expected to be more abundant, to grow faster, and to survive longer at the protected site. For the most part, this prediction was supported. All four species were either found exclusively on the protected side of the dock or had a greater percent cover on the protected side. Since *Membranipora* had higher ingestion rates at higher velocities than did the other three species, it makes sense that *Membranipora* was the only species found in abundance on the exposed side of the dock. *Membranipora* grew to a larger maximum size than did the other three species, and attained the largest colony size on the protected side. However, by the last sampling date the percent cover and the maximum size for *Membranipora* was similar

between the protected and exposed sides. This could be a result of predation by nudibranchs on the protected side. While predator densities and predation was not measured, predation was considerably more evident on the protected side of the dock (*personal observation*). The transplant experiment added further evidence that distribution and abundance is correlated with differences in growth and survival: all three species tested had higher survival and faster growth on the protected side, and *Membranipora* showed higher survival and faster growth than did the other species. Part of the reason that *Membranipora* grows faster and attains a larger size may be due to its larger zooids and to the lower energetic investment because of only making autozooids.

Overall, the results are consistent with the hypothesis that bryozoans would have greater abundance, faster growth rates, and higher survival in habitats dominated by water velocities where feeding success is high. Previous research on the effect of velocity on growth in bryozoans show mixed results. For example, many studies have investigated the effect of flow velocity on growth in *Celleporella hyalina* but the results are not consistent. *Celleporella* can have more rapid growth in slower flow (Cancino and Hughes 1987), more rapid growth with increasing flow (Hughes and Hughes 1986), or no effect of flow on growth (Hermansen et al. 2001). Some of this variation may be due to a stronger effect of season than of flow velocity on growth rate (Cancino and Hughes 1987; Hughes 1992). It should also be noted that none of these studies relate growth rate to feeding success. The only previous study to do that similarly found a correlation between the two attributes (Okamura 1992).

Ecological implications

Feeding varies with water velocity for bryozoans, and this relationship is different for different species. Bryozoan distribution and abundance at least in part may be due to how water flow affects feeding, growth, and survival. Some bryozoans, such as *Membranipora*, are especially effective at capturing particles even at higher water velocities. Thus, species such as *Membranipora* may be found in a wider range of flows in nature. Another advantage of being an especially good filterer is that rapid growth can be achieved. *Membranipora* is most often found growing on kelps and other macroalgae (Bernstein and Jung 1979; Yoshioka 1982). While kelps are perennial, the blades can be more ephemeral and generally live <6 months in *Macrocystis pyrifera* (North 1961) and

Laminaria longicuris (Chapman 1986). *Membranipora* can utilize this kind of habitat through high recruitment and rapid growth (McKinney and Jackson 1991). Not only does rapid growth give *Membranipora* a competitive advantage on such ephemeral substrata, but it also might contribute to its effectiveness as an invasive species. *Membranipora* was first seen in the Gulf of Maine in 1987, and within a few years it became the dominant organism living on kelps (Berman et al. 1992). *Membranipora* has a negative effect on the kelps (Lambert et al. 1992; Scheibling et al. 1999; Chavanich and Harris 2000; Levin et al. 2002; Saier and Chapman 2004) and as a result, substantial areas of the rocky subtidal along the Atlantic coast of Nova Scotia and the Gulf of Maine have shifted from domination by kelp to domination by the invasive macroalga *Codium fragile* ssp. *tomentosoides* (Harris and Tyrrell 2001; Levin et al. 2002; Mathieson et al. 2003; Scheibling and Gagnon 2006; Theriault et al. 2006). Understanding how water flow affects feeding in bryozoans not only provides insights about their distribution and abundance, but may also allow prediction of which bryozoans are likely to become problematic invasive species.

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