CURRENT-RELATED MORPHOLOGY AND BEHAVIOUR IN SOME PACIFIC COAST BRYOZOANS

Judith E. Winston

Department of Earth and Planetary Sciences,
The Johns Hopkins University,
Baltimore, Md. 21218

and

Discovery Bay Marine Laboratory,
P.O. Box 35, Discovery Bay, Jamaica, W.I.

ABSTRACT

Qualitative and quantitative observations on 24 species of marine bryozoans from southern California have a variety of morphological and behavioural adaptations related to feeding activities in a variety of growth forms, including massive branching, bilaminar, and reteporiform. A high degree of correlation exists between skeletal and soft-part morphology; behavioural characters are not as closely linked to morphology. Feeding behaviour in the various species ranges from passive filtration by individual polypides to highly patterned behaviour in which polypides cooperate to generate colony-wide current patterns and to remove various sizes of waste materials.

INTRODUCTION

Adaptations of morphology, orientation of feeding organs, and active behavioural mechanisms enable suspension-feeders to interact with the surrounding water currents for effective feeding. Suspension-feeders can be split into two categories: passive feeders, which rely on external water flow to move water through their filtering organs, and active feeders which have some means of forcing water through the filtering organs (Jørgensen, 1966).

The dichotomy between active and passive suspension feeders may not be complete, as LaBarbera (1977) points out. Active suspension feeders sometimes make use of hydrodynamic effects to take the place of active pumping. This is seen in solitary animals such as balanoid barnacles which filter actively at low current speeds but extend their cirri as passive fans at higher speeds (Crisp and

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Southward, 1961). Articulate brachiopods (LaBarbera,1977) can orientate their shells so that ambient currents augment the ciliary flow through the lophophore.

Studies on responses of colonial organisms are fewer. Vogel (1974) has shown that even models of sponges in moving water will pump water in one direction and that living sponges make use of ambient currents to increase water flow to their bodies. Chamberlain and Graus (1975) have examined ways in which various parameters of branching interact with currents to pattern flow through coral colonies.

The production of feeding currents by marine bryozoans and patterning of these currents have come under investigation only recently. Banta, McKinney and Zimmer (1974) were the first to point out the importance of colony-wide excurrents. Cook (1977) reported observations on colony-wide currents in 16 species of bryozoans from the North Atlantic and the Mediterranean.

The present author has described patterns in morphology and feeding behaviour of individuals and colonies for 56 species from Florida and Panama (Winston, 1978).

These studies have shown the following: (1) In species having individualized behaviour and widely separated or uniserial zooids (e.g. Aetea sp., Aeverrillia armata, Bowerbankia spp, Crisia sp., Beania intermedia, Sundanella sibogae) colony currents are weak or non-existent (Cook, 1977; Winston, 1978). (2) In erect species with a unilaminar colony structure (e.g. Bugula stolonifera, B. neritina, B. turrita, Caulibugula dendrograpta, C. pearsei, Reteporellina evelinae, Sertella sp.) strong and unrestricted unidirectional water flow is maintained allowing lophophores maximum access to suspended food particles (Cook, 1977; Winston, 1978). (3) In some encrusting forms (e.g. Conopeum seurati, C. tenuissimum, Membranipora tenuis, M. arborescens, Alcyonidium polyoum, A. polypylum) currents may be augmented by lophophore clustering and relatively unpatterned turbulent flow created (Winston, 1978). (4) However, in most encrusting forms unrestricted continuous water flow through the lophophores of the colony appears to require separation of incurrents and excurrents by polypide position and activity alone or by polypide positioning in conjunction with skeletal patterning.

Massive branching and bilaminar colonies are also common among marine bryozoans, but their feeding and current patterns have not been described until now. The work reported here, a continuation of the study of Winston (1978) is based on data for 24 species from intertidal and subtidal environments around Monterey, California. Observations were made to obtain information on more species in general and specifically to discover types of behaviour and current patterns present in massive branching and bilaminar forms.

MATERIALS AND METHODS

Specimens from intertidal and subtidal environments in the Monterey area were maintained in running seawater until they could be observed and photographed (usually within a few hours of collection). Observations were made of feeding on natural particles in the water. In addition, cultured phytoplankton were added to stimulate feeding activity. Carmine particles and plastic beads (1-30 μ m in diameter) were used to study rejection mechanisms.

Morphological parameters measured correspond with those made in the previous study: skeletal characters (including length and width of zooid, length and width of orifice), polypide characters (including tentacle length, tentacle number, tentacle width, lophophore diameter, and mouth size), and where possible, colony characters (including length and width of incurrent cells and channels and excurrent chimneys). Measurements were made on 5-10 individuals from one or two colonies and figures given in Table 1 represent mean values for each species.

Observations were made for each species on polypide morphology: lophophore shape (equi-tentacled, obliquely truncate, scalloped or campylonemidan, homomorphic or heteromorphic) mouth shape (round, ovoid, elongate, horseshoe shape); and introvert length (short, medium, long).

Behavioural observations were made concurrently on the same colony or colonies. Individual (polypide) behaviour patterns were analysed: type of scanning behaviour (multidirectional, vertical, lateral, none); individual actions (see key to Table 2); and overall level of activity. Emphasis was placed on analysis of colony-level behaviour, particularly the strength and type of colony currents produced and the general level of behavioural integration. Currents were traced with fluorescein dye, photoplankton particles, carmine particles or plastic beads, injected with a micropipette into the water adjacent to the colony.

Patterns of colony morphology and behaviour are described as previously by Types: (I) polypide behaviour individualized, (II) polypides separated and their orientation controlled by skeletal structure of the colony, (III) polypides forming temporary clusters, (IV) polypides forming fixed clusters unreflected by skeletal morphology, (V) polypides forming fixed clusters enhanced by irregular patterning of the colony skeleton, and (VI) polypides forming fixed clusters enhanced by a regular patterning of the colony skeleton. Again, it must be stressed that these categories are intended only to describe functional differences in behaviour. They are not mutually exclusive and more than one pattern may occur in a colony or a species.

RESULTS

A summary of morphological characteristics for each species studied is given in Table 1. Individual and colony behavioural characteristics are summarized in Table 2. As the main purpose of this study was to obtain information on erect growth forms (especially massive branching and bilaminar forms uncommon in the environments previously studied) the results are organized to (1) present patterns occurring in these forms and (2) give descriptions of encrusting forms encountered with emphasis on some new behaviour was noted.

Description of Erect Branching Forms

Species Characterized by Type I and II Patterns

Individualized behaviour patterns occurred in those forms in which polypides were well separated from each other by behavioural mechanisms and/or colony structure. For example, in *Filicrisia* sp., where polypides are separated by filamentous colony design, actions of one polypide have very little effect on the actions of another. In contrast to *Filicrisia* the more compactly designed colony of *Crisia serrulata* (Fig. 1*a*) functions much like a *Bugula* or reteporid colony - creating a directional current which impinges on polypide-covered surfaces and passes through the spaces between the branches. As the illustration shows, positioning of the tubes causes adjacent polypides on a branch to be directed away from each other and toward the polypides of the adjacent branches. The polypides (paralleling the direction of the orifice spines) are orientated at about a 60° angle into the branch spaces with the two bent-away tentacles opposite the orifice spine. Reteporid polypides, which also have campylonemidan lophophores, have a similar orientation into the branch spaces; the combination is most effective in creating a strong current through the branches.

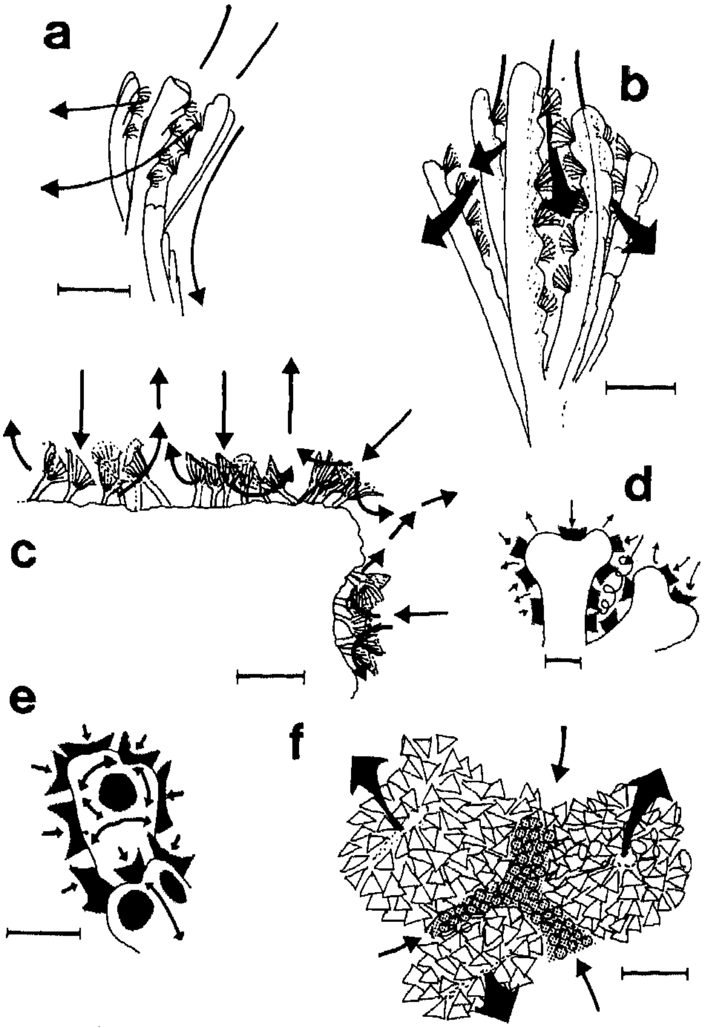

Figure 1. Current patterns in branching colonies. (a) *Crisia serrulata*. Unidirectional flow through branches. (b) *Scrupocellaria diegensis*. Currents through branch segment. Lophophores on a branch are directed away from each other and toward those of adjacent branches. (c) *Hippothoa hyalina* (erect growth form). Portion of a branch showing current directions and orientation of polypides. (d) *Hippothoa hyalina* (erect growth form). Two branches with current directions and position of lophophore clusters marked. Note excurrents at growing tips, incurrents in hollows and between branches and turbulent flow pattern between branches. (e) *Celleporina robertsoniae*. Branch with incurrent cells (shaded areas) and channels (double-ended arrows) marked. (f) *Celleporaria brunnea*. Three branches showing position of current channels (small arrows) and excurrent grooves (large arrows). ((a), (b), (c) Scale = 1mm, (d), (e) Scale = 5mm, (f) Scale = 3mm).

In *Scrupocellaria diegensis* (Fig. 1*b*), also, expanded lophophores are directed toward those of the adjacent branches so that the branch spaces are filled by tentacle Lophophores of this species are obliquely truncate, but not campylonemidan. Viewed from the distal end, the lophophore-bearing surfaces of the colony face in and branches form semi-circles rather than planar fans, yet the water current passes only once through the colony.

The unidirectional current pattern (Type II) was most strongly demonstrated in this study by *Scrupocellaria diegensis* and *Phidolopora pacifica*. *Phidolopora* is a branching fenestrate reteporid whose colonies form rigid lacy masses. In the still water of the laboratory container addition of carmine particles made visible a distinct pattern of channeling and reworking of water, but the effect of such a pattern in moving water is not known The most characteristic behaviour of polypides of this species is a bending or whipping out of the anal tentacle either singly or consecutively. This action can be used to directly reject a particle, and (since it was observed when no particles were being rejected) may also serve to increase the efficiency of water passage through the colony. The activity occurs most frequently in polypides near the tips of branches and may help pump currents through the branch spaces. As in *Reteporellina evelinae* (Winston, 1978) unified retraction of a group of polypide is used to clear branch spaces of large particles.

Species Characterized by Type III, IV and V Patterns

Other erect forms showed three basic patterns.

The occurrence of small encrusting colonies of *Hippothoa hyalina* on algae and large branching colonies rooted hard substrata provided an example of range in behaviour a morphological parameters in a species with a variable growth form. It also indicated some of the problems of attempting such studies with colonial animals - in which astogenetic as well as ontogenetic and environmentally produced differences must be considered. As Table 1 show dimensions of morphological characters measured (length o embedded zooids of the erect colonies could not be obtained) are greater for the zooids of the erect colonies, e.g. polypides have lophophores averaging 509 µm (vs. 349µ m) and an average of 14 tentacles (vs. 11). The average mouth size is doubled (from 23-46µ m), and the shape of the mouth changes from round to ovoid. Parameters of individual behaviour are almost identical; patterns of colony behaviour are somewhat altered.

Colony behaviour in the small encrusting colonies is probably best described as being of the temporary cluster (Type III) variety. Polypides can scan to form clusters (which have a longer duration than those of some other Type III species). Clusters may be repeated by the same polypides after retraction, but are not distinctly "fixed". In the erect colonies polypides also scan and lie horixontally on their introverts to make very small and more or less fixed clusters approximating Type IV (Fig. 1c). However, bending and scanning by polypides remains more important in cluster formation than in most Type IV colonies. Fig. 1d shows the current patterns observed. At the growing tips of branches there are usually no functional polypides, and these tips mark excurrent areas. Incurrents can be seen in hollows of branch tip bifurcations and at the entrance to branch spaces. In the laboratory the flow in areas between adjacent branches is turbulent rather than unidirectional, and rejected particles are shuttled back and forth between the branches. Incurrent cells are separated by fairly large excurrent areas; cells on opposing branches, however, are not offset in any distinct pattern. The result is that particles are processed by being carried or bounced back and forth in the eddies between the branches (Fig.1d). In this case colony structure and polypide activity produce areas of turbulence around the branches rather than a directional pattern of flow through the colony.

Celleporina robertsoniae is another species with an erect irregularly branching colony form. In Celleporina, however, the colony current pattern is Type V, with polypides forming fixed cells and channels that follow and exaggerate the zooecial contours of the branches. Sections of two branches of a colony with positioning of incurrent cells and channels is illustrated by fig. 1e. Unlike the polypides of Hippothoa, those of Celleporina seldom change orientation except for a slight amount of lateral scanning or waving. Lophophores are more strongly heteromorphic, ranging from equi-tentacled (at center of incurrent cells or bases of channels) to scalloped and extremely obliquely truncate. The introvert is short, about level with the top of the peristome, except in the polypides with the most unequal tentacles (bordering excurrents).

Celleporaria brunnea provides a contrast in polypide activity. Colonies of this species usually consist of an encrusting base with irregular nodular or stout branch-like protuberances. Fig. 1f shows a portion (three branches) of a Celleporaria colony with current patterns indicated. The surface of the colony produces irregularly structured channels and raised areas. When lophophores are expanded there is a modified Type V pattern consisting of current channels through the branches, though on a large branch incurrent cells about 3 mm in diameter also occur. A branch may be divided by an excurrent chimney (often a long groove) which is not reflected in a raised area of the skeleton, but which serves to divide polypides in one channel from those in another. At the tip of a branch there is usually a budding zone which forms an excurrent chimney or groove. Smaller more equi-tentacled polypides occur in channels while those with the most assymmetrical lophophores are found at the edge of branches and overhanging the channels. Addition of carmine particles showed no unidirectional path in the current channels. However, rejection of these inorganic particles may have created more turbulence than normal. The characteristic behaviour of polypides is a combination aversion retraction (partial retraction of lophophore) and writhing (snake-like curling and uncurling of tentacles). This activity may affect one zooid or a whole group and it occurs constantly. Polypides of this species also perform much limited multidirectional scanning. Individuals are so close together that edges of the tentacles touch or overlap, and scanning by one individual causes neighbours to sway. Polypides can capture prey by making a cage of the tentacle crown, though in this species the cage is very narrow, with only the bottom half closed and the upper halves of the tentacles bent out at right angles.

Description of Bilaminar Forms

Colonies of Hippoporina insculpta consist of bilaminar frills or plates arising from an encrusting base. On a flat colony surface polypides form clusters (Type IV) with incurrent cells about 2.2 mm in diameter. In areas where the skeleton flexes in, for example between branches, there are channels approximately equal in cross-section to the incurrent cells (Fig. 2a). In addition, when only a few polypides are expanded, they orientate to form temporary clusters. When most polypides are expanded they generally keep a fixed orientation, but cage capture of small protozoans occurs.

The ctenostome Pherusella brevituba has a similar colony morphology, with encrusting bases, often developing into flattened leathery lobes. In side view incurrent cells can be distinguished, cells are shallow because

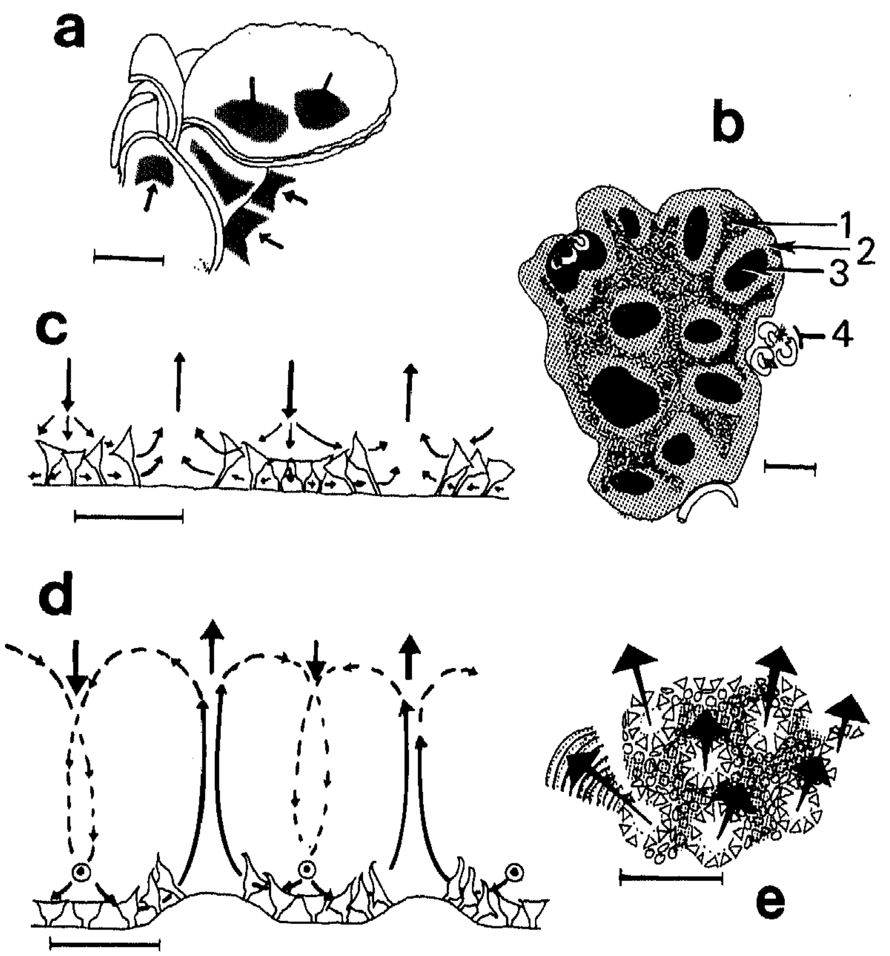

Figure 2. Caption on page 256.

Figure 2. (Caption)
Current patterns in bilaminar and encrusting colonies. (a) Hippoporina insculpta. Bilaminar branches with some incurrent cells and channels marked. (b) Cauloramphus spiniferum. Portion of colony showing channels with equitentacled lophophores at base (1), angled lophophores surrounding chimneys (2), and excurrent chimneys (3) giving "pseudosponge" effect. (4) is a cluster of serpulids. (c) Cauloramphus spiniferum. Incurrents, excurrents, lophophore clusters and chimneys in side view. (d) Porella porifera. In side view. Excurrent chimneys bare of polypides and usually with raised surface. Water flow helical in laboratory. (e) Porella porifera viewed from above, showing incurrent channels and excurrent chimneys, one with puffs of fluorescein dye (a),(b),(c),(d) scale = 2mm, (e) scale = 5mm).

their outer polypides are not strongly heteromorphic, although a few have slightly scalloped obliquely truncate lophophores. There are no wide demarcations (excurrent zones) between incurrent cells. Like Flustrellidra hispida (Winston, 1977) polypides of Pherusella can reject large particles by flattening the lophophore almost completely, but the most typical behaviour carried out by individuals is a constant slight multidirectional scanning.

Description of Encrusting Forms

Colony patterns in encrusting species ranged from Type III to Type V.

Colonies of Eurystomella bilabiata have a pattern intermediate between Type III and Type IV. Polypides have very long introverts which bend to scan and orientate the lophophores. Unlike Type III colonies, described in the previous study (Winston,1978), polypides of Eurystomella are not constantly being extruded from and retracted into the zooid. Polypides do not change their orientation frequently as long as the culture dish contains only seawater. However, the behaviour of this species changes radically when food is added. Polypides continually flick tentacles and puff away pieces of debris, but when food (cultured Nitschia and Platymonas) is added polypides perform frenetic tentacle flicking and cage-making activity. Large masses of Platymonas (Fig. 3a) are (1) grasped by tentacles, each moving individually in a snake-like motion resembling the tentacle action of a feeding sea anemone, (2) pulled into the lophophore where gulping actions of the pharynx can be seen, while the tentacles (3) form a cage with tentacle ends twisted around the mass. A mass which does not move is uncaged fairly rapidly and (4) remains at the base of the lophophore until ingested, or if too large to be ingested, is finally puffed away.

In contrast to most of the encrusting species previously observed (Winston, 1978) a number of Type IV and V encrusting species in this study had very large excurrent chimneys. To the naked eye the fuzzy bright-coloured surface formed by the expanded lophophores made these colonies resemble sponges - the excurrents being the "oscula".

Cauloramphus spiniferum (Fig.2*b*, 2*c*) and *Porella porifera* are two such "pseudo-sponges". Cross-colony channels are formed by polypides with equi-tentacled lophophores, while those with increasingly more obliquely truncate lophophores make up the angled sides of the chimneys (Fig. 2*c*). In *Cauloramphus* these chimneys are variable in size, (averaging 1.2 mm) and incurrent channels are of similar dimensions. Excurrent chimneys are bare of polypides and usually, but not always, raised above the surrounding surface. Some raised areas are formed by the colony skeleton, but most appear to be caused by the topography of the substratum beneath (e.g. the colony overgrowing small barnacles or serpulids. Also, in *P. porifera* chimneys are lined by polypides with extremely long tentacles which bend in toward the channels (Fig. 2*d*). These polypides move their anal tentacles out into the excurrent chimneys to reject particles. Injection of fluorescein dye near the colony soon resulted in little puffs of dye exiting from each chimney (Fig. 2*e*). Plastic beads were caught in the strong eddies created in this way and clogged the lophophores until they were released by puffing.

Both *Cauloramphus* and *Jullienula hippocrepis* possess a unique method of rejection of large particles (fecal pellets, debris, etc.), involving coordinated polypide action. In *Cauloramphus*, as illustrated by Fig. 3*b*, (1) a large particle enters the lophophore of a polypide which (2) makes a cage around it with the tentacles and then (3) keeping it in the cage, bends the introvert and ejects it into the next (chimney-ward) lophophore. (4) The process continues until the particle reaches the polypide bordering the chimney. (5) That polypide jerks backward and releases the particle into the chimney where it is ejected from the colony.

Jullienula hippocrepis is a third species with large excurrent chimneys. Chimneys occur on the flat surface of the colony or on projections due to the irregularity

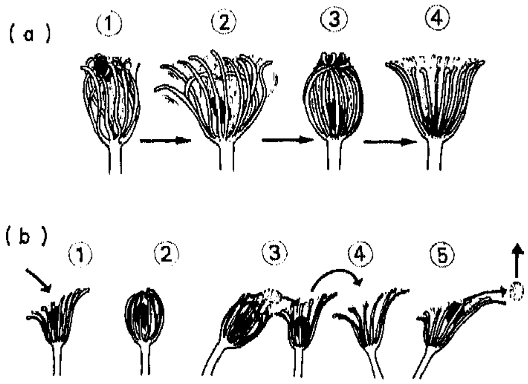

Figure 3. Behavioural sequences in two encrusting species. (a) *Eurystomella bilabiata*. Feeding sequence. (1) Masses of *Platymonas* and debris are caught by writhing tentacles, and (2) pulled into the lophophore. (3) Lophophore forms a cage (with distal ends of tentacles twisted) around the mass. (4) Non-motile mass rapidly uncaged and remains at base of lophophore until ingested. (b) *Cauloramphus spiniferum*. Rejection of a large particle. (1) Unwanted particle enters a lophophore. (2) Tentacles form cage around particle. (3) With particle still encaged lophophore jerks chimney-ward. Cage opens and particle is transferred to next lophophore. (4) Action is repeated until particle reaches lophophore bordering an excurrent chimney. (5) This lophophore bends backward over chimney releasing particle into excurrent where it is ejected from the colony.

of the surface beneath the colony. Channels average about 3.5 mm and chimneys about 1.7 mm, but they are not very uniform. In *Jullienula* polypides also form lophophore cages around fecal pellets or debris particles, and the particles are carried from lophophore to lophophore. The manoeuvre is not as efficient as in *Cauloramphus* as polypides do not bend over to transfer particles, but chimney-border polypides jerk backward to release particles into chimneys. In *Jullienula*, smaller particles ejected at the lophophore base are carried along by currents moving at the introvert level and eventually ejected into chimneys.

Such complex rejection mechanisms may be common in large-chimneyed species, but they do not always occur. For example, polypides of *Membranipora membranacea*, the first species of this type to be described (Banta, McKinney and Zimmer, 1974) is much less selective. This species will ingest 1-30μ m plastic beads, caging them in groups of six or so, or using the tentacles to knock them directly into the pharynx. In this species the type of group rejection described above has not been observed.

DISCUSSION

The results presented above as well as recent work by Cook (1977) and the present author (Winston, 1978) indicate the ubiquity of current-producing activities by bryozoans. In order to assess the significance of the current that bryozoans produce in natural situations it is necessary to take into account both the relative scale and actual size of bryozoans and the currents they produce. For example, erect branching bryozoan colonies might be compared with branching coral colonies. Chamberlain and Graus (1975) found that flow through the interiors of branching coral colonies was due entirely to interactions between outside hydrological conditions and colony morphology. Their field studies demonstrated no individual or joint polyp activity capable of influencing the currents passing through the colony.

Rigid branching bryozoan colonies (e.g. Celleporina robertsoniae and Hippothoa hyalina) strongly resemble miniature versions of branching corals, yet there are two reasons why their relationships with water currents may be quite different. First, lophophores of bryozoan colonies are actively producing currents, and the large size of the lophophores relative to branches makes it more likely that their activities will influence flow through the colony. Second, the small size of bryozoan colonies, a few millimeters to centimeters (versus several centimeters to a meter or more for corals), means that even in open water situations bryozoan colonies face a current regime different from that of corals.

One of the functions of the current patterns exhibited by branching colonies is to create turbulence. In order to entrain food particles all these bryozoans must have some method of changing water flow as it passes over the colony. Colonies of species living in high energy environments (e.g. Phidolopora or erect Hippothoa from shallow subtidal habitats) must act to slow the water flow and change it from laminar to turbulent. For colonies of species inhabiting relatively still water (e.g. Celleporaria brunnea from the undersurfaces of floating docks in the marina) efficient functioning requires creation of turbulence and flow through the colony. What looks like excessive reworking of water, the helical or whirlpool

Table 1. Morphological Characteristics of Marine Byrozoans from Monterey, California

	A	B	C	D	E	F	G	H	I	J	K	L	M	N
CHEILOSTOMES														
1.	551	398	102	192	17	595	460	584	SOT	CO	14	49	RO	L
2.	468	278	73	103	16	579	547	520	SOT	CO	18	32	R	L
3.	444	346	93	164	14	555	355	595	SOT	CO	14	49	ET	L
4.	415	248	96	133	13	342	342	379	ET	S	11	25	R	M
5.	588	369	122	167	17	1012	630	994	SSc	CO	27	58	H	M
6.	606	408	126	131	14	650	415	575	SSc	CO	14	47	R,O	S,M
7.	1411	684	178	245	19	1094	1094	1044	ET	S	18	91	H	S
8.	628	435	217	268	22	706	706	730	ET	CO	16	86	ET	L
9.	546	334	166	190	20	642	547	643	SOT	CO	14	47	ET	L
10.	417	187	107	93	11	349	311	386	SOT	CO	11	23	R	M
11.	---	171	116	119	14	509	440	544	SOT	CO	18	46	RO	L
12.	624	382	187	206	18	739	555	797	SOT	CO	14	49	RO	L
13.	929	490	180	147	18	744	744	704	ET	S,CO	23	55	RO	M
14.	680	294	99	153	14	383	357	440	SOT	S	18	35	R	M
15.	683	408	106	142	16	662	531	632	SSc	CO	18	44	RO	M
16.	521	313	116	107	12	661	309	566	SSc	CO	18	26	R	S
17.	533	191	131	104	12	632	390	593	BT	VC	18	46	RO	S
18.	433	313	102	122	14	673	357	733	SSc	CO	18	36	RO	S
19.	400	304	109	122	12	677	335	555	SSc	CO	18	34	RO	M
20.	448	269	76	127	16	528	340	577	AOT	CO	14	44	RO	S
21.	528	206	---	105	12	374	299	374	AOT	VC	14	35	RO	S
CTENOSTOMES														
22.	907	518	248	342	26	760	760	950	AOT	CO	18	102	ET	L
CYCLOSTOMES														
23.	652	116	89	73	8	273	273	335	ET,BT	VC	11	17	R	N
24.	592	122	78	89	9	186	186	273	ET	S	9	18	R	N
25.	972	166	167	131	11	564	247	433	BT	VC	14	28	R	N

KEY TO TABLE 1.

CHEILOSTOMES
1. *Aplousina* sp.
2. *Callopora circumclathrata*
3. *Cauloramphus spiniferum*
4. *Cellaria mandibulata*
5. *Celleporaria brunnea*
6. *Celleporina robertsoniae*
7. *Coleopora gigantea*
8. *Eurystomella bilabiata*
9. *Hippoporina insculpta*
10. *Hippothoa hyalina* (encrusting)
11. *Hippothoa hyalina* (erect)
12. *Jullienula hippocrepis*
13. *Lagenicella punctulata*
14. *Membranipora membranacea*
15. *Microporella californica*
16. *Parasmittina collifera*
17. *Phidolopora pacifica*
18. *Porella porifera*
19. *Rhynchozoon rostratum*
20. *Scrupocellaria diegensis*
21. *Tricellaria occidentalis*

CTENOSTOMES
22. *Pherusella brevituba*

CYCLOSTOMES
23. *Crisia serrulata*
24. *Filicrisia* sp.
25. *Tubulipora* sp.

ZOOID MORPHOLOGY
A. Mean Zooid Length µ m
B. Mean Zooid Width µ m
C. Mean Orifice Length u m
D. Mean Orifice Width µ m

POLYPIDE MORPHOLOGY
E. Mean Tentacle Number
F. Mean Tentacle Length (Long) µ m
G. Mean Tentacle Length (Short) µ m
H. Mean Lophophore Diameter µ m
I. Lophophore Shape
J. Tentacle Curvature
K. Mean Tentacle Width µ m
L. Mean Mouth Diameter µ m
M. Mouth Shape
N. Introvert Length

Lophophore Shape: ET = equi-tentacled, SOT = some polypides with obliquely truncate lophophores, AOT = all polypides with obliquely truncate lophophores, SSc = some polypides with scalloped lophophores, BT = bent-tentacled (campylonemidan) lophophores. Tentacle Curvature:S = all tentacles held straight, CO = ends of tentacles curve out, VC = tentacles variously oriented. Mouth Shape:R = round, RO = round to ovoid, ET = elongate to triangular, H = horseshoe-shaped. Introvert Length: N = none, S = short, M = medium, L = long.

Table 2. Behavioural Characteristics of Marine Bryozoans from Monterey, California.

	A	B	C	D	E	F	G	H	I
CHEILOSTOMES									
1.	A	F,MC	MS	III	M	0	0	6	Encrusting
2.	A	F,MC	LS	IV	S	0	0	6	Encrusting
3.	H	MC	LS	IV	S	-	1.2	-	Pseudosponge
4.	M	AvR	MS	II*,III	M	0	0	2-4	Adjacent polys. form temp. clusters
5.	H	MC,CC,AvR,W	LS	V	S	3.1(C)	-	-	Char.by combination of AvR and W
6.	L	O	LS	V	S	-	-	-	Thick but irreg. shaped branches
7.	A	MC,AvR,FLD	MS	I,III	M	2.8(C)	-	4	Peristms.aligned behav.individual.
8.	H	F,MC,CC,W	MS	III	S	1.9(C)	-	6	Food capt.with violent tentcl.act.
9.	M	MC,CC	LS	III,IV*,V	S	2.2(C)	-	20	Bilaminate frills
10.	M	F	MS	III	M	1.0(C)	-	4	Encrusting
11.	M	O	MS	III,IV	M	2.3(C)	-	16	Erect branching
12.	A	F,MC,FLD	LS	IV	S	3.5(CH)	1.7	-	Pseudosponge
13.	L	AvR	MS	II	W	0	0	0	Polys.well sep., behv.individual.
14.	M	MC,CC	LS	IV	S	2.1(C)	0.8	9	Encrusting
15.	M	F	LS*,MS	III	M	1.8(C)	-	4.4	Encrusting
16.	A	O	O	V	S	-	-	-	Large excurrents
17.	A	Mc,AvR,W	O	II	S	0	0	0	Polys.whip anal tentacls.outward.
18.	H	O	O,VS	IV,V	S	1.7(C)	1.7	-	Pseudosponge
19.	H	O	O	V	S	2.3(C)	1.1	-	Both in- & ex-currents sharply defined.
20.	M	F,AvR	VS	II	S	0	0	0	Bnchs.form funnel not strgt fan.
21.	M	MC,AvR	VS	II	M	0	0	0	Unilaminar branching.
CTENOSTOMES									
22.	M	MC,FLD	MS	I,IV*	M	3.8	-	22	In & ex-currents not sharply defd.
CYCLOSTOMES									
23.	M	O	O	II	W	0	0	0	Current weak but undirectional
24.	L	O	O	II	W	0	0	0	Very passive
25.	M	MC	O	V	S	-	-	-	Campylonemidan Lophophore directs current in at an angle.

KEY TO TABLE 2

CHEILOSTOMES
1. *Aplousina* sp.
2. *Callopora circumclathrata*
3. *Cauloramphus spiniferum*
4. *Cellaria mandibulata*
5. *Celleporaria brunnea*
6. *Celleporina robertsoniae*
7. *Coleopora gigantea*
8. *Eurystomella bilabiata*
9. *Hippoporina insculpta*
10. *Hippothoa hyalina* (encrusting)
11. *Hippothoa hyalina* (erect)
12. *Jullienula hippocrepis*
13. *Lagenicella punctulata*
14. *Membranipora membranacea*
15. *Microporella californica*
16. *Parasmittina collifera*
17. *Phidolopora pacifica*
18. *Porella porifera*
19. *Rhynchozoon rostratum*
20. *Scrupocellaria diegensis*
21. *Tricellaria occidentalis*

CTENOSTOMES
22. *Pherusella brevituba*

CYCLOSTOMES
23. *Crisia serrulata*
24. *Filicrisia* sp.
25. *Tubulipora* sp.

A. Tentacle Flicking Activity. *B*. Other Individual Actions. *C*.Scanning Behaviour. *D*. Type of Colony Current Pattern. *E*. Strength of Colony Currents. *F*. Size of Incurrents mm. *G*. Size of excurrent Chimneys mm. *H*. Number of Lophophores/ Cluster. *I*. Comment.

Tentacle Flicking Activity: L= little activity, M= moderate activity, A=high degree of activity, H= high degree of activity and greater range of activity. *Other Individual Actions*: F=fans several tentacles in unison, MC=makes cage of tentacles, no prey observed, CC=cage capture, AvR=avoidance retraction, W=writhing of tentacles, FLD=flattens lophophore to disk. *Scanning Behaviour*: O=not present, MS=multidirectional scanning, VS=chiefly vertical scanning, LS=chiefly lateral scanning. *Type of Colony Current Pattern*: I=behaviour individualized, II=colony skeleton separates polypides, colony current generally unidirection, III=polypides form temporary clusters, not relected in skeletal morphology, IV=Polypides form fixed clusters, not reflected in skeletal morphology, V=Polypides form fixed clusters, reflected in skeletal morphology, patterning irregular. *Strength of Colony Currents*:W=weak, M=moderate, S=strong. *Size of Incurrents*: O=not present, C=incurrent cell or cluster, CH=incurrent channel. *Size of Excurrents*:O= not present. (For further expln. see Winston, 1978).

patterns seen in the laboratory (e.g. Figs. 1d,2d), may be necessary in nature to move food particles from the macro-currents into a microenvironment for extraction.

In spite of the differences in size and scale between branching bryozoan and branching coral colonies, some of the same factors that influence water flow through coral colonies will probably be found to apply to bryozoans. For example, coral colonies with a flow pattern in which most of the water entering the colony is directed diagonally outward may develop stagnant regions in the interior. Such interior stagnation leads to a critical size above which such colonies have dead interiors (Chamberlain and Graus, 1975). Diagonally directed outward flow in bryozoan colonies might be important in slowing down water movement to the point where colony created currents could be effective, while the interior polypide-produced currents might keep the interior from stagnation. Nevertheless, branching bryozoan colonies might reach a certain size above which polypide produced currents would not be sufficient to keep water moving.

Horizontal flow (in which most of the water entering passes through the colony) obtains in open structured coral colonies and is characteristic of corals living in high-energy environments. It is postulated by Chamberlain and Graus (1975) that the ability to cope with fast water movement may depend on adaptations (such as roughening of the surface to create a branch boundary layer) for protecting the polypides from extremes that would preclude feeding activities. The relationship between functionally open-structured bryozoan colonies and high energy regimes is not yet known. One open-structured species from this study, Hippoporina insculpta, with a frilled bilaminar morphology, does occur in a high energy intertidal environment; perhaps the curving platy branches act as current baffles to protect lophophore surfaces. The knobs and spines so characteristic of certain erect and encrusting bryozoans may also be found to have this function. However, such a function could not be provided by projections (like those of some Celleporaria species) not reaching the level of the expanded lophophores.

With encrusting colonies various current patterns are possible. In some colonies only temporary clusters are formed, usually with 3 to 6 lophophores, e.g. 12 species observed by Winston (1978) and 6 species in the present study). The activity of the lophophores in this type of encrusting colony acts to create turbulence and enhance water movement over the colony surface, without resulting in any kind of directional flow. In other encrusting colonies fixed clusters of lophophores occur, either visible in the expanded polypides only, or reflected in the configuration of the colony skeleton itself. In all but the youngest and/or smallest colonies excurrent chimneys or channels occur between the incurrent cells or clusters.

Cook (1977) described three basic patterns of colonial water currents in encrusting forms: (1) the centripetal currents occurring in certain cyclostome colonies (see also Winston, 1978), and patterns characterized by (2) passive exhalent chimneys (areas devoid of feeding lophophores for various reasons), and (3) active excurrent chimneys surrounded by polypides with obliquely truncate lophophores. Winston (1978) did not distinguish between active and passive excurrent chimneys but emphasized the incurrent cells and the development of regular patterning for current channelling.

The results given above cover both incurrent and excurrent aspects of colony current patterns, and also emphasize the necessity to look at species from as many different areas and environments as possible. In the majority of the encrusting species observed in Panama and Florida (Winston, 1978) the incurrent cells were much more obvious than excurrent chimneys or channels - the excurrents being often just the distance between opposing obliquely truncate lophophores at the edges of adjacent incurrent cells. Some species observed by Cook (1977), e.g. Cleidochasma contractum, are also small-chimneyed in the sense of having chimneys formed by a non-feeding zooid or at the bifurcation of a zooid row. In contrast excurrent chimneys are immediately apparent in several of the encrusting species described above. These chimneys (0.8-1.7 mm in diameter) can be formed either by the presence of a raised area in the skeleton or in the substratum beneath the skeleton, or by the occurrence of a gradational heteromorphy of the lophophores surrounding the chimney.

Banta, McKinney and Zimmer (1974) use the relatively constant size (1-2 mm) and distance between monticules (2-3 mm) among Palaeozoic bryozoans (Cystoporata and Trepostomata) as an argument for a probable excurrent function for these raised areas. This consistency in size would be expected if the number of cilia per unit area of colony surface is approximately equal among species with monticules. Cook (1977) also notes the similarity in chimney size distribution in encrusting species. This apparent similarity may again be a matter of scale. The number of cilia per unit area of colony is a function of lophophore size (tentacle length and number) which we know varies among living marine bryozoans (Winston, 1977). If lophophore diameter is used as an estimate of size, chimney diameter can be seen to vary with lophophore size (Fig.4) in the five species for which this information is available so far. Whether large chimneyed species are more characteristic of one environment than another is a question that can only be settled by more observation.

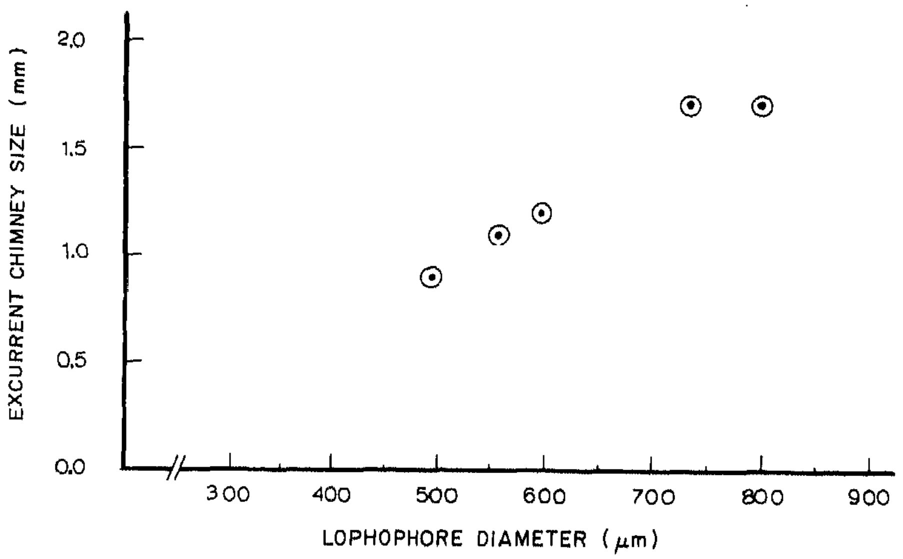

Figure 4. Excurrent chimney size with respect to lophophore diameter in five encrusting species. The species *Membranipora membranacea*, *Rhynchozoon rostratum*, *Cauloramphus spiniferum*, *Porella porifera*, *Jullienula hippocrepis* are illustrated in order of increasing lophophore diameter.

It is of interest that regularly patterned (Type VI) colonies did not occur among the California bryozoans sampled. Regular patterning of chimneys, mentioned by Cook (1977) as well as by Banta, McKinney and Zimmer (1974) could be expected to enhance the efficiency of current processing and thus might be expected to occur in habitats where the food resource is low and/or water movement or exchange limited (unlike the habitats of species in this study). There is not yet enough information on species from different environments to do more than speculate.

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