

COLONY-WIDE WATER CURRENTS IN LIVING BRYOZOA

by

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Résumé

Les divers types de courants d'eau des colonies de Bryozoaires sont décrits et analysés. Pour les formes encroûtantes, il en existe au moins trois à l'heure actuelle. Pour les petites colonies de Cyclostomes (*Lichenopora*), il n'existe qu'un courant centripète se dirigeant vers l'extérieur. Chez certaines Chéilostomes (*Hippoporidra*) et Cténostomes (*Alcyonidium nodosum*), des « monticules » sont formés par des groupes de zoïdes dont les couronnes de tentacules sont absentes, réduites ou ne se nourrissent pas. Les « monticules » sont le siège de courants passifs, dirigés vers l'extérieur. Chez d'autres Chéilostomes (*Schizoporella*, *Hippoporina* et *Cleidochasma*) et des Cténostomes (*Flustrellidra hispida*), des groupes de zoïdes à couronnes de tentacules hétéromorphes constituent des « cheminées » produisant des courants actifs se dirigeant vers l'extérieur. Des suggestions sont faites concernant une suite d'observations sur les colonies vivantes.

Introduction

Observation of living colonies is increasingly becoming an essential feature in the study of Bryozoa. Not only is it the primary method of discovering the function of zooids or parts of zooids, it is the first step in testing the established inferences about analogous and homologous structures in preserved material. The study of the functions of whole colonies and the degree and kind of integrative factors contributing to colony-control of these functions is in its early stages. These primary observations can only be made on living colonies.

The wide variation in astogeny and ontogeny of structures and their functions in Bryozoa require much further work on many species before any general patterns may become obvious. The information already available has great taxonomic potential. Until the analogous functions performed by different structures and the differing functions performed by apparently homologous structures have been tested by observation of living, growing colonies, that potential may remain largely unrealized.

Recently, there has been a rapid increase in the number of studies of the lophophore and tentacles. Some of these have been on structure (Smith, 1973; Gordon, 1974), others on behaviour in living colonies (Bullivant, 1968b; Dudley, 1970; Jebram, 1973; Ryland, 1975). The existence of patterned, colony-wide water currents, involving groups of zooids with heteromorphic tentacle crowns has been demonstrated by Banta *et al.* (1974).

Observation of 13 species described here has shown that water current patterns may be an intrinsic part of colony function in many Bryozoa. In addition, the nature of the patterns themselves are apparently related

in varying degrees to the growth habit (astogenetic structure) of the colony and to both continuous and cyclic ontogenetic changes.

Preliminary observations show that water current patterns are inherent in the colony structure of some erect forms. In encrusting forms, they are a resultant both of position of zooids within the colony and of the presence of heteromorphic lophophores and tentacles.

The lophophore in Bryozoa supports a distal ring of ciliated tentacles and is continuous proximally with the tentacle sheath. When the zooid is feeding, there is great variability in the amount of eversion of the tentacle sheath. In some forms, notably Cyclostomata, the tentacle sheath is not visible in feeding zooids and the proximal part of the tentacle crown may remain within the peristome. In some Cheilostomata, notably in *Exechonella antillea* (Osburn), which has been observed in many living specimens from West Africa, the tentacle sheath is completely everted, raising the tips of the long tentacles as much as 2 mm above the colony surface. The greater part of the gut passes up into the everted sheath cavity during feeding.

In all cases, the normal feeding water current produced by the cilia is into the tentacle crown toward the mouth, then between the tentacles and outward toward the surface of the colony. The directional beat of the cilia can be reversed (see Ryland, 1970:44) and unwanted particles can be rejected by this method which is often combined with rapid closure of the basal part of the tentacle crown, by reversal of the pharyngeal ciliary current and by muscular contraction of the pharynx.

There is generally considerable turbulence over the surface of a colony in which most zooids are feeding. In many erect forms, the position of the zooids forming the branches is such that the current passing between the tentacles is unrestricted. In large expanses of encrusting forms, it would appear much more difficult for water to flow in an unrestricted manner (see also Banta *et al.*, 1974). These authors noted that in a species of *Membranipora* which formed large, encrusting colonies on algae, groups of zooids were modified to form "chimneys" or excurrent water outlets. These provided regularly spaced outlets across the colony surface and comprised circlets of zooids with very long tentacles, each surrounding a zooid which either did not possess or did not protrude its lophophore.

Materials and Methods

The Bryozoa upon which the observations described here were made, were collected and observed respectively:

1. - near Marseilles and at the Station marine d'Endoume (France);
2. - in or near Buzzards Bay, Cape Cod and at the Marine Biological Station, Woods Hole (U.S.A.);
3. - from Dovercourt Beach, Essex and at the British Museum (Natural History) (England).

Specimens were maintained in tanks of running seawater at Woods Hole and in a closed, filtered and aerated system in London.

RESULTS

Observations have been made on erect, unilaminar colonies and colonies encrusting algae and shells.

Unilaminar, erect forms of growth may be uni- to multiserial, bifurcating or reticulate, flexible or rigid. Generally, the water current

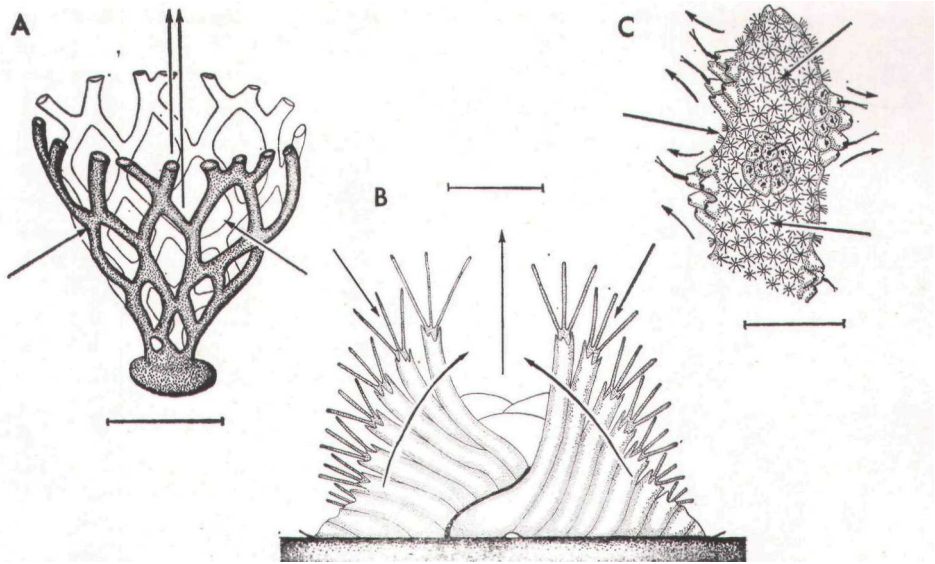
in unilaminar forms passes from the frontal to the basal side of the colony. A unilaminar, rigid, reticulate colony of a cheilostome "reteporid", probably *Sertella* sp., was observed at Marseilles. The colony was very young and small, approximately 20 mm in height, with the zooid orifices facing outward. Zooids bordering the trabeculae protruded their tentacle crowns into the fenestrae laterally. The resultant, colony-wide water current passed inward through the fenestrae and out of the funnel formed by the colony, as a column of water moving at about 1 mm per second. Other Sertellidae since observed had the zooid orifices facing the inner side of the colony funnels and the current was therefore the reverse of that shown in Text-fig. 1, A. It is very interesting to compare the currents seen in Recent Sertellidae with those postulated for similarly constructed fossil Fenestellidae by Cowen and Rider (1972:157, text-figs. 3 B, C).

A similar pattern to that of the Sertellidae occurs in the erect, unilaminar but flexible cheilostome, *Bugula turrita* Verrill. Specimens from Buzzards Bay had spirally arranged branches (see Ryland, 1960b: 98), with the biserial zooids facing the inner side of spiral. Generally, only the astogenetically younger six generations of zooids at the ends of the branches were seen to feed actively. The tentacle crowns were well protruded, the everted tentacle sheaths raising the tips of the tentacles 0.5-0.6 mm beyond the surface of the branches. The tentacle crowns formed a reticulate pattern and were all of the same length. Water currents passed between the tentacles to the reverse, outer side of the branch and then downward to the base of the colony. The currents thus passed successively through each spiral array of branches. Cowen and Rider (1972) postulated a somewhat similar current pattern for the spirally constructed fossil, *Archimedes*.

In contrast, some erect forms observed had no appreciable colony-wide water current. In a species of the cyclostome, *Crisia*, growing on algae washed up at Manomet, Cape Cod, the zooids were biserial but their orifices were widely separated and the branches not spirally arranged. The tentacle crowns were protruded just beyond the edge of the peristome. Another erect but very dissimilar form of colony occurred in the ctenostome, *Alcyonidium gelatinosum* (Linnaeus) from the Essex coast. It consisted of elongated, sometimes palmate gelatinous masses, often more than 20 cm in length. The earliest astogenetic stages encrusted small stones and shells and were followed by a long "stalk-like" portion about 5 cm long and 10 mm wide. Later stages consisted of an increased number of zooids and confused areas of overgrowth. Although the tentacles of some zooids were longer than those of the majority, there was no evidence of any colony-wide water current.

The remaining colonies observed were all encrusting. Extensive colonies of *Aetea* sp. from Buzzards Bay had uniserial encrusting basal portions to each zooid, but the orifices were raised at the distal end of a long erect portion of the zooid. When the tentacle crowns were protruded, the tips of the tentacles of some zooids were raised nearly 1 mm above the substratum. The irregular, uniserial mode of growth of the basal portion of each zooid resulted in a very irregular distribution of tentacle crowns and no appreciable colony-wide water current was seen.

An entirely different type of encrusting colony was seen in the cyclostome *Lichenopora*. Colonies were observed from the Mediterranean, from Buzzards Bay and Manomet, Cape Cod. These latter colonies were small (2-7 mm in diameter), discoid and domed. The central, astogenetically older zooids had longer peristomes (0.4 mm) than those at the growing edge (0.2 mm) and their tentacles were also longer (Text-fig. 1,B). The zooids are arranged in radial rows. Water currents, passed between the tentacles and moved centripetally between the zooids rows, below the level of the peristomes and tentacle



TEXT-FIG. 1.

- A. **Water currents in an erect, unilaminar, fenestrate colony with orifices facing externally.** Currents pass inward through the fenestrae and « upward » and **outward** from the centre of the colony. Note that many similar colonies have the orifices facing internally, and the current is therefore the reverse of that shown. The orientation of the entire colony in life is frequently also the reverse of that shown.
Scale 8.00 mm.
- B. Diagrammatic section through a small lichenoporidae colony, passing between zooid rows (partially from Boardman and Cheetham, 1973, text-fig. 8). Note the elongation of the tentacles with cyclic ontogenetic changes, so that zooids of earliest astogeny have the longest tentacles. The centripetal water current flows between zooid rows and « upward » and outward from the central area.
Scale 1.00 mm.
- C. **Inferred method of production of water current in part of a branched colony of Hippoporidra.** Groups of raised, frontally budded male zooids have **no cilia on the tentacles, and form** passive excurrent outlets.
Scale 3.00 mm.

crowns. When all zooids were feeding, a steady colony-wide current was produced which passed upward from the centre of the colony at about 1 mm per second. When colonies were deliberately covered with a thin layer of fine mud, the surface current passing between the zooid rows cleared a colony 5 mm in diameter of all detritus in 10-15 minutes.

Colonies of the cheilostome *Electra pilosa* (Linnaeus) encrusted *Chondrus* at Manomet and *Fucus* at Dovercourt. In colonies where

the number of zooids in lateral series exceeded 20-25, some heteromorphic tentacle crowns were seen. In colonies with only a few zooids in lateral series, all the tentacle crowns appeared to be the same. *E. pilosa* tended to grow in uniserial rows, especially under conditions of restricted substratum. Under less restricted conditions, apparently multiserial expanses were formed by "infilling" between uniserial rows. Each zooid of a uniserial row produced paired lateral-distal buds in a sequence which followed that of the primary series, but which was much later in time. Instead of developing at an angle to the primary series and forming secondary uniserial rows, these buds grew parallel to the primary growth direction, forming lateral communication with the next distal zooid of the primary series. When this zooid produced paired lateral buds, the previous pair formed distal communication with them. Further series of single, distal lateral buds on either side of the central group formed a regular quincuncial arrangement of zooids which eventually developed into a simple growing edge. The astogenetic sequences involved were, however, quite unlike those of many other encrusting expanses and formed a mosaic of rectangular zooid groups. This was reflected in the position of the heteromorphic zooids with long tentacles which tended to occur in rectangular zones, not the circular groups observed in *Membranipora* by Banta *et al.* (1974). Observations on *E. pilosa* were complicated by the tendency for the everted tentacle sheath and tentacles to vary in size directly with the size of the zooids which were very subject to micro-environmental crowding influences as a resultant of the mosaic growth form of the colonies. The groups of zooids with longer tentacles did not appear to be acting as "chimneys" and no appreciable colony-wide water current was seen.

Colonies of the ctenostome *Flustrellidra hispida* (Fabricius) were common on *Fucus* from Dovercourt. Colonies collected from January to March 1975 were generally found at the base of the algal fronds and had zones of actively feeding zooids which appeared to have budded from non-feeding zooids in a quiescent phase, probably a winter state. Young colonies and ancestrulae were present on the upper parts of the *Fucus* fronds from late February onward and both old and young colonies included zooids without lophophores but with four to six bright orange embryos. The zooids and tentacle crowns of *F. hispida* were large and the everted tentacle sheath protruded the tips of the tentacles over 2 mm above the colony surface. Some small groups of zooids had some tentacles longer than the rest. The zooids formed circlets of four to six, surrounding a central zooid which either did not protrude its lophophore or did not possess one. Occasionally, the central zooid contained embryos. The circlets of zooids were very irregularly distributed and the zooids tended to hold tentacle crowns toward the centre, forming a "chimney" (Plate A, 3). In areas where the growing edges of two colonies met, kenozooids were budded by each colony. The zooids from each colony nearest the kenozooids held the tentacle crowns alternately over the kenozooidal rows. The chimneys formed distinct excurrent water outlets when the whole colony was feeding, the other tentacle crowns forming a very regular, reticular pattern.

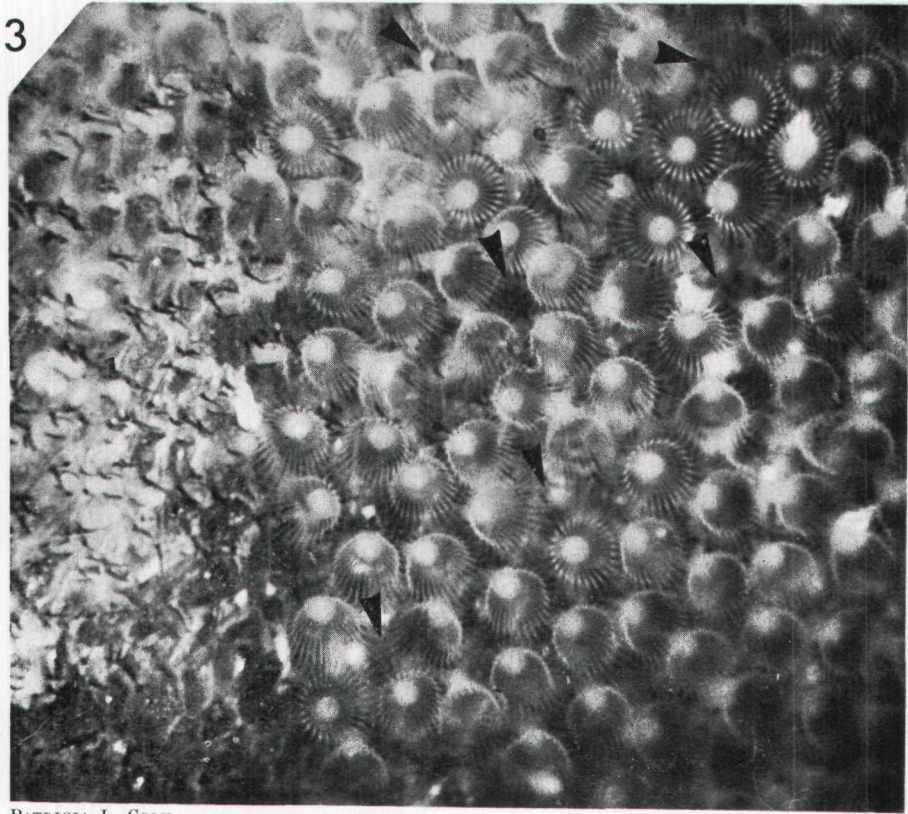
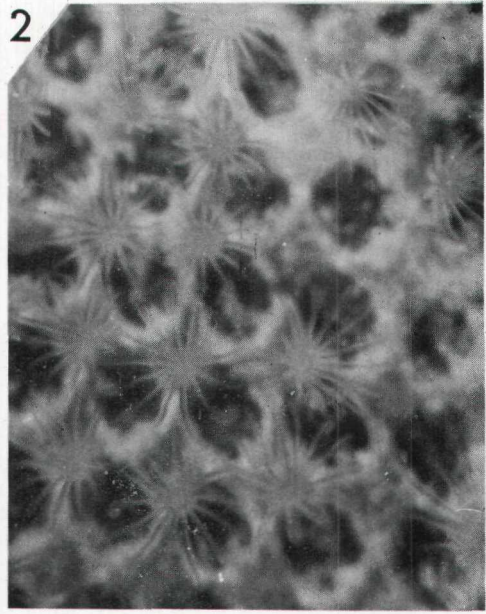
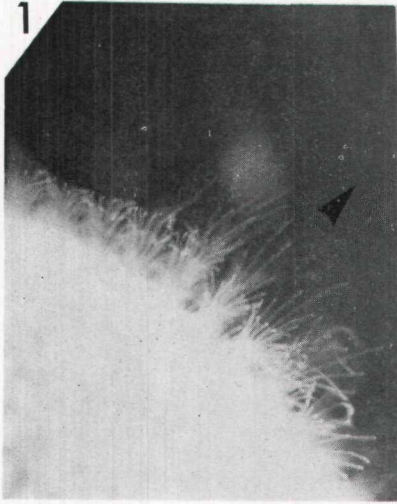
Very young colonies, comprising 25-30 zooids, had no chimneys.

There was an increase in size of both zooids and tentacle crowns with colony growth, as a zone of astogenetic repetition had not been reached. The crowns of the largest, subperipheral zooids were held outward, over the growing buds. This produced a distinct, centrifugal water current within the colony.

All the remaining colonies observed were of cheilostomes encrusting lamellibranch shells from Buzzards Bay or deeper water off Cape Cod. Among these were several colonies of *Cleidochasma contraction* (Waters), the largest measuring approximately 15X25 mm. Groups of zooids were present in which the everted tentacle sheath and some of the tentacles were considerably longer than those of other zooids (Plate A, 1). The heteromorphic zooids were arranged in circlets and surrounded by zooids with some slightly elongated tentacles. These groups were interspersed and merged with zooids in which the tentacles were shorter and all of the same length. The very long tentacles occurred in direct relationship to zooid position in a chimney group. Zooids astogenetically proximal to a chimney had four very long distal tentacles, those occurring laterally had four to six long lateral tentacles on the inward side, and those occurring distally to a chimney had four long proximal tentacles. The centre of a chimney consisted either of a non-feeding zooid or of a bifurcation in the zooid rows. The presence of both developing and complete ovicells did not affect the type of lophophore present and ovicells were not related in position to the distribution of chimneys.

The colony-wide water currents moved alternately inward toward the short-tentacled zooids, passed between their tentacles, along the surface of the colony and outward through the chimneys. The current running over the surface of the zooids passed toward the growing edge in the more peripherally placed zooids. Zooids at the growing edge were also heteromorphic in many cases and had long distal tentacles. The tentacle crowns were held over the developing buds almost horizontally. The surface current passing below the tentacle crowns near the periphery of the colony was very rapid, running at 2-3 mm per second. Small particles (0.01 mm in diameter) were cleared rapidly from the surface of subperipheral and peripheral zooids by this current. Larger particles (up to 0.05 mm) were expelled by the chimney currents 2-3 mm above the colony surface in 1-2 seconds. Microenvironmental obstructions (such as small barnacles, serpulid worms and boring sponges) round and over which the bryozoan had grown, were also the site of chimneys. The elongated tentacles were developed on the same side as the obstruction and the tentacle crowns were held away from the obstruction (Text. - fig. 2, A and B).

Colonies of *Schizoporella cornuta* (Gabb and Horn) on *Pecten* had reddish-orange coelomic tissue, pale orange tentacles and dark red-to-pink embryos. The form and distribution of chimneys were similar to those seen in *C. contractum*, except that tentacle crowns bordering microenvironmental obstructions were not held away from the obstruction. Larvae, released from the ovicells while the colony was feeding, passed to the periphery in the surface currents, below the level of the extended tentacle crowns and were not expelled by the chimney currents. In young colonies, the ancestrula had a large orifice bordered by 10 spines and the lophophore had 10 tentacles

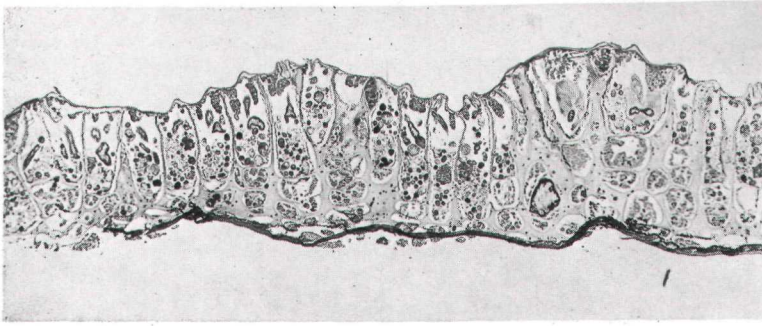


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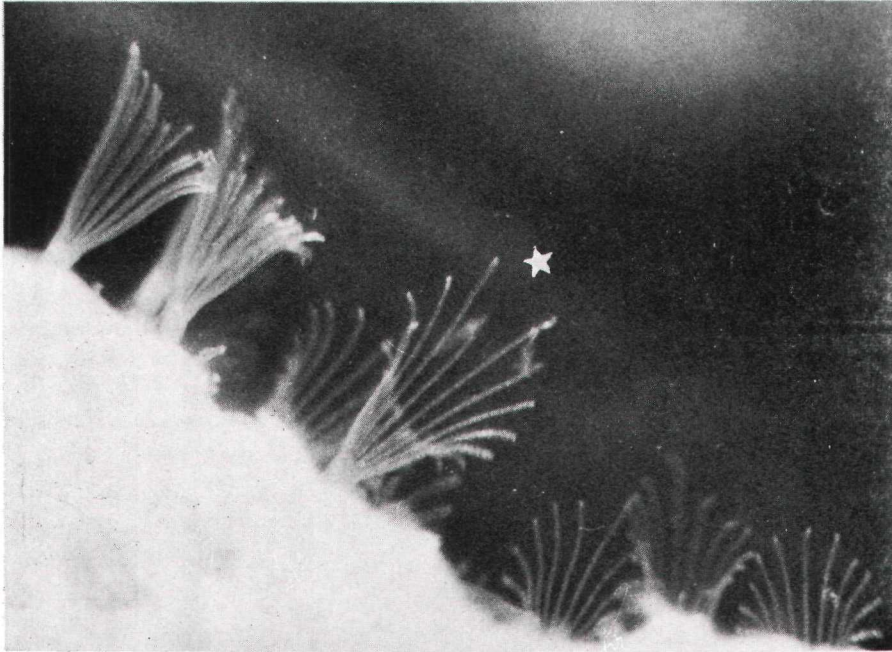
PLATE A

1. *Cleidochasma contractual* (Waters), Buzzards Bay, Cape Cod.
Part of a colony in lateral view with tentacle crowns expanded. Direction of current from chimney zooids arrowed. X 20.
2. *Electra pilosa* (Linn.), Manomet, Cape Cod.
Frontal view of expanded tentacle crowns. X 40.
3. *Flustrellidra hispida* (Fabricius), Dovercourt, Essex.
Groups of expanded tentacle crowns with several irregularly spaced chimneys arrowed. X 12.

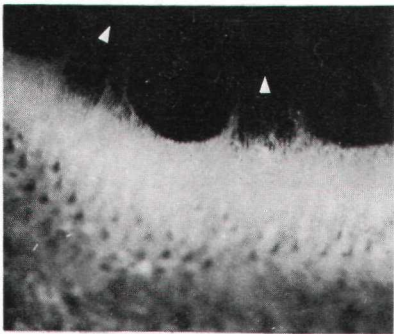
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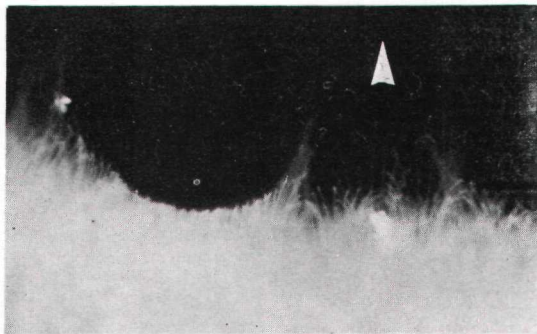
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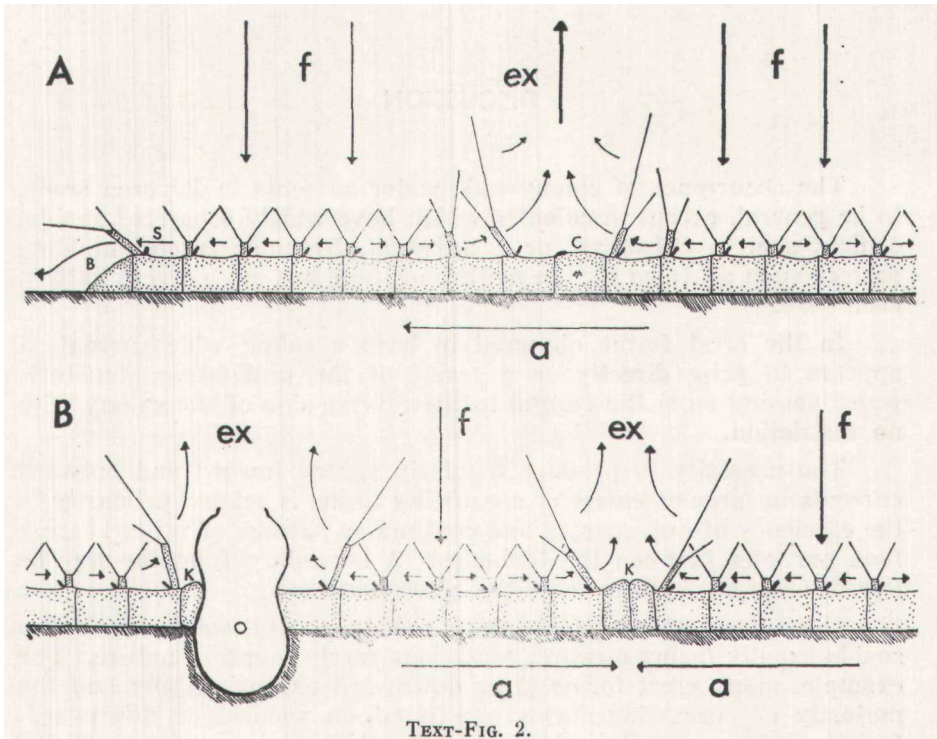
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PLATE B

1. *Alcyonidium nodosum* O'Donoghue and de Watterville, Port Nolloth, S. Africa. Vertical section through two "monticules" consisting of large zooids with embryos. X 17.
2. *Hippoporina porosa* (Verrill), Buzzards Bay, Cape Cod. Expanded tentacle crowns. The marked crown (*) is from a zooid just peripheral to a chimney zooid, note elongation of some tentacles. X 50.
3. *H. porosa*, as above. Two chimneys in silhouette. Direction of current from chimney zooids arrowed. X 16.
4. *H. porosa*, as above, one of the chimneys of Figure 3 enlarged. Direction of water current arrowed. X 34.

(0.10 mm long). The next generation of 2-3 zooids had 12 tentacles (0.02 mm long) and subsequent zooids had 12-13 tentacles in which the distal four were longer than the remainder (range 0.20-0.30 mm). The subperipheral tentacle crowns were held almost horizontally over the growing edge and although they were not heteromorphic, produced a strong centrifugal colony-wide water current.

In *Hippoporina porosa* (Verrill), the coelomic tissues were orange-red, the tentacles orange and the embryos bright red. Heteromorphic zooids forming chimneys had extremely long tentacles and, in lateral view, the tentacle tips form a series of curves across the colony (Plate B, 3 and 4).



TEXT-FIG. 2.

- A. Diagrammatic section through an encrusting colony with a growing edge and a chimney.
 a: direction of growth; b: peripheral zooid bud; c: central zooid of chimney; ex: outward current; f: inward current; s: surface current.
- B. Similar section through two colonies which have met, producing rows of kenozooids at the adjacent growing edges. One colony has grown round a microenvironmental obstruction.
 k: kenozooid; o: microenvironmental obstruction.

The structure and distribution of chimneys were virtually the same in colonies of *Cryptosula pallasiana* (Moll) and *Parasmittina nitida* (Verrill) which were also observed.

In all these cheilostome species, the occurrence of chimneys was correlated to a varying extent with astogenetic changes in the colony pattern. In more than 75 per cent of occurrences in *H. porosa*, approximately 50 per cent in *S. cornuta* and 25 per cent in *P. nitida* and *C. contractum*, the chimneys were associated with the bifurcation

of zooid series. This positional correlation was not exact but often the central, non-feeding zooid of a chimney was one proximal to a bifurcation. In other cases, this zooid was one of the proximal members of a chimney and the central zooid was provided by one of the distal pair of zooids of the bifurcation.

In none of the species observed was there any visible heteromorphism except that of the length of tentacle and tentacle sheath and of behaviour. The ciliary movement of the elongated tentacles appeared to be of the same speed as other tentacles and there was no significant difference in the size of the orifice or width of the tentacle sheath of the heteromorphic zooids.

DISCUSSION

The occurrence of colony-wide water currents in Bryozoa seems to be general, except in colonies which have widely separated zooidal orifices such as *Crisia* sp. or a uniserial, irregular colony budding pattern such as *Aetea* sp. In neither of these has any current pattern been seen.

In the erect forms observed to have a colony-wide current, it appears to arise directly as a result of the unilaminar structure, water passing from the frontal to the reverse side of the colony with no restriction.

The necessity to produce regularly spaced inward and outward currents in large expanses of encrusting forms is related primarily to the efficiency of unrestricted and continuous passage of water bearing food particles between the tentacles. A secondary function may be the clearing of detritus from the colony surface.

Laboratory observations were made in still water, with the zooids usually facing upward, conditions rarely found in nature. For example, many erect forms grow downward or horizontally and the majority of encrusting forms are found on vertical or downward-facing surfaces, whether they grow on algae or on rocks or shells. In the laboratory, detritus removed by the chimney currents, tended to be drawn in toward the colony again by the inward currents. This would probably not occur under natural conditions where the orientation of the colony was different and where there was some turbulence, however slight, in the surrounding water.

In encrusting colonies, the methods known at present by which colony-wide excurrent outlets are produced fall into three groups. It is very probable that other, as yet unobserved or unrecognized methods, exist.

The first method is that found in small discoid colonies of limited size, such as *Lichenopora*. Here, there is only one chimney placed at the centre of the colony. The radial arrangement of the zooids and the continuous extension during ontogeny of the peristomes of the astogenetically older zooids, is accompanied by elongation of living chambers. The cyclic degeneration and regeneration of the

lophophore and other viscera result in the larger tentacle crown being found at the centre of the colony. This produces a colony-wide, centripetal current. The very young colonies of ctenostomes and cheilostomes observed have the potential to grow much larger and the colony-wide currents observed in them are entirely different from those seen in *Lichenopora*. The size of the living chamber, viscera and tentacles does not enlarge with ontogeny. Instead, the size of the zooids increases with astogeny in the primary zone of astogenetic change and, thus, the size of the tentacle crowns increases toward the periphery of the colony, resulting in a centrifugal water current.

Once such colonies have grown larger, the second method, in which regularly placed chimneys are developed, is found. The heteromorphic zooids apparently occur as a response to astogenetic position in the colony and are presumably maintained throughout cyclic ontogenetic changes involving the lophophores and viscera. The degree of heteromorphism differs but the excurrent function of the chimneys is dependent upon the differential current directions induced by alternating groups of actively feeding zooids. These colonies may be regarded as having "active" chimneys (cf. below).

The third method is that in which the chimney is formed by heteromorphic zooids which do not have active, feeding tentacle crowns. This method is one which may be inferred from preserved material. For example, apparent "monticules" occur in the Recent ctenostome, *Alcyonidium nodosum* (see O'Donoghue and de Watteville, 1944:428, pl. 16, figs. 17, 18), from South Africa. The colonies encrust the shell of a gastropod, *Comminella papyracea*, and have regularly spaced, raised groups of large zooids, surrounded by relatively depressed, smaller ones. Sections through the colony show that both types of zooids have lophophores and that the tentacles all appear to be of the same length. Many of the zooids forming the raised monticules (between 30-75 per cent) do not possess lophophores, however, and in approximately half of these the zooid living chamber is full of developing embryos (see Plate B, 1). Such groups of zooids would act as "passive" chimneys in that the inward current would pass between the tentacles of the smaller zooids and the outward currents would automatically form above the monticules, which would have few or no zooids feeding. A combination of function (brooding and providing excurrent outlets) is similar to that inferred for some fossil forms and has been recently discussed by Banta *et al.* (1974). Somewhat similar colonies with monticules have also been recently reported by Taylor (1975), in a multilaminar jurassic cyclostome which encrusted mollusc shells which had probably been inhabited by pagurids. The monticules were inferred to be the site of passive excurrent outlets.

Passive chimneys are also inferred from the presence of monticules in the Recent and fossil genus *Hippoporidra* which is usually associated with gastropod shells inhabited by pagurids. Here the raised groups of large, male zooids are formed by "frontal budding" (see Banta, 1972). The male zooids have modified lophophores and viscera and the tentacles are greatly reduced in number and not ciliated. Male zooids, therefore, do not feed and, as they occur in groups, may also act as passive excurrent outlets (see Text-fig. 1, C).

There is a distinct positive correlation between the occurrence of raised monticules and a symbiotic association of the bryozoan with gastropods or gastropod shells inhabited by pagurids. However, similar regularly spaced, protuberant areas, comprising frontally budded zooids, are common in many encrusting cheilostomes, particularly in the celleporiform type of colony. It is very probable that these, too, may be the site of active or passive chimneys but no species has as yet been examined alive for water current patterns.

The similarity in the size and distribution of chimneys among encrusting forms is striking (Table 1). The average distance between chimneys is similar to that reported for the monticules studied by Banta *et al.* (1974) and by Taylor (1975) and this strengthens the inference that they had one function in common, at least.

The demonstration of colony-wide currents shows a gradient in correlated structure and function somewhat similar to that known in male zooids. Here, the most undifferentiated form is found in *E. pilosa* (Silén, 1966) where the heteromorphism is expressed only in behaviour and then only at certain cyclically occurring ontogenetic stages involving the viscera and lophophores. The next stage is found in *Hippopodinella adpressa* (Busk) where the difference in morphology and behaviour between the male zooids and autozooids is considerable, but still confined to certain stages in cyclic ontogeny (Gordon, 1968). The final element known at present is that found in *Hippoporidra* where the behaviour and morphology of the males is accompanied by differences in the morphology of the calcified walls from those of the autozooids and is thus recognizable at all astogenetic and ontogenetic stages (Cook, 1968 c).

The astogenetic and ontogenetic gradients exhibited by the species observed indicate varying kinds and the degrees of colony control in the production of water currents (Boardman and Cheetham, 1973). Generally, it may be assumed that the methods of producing currents show more integration in the encrusting species than the erect species. Which of the three methods found in encrusting colonies shows the highest degree of colony control requires further study.

The presence and form of chimneys in other species, especially those with encrusting colonies require confirmation. It is necessary to discover if the heteromorphic lophophores arise in regularly patterned units as part of the astogenetic process or are the result of colony-controlled cycles of degeneration and regeneration. A combination of these alternatives is, of course, also possible. The constancy of position of chimneys during the life of a colony and their occurrence in areas of frontal budding and overgrowth also requires observation.

The occurrence and form of water currents in other types of colony, particularly those which are bilaminar and lunulitiform are as yet unknown. Investigation is also needed into the occurrence of chimneys in species which have an unstable colony form (i.e. are encrusting under some environmental conditions and erect under others: Cook, 1968 b).

Many heteromorphic zooids are known in cheilostomes which, in addition to having lophophores and a feeding function, have orifices and opercula which differ from those of the majority of zooids in a colony. Often, these heteromorphic zooids occur in distinct patterns.

TABLE I
Data of heteromorphic zooids

Name	Locality data	Dimensions of colony	Estimated no. of zooids	Length of zooids	Diameter of chimney	Distance between chimneys	Length of heteromorph tentacles	Length of tentacle sheath of heteromorph	No. of tentacles of heteromorphs	Length of ordinary tentacles	Length of tentacle sheath of ordinary zooids	No. of tentacles of ordinary zooids
<i>Cleidochasma contractum</i>	Buzzards Bay on <i>Pecten</i>	15 × 25 mm	2,000	0.55 - 0.60 mm	0.60 - 0.80 mm	1.70 - 2.50 mm	0.35 - 0.84 mm	0.40 mm	13-14	0.25 - 0.28 mm	0.20 mm	10-13
<i>Schizoporella cornuta</i>	Buzzards Bay on <i>Pecten</i>	20 × 30 mm	3,000	0.40 - 0.55 mm	0.80 mm	2.00 mm	0.30 - 0.90 mm	0.50 mm	13-14	0.60 - 0.70 mm	0.40 mm	13-14
<i>Hippoporina porosa</i>	Buzzards Bay on <i>Pecten</i>	30 × 40 mm	4,000	0.45 - 0.55 mm	0.50 - 0.60 mm	1.80 - 2.00 mm	0.50 - 0.90 mm	0.50 mm	16	0.40 - 0.50 mm	0.15 mm	13-14
<i>Cryptosula pallasiana</i>	Manomet on <i>Mytilus</i>	15 × 20 mm	1,000	0.60 - 0.75 mm	0.70 - 1.00 mm	1.60 - 2.00 mm	0.40 - 0.90 mm	0.40 mm	16	0.40 - 0.42 mm	0.15 - 0.20 mm	16
<i>Parasmittina nitida</i>	Buzzards Bay on shells	30 × 30 mm	3,000	0.50 - 0.60 mm	0.60 mm	1.70 - 2.00 mm	0.30 - 0.90 mm	0.40 - 0.50 mm	16	0.24 - 0.40 mm	0.30 mm	16
<i>Flustrellidra hispida</i>	Dovercourt on <i>Fucus</i>	30 × 30 mm	2,000	0.60 - 1.00 mm	1.00 mm	1.00 - 4.00 mm	0.50 - 1.20 mm	0.67 - 0.80 mm	28-30	0.50 - 0.67 mm	0.50 - 0.60 mm	28
<i>Lichenopora</i> sp.	Manomet on 2 mm diam. <i>Chondrus</i>		80	—	0.60 mm	—	0.40 mm (central)	—	10-11	0.20 mm (peripheral)	—	10-11

Some are known or inferred to have a brooding function, others are inferred to be male zooids (Cook, 1973 b). Generally, if brooding structures are already known for a species, these zooids tend to be interpreted as "avicularia". The function of some avicularia without lophophores, but with highly modified opercula and muscle systems, is known from direct observation of living colonies (Kaufmann, 1971; Cook, 1963). That of the great majority, including those with and without tentacles, has never been demonstrated by direct observation. For example, the "B-zooids" in most species of *Steganoporella*, which have lophophores with long, ciliated tentacles and enlarged, modified opercula, are reasonably interpreted as "avicularia" because one species, *S. mandibulata* Harmer, has such highly modified structures without lophophores and does not possess "B-zooids" (see also Banta, 1973). Other, similar generic groups show series of such heteromorphs (e.g. *Labioporella*). The actual function of "B-zooids" and similar forms may perhaps be related to water current formation and the possibility of alternative or additional functions in such a series requires investigation.

Cheilostome species with chimneys seen so far either produce unbrooded eggs or develop brooding structures (ovicells) fairly late in the ontogeny of the zooids concerned. It would be useful to know if the distribution and development of chimneys is different in colonies where ovicells are produced as part of the primary ontogenetic process.

Today, the presence of heteromorphic tentacle crowns has only been demonstrated in living colonies. It is possible that differences in tentacle number and length may be recognized in suitably preserved material.

Many more observations of fossil species and analyses of the distribution and ontogeny of heteromorphic zooids are needed. Eventually, more series of integrative characters may become apparent for comparison with those which may be recognized in living colonies.

Notes on the observation of living colonies

The very recent recognition of colony-wide water currents underlines how little is known of total colony reaction and function in Bryozoa. To a certain extent, this is the result of the relative sizes of zooids and colonies. Colonies of some cyclostomes, such as those of *Lichenopora*, are usually small enough to be totally visible at low-power magnification. Colony-wide reactions are thus more noticeable than they are in larger forms. Even higher powers of magnification are commonly used in the study of the behaviour of heteromorphs such as avicularia, and this has obscured their relationships to other zooids and their possible role in the function of the whole colony.

A great deal of information on functional morphology is based on a few species only and, often, on observations made in the last century which have not been repeated (Dalyell, 1847, 1848). Assumptions for most species are thus almost totally inferential and parallel studies on a wide range of forms is required. It seems appropriate here to suggest some of the observations which should be included where possible in the study of living colonies.

It must be stressed that these are not the total number of features which could be observed and that many other as yet unknown reactions and

functions may be discovered. Some of these observations may also be made or inferred from a study of preserved material. The approximation of these inferences to the actual can only be strengthened by study of the living colonies. Obviously, not all these observations are possible in all colonies. It must also always be understood that laboratory observations are made in conditions which approximate to an unknown degree to the "normal" environment. Results should, therefore, be interpreted in the understanding that practically nothing is known of "normal" behaviour in the sea. Demonstration of one function in a structure should not preclude inquiry into other possible functions. Apparently homologous structures may have different behaviour patterns, functions and physiology. For example, the closely similar avicularian setae of *Caberea* and *Cupuladria* differ in behaviour, function and irritability. Structures with the same function may not be homologous. For example, the external brooding chambers (ovicells) of cheilostomes have several different astogenetic origins and ontogenetic developments (see also Woollacott and Zimmer, 1972; Harmelin, 1973b).

Once many more series of observations have been made, some general patterns of behaviour and function and their relationship to morphology may become apparent. It will then be possible to make stronger inferences about preserved, Recent or fossil material of the same or similar species and, eventually, to construct generalized models which may approximate increasingly to actual colony function. Some references are included under the headings below, illustrating recent studies on these subjects.

1. General data should include information on temperature and salinity ranges, turbulence, turbidity and depth.

2. Substratum data should include notes on the general nature of the area, such as rock type and conformation, orientation and position of colonies, size and type of shell, grain size of sediments and availability of substratum generally (Cook, 1968a; Maturo, 1966; Eggleston, 1972; Moore, 1973).

3. Associated plants and animals should include a survey of Bryozoa themselves as substrata, space competition and predator, symbiotic and cleaning associations (Haderlie, 1969; Gordon, 1972; Stebbing, 1971, 1973; Wyer and King, 1973).

4. Abundance and diversity data should include maximum size of colonies, an estimate of numbers of zooids and seasonal as well as substratum and locality distribution (Ryland, 1962, 1974; Ryland and Stebbing, 1971; Abbott, 1973a; Humphries, 1973).

5. Pigments in coelomic tissues, embryos, etc. may be recorded in terms of colour charts (Ryland, 1958; Eggleston, 1970; Gordon, 1970; Redier, 1972).

6. Observations on astogenetic changes include study of growth rates and patterns within and among colonies, growth of rooting systems, development of nodes and sequences of development of brooding structures, seasonal regeneration and development of resistant zooids (Gordon, 1971a; Abbt, 1973b; Dudley, 1973; Hayward and Harvey, 1974b).

7. Observations on ontogenetic changes include study of changes in morphology of zooids which may be continuous, cyclical or seasonal. Development of calcified frontal walls, communicating organs and brooding structures are particularly important (Gordon, 1971b; Cook, 1973b; Harmelin, 1973b).

8. Microenvironmental and environmental changes may be studied by direct observation during growth or by comparing growth patterns and zooidal ontogeny within and among colonies. Studies of species displaying unstable colony forms from different environments are important (Boardman *et al.*, 1969; Boardman and Cheetham, 1973; Harmelin, 1973a).

9. Breeding, brooding and larval development data should include zoning of reproductive zooids, fertilization behaviour, passage of ova into external ovicells and internal ovisacs, duration of brooding, larval release and behaviour and growth phases of planktotrophic larvae (Atkins, 1955; Silén, 1945, 1966, 1972; Bullivant, 1967; Cook, 1968c; Gordon, 1968, 1970).

10. Settlement, metamorphosis and early astogeny; data should include observations on hierarchies of substratum preferences, positional preferences, rates of change and type of development through metamorphosis and early astogeny and early budding patterns (Wisely, 1958; Ryland, 1960a; Cook and Hayward, 1966; Gordon, 1970; Eitan, 1972; Cook, 1973a; Dudley, 1973; Hayward and Harvey, 1974a).

11. Polymorphism data includes study of kenozooids and behaviour and function of heteromorphic zooids, direct observation and experimental evidence of defensive, supportive and cleaning functions (Marcus and Marcus, 1962; Cook, 1963; Kaufmann, 1971; Silén and Harmelin, 1974).

12. Functions of tentacles; data should include studies through zones of astogenetic change and repetition. Apart from observation of water currents, food preferences and particle sizes should be noted. The size and height of tentacle crowns, in comparison with those of surrounding, perhaps competitive forms, are also of interest. Reaction to light intensity, temperature changes and turbulence should also be noted (Bullivant, 1968 a, b; Dudley, 1970; Jebram, 1973; Ryland, 1975).

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Summary

Colony-wide water current patterns are described and analyzed. In encrusting forms, at least three methods of producing water currents are now known. In small colonies of Cyclostomata (*Lichenopora*), there is a single, centripetal, outwardly directed current outlet. In some Cheilostomata (*Hippoporidra*) and Ctenostomata (*Alcyonidium nodosum*), « monticules » are formed by groups of zooids where the tentacle crowns are absent, reduced in number, or do not feed. The monticules are the site of passive, outwardly directed current outlets. In other Cheilostomata (*Schizoporella*, *Hippoporina* and *Cleidochasma*) and Ctenostomata (*Flustrellidra hispida*), groups of zooids with heteromorphic tentacle crowns form "chimneys" which produce active outwardly directed current outlets. Some suggestions are made toward a sequence of observations on living colonies.

Zusammenfassung

Die Systeme der Wasserströme ganzer Kolonien werden beschrieben und analysiert. Von inkrustierenden Formen sind jetzt wenigstens drei Methoden zur Strömungserzeugung bekannt. In kleinen Kolonien der Cyclostomata (*Lichenopora*) gibt es einen einzigen, centripetal auswärts gerichteten Strom. In einigen Cheilostomata (*Hippoporidra*) und Ctenostomata (*Alcyonidium nodosum*) werden « Monticulen » gebildet aus Zooidgruppen mit fehlenden Tentakelkronen oder mit Tentakelkronen mit reduzierter Tentakelzahl oder aus Zooiden, die nicht fressen. Diese « Monticulen » sind die Stellen mit passiv auswärts gerichtetem Strom. In anderen Cheilostomata (*Schizoporella*, *Cleidochasma*, und *Hippoporina*) und Ctenostomata (*Flustrellidra hispida*) bilden Gruppen von Zooiden mit heteromorphen Tentakelkronen Schornsteine für aktive auswärts gerichtete Ströme.

Eine Reihenfolge der Beobachtungen an lebenden Kolonien wird vorgeschlagen.

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