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Colony growth rate of encrusting marine bryozoans (*Electra pilosa* and *Celleporella hyalina*)

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Abstract

Growth experiments were performed in a strong current environment (Menai Strait, UK) with cloned, transplanted colonies of encrusting *Electra pilosa* and *Celleporella hyalina* growing on microscope slides mounted on a raft. Colony growth was also recorded for the same species, both appearing naturally on macroalgae and in controlled laboratory experiments. For the laboratory experiments, the lowest algal concentration that still resulted in maximum growth rate (about 0.07 day^{-1}) for *E. pilosa* was at most 1500 *Rhodomonas* cells ml^{-1}, corresponding to 1.9 μg chl *a* l^{-1}, close to but greater than the mean value measured in the Menai Strait. For the raft experiments, colonies were exposed to naturally occurring fast flow (about 40 cm s^{-1}) and to reduced flow (about 30 cm s^{-1}). The mean phytoplankton concentration was 1.1 ± 0.6 μg chl *a* l^{-1}, and the specific growth rate was 0.10–0.12 day^{-1}, regardless of species and flow regime. The somewhat slower growth of natural bryozoan colonies on macroalgae (0.08 day^{-1}) may be due to their larger initial size. Based on estimates of the thickness of the viscous sublayer it is concluded that suspension feeding by encrusting bryozoans may be restricted to the viscous sublayer, and that increasing current velocities do not reduce the growth (and thus feeding).

Keywords: Bryozoans; Specific growth rate; Algal concentration; Current strength; Cloning; Transplantation

1. Introduction

Bryozoans are sessile, colonial suspension feeders that mainly feed on phytoplankton (Bullivant, 1968a,b; Menon, 1974; Winston, 1978; McKinney, 1990; Best and Thorpe,

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1983; Riisgård and Manriquez, 1997; Nielsen and Riisgård, 1998). The phylum Bryozoa contains nearly 4000 extant species, but there is an extensive fossil record beginning 500 million b.p., with about four times as many species (Ryland, 1970). Most bryozoans live in the sea and the largest numbers are found at salinities around 35‰, and observations show that bryozoans thrive well in strong current environments (Ryland, 1970). Bryozoans are distributed all over the world and in the Antarctic they constitute an important group of benthic suspension feeders (Barnes and Clarke, 1994). Bryozoans are often found on rocks and seaweeds, but a few live on soft sediment.

The two calcareous encrusting species *Electra pilosa* and *Celleporella hyalina* were used for growth experiments in the present work. Both species belong to the class Gymnolaemata and the order Cheilostomata and both are intertidal species living at maximum water depths of about 50 m (Ryland and Hayward, 1977; Hayward and Ryland, 1979). *E. pilosa* is universally distributed (Ryland and Hayward, 1977) and *C. hyalina*'s distribution extends from the Arctic to the Bay of Biscay and along the Pacific Coast to California and parts of Mexico as well as on the Eastern coast of North America (Hayward and Ryland, 1979). *E. pilosa* can be found on almost any firm substratum, but are often conspicuous on *Fucus* sp. (Ryland and Hayward, 1977). *C. hyalina* grows on macroalgae and is often very abundant on *Laminaria* sp. (Hayward and Ryland, 1979).

Near a surface exposed to a freestream current, there is a boundary layer in which the velocity increases from the no-slip condition at the surface (Vogel, 1994; Mann and Lazier, 1996) to the freestream velocity. At high Reynolds numbers, the boundary layer is turbulent and for a smooth surface viscous forces dominate the inner wall layer, the viscous sublayer, in which velocity increases linearly with wall distance. Further away from the surface turbulence prevails and in a region, the logarithmic layer, velocity increases logarithmically with wall distance (Mann and Lazier, 1996).

The viscous sublayer, usually a few millimeters thick, is a barrier to exchange of matter because of the absence of turbulence, and it is known to reduce the transport of nutrients to macoalgal surfaces. Depending on the benthic activity and the level of mixing in the boundary layer, part or all of the boundary layer may be subject to waste accumulation and food depletion (Hurd et al., 1997; Vogel, 1994; Wildish and Kristmanson, 1997). The thickness of the viscous sublayer and the whole boundary layer decreases and the turbulence level increases with increasing freestream current. Therefore, fast moving water is beneficial for sedentary organisms since it assists a better exchange of substances. Encrusting bryozoans most likely feed in the viscous sublayer as they only extend about 1 mm above the substratum (Lidgard, 1981; Lidgard and Jackson, 1989; Grünbaum, 1995; Larsen et al., 1998). For non-smooth surfaces, depending on size of roughness elements and Reynolds number, there may be no viscous sublayer (Schlichting, 1968, p. 617). It is not clear if such conditions prevail in areas of bryozoan growth.

Encrusting bryozoans have few predators in high current environments and may, therefore, be regarded as specialists in the viscous sublayer. The most conspicuous danger for the bryozoans living in the viscous sublayer may actually be that the water flow gets too slow so that the animals deplete the layer of food particles. The growth of bryozoans has so far mainly been studied in the laboratory in gently mixed water

(Menon, 1972; Jebram, 1973, 1980; Winston, 1976; Jebram and Rummert, 1978; Hunter and Hughes, 1993a; Bayer et al., 1994; Bayer and Todd, 1996; Riisgård and Goldson, 1997), and some of the experiments have been performed at high algal concentrations with only little resemblance to conditions that bryozoans experience in their natural environment. Only few attempts have been made to study the influence of current velocity on bryozoan food uptake (Okamura, 1984, 1985, 1990; Eckman and Okamura, 1998) and growth (Cancino and Hughes, 1987; Okamura, 1992; Eckman and Duggins, 1993; Okamura and Partridge, 1999).

The purpose of this study was to further investigate the importance of algal concentration, and to some extent the ambient velocity, for colony growth of two encrusting bryozoans. This was done in controlled laboratory feeding and growth studies, as well as in field experiments where current velocity and phytoplankton concentration were concurrently recorded along with measurements of the specific growth rate of cloned, transplanted colonies. To further characterize the experiments, estimates have been made of the friction velocity and the viscous sublayer thickness.

2. Materials and methods

2.1. Cloning and growth of E. pilosa

Fucus serratus with colonies of *E. pilosa* was collected on March 9, 1998 at Kerteminde harbour, close to the Research Centre for Aquatic Biology, Kerteminde, Denmark, where the laboratory growth experiments were performed. Colonies with active autozooids and large budding zones were selected for cloning. The budding zones were cut into smaller pieces which were clamped onto microscope glass slides by putting a coverslip on the top of part of the algae and using slit polyvinyl tubing as clamps (see Fig. 1). To ensure that the coverslip was leveled with the colony, the piece of macroalgae below the coverslip was thinned by cutting off the top layer of the algae. The microscope slides were then placed in histological staining racks and suspended in aquaria with 9 l of bio-filtered (*Mytilus edulis*) seawater. To ensure maximum growth (Riisgård and Goldson, 1997), the bryozoans were fed 6-μm diameter flagellates (*Rhodomonas* sp.) at an average concentration of about 5000 cells ml^{-1}. *Rhodomonas* sp. was cultured on a standard media and grown in 1-l bottles. The growth of the colonies was monitored both by counting the total number of zooids and by measuring the colony area. A dissection microscope (Wild) with an attached *camera lucida* was used to make traces of the colonies in order to estimate the area.

The above ‘preliminary’ growth experiment was supplemented by growth experiments using different algal concentrations. The ‘supplementary’ growth experiments were made over a 14-day period with five *E. pilosa* colonies of the same genotype in six aquaria containing 1.8 l of bio-filtered water each with a specific mean concentration of *Rhodomonas* sp. There were five colonies in each aquarium, and all colonies were reduced to the same size, around 20 zooids. The average algal concentrations were 1000 ± 280, 1500 ± 230, 2500 ± 410, 3300 ± 630, 4100 ± 930, 4700 ± 910 cells ml^{-1}. The algal concentration was measured by means of an electronic particle counter

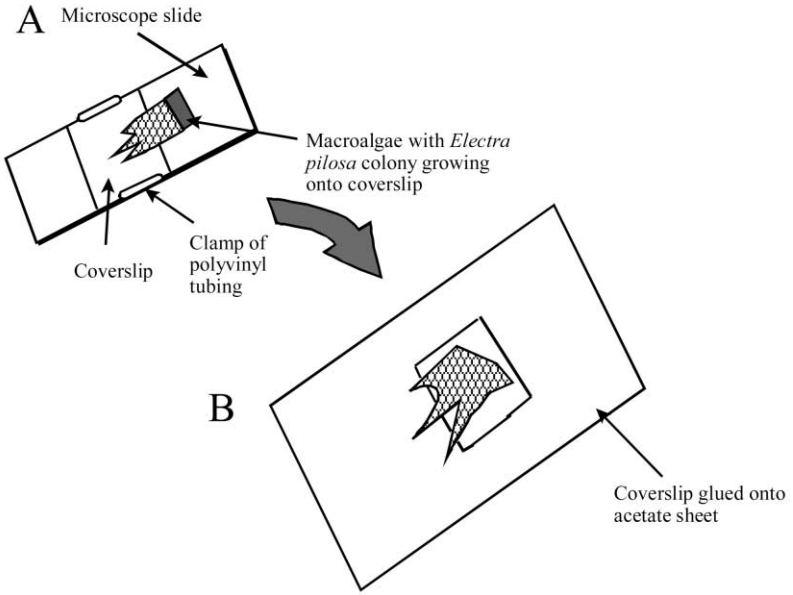

Fig. 1. *E. pilosa* cloning. (A) A piece of macroalga with a part of the budding zone clamped with polyvinyl tubing between a microscope slide and a coverslip. The zooids have started to grow onto the coverslip. (B) A coverslip with an established colony glued onto a piece of acetate.

(Elzone 80 xy) 10 min after a new addition of algal cells and 24 h later, and the average daily concentration was then calculated assuming an exponential decrease over time. The specific growth rate was calculated according to Eq. (4) (see later). The algal concentration of *Rhodomonas* sp. (C, $\times 10^3$ cells ml^{-1}) was converted to chlorophyll *a* concentration (μg chl *a* l^{-1}) by the relationship (Clausen and Riisgård, 1996): chl $a = 1.25C$ (based on regression analysis of relationship between measured chl *a* at five algal concentrations in the range 2000–30,000 cells ml^{-1} and triple determination on each sample; $r^2 = 0.999$).

2.2. Growth of bryozoans in the Menai Strait

The growth of bryozoans at natural current velocities was measured in the Menai Strait, a narrow channel between the island of Anglesey and the North Wales mainland, UK. The narrowness of the strait creates a strong bi-directional tidal current. The velocity is stronger in the southwesterly than in the northeasterly direction. During spring tide the maximum velocities, at a depth of 4–6 m, are 1.2 m s^{-1} (SW) and 0.8 m s^{-1} (NE), and the mean spring and neap tidal range are 6.6 and 3.4 m, respectively (Harvey, 1968). The bryozoan colonies growing on macroalgal fronds experience unidirectional flow because the fronds are flexible and extend out in the direction of the current flow.

2.2.1. Collection and cloning of bryozoans

F. serratus and *F. vesiculosus* with colonies of *E. pilosa* on the fronds were collected at Church Island in the Menai Strait in July 1998. The macroalgae were transported to the laboratory (School of Biological Sciences, University of Wales, Bangor) where replicates of the same genotype were made by cutting large budding zones of one colony into several smaller pieces. Then the previously described cloning method was applied (Fig. 1A). After 19 days of growth, the coverslips with bryozoan colonies were glued onto acetate sheets (Fig. 1B). During the cloning experiment the bryozoans were kept in aquaria with 1.5 l of UV-irradiated and 20 μm filtered seawater added *Rhodomonas* sp. in an average daily concentration of about 5000 cells ml^{-1}. The algal concentration was measured by use of a haemocytometer, and the seawater in the aquarium was changed every second day. Two genotypes of *C. hyalina* colonies (H and T) growing on pieces of acetate were used. The colonies were reared after the methods described by Hunter and Hughes (1993b) and Riisgård and Manríquez (1997), and small pieces on acetate were glued onto microscope slides.

2.2.2. Growth of colonies transferred to Menai Strait

Both *E. pilosa* (genotypes F and L) and *C. hyalina* (genotype H and T) were placed off an anchored raft in Menai Strait. From the raft a metal frame was suspended in the water (Fig. 2). A device was attached to the frame to create two different flow conditions for the bryozoans. The device consisted of two pieces of plywood (60×90 cm) placed 4.5 cm apart, forming a plane flow channel. Plastic mesh (1×1 mm) was put over the space between the two boards. Inside the channel, the water flow was somewhat reduced because of the closeness of the two boards and the plastic mesh at inlet and outlet. The bryozoans on microscope slides were secured onto 15×17 cm plastic frames on both the in- and outside of the channel walls. The plastic mesh was cleaned weekly to avoid fouling growth. *C. hyalina* colonies (reduced to about 10 zooids) were placed in the Menai Strait on September 17, 1998 while reduced *E. pilosa* colonies were put out on September 25 (genotype L) and October 1 (genotype F). Growth measurements were made weekly using a digitizer to estimate the area of the colonies brought to the laboratory. All colonies were collected on October 20 and the final area measurements were subsequently made. A 'control' or reference group of each species and genotype were kept in the laboratory in 1.5-l tanks and fed a daily average concentration of about 5000 cells ml^{-1} (15°C) to ensure maximum growth.

2.2.3. Growth of colonies on macroalgae

The area of natural bryozoan colonies growing on macroalgae was measured over a 2-week period (from September 29 to October 13) to compare how the specific growth rate on a natural substratum relates to colony growth on microscope slides. The measurements were made at St. Georges pier in the Menai Strait where the flow environment experienced by the bryozoans were near identical to the conditions at the raft. Several fronds of *Laminaria saccharina* growing at the pier were marked with plastic ties. Eighteen colonies of *E. pilosa* and eight colonies of *C. hyalina* were used in the experiment. The area of colonies growing on the macroalgae was traced onto acetate sheets at the beginning and at the end of the growth period.

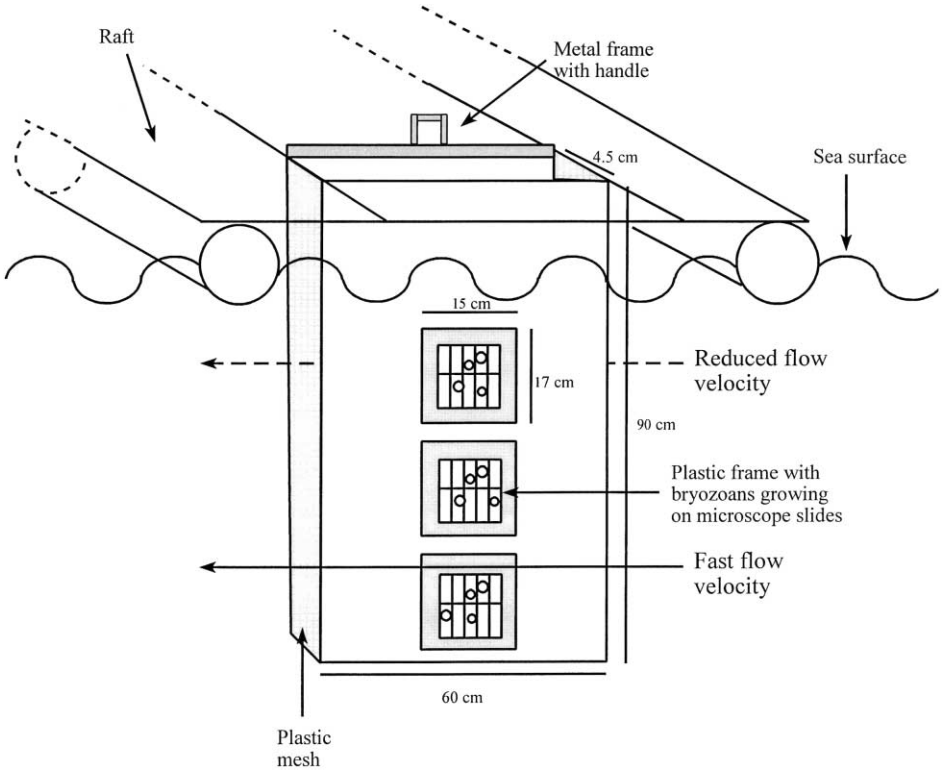

Fig. 2. Sketch of plane channel flow used for field growth experiments in Menai Strait. The bryozoans were placed both on the inside (reduced flow) and on the outside of the pipe (fast flow).

2.3. Calculation of specific growth rate

The initial growth rate of bryozoan colonies is exponential and can be expressed by the equation $\mathrm{d}N/\mathrm{d}t = \mu N$, or:

$$N = N_0 \exp(\mu t), \tag{1}$$

where N is the size of the colony at time t, N_0 is the size of the colony at the beginning of the experiment $t = 0$, and μ is the specific growth rate. The colony size can be expressed as total number of zooids or the colony area. Eq. (1) can also be written as $\log_{10} N = \mu t \log_{10} e + \log_{10} N_0$. In this present work, the colony size N was plotted as a function of time t in a semi-log plot and a regression line calculated, yielding the slope $\mu \log_{10} e$, hence, the specific growth rate. Inserting $N = 2N_0$ into Eq. (1) gives the doubling time:

$$t_2 = \ln 2/\mu. \tag{2}$$

When only the initial and final colony size is known, the specific growth rate can also be calculated as:

$$\mu = \ln(N/N_0)/t. \quad (3)$$

The above development assumes colony growth to be proportional to area of colony. However, if colony growth is governed by budding along the periphery and proportional to its length P, we expect $dP/dt = \mu_P P$, hence, $P = P_0 \exp(\mu_P t)$. Assuming again the number of zooids to be proportional to colony area A and expressing colony shape by the parameter $C = A/P^2$ the exponential growth becomes:

$$N = N_0(C/C_0)\exp(\mu t), \quad (4)$$

where C and C_0 denote the shape parameter at time t and at time $t = 0$, respectively, and $\mu = 2\mu_P$. If colony shape is preserved during growth in the sense that $C = C_0 =$ constant, we recover the usual form (Eq. (1)). On the other hand, if colony shape changes, say from initially circular to an oblong or dendritic shape, C/C_0 would decrease with time and the semi-log plot of zooid number versus time would no longer be linear, even when μ is constant. Values of the shape parameter are readily calculated for simple shapes, e.g. $C\{\text{equilateral triangle, circle, square, } 2 \times 1 \text{ rectangle}\} = \{1/10.4, 1/12.6, 1/16, 1/25\}$. The principal categories of budding (intrazooidal, zooidal and frontal budding) among encrusting cheilostomes have been described by Lidgard (1985a,b), McKinney and Jackson (1988), and Lidgard and Jackson (1989).

2.4. Current velocities

Current velocities were measured during spring and neap tide on October 7 and 15 1998, respectively, using a current meter (Valeport model 108 MkIII) placed below the raft. Readings, with 15-min intervals, were made close to the bottom, at medium depth and just below the raft. The difference in freestream velocity outside boundary layers for reduced and fast flow conditions at the raft in Menai Strait was measured with plaster of Paris cylinders, which dissolves in seawater so that the weight loss of plaster can be used as an indicator of the water movement (Muus, 1968; Thompson and Glenn, 1994). To make the plaster of Paris cylinders, a piece of plastic pipe (height 21 mm, diameter 15 mm) was used as a mould, and the cylinders were dried at 50°C for 24 h. Then each cylinder was glued onto a marked microscope slide, attached to the same frames as the bryozoans, and left in the field for 24 h. The ratio of average weight loss of the cylinders in the fast and reduced flows was found to be 1.9:1.

Using the analogue between heat and mass transfer and approximating the separated flow past the plaster of Paris cylinders by two-dimensional flow past cylinders, the weight loss is expected to be proportional to $Re^{0.6}$, or proportional to velocity $U^{0.6}$ (for the relevant Reynolds numbers of the order of $Re = dU/\nu = 0.015 \times 0.4/1.4 \times 10^{-6} \approx 4300$, Lienhard, 1981, p. 333). Thus, the ratio of flow on the outside and inside the flow channel is estimated to be about $1.9^{0.6} \approx 1.47$. However, a smaller ratio of about 1.34 is found by approximate flow calculations (see Appendix A), which confirms that the use of the plaster of Paris cylinders is questionable (cf. Porter et al., 2000; Wildish et al., 2000).

2.5. Measurement of chl a

Water samples taken at 0.3-m depth were collected weekly for measurement of chlorophyll *a* (chl *a*) concentration at the field growth site. The water samples were immediately filtered through an 80-μm filter to remove zooplankton, and 300-ml water samples (five replicates) were filtered through Millipore GF/C filters and kept in a freezer until the end of the sampling period. Then the filters were extracted in 10 ml 90% acetone (12 h) and readings of chl *a* made using a Turner Designs Flourometer. The following equation was used (Parsons et al., 1984): chl $a = (F/F_b)/RK_f\ (v/V)$, where F = fluorescence, F_b = fluorescence of a blank sample, R = range, $K_f = 0.09$ μg l^{-1} (calibration constant), v = volume (ml) of the extract, V = volume of the filtered water (l).

The temperature in Menai Strait was measured with a temperature data logger (Hobo) every hour during the whole period.

3. Results

3.1. Colony growth in laboratory

E. pilosa colonies exposed to a near constant concentration of about 5000 algal cells ml^{-1} started to grow onto the coverslips after 3 days, and $>50\%$ of the colonies had grown onto the coverslips within 5 days. Fig. 3A shows the calculated regression lines in plots of colony size as a function of time for all the colonies. The coefficient of determination of the regression lines varied between $r^2 = 0.97$ and 0.99 (growth based on area), and between 0.87 and 0.99 (growth based on number of zooids) (see Table 1). The average specific growth rate was $\mu = 0.09 \pm 0.02$ day^{-1} (area) and 0.11 ± 0.02 day^{-1} (zooids). The estimated doubling times for all colonies are shown in Table 1. The mean doubling times were $t_2 = 7.61 \pm 1.54$ days (area) and 6.65 ± 1.49 days (zooids). The growth results are quite similar, regardless of the method used to determine the colony growth. This is illustrated by Fig. 3B showing that the number density of zooids (calculated as total number of zooids in colony divided by colony area in square millimeter) is nearly constant as a function of time for all the colonies, although values vary in the range about 5–8 zooids mm^{-2}. When the number of zooids is counted, only fully formed zooids are taken into account, excluding the buds along the colony edge. Therefore, only growth data based on colony area are mentioned in the following.

To test the hypothesis that the shape parameter $C = A/P^2$ could vary during growth this parameter was calculated for a number of well-fed *E. pilosa* ($n = 4$) and *C. hyalina* ($n = 8$) colonies during a growth period of 25 days (Fig. 3C and D). Trend lines (parabolas) for the estimated *C*-values as a function of time showed a decreasing tendency for *E. pilosa* (initial *C*-value of 0.045 decreased by about 50 % at the end of the growth period in accordance with its stellate or irregular colony growth pattern) whereas an increasing tendency was found for *C. hyalina* (initial $C = 0.05$ increased by about 20 % in accordance with its circular growth pattern). This confirms the hypothesis that the shape parameter C varies during growth, depending on species and growth form.

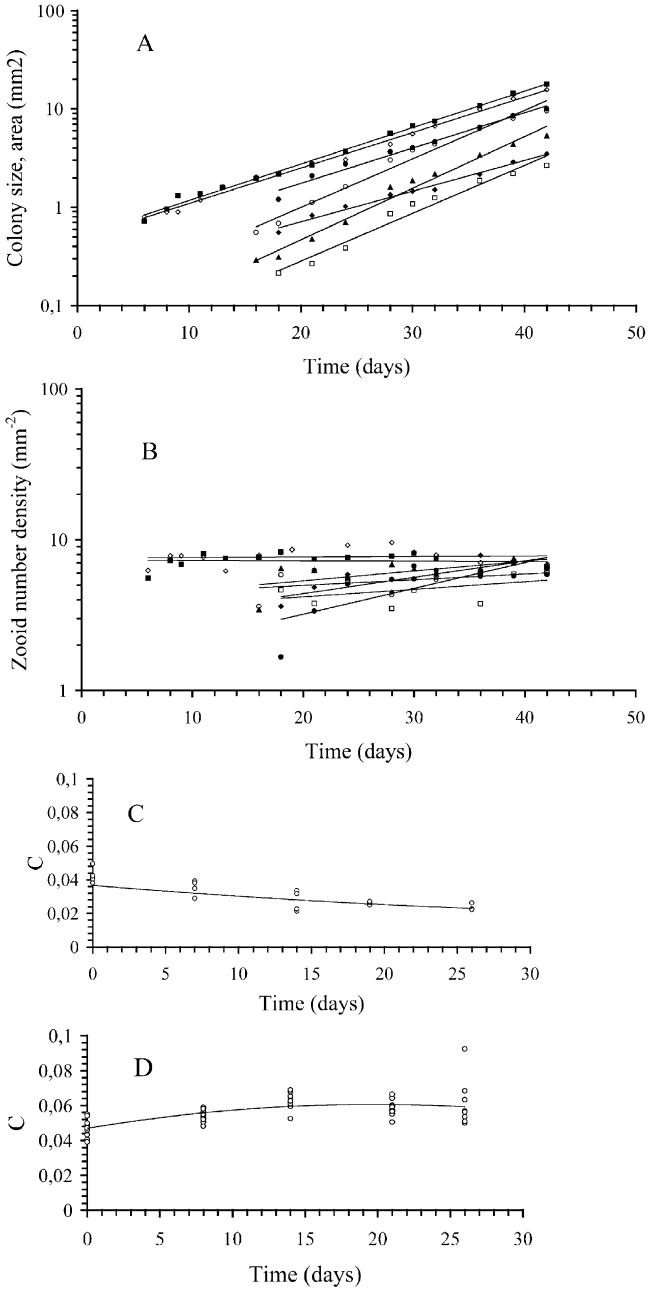

Fig. 3. *E. pilosa.* (A and B) Growth of the bryozoan colonies exposed to about 5000 *Rhodomonas* cells ml^{-1} in laboratory experiments. Colony size based on area and number density are plotted as a function of time and the calculated regression lines are indicated. (A) Colony size based on area measurements. (B) Number density of zooids (total number of zooids in colony divided by colony area in mm^2; see also case of 5000 cells ml^{-1} in Table 1). (C and D) Calculated shape parameter $C = A/P^2$ as a function of time for 'genotype H, fast flow' *E. pilosa* (C) and 'genotype L, fast flow' *C. hyalina* (D). The trend lines (parabolas) are shown.

Table 1
Laboratory growth measurements of colonies of *E. pilosa* at different algal (*Rhodomonas*) concentrations (C, $\times 10^3$ cells ml^{-1}). Average ($\pm$S.D.) specific growth rate and doubling time are indicated

Algal concentration (C)	Colony area					Total number of zooids				
	N_0	N_t	r^2	μ	t_2	N_0	N_t	r^2	μ	t_2
1	7.13	13.97	0.97	0.05	13.86	20	81	0.96	0.09	7.70
	8.27	17.68	0.98	0.05	13.86	18	83	0.98	0.10	6.93
	5.99	11.12	0.98	0.04	17.33	20	47	0.99	0.06	11.55
	6.84	12.55	0.97	0.04	17.33	19	51	0.96	0.07	9.90
	8.27	17.39	0.96	0.06	11.55	20	76	0.98	0.09	7.70
				0.05 $\pm$ 0.01	14.79 $\pm$ 2.51				0.08 $\pm$ 0.02	8.76 $\pm$ 1.92
1.5	6.92	16.20	1.00	0.06	11.55	20	72	0.99	0.09	7.70
	6.36	16.49	0.99	0.07	9.90	20	69	0.97	0.09	7.70
	6.94	17.07	1.00	0.07	9.90	19	64	0.92	0.08	8.66
	5.50	14.46	1.00	0.07	9.90	20	54	0.91	0.06	11.55
	8.68	20.82	1.00	0.06	11.55	20	69	0.94	0.09	7.70
				0.07 $\pm$ 0.01	10.56 $\pm$ 0.90				0.08 $\pm$ 0.01	8.66 $\pm$ 1.67
2.5	7.13	17.40	0.99	0.07	9.90	20	76	0.97	0.09	7.70
	7.13	18.82	0.99	0.07	9.90	19	81	0.98	0.10	6.93
	6.84	14.54	0.99	0.06	11.55	18	61	0.94	0.08	8.66
	7.41	18.25	0.99	0.07	9.90	20	75	0.96	0.09	7.70
	7.41	17.11	0.99	0.06	11.55	20	62	0.97	0.08	8.66
				0.07 $\pm$ 0.01	10.56 $\pm$ 0.90				0.09 $\pm$ 0.01	7.93 $\pm$ 0.74
3.3	5.42	19.11	1.00	0.09	7.70	20	68	0.98	0.08	8.66
	6.56	16.54	0.99	0.06	11.55	19	65	0.91	0.08	8.66
	6.84	21.39	1.00	0.08	8.66	18	86	0.97	0.11	6.30
	6.84	16.25	0.99	0.06	11.55	20	69	0.96	0.08	8.66
	6.84	19.11	0.99	0.07	9.90	20	76	0.97	0.09	7.70
				0.07 $\pm$ 0.01	9.87 $\pm$ 1.72				0.09 $\pm$ 0.01	8.00 $\pm$ 1.04
4.1	7.41	25.38	1.00	0.09	7.70	20	92	0.98	0.11	6.30
	7.70	22.53	0.99	0.08	8.66	20	88	0.98	0.10	6.93
	5.42	19.39	1.00	0.09	7.70	19	81	0.98	0.10	6.93
	7.41	23.67	0.99	0.08	8.66	20	83	0.98	0.10	6.93
	6.84	22.24	1.00	0.09	7.70	20	90	0.98	0.10	6.93
				0.09 $\pm$ 0.01	8.08 $\pm$ 0.53				0.10 $\pm$ 0.00	6.80 $\pm$ 0.28
5.0	0.80	15.74	0.99	0.08	8.66	5	108	0.99	0.08	8.66
	0.72	17.82	0.99	0.09	7.70	4	117	0.98	0.08	8.66
	0.29	5.34	0.98	0.12	5.78	1	36	0.97	0.14	4.95
	0.56	9.57	0.98	0.11	6.30	2	58	0.97	0.12	5.78
	0.22	2.67	0.97	0.11	6.30	1	16	0.97	0.12	5.78
	1.20	10.05	0.98	0.08	8.66	2	59	0.87	0.12	5.78
	0.55	3.50	0.98	0.07	9.90	2	23	0.96	0.10	6.93
				0.09 $\pm$ 0.02	7.61 $\pm$ 1.54				0.11 $\pm$ 0.02	6.65 $\pm$ 1.49

Symbols: μ (day^{-1}) = specific growth rate based on the slope of the estimated regression lines (cf. Fig. 3 which shows example case of 5000 cells ml^{-1}); t_2 (day) = doubling time; N_0 = number of total zooids or colony area (mm^2) at time 0; N_t = final number of total zooids or final colony area (mm^2); r^2 = coefficient of determination for the regression lines.

3.2. Colony growth in Menai Strait

During September, the average temperature was about 15°C, and in October the average temperature was close to 14°C. During the last few days of the field experiment the temperature dropped to about 12.5°C. The salinity was near constant 33‰. The

Table 2
Growth of transplanted *C. hyalina* (genotype H) in Menai Strait during 34 days (September 17–October 20), and control colonies grown in the laboratory

Colony area					Total number of zooids				
N_0	N_t	r^2	μ	t_2	N_0	N_t	r^2	μ	t_2
Control									
2.08	45.31	0.97	0.10	6.93	10	474	0.96	0.12	5.78
2.39	39.98	0.97	0.09	7.70	10	424	0.96	0.11	6.30
2.37	46.21	0.97	0.09	7.70	11	466	0.97	0.11	6.30
1.92	41.92	0.98	0.10	6.93	10	441	0.98	0.12	5.78
2.25	58.00	0.96	0.10	6.93	10	568	0.95	0.12	5.78
1.91	55.46	0.96	0.10	6.93	10	589	0.95	0.12	5.78
1.97	52.37	0.97	0.10	6.93	10	535	0.95	0.12	5.78
2.23	62.16	0.96	0.10	6.93	12	649	0.95	0.12	5.78
2.25	37.69	0.99	0.09	7.70	10	343	0.99	0.11	6.30
			0.10 ± 0.01	7.19 ± 0.39				0.12 ± 0.01	5.95 ± 0.26
Fast flow									
2.75	64.66	0.99	0.10	6.93	11	460	0.97	0.11	6.30
2.33	63.12	0.99	0.10	6.93	10	431	0.98	0.11	6.30
2.10	62.33	0.99	0.10	6.93	9	505	0.98	0.12	5.78
2.16	50.11	0.99	0.09	7.70	10	387	0.99	0.11	6.30
2.19	38.74	0.99	0.11	6.30	9	309	0.95	0.14	4.95
2.25	57.78	1.00	0.10	6.93	10	433	0.98	0.11	6.30
2.61	71.07	0.99	0.10	6.93	11	495	0.97	0.11	6.30
2.28	60.19	1.00	0.10	6.93	10	407	0.98	0.11	6.30
2.00	40.74	0.99	0.09	7.70	10	260	0.97	0.10	6.93
1.81	50.60	1.00	0.10	6.93	10	346	0.99	0.11	6.30
			0.10 ± 0.01	7.02 ± 0.41				0.11 ± 0.01	6.18 ± 0.51
Reduced flow									
2.21	42.62	0.99	0.09	7.70	11	315	0.96	0.10	6.93
2.01	47.21	0.97	0.09	7.70	10	363	0.92	0.11	6.30
2.16	45.12	0.99	0.09	7.70	10	311	0.96	0.10	6.93
2.49	43.87	0.97	0.08	8.66	12	314	0.92	0.09	7.70
2.45	39.88	0.99	0.08	8.66	10	281	0.94	0.10	6.93
2.23	47.52	0.97	0.09	7.70	10	341	0.91	0.10	6.93
1.92	59.50	0.97	0.10	6.93	9	385	0.89	0.11	6.30
1.70	42.61	0.96	0.09	7.70	9	301	0.91	0.10	6.93
2.35	46.51	0.98	0.09	7.70	11	329	0.92	0.10	6.93
2.36	63.79	0.97	0.10	6.93	10	477	0.92	0.11	6.30
			0.09 ± 0.01	7.74 ± 0.58				0.10 ± 0.01	6.82 ± 0.43

growth data for all transplanted colonies are shown in Tables 2–6. It is seen that the coefficient of determination is high for all the replicates. For *C. hyalina*, genotype H: $r^2 = 0.96–1.00$; genotype T: $r^2 = 0.94–1.00$. For *E. pilosa*, genotype F: $r^2 = 0.95–0.99$; genotype L: $r^2 = 0.95–0.99$. The average specific growth rates for the four transplanted genotypes are depicted in Fig. 5 along with the growth rates for natural colonies growing on macroalgae. The *Celleporella* colonies in the fast flow achieved specific growth rates equal to the rates of the 'control' colonies grown at optimal laboratory conditions at 5000 cells ml^{-1} (genotype H: $\mu = 0.10$ day^{-1}, genotype T: $\mu = 0.09$ day^{-1}), whereas the growth of the colonies in the reduced flow was less. The fastest growth of *E. pilosa*, genotype F ($\mu = 0.12$ day^{-1}) was seen in the reduced flow, whereas for genotype L the fastest growth ($\mu = 0.12$ day^{-1}) was in the control colonies, and in both flow regimes the rates were smaller ($\mu = 0.10$ day^{-1}). It can be stated that the average specific growth rate for all colonies regardless of genotype, species, or flow regimes was close to 0.11 day^{-1}. For the two species growing on macroalgae the average specific growth rate was smaller than the growth rate of the colonies growing on microscope slides, about 0.06 and 0.08 day^{-1}, respectively, for *C. hyalina* and *E. pilosa* colonies (see Table 6).

Table 3
Growth of transplanted *C. hyalina* (genotype T) in Menai Strait during 34 days (September 17–October 20), and control colonies grown in laboratory

Colony area					Total number of zooids				
N_0	N_t	r^2	μ	t_2	N_0	N_t	r^2	μ	t_2
Control									
2.36	42.38	0.98	0.09	7.70	10	472	0.97	0.12	5.77
1.45	31.58	0.98	0.10	6.93	5	353	0.97	0.13	5.33
2.13	44.21	0.97	0.09	7.70	10	475	0.96	0.12	5.77
2.22	45.05	0.96	0.09	7.70	10	511	0.97	0.12	5.77
2.35	46.38	0.96	0.09	7.70	10	510	0.95	0.12	5.77
0.90	23.28	0.99	0.10	6.93	3	249	0.99	0.14	4.95
			0.09 ± 0.01	7.44 ± 0.40				0.13 ± 0.01	5.56 ± 0.35
Fast flow									
1.85	40.62	0.99	0.10	6.93	11	287	1.00	0.10	6.93
1.68	28.20	0.98	0.09	7.70	9	217	0.99	0.10	6.93
1.89	47.82	0.99	0.10	6.93	10	322	0.96	0.11	6.30
2.64	40.61	0.99	0.09	7.70	11	269	0.95	0.10	6.93
2.38	42.28	0.99	0.09	7.70	10	307	0.95	0.11	6.30
			0.09 ± 0.01	7.39 ± 0.42				0.10 ± 0.01	6.68 ± 0.35
Reduced flow									
2.12	28.19	0.98	0.08	8.66	10	223	0.91	0.09	7.70
2.03	20.62	0.96	0.07	9.90	11	183	0.91	0.08	8.66
2.40	26.95	0.94	0.07	9.90	10	226	0.88	0.09	7.70
2.17	27.34	0.95	0.07	9.90	11	211	0.92	0.09	7.70
2.07	40.69	0.96	0.09	7.70	10	257	0.89	0.10	6.93
			0.08 ± 0.01	9.21 ± 1.00				0.09 ± 0.01	7.73 ± 0.61

Table 4
Growth of transplanted *E. pilosa* (genotype F) in Menai Strait during 26 days (September 25–October 20), and control colonies grown in the laboratory

Colony area					Total number of zooids				
N_0	N_t	r^2	μ	t_2	N_0	N_t	r^2	μ	t_2
Control									
3.02	23.13	0.97	0.11	6.30	10	64	0.98	0.10	6.93
3.65	22.70	0.99	0.10	6.93	11	53	0.95	0.08	8.66
3.61	23.17	0.98	0.10	6.93	11	68	0.99	0.10	6.93
4.17	27.24	0.98	0.10	6.93	11	81	0.98	0.11	6.30
3.74	23.84	0.98	0.10	6.93	11	66	1.00	0.09	7.70
			0.10 ± 0.00	6.80 ± 0.28				0.10 ± 0.01	7.30 ± 0.91
Fast flow									
3.75	36.91	0.97	0.12	5.77	10	188	0.99	0.14	4.95
3.28	29.54	0.98	0.11	6.30	11	159	1.00	0.13	5.33
4.10	30.40	0.95	0.10	6.93	10	161	1.00	0.14	4.95
4.04	34.70	0.97	0.11	6.30	11	171	1.00	0.14	4.95
3.27	30.70	0.96	0.11	6.30	11	154	1.00	0.13	5.33
			0.11 ± 0.01	6.32 ± 0.29			1.00	0.14 ± 0.01	5.10 ± 0.21
Reduced flow									
4.46	48.93	0.98	0.12	5.77	11	248	0.99	0.15	4.62
5.22	43.82	0.99	0.11	6.30	11	219	0.99	0.15	4.62
4.19	48.39	0.99	0.12	5.77	12	232	0.99	0.15	4.62
4.87	41.95	0.99	0.11	6.30	14	211	0.98	0.13	5.33
4.03	55.79	0.99	0.13	5.33	12	257	1.00	0.15	4.62
			0.12 ± 0.01	5.89 ± 0.41				0.15 ± 0.01	4.76 ± 0.32

3.3. Current velocities

During spring tide, the highest velocities were measured at the middle depth of 4–6 m, ranging from 10 to 150 cm s^{-1}. At the surface level, the lowest and the highest measured current velocity was close to 0 and 40 cm s^{-1}, respectively, and the average velocity was 20 cm s^{-1}. During neap tide the maximum velocity varied from 0 to 60 cm s^{-1} at the middle depth. At the surface level the maximum current velocity was 10 cm s^{-1}, and the average velocity 4 cm s^{-1}. In the following, the average value of current corresponding to fast flow condition at the raft in Menai Strait was taken to be 40 cm s^{-1}.

To determine the flow conditions experienced by bryozoans exposed to a given current velocity it is of interest to estimate the height of the viscous sublayer (δ) which can be calculated as in Grünbaum (1997):

$$\delta = 7\upsilon/u^*, \tag{5}$$

where υ is the kinematic viscosity of the seawater (1.4×10^{-6} m^2 s^{-1} at 10°C), and $u^* = \sqrt{(\tau_w/\rho)}$ is the shear velocity which may be estimated from a boundary layer calculation. Assuming a smooth flat surface subject to a turbulent freestream flow with

Table 5
Growth of transplanted *E. pilosa* (genotype L) in Menai Strait during 26 days (September 25–October 20), and control colonies grown in the laboratory

Colony area					Total number of zooids				
N_0	N_t	r^2	μ	t_2	N_0	N_t	r^2	μ	t_2
Control									
5.08	85.09	0.98	0.11	6.30	13	304	0.97	0.13	5.33
5.72	92.35	0.99	0.11	6.30	14	337	0.98	0.13	5.33
6.54	113.90	0.99	0.12	5.77	13	301	0.96	0.12	5.77
6.24	108.58	0.99	0.12	5.77	8	381	0.95	0.15	4.62
5.74	111.74	0.99	0.12	5.77	13	393	0.98	0.14	4.95
6.05	104.08	0.99	0.12	5.77	6	340	0.95	0.16	4.33
4.17	72.06	0.99	0.12	5.77	7	240	0.96	0.14	4.95
			0.12 ± 0.00	5.92 ± 0.26				0.14 ± 0.01	5.04 ± 0.48
Fast flow									
6.57	84.05	0.99	0.10	6.93	14	400	0.93	0.13	5.33
6.97	87.94	0.99	0.10	6.93	13	377	0.93	0.13	5.33
5.15	64.74	0.99	0.10	6.93	14	265	0.97	0.11	6.30
5.36	59.86	0.99	0.09	7.70	13	278	0.96	0.12	5.77
5.72	73.12	0.99	0.10	6.93	14	306	0.91	0.12	5.77
4.53	69.58	0.97	0.10	6.93	12	321	0.94	0.13	5.33
			0.10 ± 0.00	7.06 ± 0.31				0.12 ± 0.01	5.64 ± 0.39
Reduced flow									
5.22	75.50	0.95	0.10	6.93	12	374	0.92	0.13	5.33
4.83	50.56	0.97	0.09	7.70	11	234	0.86	0.12	5.77
5.54	55.81	0.96	0.09	7.70	14	275	0.97	0.11	6.30
5.01	84.79	0.98	0.11	6.30	10	312	0.96	0.13	5.33
6.03	68.71	0.98	0.09	7.70	10	333	0.90	0.13	5.33
5.43	75.12	0.97	0.10	6.93	13	261	0.91	0.12	5.77
			0.10 ± 0.01	7.21 ± 0.58				0.12 ± 0.01	5.64 ± 0.39

velocity U_0, the skin friction coefficient may be approximated by that of a turbulent boundary layer (Schlichting, 1968, p. 600):

$$c_x \equiv 2\left(u^*/U_0\right)^2 \approx 0.0296\, Re_x^{-0.2}, \tag{6}$$

where x denotes the distance downstream from the start of the plate. For the present experiment, x is small, yielding a relatively small Reynolds number, $Re_x = xU_0/\upsilon$, hence, a large u^* and a small δ. For the transplanted colonies exposed to fast flow, for example, $x = 0.3$ m and $U_0 = 0.40$ m s^{-1}, Eq. (6) gives $u^* = 0.0156$ m s^{-1}, and Eq. (5) gives $\delta = 0.63$ mm. Corresponding values for the reduced flow at the raft in Menai Strait (cf. Fig. 2), $U_0 = 0.30$ m s^{-1} are $u^* = 0.012$ m s^{-1} and $\delta = 0.81$ mm. These values may be typical of maximum flows past encrusting bryozoan colonies growing on flat macroalgal fronds aligned with a turbulent flow, although depending on length from start of boundary layer to location of colony. It, thus, appears that encrusting bryozoans on fronds most often, in spite of relatively high freestream flows as measured in the Menai Strait, be restricted to feed in or at the edge of the viscous sublayer. In

Table 6
Growth of natural *C. hyalina* and *E. pilosa* colonies on macroalgae in Menai Strait during 15 days (September 29–October 13)

Colony area			
N_0	N_t	μ	t_2
C. hyalina			
12.87	23.44	0.04	17.33
12.76	34.44	0.07	9.90
10.70	25.63	0.06	11.55
14.12	21.27	0.03	23.10
16.10	36.47	0.06	11.55
4.27	21.62	0.12	5.78
6.32	18.92	0.08	8.66
35.42	53.26	0.03	23.10
		0.06 ± 0.03	13.87 ± 6.56
Electra pilosa			
5.28	16.56	0.08	8.66
8.93	37.52	0.10	6.93
16.87	47.20	0.07	9.90
34.95	66.87	0.05	13.86
38.48	94.73	0.06	11.55
7.01	21.66	0.08	8.66
12.90	28.55	0.06	11.55
32.40	82.03	0.07	9.90
5.43	18.20	0.09	7.70
5.30	24.40	0.11	6.30
8.18	42.52	0.12	5.78
31.11	54.15	0.04	17.33
47.33	112.77	0.06	11.55
5.18	24.60	0.11	6.30
7.87	32.20	0.10	6.93
61.05	97.92	0.03	23.10
9.18	41.97	0.11	6.30
119.60	307.20	0.07	9.90
22.02	86.46	0.10	6.93
		0.08 ± 0.03	9.95 ± 4.37

visualisation studies Hurd et al. (1997) found boundary layers on blades of the giant kelp *Macrocystis integifolia* to be turbulent and thick at Reynolds numbers smaller than those suggested above, but it is unclear if the surface of flat macroalgae may in general be considered hydraulically smooth. If equipped with roughness elements of height comparable to those of bryozoans the algal surface would be considered to be hydraulically rough, and turbulence would persist to the level of the inlet to the lophophores.

4. Discussion

Earlier laboratory experiments on *E. pilosa* performed by Riisgård and Goldson (1997) showed that maximum growth occurred at concentrations above 2000

Rhodomonas cells ml^{-1}, but a more precise statement about the lowest algal concentration that would result in maximum growth was not given. The present laboratory study of growth of *E. pilosa* in response to various algal concentrations indicates that maximum growth occurs at a *Rhodomonas* sp. concentration between about 1000 and 1500 cells ml^{-1} (Table 1, Fig. 4), equivalent to about 1.3–1.9 μg chl *a* l^{-1} which is close to the mean concentration measured in Menai Strait in this work (1.1 ± 0.6 μg chl *a* l^{-1}), and by Blight et al. (1995). This indicates that the bryozoans were not food limited in the field although the mean chl *a* concentration was relatively low compared to e.g. Danish coastal waters with a the median concentration of 5.1 μg chl *a* l^{-1} (Sand-Jensen et al., 1994). Noting the large variation in concentrations measured in the field, and the fact that bryozoans are continuous filter-feeders, it is appropriate to employ the mean concentration as an indicator of the food supply, although Wildish and Kristmanson (1988) in the case of giant scallops has suggested an adaptation to tidal periodicity so as to maximize feeding/growth.

The present growth experiments on the raft in Menai Strait with transplanted *E. pilosa* and *C. hyalina* showed that the specific growth rates were 0.10–0.12 and 0.08–0.10 day^{-1}, respectively, regardless of flow regimes, species, and genotype

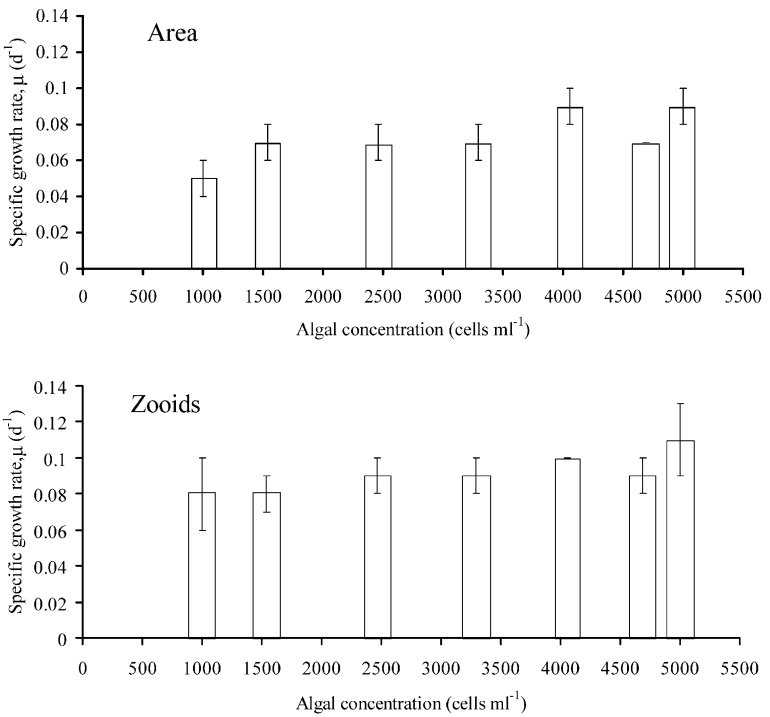

Fig. 4. Colony growth of *E. pilosa* at different algal concentrations in laboratory experiments. The mean (±S.D.) specific growth rate of clones was measured over a 14-day period. Upper: calculations based on colony area. Lower: calculations based on total number of zooids. Data from Table 1.

studied (*E. pilosa*: Tables 4 and 5; *C hyalina*: Tables 2 and 3). These growth rates are comparable to the rates obtained in 'control' or reference colonies kept under optimal growth conditions in the laboratory (Fig. 5). The somewhat slower growth of natural bryozoan colonies on macroalgae in the Menai Strait (Table 6) may be due to their larger size, as they were not reduced previous to the growth measurements. According to Bishop and Bahr (1973) the feeding rate—and thus growth—seems to decrease with increasing colony size, which may be due to changes in shape parameter *C* (cf. Eq. (4)). So far, for colony growth in the laboratory, it has been found that the shape parameter *C* varies during growth, depending on species and growth form.

Experiments performed by other workers have also attempted to determine relationship between algal concentration and growth (Table 7). It is striking that most previous experiments have been performed at algal concentrations much higher than actual field values. Field experiments made in Australian waters by Wass and Vail (1978) showed specific growth rates close to 0.11 day^{-1} for the encrusting species *Valdemunitella valdemunita* (Table 7). Cancino and Hughes (1987) made field experiments with *C. hyalina* in Menai Strait where they grew colonies in different flow regimes described as

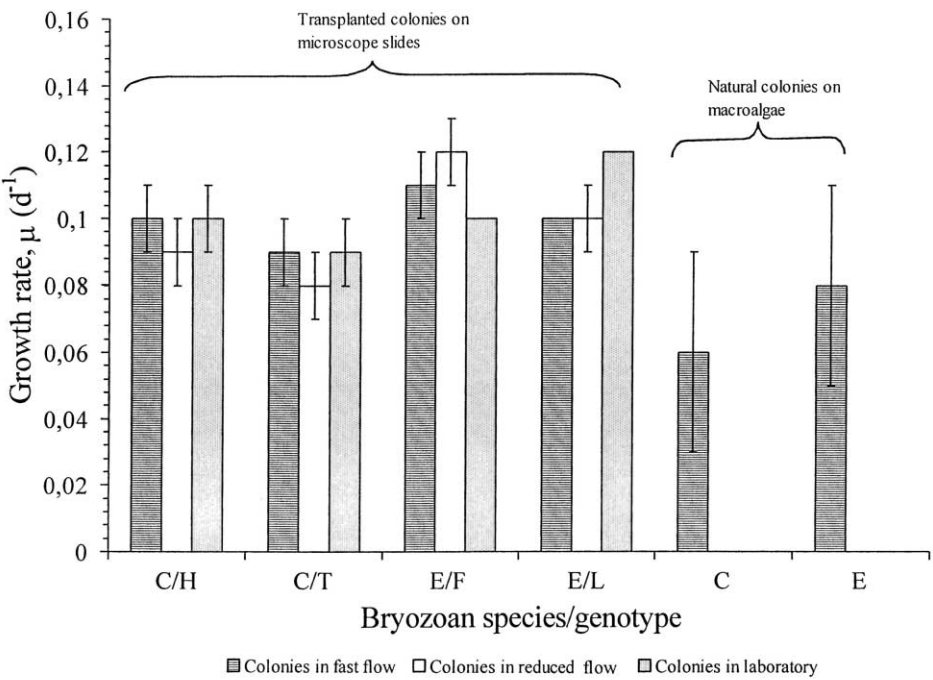

Fig. 5. The mean (±S.D.) specific growth rate (from Tables 3–7) based on colony area measurements for all transplanted colonies growing on microscope slides, and for natural colonies growing on macroalgae. The transplanted colonies were grown in both fast and reduced flow conditions, and colonies grown at optimal conditions in the laboratory served as 'controls' or references. The natural colonies were grown in the fast flow regime. C/H: *C. hyalina*, genotype H; E/F: *E. pilosa*, genotype F and so forth.

Table 7
Specific growth rate and doubling time in various field (A) and laboratory (B) growth experiments
The initial or mean algal concentrations are indicated. Algae used were *Rhodomonas* sp. unless otherwise indicated. NA = not available. Doubling time is calculated according to Eq. (3).

	Species	Algal concentration (cells ml^{-1})	Flow velocity (cm s^{-1})	Growth rate (day^{-1})	Doubling time (day)	Sources
(A)	*C. hyalina*	250–1850[a]	0–40[b]	0.10[c]	6.93	Present study
			reduced	0.09	7.70	
	E. pilosa	250–1850[a]	0–40[b]	0.11[d]	6.30	Present study
			reduced	0.11	6.30	
	C. hyalina	NA	Unrestricted[e]	0.13[f]	5.33	Cancino and Hughes (1987)
			Semirestricted	0.13	5.33	
			Restricted	0.13	5.33	
	M. membranacea	NA	0–60[g]	0.13[h]	5.33	Okamura and Partridge (1999)
			0–90	0.14	4.95	
	V. valdemunita	NA	NA	0.11[i]	6.30	Wass and Vail (1978)
	B. neritina	NA	NA	0.43[j]	1.61	Kitamura and Hirayma (1984)
(B)	*C. hyalina*	10 000	NA	0.02[k]	34.66	Hunter and Hughes (1993a)
		50 000		0.06	11.55	
		100 000		0.07	9.90	
	C. hyalina	4000 (mean)	NA	0.10[l]	6.93	Riisgård and Goldson (1997)
	E. pilosa	4000 (mean)	NA	0.12[l]	5.78	Riisgård and Goldson (1997)
	E. pilosa	100 (initial)	NA	0.03[m]	23.10	Bayer et al. (1994)
		1000		0.10	6.93	
		10 000		0.24	2.89	
		100 000		0.25	2.77	
	E. pilosa	43 000 (initial)	NA	0.06[n]	11.55	Bayer and Todd (1996)
	Con. seurat	> satiation concentration	NA	0.34[o]	2.04	Jebram and Rummert (1978)
	C. tenuissimum	118 000 (initial)	NA	0.26[p]	2.67	Winston (1976)

[a] The chl *a* concentration varies between 0.3 and 2.3 μg chl *a* l^{-1}. The corresponding algal concentration (cells l^{-1}) is calculated by use of Eq. (1).

[b] See Fig. 5 in this paper; the reduced flow was about 75% of the fast flow.

[c] The specific growth rate is the average of genotype H and T from Tables 3 and 4 based on colony area measurements.

[d] The specific growth rate is the average of genotype F and L from Tables 5 and 6 based on colony area measurements.

[e] The difference in flow is 1:1.8:3.0 for restricted, semi-restricted and unrestricted flow, respectively.

[f] The grand mean instantaneous growth rate (= specific growth rate) see results first paragraph.

[g] Flow velocity is based on the overall mean velocities (measured at the level of the algal canopy) plotted in Fig. 4 for the inflow measurements.

[h] The specific growth rate is calculated by data supplied by B. Okamura.

[i] The specific growth rate is based on the values in Table 1 for the first 21 days for colony 1.

[j] The value is based on the slope of the regression line A in Fig. 2.

[k] Values based on Table 1.

[l] Specific growth rates from Table 3.

[m] Maximal growth rates from Fig. 2 are transformed according to Eq. (4).

[n] Calculation based on Fig. 3 and the assumption that the initial area was close to 3.2 mm^2.

[o] Calculated from Fig. 1 (algae: *Oxyrrhis*).

[p] Calculated from Fig. 2 (algae: *Dunaliella*).

unrestricted, semi-restricted, and restricted flow (Table 7). The different flow regimes were established by placing conical baffles around the bryozoan colonies. Their results showed a specific growth rate of 0.13 day^{-1}, regardless of flow treatment. Experiments performed by Okamura and Partridge (1999) in Lough Hyne (Ireland) over a 10-day period showed specific growth rate at 0.13 and 0.14 day^{-1} for *Membranipora membranacea* at two field sites with different flow velocities. Lough Hyne is a narrow channel where the tidal current dominates the flow, as is the case in Menai Strait, but the flow velocities measured at Lough Hyne were higher.

Growth experiments with *Membranipora membranacea* kept in tubes by Eckman and Duggins (1993) showed a different effect, as the growth decreased when the flow was increased, possibly because the hydrodynamics of flow in tubes are different from flow in natural benthic boundary layers (Wildish and Kristmanson, 1997). Kitamura and Hirayma (1984) found a very high specific growth rate of 0.43 day^{-1} for the erect *Bugula neritina* (Table 7), but as a general rule for encrusting bryozoans the maximum growth rate appears to be about 0.12 day^{-1}, expect for encrusting *Coneopeum seurati* colonies kept at *Oxyrrhis* concentrations "larger than satiation concentrations" (Jebram and Rummert, 1978).

In this study, estimated values of average shear velocities and height of viscous sublayers for transplanted colonies exposed to normal and reduced flow, respectively, were $u^* = 15.6$ and 12 mm s^{-1}, and $\delta = 0.63$ and 0.81 mm, respectively. Estimates made by Grünbaum (1997) for "moderate flow" conditions showed lower shear velocities (2.2–8 mm s^{-1}) and greater heights of the viscous sublayer (1.2–4.2 mm). In a flume study performed by Larsen et al. (1998), using video to measure water flow velocity and particle capture, it was demonstrated that the upstream flow was laminar, that the velocity profile above a row of bryozoans was linear, and that the bryozoans were actively feeding in this viscous layer. According to Larsen et al. the values of the shear rates $\partial u/\partial y = 1–4$ s^{-1}, corresponding to shear velocity $u^* = 1–3$ mm s^{-1}, are similar to those found in the viscous sublayer of turbulent flow over smooth surfaces.

Numerical simulations by Larsen et al. (1998) suggest that when the flowrate was doubled the water space available for particle capture was decreased, yet feeding rate increased because the particle flux increased in the thinner boundary layer. This is also in accord with the model developed by Eckman and Okamura (1998) who predicted that the capture rate increases with increasing external flow.

On the other hand, earlier laboratory studies by Okamura (1985, 1988) showed the opposite effect: when the flow was increased, the feeding rates decreased. This is perhaps explained by the very strong flume flow (10–12 cm s^{-1}) just above the bryozoan colony resulting in much higher velocities in the viscous sublayer than bryozoans may experience in nature. Two studies of bryozoans in flume flow show that the bryozoans are affected by high velocity just above the colony. Thus, lophophores were retracted at flow velocities between 2–5.5 cm s^{-1} (Lidgard, 1981) and above 10 cm s^{-1} (Eckman and Duggins, 1993). Fig. 4 in Larsen et al. (1998) shows that the flow velocity is 0.75 mm s^{-1} about 0.1 mm above the bryozoan colony, which probably are closer to the natural conditions. It appears that further progress in understanding requires experimental data (or reliable theoretical predictions) characterizing the flow above a colony in terms of parameters such as shear velocity u^* and whether or not a laminar

sublayer exists just above the lophophores. Although the flow conditions in laboratory experiments may involve turbulent water motion due to air-bubble mixing in the bulk the bryozoans feed from a non-turbulent (laminar) sublayer, hence, have conditions equivalent to those in the field.

The flume experiment by Larsen et al. (1998) seems to reflect what could be expected when bryozoans are feeding in a laminar boundary layer. The present field experiments showed that the bryozoans could be assumed to feed adequately during the tidal cycle in Menai Strait, irrespective of even very high flow velocities. The bryozoans are believed to reside within the viscous sublayer, which does not seem to get food depleted. High flow environments may most likely lead to optimal feeding and growth, as shown in the present and earlier field studies performed by Cancino and Hughes (1987) and Okamura and Partridge (1999), probably because colonies are exposed to thin laminar sublayers.

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Appendix A. Estimate of reduced velocity in channel

Consider the channel formed by two parallel plates on the raft, spaced 4.5 cm apart, 60 cm long, and aligned with the current of freestream velocity, $u_\alpha = 40$ cm s^{-1}. Due to the resistance to flow of the 1×1 mm mesh at inlet and outlet, and the boundary layers developing along the plates, the freestream velocity in the channel will be reduced, say to u_1. Here, only the frictional pressure drop across meshes is important, exceeding by at least an order of magnitude the contributions from the boundary layers. For one mesh the pressure drop may be estimated from $\Delta p = \zeta\{1/2\}\rho u_1^2$, where $\zeta \sim 0.8$ (Idelchik, 1994, p. 522). Equating twice this pressure drop (for two meshes) to the driving excess pressure at the channel inlet, arising from the deceleration of the current, $\Delta p = 1/2\ \rho (u_\alpha^2 - u_1^2)$, gives an estimate of the reduced flow, $u_1 = u_\alpha/(1+\zeta)^{1/2} = 40/1.34 \sim 30$ cm s^{-1}. During periods between cleaning of meshes, fouling may have reduced the velocity further, as would a misalignment of the raft relative to the current.

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