Testing Habitat Complexity As A Control Over Bryozoan Colonial Growth Form And Species Distribution

By: **Steven J. Hageman**, Frank K. McKinney, and Andrej Jaklin

Abstract

The aim of this study is to test the effects of fine scale (microhabitat) environmental variation on the distribution of bryozoan species and potential variation in growth habit diversity and disparity. Data are derived from six microhabitats in replicate, on designed apparatuses, providing surfaces of varied complexity and orientation. The apparatuses were deployed on a sediment substrate at 24 m depth offshore of Rovinj, Croatia and recovered 14 months later. Species distributions were documented for each microhabitat and indexed for relative abundance. Twenty-five bryozoan species were recorded in multiple 0.5 x 0.5 cm cells in multiple patches on each microhabitat. Species richness was relatively uniform in each microhabitat, but most individual species and several growth habit attributes differed in abundance or presence among microhabitats.

Hageman, S.J., McKinney, F.K., and Jaklin, A. (2011). Testing Habitat Complexity As A Control Over Bryozoan Colonial Growth Form And Species Distribution. *Bryozoan Studies*, 2010 (pp.105-119). Lecture Notes in Earth System Sciences 143. DOI:10.1007/978-3-642-16411-8_8

Testing Habitat Complexity as a Control over Bryozoan Colonial Growth Form and Species Distribution

Colonial Growth Form Ecology

Steven J. Hageman, Frank K. McKinney (deceased), and Andrej Jaklin

Abstract The aim of this study is to test the effects of fine scale (microhabitat) environmental variation on the distribution of bryozoan species and potential variation in growth habit diversity and disparity. Data are derived from six microhabitats in replicate, on designed apparatuses, providing surfaces of varied complexity and orientation. The apparatuses were deployed on a sediment substrate at 24 m depth offshore of Rovinj, Croatia and recovered 14 months later. Species distributions were documented for each microhabitat and indexed for relative abundance. Twenty-five bryozoan species were recorded in multiple 0.5 × 0.5 cm cells in multiple patches on each microhabitat. Species richness was relatively uniform in each microhabitat, but most individual species and several growth habit attributes differed in abundance or presence among microhabitats.

Keywords Recruitment • Species richness • Growth habit • Ecology • Adriatic Sea

Introduction

This study arose from a long-term search for a better understanding of the environmental factors that control the distribution and abundance of bryozoan colony growth forms and species richness in space and time. The broad correlation of sedimentary environments with the dominance and diversity of colony growth forms (Stach 1936) has been used in reverse in many publications in which growth forms of ancient bryozoans have been used to infer paleoenvironments.

S.J. Hageman (✉) • F.K. McKinney (deceased)
Department of Geology, Appalachian State University, Boone, NC, USA
e-mail: hagemansj@appstate.edu

A. Jaklin
Ruđer Bošković Institute, Center for Marine Research, Rovinj, Croatia
e-mail: jaklin@cim.irb.hr

A. Ernst, P. Schäfer, and J. Scholz (eds.), *Bryozoan Studies 2010*,
Lecture Notes in Earth System Sciences 143, DOI 10.1007/978-3-642-16411-8_8

Although the ultimate goal of this project is to understand controls on growth habits, this paper deals only with microhabitats and the bryozoan fauna found in them. The question addressed is: Given a range of microhabitats expressed by textural complexity and orientation, is there an apparent effect on species richness and difference in microhabitat specificity of taxa and growth habit?

Previous Work

There is a rich literature reporting results of in situ and of laboratory studies of bryozoans' behaviour and/or survivorship in response to specific environmental influences on the entire life cycle from embryo to sexually mature colony. Citing only single examples from the literature base of representative topics, successful completion of a life cycle involves seasonality of larval release (Mariani et al. 2005), larval swimming duration and dispersal distance (Pemberton et al. 2007), larval behaviour before (Ryland 1977) and after (Burgess et al. 2009) contact with a potential substrate, substrate pre-emption (Sutherland and Karlson 1977), substrate quality (Dobretsov and Qian 2006), and post-settlement interactions with competitors (Barnes and Dick 2000) and predators (Lidgard 2008).

All of these topics – and others – are critically important to whether or not a given species is present or absent on a given substrate. For this study, however, they comprise a contextual background for an abundant pool of larvae from which a species-rich (Hayward and McKinney 2002) bryozoan fauna could potentially be recruited onto various microhabitats provided within experimental apparatuses.

Material and Methods

Apparatuses consisting of multiple substrates (e.g. panels) with varied orientations and textures replicated in each apparatus were constructed for this study (Fig. 8.1a). The goals of the design were to provide equal access for bryozoan larvae to varied microhabitats (treatments) within a local environment, but with minimal interaction among microhabitats. All substrates were composed of plastic and the surfaces were mildly abraded with fine sandpaper. Treatment panels were attached to the frame by plastic cable ties via holes drilled in the PVC pipes. Each of the microhabitats provided a minimum of 600 cm^2 available for settlement.

Apparatuses and Microhabitat

The microhabitats created for this study (Fig. 8.1a) included: (1) vertical smooth panels (Fig. 8.1f), (2) strings of nylon netting (0.5 mm diameter) composed of

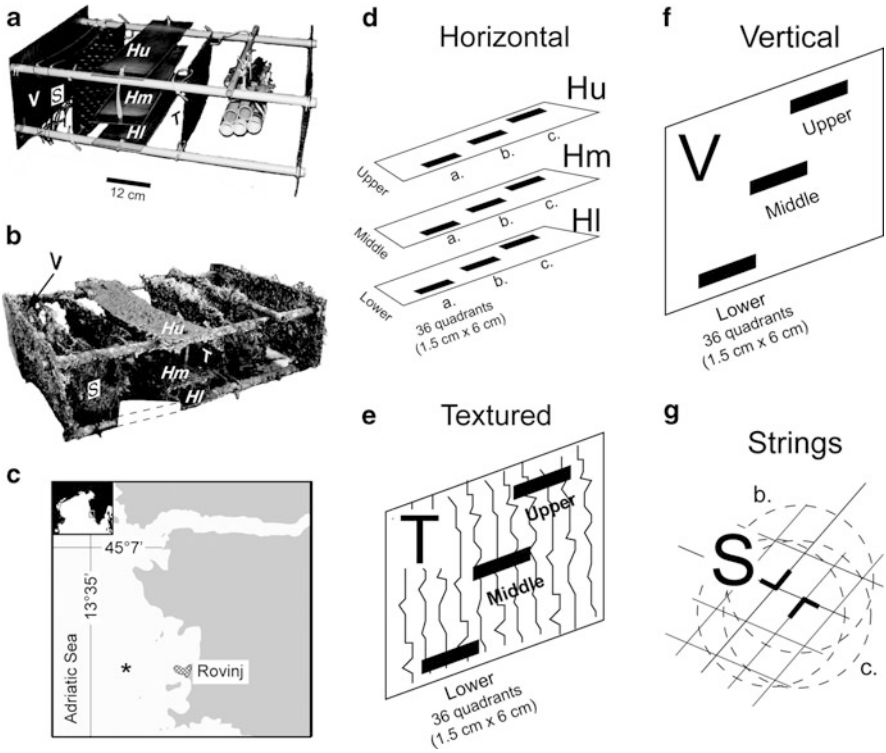

Fig. 8.1 Experimental apparatus and deployment location. (**a**) PCV-supported microhabitat panel prior to deployment; (**b**) Microhabitat panel after deployment. V = vertical, S = Strings, H = Horizontal, u = upper, m = middle, l = lower, T = textured; (**c**) Location of deployment in the northeastern Adriatic Sea (*), approximately 2.0 km WSW of Rovinj peninsula, beneath oceanographic observation buoy at 45° 04.960′ N, 13° 36.233′ E, (**d**–**g**), Microhabitat panels

multiple twisted strands (Fig. 8.1g), (3) the under side of horizontal panels mounted separately on the upper, middle and lower part of the device (Fig. 8.1d), (4) vertical panels with an irregular corrugated surface with ~2.0 mm of relief (Fig. 8.1e). Other microhabitat panels were used in the apparatuses, but are not included in this study.

Two replicate apparatuses (A and B) were deployed beneath the moored oceanographic observation buoy 2.0 km WSW of the peninsula of the town of Rovinj (Fig. 8.1c). The apparatuses were deployed by SCUBA in March of 2007 in 24 m water depth and secured to the sandy sea floor approximately 2 m apart. The apparatuses were recovered by SCUBA in May 2008, with no signs of significant natural or artificial disruption to their placement.

Apparatuses were returned to the laboratory in sea water and photographed whole (Fig. 8.1b) immediately upon exposure to the air. Apparatuses were then disassembled and each microhabitat surface photographed in its entirety in the original wet state with 7.1 Mb digital images. Each treatment panel was then thoroughly rinsed in fresh water and allowed to air dry in a natural setting. Large

soft-bodied organisms such as sponges and ascidians and macro-invertebrates such as ophiuroids and polychaetes were noted and removed. Dried treatment panels were individually wrapped and transported to Appalachian State University for detailed study. Due to their fragile state, bryozoan specimens were studied with dried cuticle and soft tissue intact.

Experimental Design

Data for this study are hierarchically arranged. In descending order, levels are:

5. *Replicate* apparatuses: A and B at the one locality (observation buoy)
4. *Microhabitat*: six within each replicate, Horizontal Upper, Horizontal Middle, Horizontal Lower, Vertical, Textured, Strings (Fig. 8.2).
3. *Patch*: three (1.5 × 6 cm) within each microhabitat.
2. *Grid*: 36 (0.5 × 0.5 cm) grids within each Patch (3 × 12)
1. *Occurrence* of species: scored as 1 for present and 0 for absent.

The fundamental unit of observation in this study is presence or absence (occurrence) of each bryozoan species in a (0.25 cm^2) grid cell. Within five of the microhabitats each 1.5 × 6 cm patch, represented by black strips on panels in Fig. 8.1, was divided into 36 grid squares each 0.5 × 0.5 cm. Thus, the maximum score for each species for each patch is 36 and each microhabitat was 108 for each replicate apparatus (total pooled 216 per treatment). For the String microhabitat, the netting was cut between each knot, resulting in an "X" (Fig. 8.1g). The surface area of one half of this unit, a "V" is approximately equivalent to one grid (0.25 cm^2) and thus was used as a unit of observation. The string "Vs" were randomly placed in three groups of 36 (n = 108) for each Apparatus Replicate (position within the string treatment was not identified).

The experimental design of this study was exploratory and does not allow for a full factorial partitioning of sources of variation. Other potential sources of variation (distribution of colonies of bryozoan species) include: (1) positional (edge) effects within the apparatus and among microhabitats (effects presumed to be minimal, but unknown), (2) positional (edge) effects within microhabitats (effects apparently significant, and partially accounted for in this study), (3) compositional effects of different plastics among the microhabitat substrates (effects presumed to be minimal). In spite of these limitations, results from this study can provide valuable insight into the distribution of bryozoan species at the microhabitat level.

Data Collection

Panels (microhabitats) were examined with an Olympus SZX 12 microscope with a field of view of approximately 1.5 × 4 cm, and digital photos were taken. A 3 × 4

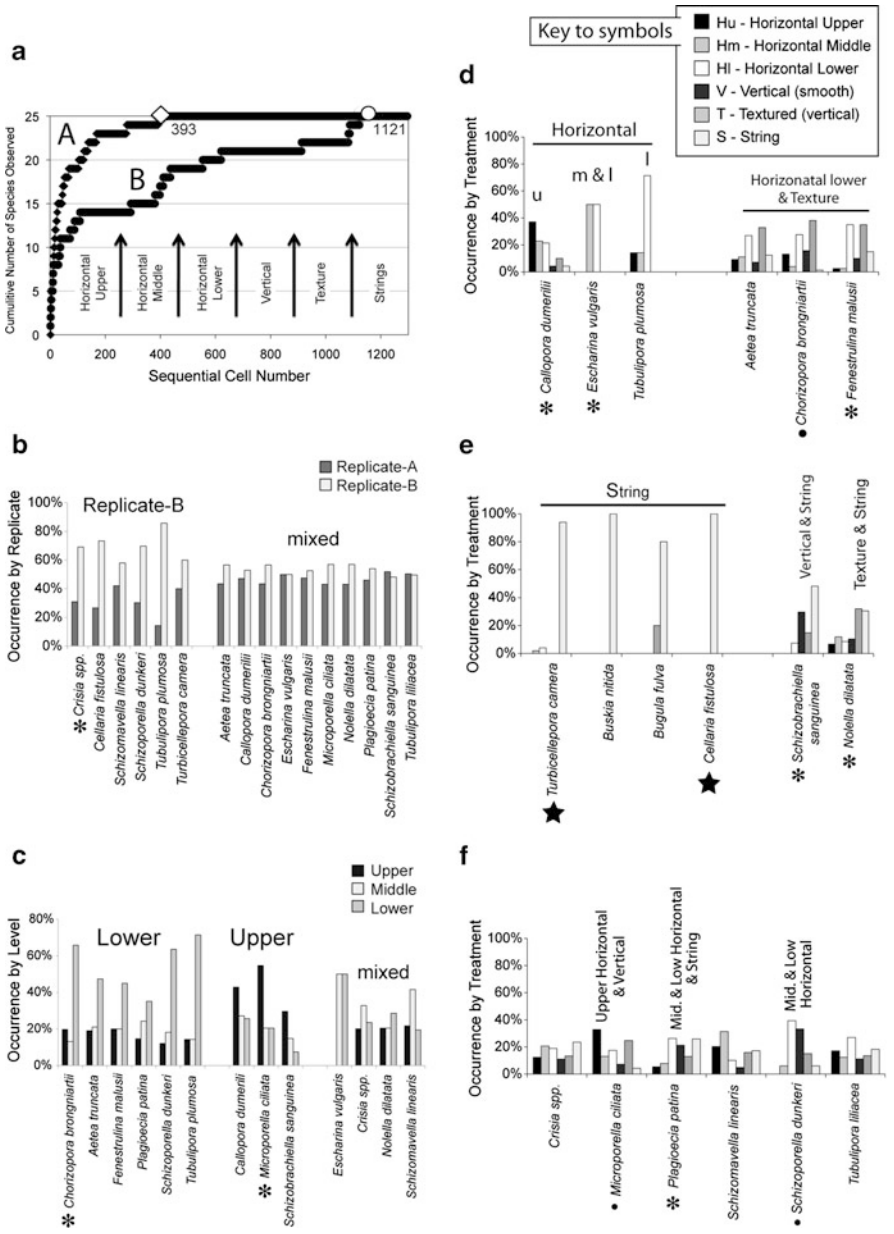

Fig. 8.2 Observed and modeled cumulative sampling curves. (**a**) Sampling *curves* (number of species observed per successive observation) for A = data randomized by collecting sequence and B = observed by collected through successive microhabitats. All 25 species were encountered by the 393rd cell in the random distribution, but the same 25 species were not observed until the 1,121st cell was censused in the actual sequence collected sequentially by microhabitat; (**b–f**) Relative abundance of common species (present in 14 or more cells) calculated within taxa among

grid (0.25 cm^2 each cell) was digitally burned into the image and printed as a reference map. Using higher magnification, each grid cell was evaluated using the reference map and all bryozoan species were identified using Hayward and McKinney (2002) and scored 1 if present and 0 if absent. Criteria for occurrence counting was based on presence/absence of a species in a cell, not frequency or dominance, thus: (1) species with multiple colonies in a cell, whatever their origin, were counted as a single occurrence; (2) a single colony overlapping into two adjacent cells was counted as occurring once in each cell; (3) colonies represented only by ancestrulae or the primary zone of astogenetic variation were not counted.

Data Analysis

Sampling Curve to Evaluate Species Heterogeneity Among Microhabitats

If bryozoan species are randomly distributed across all microhabitats within an apparatus, then a plot of the number of successive observations, here grid cells, against the cumulative number of species observed should plot as a relatively smooth curve (Sanders 1968). The curve is expected to initially increase rapidly and then asymptotically approach the maximum number of observed species for the assemblage. A sampling curve was modeled subsequent to data collection by generating a curve of species richness from data randomized by the order of their collection (Fig. 8.2a). In contrast, if species are not randomly distributed (i.e. heterogeneity related to microhabitat) and a cumulative species sampling curve is generated by systematically collecting across the apparatus one microhabitat at a time, the curve should stair step as the sampling progresses.

Comparing Replicate Among and Within Microhabitat Variation

Non-parametric Kruskal-Wallace tests were performed using PAST v. 2.01 (Hammer 2010) in order to determine the relative importance of differences among Replicates, Microhabitats and Level above substrate. Data were pooled for patches based on their

Fig. 8.2 (continued) treatments, i.e. total for each species = 100%. Asterisk indicate significance a $p \leq 0.05$ for Kruskal-Wallace test, stars indicate a high degree of significance at $p \leq 0.001$ and a *dot* indicates those approaching significance $0.1 \leq p \leq 0.05$; (**b**) Species distribution between replicate apparatuses; (**c**) distribution of species based on relative height above the primary substrate; (**d**) distribution of species showing preference for horizontal and textured microhabitats; (**e**) distribution of species showing preference for strings, vertical and textured microhabitats; (**f**) distribution of species showing less pronounced preference of individual microhabitats

relative position as measured on vertical panels (lower ~5 cm, middle ~15 cm and upper ~25 cm above the primary substrate) and the three patches each from the respective horizontal panels. For each replicate, microhabitat and level, the relative abundance of species with 14 or more occurrences in the entire study was plotted in histograms.

Microhabitat Preference of Individual Species

Typically, occurrence data are reported by treatment and species are indexed by which species is most common/abundant at a given treatment or site. This obscures the potential recognition of microhabitats or locations that are of particular importance for a given species, which may otherwise not dominate at any habitat or location. In this study, species occurrences are evaluated as to the distribution (percent occurrence) of one species among all microhabitats. (number of grid cells in which "species X" is present for a microhabitat, divided by the total number of all occurrences for "species X" in all microhabitats $\times$ 100) from raw data in Table 8.1. This value expressed as a percentage allows for comparison of the most or least "important" microhabitat for each species as in Fig. 8.2.

Results

Sampling Curve to Evaluate Species Heterogeneity Among Microhabitats

In hypothetical random data collection design (or species distribution), the total number (25) should be observed before the 400th cell observed (curve "A" in Fig. 8.2a). In the actual curve (curve "B" in Fig. 8.2a), the total species abundance was not observed until after the 1,100th cell, after data from the sixth microhabitat was included. This suggests that microhabitat heterogeneity is at least partially responsible for the distribution of the species. It is possible that factors other than microhabitat differences could be responsible for the deviation from the expected curve (randomized across apparatus in Fig. 8.2a, line a) but none are in evidence.

Frequency and Distribution of Species

The absolute occurrence totals of the 25 species are given in Table 8.1. The number of occurrences (sum of species presences in cells) organized by Replicate and Microhabitat ranged from 112 (Vertical–Replicate-A) to 476 (Strings–Replicate B). The total number of occurrences was greater for Replicate-B relative to Replicate-A

Table 8.1 Columns are 36-cell patches within a microhabitat treatment for a given replicate apparatus. The value for each species is the number of grid cells for which the species was present. Label abbreviations are: A-B for replicate, H-V-S for Horizontal, Vertical or String orientation of the treatment, S-T for smooth or textured surfaces, U-M-L for upper, middle or lower level above the primary substrate, and a-b-c for random replicates patches within horizontal and string treatments

Species	A_H_S_U_a	A_H_S_U_b	A_H_S_U_c	A_H_S_M_a	A_H_S_M_b	A_H_S_M_c	A_H_S_L_a	A_H_S_L_b	A_H_S_L_c	A_V_S_L	A_V_S_M	A_V_S_U	A_V_T_L	A_V_T_M	A_V_T_U	A_S_a	A_S_b	A_S_c	Total
Aetea sica	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	3
Aetea truncata	0	0	0	3	6	2	18	3	1	0	0	3	19	0	0	4	5	2	66
Bugula fulva	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	2
Buskia nitida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Callopora dumerilii	6	2	4	2	4	0	4	2	1	0	0	1	2	2	1	1	0	1	33
Cellaria fistulosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	4
Celleporina caminata	0	0	2	0	0	0	1	0	0	0	0	1	0	0	3	0	0	0	7
Chartella tenella	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	4
Chorizopora brongniartii	0	2	2	0	1	1	0	1	10	4	0	0	9	3	0	0	0	0	33
Crisia spp.	4	2	5	12	7	3	6	11	3	5	13	2	0	8	4	6	3	6	100
Cryptosula pallasiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Escharina vulgaris	0	0	0	0	4	0	2	2	0	0	0	0	0	0	0	0	0	0	8
Fenestrulina malusii	1	0	0	0	0	0	0	1	3	0	1	3	3	5	1	0	0	1	19
Hippothoa flagellum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microporella ciliata	5	6	15	9	0	0	2	0	0	1	2	7	3	3	5	0	1	0	59
Nolella dilatata	2	5	2	8	3	9	8	6	0	0	2	0	9	8	21	14	13	6	116
Plagioecia patina	1	3	6	3	7	1	20	0	3	6	11	10	1	12	3	10	5	8	110
Schizobrachiella sanguinea	0	0	0	0	0	0	2	0	0	0	0	0	0	4	0	2	5	1	14
Schizomavella linearis	0	14	12	0	11	8	4	1	9	5	6	0	11	0	1	2	3	8	95
Schizomavella subsolana	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Schizoporella dunkeri	0	0	0	0	1	0	0	0	0	8	0	0	0	0	1	0	0	0	10
Schizoporella magnifica	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	7

Tubulipora liliacea	18	6	9	10	9	6	21	14	14	4	11	5	5	8	9	5	7	9	170
Tubulipora plumosa	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Turbicellepora camera	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	9	8	20
Patch total	37	40	57	49	54	31	93	42	44	34	46	32	62	61	49	48	52	53	
Treatment total	134			134			179			112			172			153			884
Number of species	10			14			15			13			15			16			23

Species	B_H_S_U_a	B_H_S_U_b	B_H_S_U_c	B_H_S_M_a	B_H_S_M_b	B_H_S_M_c	B_H_S_L_a	B_H_S_L_b	B_H_S_L_c	B_V_S_L	B_V_S_M	B_V_S_U	B_V_T_L	B_V_T_M	B_V_T_U	B_S_a	B_S_b	B_S_c	Total
Aetea sica	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	5
Aetea truncata	13	1	0	0	6	0	10	9	0	0	0	8	12	15	4	0	6	2	86
Bugula fulva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	3
Buskia nitida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	4
Callopora dumerilii	5	9	0	6	4	0	2	1	5	0	1	1	1	0	1	0	1	0	37
Cellaria fistulosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	4	3	11
Celleporina caminata	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	1	5
Chartella tenella	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	2
Chorizopora brongniartii	0	5	1	0	1	0	0	4	6	8	0	0	8	4	5	0	0	1	43
Crisia spp.	21	5	3	11	7	27	1	23	17	2	12	2	8	6	17	18	20	23	223

(continued)

(continued)

Species	B_H_S_U_a	B_H_S_U_b	B_H_S_U_c	B_H_S_M_a	B_H_S_M_b	B_H_S_M_c	B_H_S_L_a	B_H_S_L_b	B_H_S_L_c	B_V_S_L	B_V_S_M	B_V_S_U	B_V_T_L	B_V_T_M	B_V_T_U	B_S_a	B_S_b	B_S_c	Total
Cryptosula pallasiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Escharina vulgaris	0	0	0	0	4	0	0	4	0	0	0	0	0	0	0	0	0	0	8
Fenestrulina malusii	0	0	0	1	0	0	10	0	0	0	0	0	1	1	3	3	1	1	21
Hippothoa flagellum	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	6
Microporella ciliata	6	8	5	9	0	0	14	7	1	0	0	0	0	5	18	0	3	2	78
Nolella dilatata	1	5	3	9	3	0	5	4	0	25	0	1	20	13	15	19	15	15	153
Plagioecia patina	1	0	2	0	7	1	6	14	20	10	10	4	4	6	5	15	12	12	129
Schizobrachiella sanguinea	0	0	0	0	0	0	0	0	0	0	0	8	0	0	0	3	0	2	13
Schizomavella linearis	0	4	16	20	11	21	0	0	9	0	0	0	5	17	2	3	12	11	131
Schizomavella subsolana	1	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	4
Schizoporella dunkeri	0	0	0	0	1	0	7	6	0	0	0	3	0	4	0	1	0	1	23
Schizoporella magnifica	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Tubulipora liliacea	6	9	10	4	9	4	14	13	15	7	4	7	6	8	10	14	13	14	167
Tubulipora plumosa	2	0	0	0	0	0	7	1	2	0	0	0	0	0	0	0	0	0	12
Turbicellepora camera	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	11	7	10	30
Patch total	60	46	40	60	54	53	76	88	83	54	27	35	67	79	81	94	99	102	
Treatment total	146			167			247			116			227			295			1,198
Number of species	13			13			15			11			13			18			25
Treatment total	H_U			H_M			H_L			V			T			S			
Study total	280			301			426			228			399			448			2,082

Table 8.2 Results from Kruskal-Wallis Tests for significant differences between ranked Raw occurrence data for equivalence among factors for each species (p-values reported from 1-way test Chi Square approximation). Factors and their cases are (1) Replicate, A and B are replicate devices for all treatments at one locality, (2) Level, is the height above the primary substrate, U = upper (~25 cm), M = Middle (~15 cm), L = lower (~5 cm), (3) Microhabitat, is an incomplete decomposition of orientation of the panel (H = Horizontal and V = vertical, both smooth surfaces), Surface texture (T = Texture) and substrate type (S = string). Only species with n ≥ 14 occurrences are reported. Significant effects are highlighted in bold and [a] indicates a result approaching significance (potentially significant with larger n)

		Replicate	Level	Treatment
Species	n	A vs. B	U vs. M vs. L	Hu vs. Hm vs. Hl vs. V vs. T vs. S
Aetea truncata	152	0.52	0.33	0.30
Callopora dumerilii	70	0.64	0.60	**0.020**
Cellaria fistulosa	15	0.53	–	<**0.0001**
Chorizopora brongniartii	76	0.58	**0.032**	0.07[a]
Crisia spp.	323	**0.022**	0.11	0.45
Escharina vulgaris	16	0.71	0.22	**0.040**
Fenestrulina malusii	40	0.72	0.76	**0.027**
Microporella ciliata	137	0.76	**0.040**	0.07[a]
Nolella dilatata	269	0.61	0.83	**0.002**
Plagioecia patina	239	0.60	0.25	**0.014**
Schizobrachiella sanguinea	27	0.50	0.99	**0.012**
Schizomavella linearis	226	0.65	0.37	0.17
Schizoporella dunkeri	33	0.14	0.71	0.72
Tubulipora liliacea	337	0.90	0.23	**0.007**
Tubulipora plumosa	14	0.16	0.40	0.10[a]
Turbicellepora camera	50	0.88	–	<**0.0001**

(1,198 vs. 884, Table 8.2). All 25 observed species were found in Replicate-B, while the two rarest species (*Cryptosula pallasiana*, *Hippothoa flagellum*) were not present on Replicate-A (Table 8.1). The number of species present on any given microhabitat/replicate combination ranged from 10 to 19 with a mean of 13.8 (Table 8.1). The number of species present on any microhabitat (pooled replicates) ranged from 15 to 19, with an average of 16.7.

Large, sessile macroinvertebrates (polychaete worms, *Anomia* pelecypods, ascidians, sponges) recruited most abundantly onto the Middle and Upper Horizontal microhabitats, resulting in low numbers of observations (though more than for the Vertical microhabitat) and number of species (Table 8.1).

Kruskal-Wallis Test for Apparatus, Level, and Microhabitat Effects

Kruskal-Wallis tests for each bryozoan species with 14 or more occurrences result in a progressively higher number of significant ($p \leq 0.05$) distributional patterns from Apparatus to Level to Microenvironment (Table 8.2). Only *Crisia* spp. is

significant at the $p \leq 0.05$ level between Apparatus A vs. B. That is, there is no difference between the replicate apparatuses when examined species by species ($n \geq 14$), except that *Crisia* spp. is more abundant on Apparatus-B, which has more occurrences overall ($n = 1{,}198$ vs. $n = 884$, Table 8.1). Occurrences of only two species are significant ($p \leq 0.05$) in tests for difference among Levels above the substrate (lower, middle, upper). *Chorizopora brongniartii* is more common in the lower region and *Microporella ciliata* is more abundant in the upper region (Table 8.2).

Nine species have significantly different occurrences among Microhabitats (Table 8.2), and two of the nine species (*Cellaria fistulosa*, *Turbicellepora camera*) are highly significant ($p \leq 0.0001$). Three additional species approach significance ($0.10 > p > 0.05$) and could potentially achieve significance with a larger sample size. Four species displayed no recognizable difference among microhabitat treatments.

Microhabitat Preference of Individual Species

When interpreting the preference of species by microhabitat, affinities are complex and best treated case by case (Fig. 8.2b–f). First considering species most important on the Horizontal treatment, *Callopora dumerilii* is common throughout, but is most important on the Upper Level of the Horizontal microhabitat (Fig. 8.2d). *Escharina vulgaris* is restricted to the Middle and Lower Levels of the Horizontal microhabitat (Fig. 8.2d). *Tubulipora plumosa* is restricted to the Horizontal microhabitat and is most abundant on the Lower Level. *Aetea truncata, Chorizopora brongniartii*, and *Fenestrulina malusii* are present in all microhabitats, but are most abundant on the Texture and Lower Horizontal microhabitats (Fig. 8.2d). The strongest preference was shown for several species limited or nearly limited to the Strings (Fig. 8.2e). *Turbicellepora camera* and *Cellaria fistulosa* were observed in other microhabitats outside of the study grids but nowhere as abundant as on Strings. *Bugula fulva* was rare ($n = 5$), but was observed exclusively in the String and Texture microhabitats. *Buskia nitida* was also rare ($n = 4$), and all observed colonies were well developed and found exclusively on Strings. No specimens of *Buskia nitida* were observed in natural microhabitats beyond the scope of the study grid either.

Two species that were preferentially abundant in the String microhabitat were also associated with a second treatment (Fig. 8.2e). *Nolella dilatata* formed extensive mats of runners in both String and Texture microhabitats. *Schizobrachiella sanguinea* formed large hollow conical colonies centered on Strings but in contrast formed large encrusting disks in Vertical (smooth) microhabitat.

The most evenly distributed species among microhabitats were *Crisia* spp., *Schizomavella linearis*, and *Tubulipora liliacea* (Fig. 8.2f). Other widely distributed species that showed slight preferences for a microhabitat(s) included: *Microporella ciliata* (Vertical and Upper Horizontal), *Plagioecia patina* (Strings and Middle & Lower Horizontal), and *Schizoporella dunkeri* (Middle & Lower Horizontal).

Discussion

The question addressed in this study was: Given a range of textural complexities (flat plates, corrugated plates, woven strings) and orientations (horizontal or vertical plates, omnidirectional string surfaces), is there an apparent difference in microhabitat specificity among the bryozoans recruited onto the different microhabitats? Results suggest (but do not directly test) the idea that an increase in the number of kinds of microhabitats within a local environment (in this study <1 m^3), will result in an increase in species richness and individual occurrences relative to an equal area of uniform microhabitat.

The fact that the species list and general abundance did not differ significantly between apparatuses (Fig. 8.2b), suggests that there was no difference in bryozoan recruitment between A and B, i.e. equivalent sampling from a common larval pool. The slightly greater number of occurrences on Apparatus B (Fig. 8.2b and Table 8.1) suggests more favourable conditions for colony growth (size) rather than absolute colony number.

Species Richness Among Microhabitats

Species richness was relatively constant among the microhabitats (average of 16.7); only about two-thirds of the total number of species observed (25) was present in any given microhabitat. Thus, although diversity is relatively constant, the combination of species present within microhabitats varies. This suggests some level of selection (preferences or differential survival) at the microhabitat level. The presence of many species within and among many microhabitats suggests that larvae had an equal chance of encountering any of the microhabitat treatments. That is, no "hot zones" or "dead zones" of overall settlement frequency were observed within or between apparatuses.

Clearly some but not all species have better success in certain microhabitats than others. That is, not every species has a preferred microhabitat. In addition, some 36-cell patches within one microhabitat are more similar in species composition to patches in other microhabitats than other regions of the same microhabitat. This means that either unobserved environmental conditions control these distributions, or more likely, that controls and preferences are loose enough at this scale that strict boundaries between species compositions are not established.

Regardless of the controlling ecological factors, it is evident that microhabitat variation does have *some* influence in the distributions and abundance of bryozoan species in a community in an early stage of development (<1.2 year).

In this study, the total species richness is not a simple function of the area of substrate sampled. The number of kinds of substrate sampled (microhabitats) plays an important role in determining the over all species richness (Fig. 8.2a, Table 8.1).

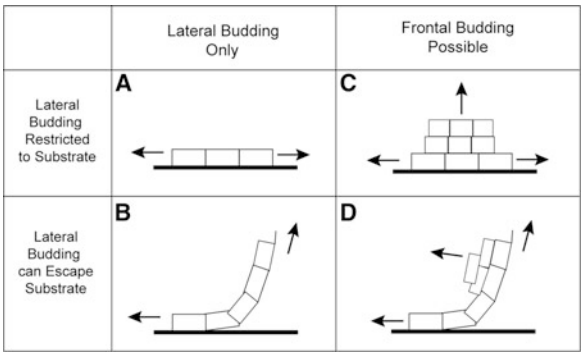

Fig. 8.3 Four primary growth habit characteristics associated with microhabitat preference defined by combinations of restricted and non-restricted lateral and frontal budding. Type-A was found only rarely in the String microhabitat, but was common in the horizontal and vertical microhabitats. Type-C was rare in the horizontal and vertical habitats, but common to abundant in the String microhabitat. Types-B and D were common to abundant in all microhabitats

Distribution of Growth Habit Characters Among Microhabitats

The most abundant species in the study were "weedy" cyclostomes (*Crisia* spp., *Tubulipora liliacea*, *Plagioecia patina)* and gynmolaemates (*Aetea truncata*, *Nolella dilata*) and were widely distributed. However, many taxa exhibited growth habit attributes that were relatively informative about microhabitat preferences. Some of the more obvious patterns were:

1. Frontal budding (*Celleporina caminata*, *Turbicellepora camera*) – much better represented on Strings; present but not abundant elsewhere.
2. Rhizoidal attachments (*Bugula fulva, Cellaria fistulosa,* but not *Crisia* spp.) – much more abundant on Strings; present but less common elsewhere.
3. Encrusting sheets with multizooidal budding zone that can escape substrate (*Schizomavella linearis, Plagioecia patina*, *Schizobrachiella sanguinea*) – prominent on Strings; common on other microhabitats. *S. sanguinea* is the only species that exhibited two growth habits, encrusting on flat substrates but forming large, hollow, conical colonies on Strings.
4. Encrusters with growing edge restricted to substrate (*Callopora dumerilii, Chorizopora brongniartii, Escharina vulgaris, Fenestrulina malusii, Hippothoa flagellum, Microporella ciliata, Schizomavella subsolana, Schizoporella dunkeri*, *Schizoporella magnifica*) – rare on Strings.
5. Runners (*Aetea sica, Aetea truncata*, *Nolella dilatata)* – most abundant on String and Texture microenvironmets and on Lower levels, but present throughout.

In summary, the greatest contrast in growth habit attributes among microhabitats is between Strings, favorable to bryozoan species with some attribute that allows some degree of escape from the substrate (Fig. 8.3 Types-B, C and D), and the less flexible broader microhabitats, favored by encrusting species with the growing edge

restricted to the substrate (Fig. 8.3 Type-A). Thus, morphological characters related to interaction with the substrate, such as multizooidal budding (Lidgard and Jackson 1989), rhizoid attachments and those that allow for upward growth, such as frontal budding and budding zones raised from the substrate (Lidgard and Jackson 1989), may be of more ecological importance for determining growth habit disparity than selection on other characters (Fig. 8.3).

Our understanding of broader environmental and phylogenetic controls on the distribution of bryozoan colonial growth habits remains incomplete. However, the methods employed in this study, potentially with more simplified designs, performed in a wide range of settings, promise insights into controls over local species richness and morphological disparity.

Acknowledgements We thank M. Novosel and A. Novosel for their help and advice in acquiring materials for constructing the experimental apparatuses. This research was supported by a Fulbright Research Fellowship to SJH, and the University Research Council of Appalachian State University.

References

Barnes DKA, Dick MH (2000) Overgrowth competition in encrusting bryozoan assemblages of the intertidal and infralittoral zones of Alaska. Mar Biol 136:813–822

Burgess SC, Hart SP, Marshall DJ (2009) Pre-settlement behavior in larval bryozoans: the roles of larval age and size. Biol Bull 216:344–354

Dobretsov S, Qian P-Y (2006) Facilitation and inhibition of larval attachment of the bryozoan *Bugula neritina* in association with mono-species and multi-species biofilms. J Exp Mar Biol Ecol 333:263–274

Hammer O (2010) PAST, PAleontological STatistics version 2.01 reference manual. Natural History Museum, University of Oslo

Hayward PJ, McKinney FK (2002) Northern Adriatic Bryozoa from the vicinity of Rovinj, Croatia. Bull Am Mus Nat Hist 270:1–139

Lidgard S (2008) Predation on marine bryozoan colonies: taxa, traits and trophic groups. Mar Ecol Prog Ser 359:117–131

Lidgard S, Jackson JBC (1989) Growth in encrusting cheilostome bryozoans. Paleobiology 15:255–282

Mariani S, Alcoverro T et al (2005) Early life histories in the bryozoan *Schizobrachiella sanguinea*: a case study. Mar Biol 147:735–745

Pemberton AJ, Hansson LJ et al (2007) Microscale genetic differentiation in a sessile invertebrate with cloned larvae: investigating the role of polyembryony. Mar Biol 153:71–82

Ryland J (1977) Taxes and tropisms of bryozoans. In: Woollacott RM, Zimmer RL (eds) Biology of bryozoans. Academic, New York

Sanders H (1968) Marine benthic diversity: a comparative study. Am Nat 102:243–282

Stach LW (1936) Correlation of zoarial form with habitat. J Geol 44:60–65

Sutherland J, Karlson R (1977) Development and stability of the fouling community at Beaufort, North Carolina. Ecol Monogr 47:425–446