N.N. Shunatova · A.N. Ostrovsky

Group autozooidal behaviour and chimneys in marine bryozoans

Abstract Marine bryozoans have a variety of behavioural reactions that are associated with different functions: feeding, cleaning, removal of filtered water, gamete release, avoidance reactions and, probably, sensation. Coordinated activities of polypides are regulated neurophysiologically, physiologically, structurally and, possibly, hormonally. Several group reactions are supposedly non-coordinated. Group autozooidal reactions and different types of colonial behaviour were observed and recorded for 17 bryozoan species and subspecies from the White and Barents Seas. Three local collective reactions (synchronised scanning, repeated particle transfer by circular water currents, and feeding and cleaning of the colony surface by "chains" of inclined lophophores) are described for the first time. The formation of water outlets (chimneys) was observed in four species with encrusting colonies. A new type of chimney was discovered in large colonies of *Tegella armifera*, in which chimneys are formed by temporary retraction of 10–12 neighbouring polypides. The space thus formed is surrounded by equitentacled lophophores standing vertically. Chimneys associated with elevated areas on the colony surface (monticules) were found in two species. In contrast to all previously published speculations and observations, the monticules were often places of incurrent rather than excurrent flow, and water outlets were formed in depressions between monticules. In *Schizomavella lineata*, monticules change their function from incurrent to excurrent after polypide degeneration. Conditions for the origin of various types of water outlets are discussed.

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Introduction

Bryozoa are colonial epibionts that actively filter feed on suspended matter (Hunt 1925; Wildish and Kristmanson 1997). Each feeding member of a bryozoan colony (autozooid) uses a crown of ciliated tentacles to capture and accumulate suspended food particles, the majority of which are then ingested. The tentaculate structure gathering food is called the lophophore. In marine bryozoans it is a conical or bell-shaped crown of tentacles surrounding the mouth and supported by the extended anterior part of a body-wall (introvert). The lophophore and introvert, together with the alimentary canal and associated musculature, are termed the polypide (Ryland 1970, 1976; Boardman et al. 1983; McKinney and Jackson 1989). All bryozoans use a common basic lophophore filter-feeding principle (Riisgård and Manríquez 1997; Nielsen and Riisgård 1998). The work of lateral ciliary tracts of bryozoan tentacles, in combination with the funnel-like design of the lophophore, generates a descending water flow. This provides the transfer of suspended food particles from the environment into the tentacle crown. The particles are caught there in different ways (reviewed by Gordon et al. 1987; McKinney 1990; Riisgård and Manríquez 1997; Nielsen and Riisgård 1998), and filtered water leaves the lophophore between the tentacles. The filtration process is often accompanied by different movements of the tentacles, lophophore and introvert (summarised in Borg 1926; Ryland 1970, 1976; Winston 1977, 1978, 1981; McKinney 1990; Shunatova and Ostrovsky 2001).

In Bryozoa all autozooidal behavioural reactions known may be assigned to one of two hierarchical levels.

Autozooidal behaviour, occurring independently of the activities of other colony members and including the work of ciliature (except in cases when cilia are absent in male autozooidal polymorphs) together with different movements of tentacles and the entire polypide, is considered here as *individual*. It is the basic activity that enables feeding and cleaning (e.g. Bullivant 1968; Strathmann 1973, 1982; Winston 1977, 1978; Dick 1984; McKinney 1990; Riisgård and Manríquez 1997;

Nielsen and Riisgård 1998; reviewed in Shunatova and Ostrovsky 2001), including faecal pellet removal (Best and Thorpe 1987; McKinney 1997), and participates in reproduction, i.e. gamete and larval release (Borg 1926; Marcus 1926; Silén 1945, 1966, 1972; Bullivant 1967; Cook 1968, 1985; Gordon 1968; Chimonides and Cook 1981; Cancino and Hughes 1988; Temkin 1994, 1996) and oviposition (Gerwerzhagen 1913; Silén 1945; Corrêa 1948; Nielsen 1981; Dyrynda and King 1983) (reviewed in Reed 1991).

Group autozooidal behaviour implies collective (simultaneous or successive) activity of zooids and, in addition to synchronised polypide protrusion and retraction, includes: (1) joint work of from two to several neighbouring autozooids to intensify feeding, cleaning or removal of filtered water (Winston 1978, 1979) and simultaneous activity of several neighbouring autozooids (sometimes, autozooidal polymorphs) during liberation of spermatozoa (Silén 1966; Chimonides and Cook 1981); and (2) the total activity of all autozooids in a colony resulting in patterning of feeding currents (e.g. Banta et al. 1974; Cook 1977; Winston 1978, 1979; Cook and Chimonides 1980; McKinney 1990). In the present paper the activities included in the first section are called "local group behaviour", whereas, for the second, the term "colonial behaviour" was adopted from Winston (1979). In some marine bryozoans, a supposed sensory activity of "sentry" zooids (Silén and Harmelin 1974; Shunatova and Ostrovsky 2001), the simultaneous zooidal activity performed during sperm release and sometimes embracing large parts of the colonies (Silén 1966), and collective movements of entire zooids (reviews: Silén 1950; Hyman 1959) may also

be considered as colonial reactions. These three kinds of activities, as well as individual reactions, are, for the most part, beyond the scope of this paper. The principal aims of the present paper are: (1) to describe comparatively the autozooidal group behaviour and colony-wide water currents in some bryozoans from the White and the Barents Seas and (2) to discuss various group autozooidal activities and the sources of their regulation.

Materials and methods

Forty species and subspecies of boreal marine bryozoans belonging to different taxa were examined in the course of this study (see Shunatova and Ostrovsky 2001). Group activity was recorded only in 17 species and subspecies of cheilostomatids and cyclostomatids (see Table 1). Observations were made during the summer–autumn field seasons 1994–1996, at the Marine Biological Station (St. Petersburg State University) and the Dalnie Zelencji Field Station (Murmansk Marine Biological Institute). Living colonies were collected by boat dredging and SCUBA from 0 to 20 m depth in the Chupa Inlet (Kandalaksha Bay, the White Sea) and the Yarnjishnaja and Dalnezelenetskaja Inlets (the Barents Sea). Upon arrival in the laboratory the colonies were cleaned and placed in plastic and glass containers with aerated seawater (7–15°C depending on the season). The observations were made mainly in still water; slow local currents were also created by a pipette in the close vicinity of the colonies. The observations were generally started on the day of sampling and were sometimes continued for 3 weeks with the same colonies. Bryozoans were observed under 16× and 28× magnifications, using binocular microscopes. Some colonies were starved by keeping them in containers with filtered seawater for 3 days. Particles used in the experiments included Chinese ink, carmine, activated carbon of different concentrations, as well as detritus and diatoms (genera *Isochrysis*, *Dunaliella*, *Phaeodactilum*).

Table 1 Occurrence of the behavioural reactions in bryozoans from the White and Barents Seas. Reactions: group scanning behaviour (*1*); formation of temporary clusters of polypides to increase and direct water currents (*2*); joint polypide activity for particle removal and colony surface cleaning at high particle concentrations (*3*): repeated particle transference from one lophophore to another in a chain succession (*3a*), inclination of lophophores (*3b*); formation of a chimney by the temporary retraction of a group of polypides (*4*); long-term chimneys (*5*); and sensory behaviour (*S*) (+, the reaction is typical for this species; –, the reaction was not observed in this species; x, the reaction is typical but it is used rather rarely). The designations for reactions are used in the text

Species	Reactions						
	1	2	3a	3b	4	5	S
Electra pilosa	+	+	+	+	–	–	–
E. pilosa var. *dentata*	–	+	–	–	–	–	–
E. crustulenta var. *baltica*	–	+	–	–	–	–	–
Callopora aurita	–	–	+	–	–	–	–
C. lineata	–	–	+	–	–	–	–
C. craticula	–	–	+	–	–	–	–
Tegella armifera	–	–	+	–	+	–	–
Cauloramphus spiniferum	–	–	+	+	–	–	+
Cribrilina annulata	–	x	–	–	–	–	–
C. punctata	–	x	+	+	–	–	–
Celleporella hyalina	–	–	+	–	–	–	+
Escharella immersa	–	–	+	–	–	–	+
Porella compressa	–	–	+	–	–	–	+
P. smitti	–	–	+	–	–	+	–
Hippoporina ussowi	–	–	–	–	–	+	+
Schizomavella lineata	–	+	–	–	–	+	–
Tubulipora flabellaris	–	–	+	–	–	–	–

Results

Local group behaviour

1. Group scanning behaviour was observed in *Electra pilosa* (Linnaeus). Lophophores performed synchronous nods in groups of from five to seven, up to ten, simultaneously bending in the same direction. The scanning continued no longer than 3–4 min, during which time nod directions were constantly changing. In spite of the fact that lophophore rotations are very common in individual scanning behaviour, we never saw them in the lophophore groups. A similar reaction was apparently noted by Winston (1978, p. 28) in *Celleporaria albirostris* (Smitt), and she suggested that this "could... be important in directing current flow".

2. Formation of temporary clusters of polypides to increase and direct water currents was first described in Winston (1978, p. 22; see also Winston 1979; McKinney 1990; Shunatova and Ostrovsky 2001). In *E. pilosa*, *E. pilosa* var. *dentata* (Ellis and Solander), *E. crustulenta* var. *baltica* (Borg) and *Schizomavella lineata* (Nordgaard), expanded lophophores are often oriented towards each other to form clusters (Fig. 1). We also occasionally observed such groups in *Cribrilina annulata* (Fabricius) and *C. punctata* (Hassall). In all cases mentioned, the temporary clusters consisted of equitentacled polypides. The formation of the clusters starts from two to three feeding lophophores, the number of which may increase up to seven. After protrusion and a short period of scanning, a polypide bent its tentacle crown towards the nearest lophophore, sometimes leading to a corresponding change in orientation of the latter. In the close vicinity of these, from one to five polypides often bend towards them. Some polypides may retract and be replaced by others, so the cluster is a dynamic association, in which "readjustments occur as new lophophores join or as former members of the cluster retract" (McKinney 1990, p. 262). At the same time, the position of the group in a colony is rather constant; we observed temporary clusters lasting about 10 min and longer. Total polypide retraction leads to a new pattern in the distribution of the clusters, depending on the position of the first polypides protruded (see also McKinney 1990). This kind of local group activity was most often recorded in starving bryozoans, although it was observed in normally fed colonies as well.

3. Joint polypide activity enables particle removal and colony surface cleaning at high particle concentrations. Several variants of this behaviour are possible:

    a. Repeated particle transference from one lophophore to another may occur in a chain succession towards the periphery or towards the central part of the colony if it consists of non-functional au-
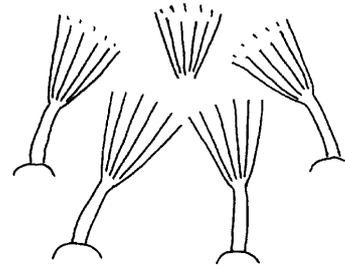

Fig. 1 Temporary cluster of feeding polypides (observed in *Electra pilosa*, *E. pilosa* var. *dentata*, *E. crustulenta* var. *baltica*, *Schizomavella lineata*, *Cribrilina annulata*, *C. punctata*)

tozooids (Fig. 2). Each feeding autozooid generates circular water currents (Grünbaum 1995) that interact with those of its neighbours. In still water, colonial hydrodynamics is the sum of the total interacting zooidal currents (see also Bishop and Bahr 1973). The particles removed may escape singly or in groups between the bases of tentacles and then are elevated and are involved in the process of refiltering (repeated particle transference to the lophophore) by circular currents. Alternatively, particles are often dragged to a neighbouring lophophore at the final stage of such transference, after which the process may occur over and over until the particles are expelled from the colony (Fig. 2a). Such a reaction was recorded in *Electra pilosa*, *Callopora aurita* (Hincks), *C. lineata* (Linnaeus), *C. craticula* (Alder), *Tegella armifera* (Hincks), *Cauloramphus spiniferum* (Johnston), *Celleporella hyalina* (Linnaeus) and *Tubulipora flabellaris* (Fabricius). In *Porella compressa* (Sowerby), *P. smitti* (Kluge) and *Escharella immersa* (Fleming) particle removal may also be performed by lophophore contractions in the successive zooids (Fig. 2b). In *Cribrilina punctata* and *Cauloramphus spiniferum* these contractions are accompanied by simultaneous nods of polypides (Fig. 2c). For the latter species a similar rejection method was first recorded by Winston (1979, p. 257), who believed that this behaviour involves a "coordinated polypide action". The only difference between the activity described by Winston (1979) and that we observed is the absence of cage-making (Winston 1978) at the beginning of this reaction. The successive transference of released eggs in *Electra* species that was described by Borg (1926) is probably based on the same mechanisms. All these reactions are repeated until the particles are removed from the colony. Particle removal is not always performed along a straight line, but always towards the periphery or the central part of the colony when it consists of non-feeding zooids. In obliquely truncate and bent-tentacled lophophores, the particles are always removed towards the side of the longest tentacles.

Fig. 2 Repeated particle transference from one lophophore to another in a chain succession by: **a** ciliary currents (*Electra pilosa, Callopora aurita, C. lineata, C. craticula, Tegella armifera, Cauloramphus spiniferum, Celleporella hyalina, Tubulipora flabellaris*), **b** lophophore contractions (*Porella compressa, P. smitti, Escharella immersa*) and **c** lophophore contractions accompanied by polypide nods (*Cribrilina punctata, Cauloramphus spiniferum*)
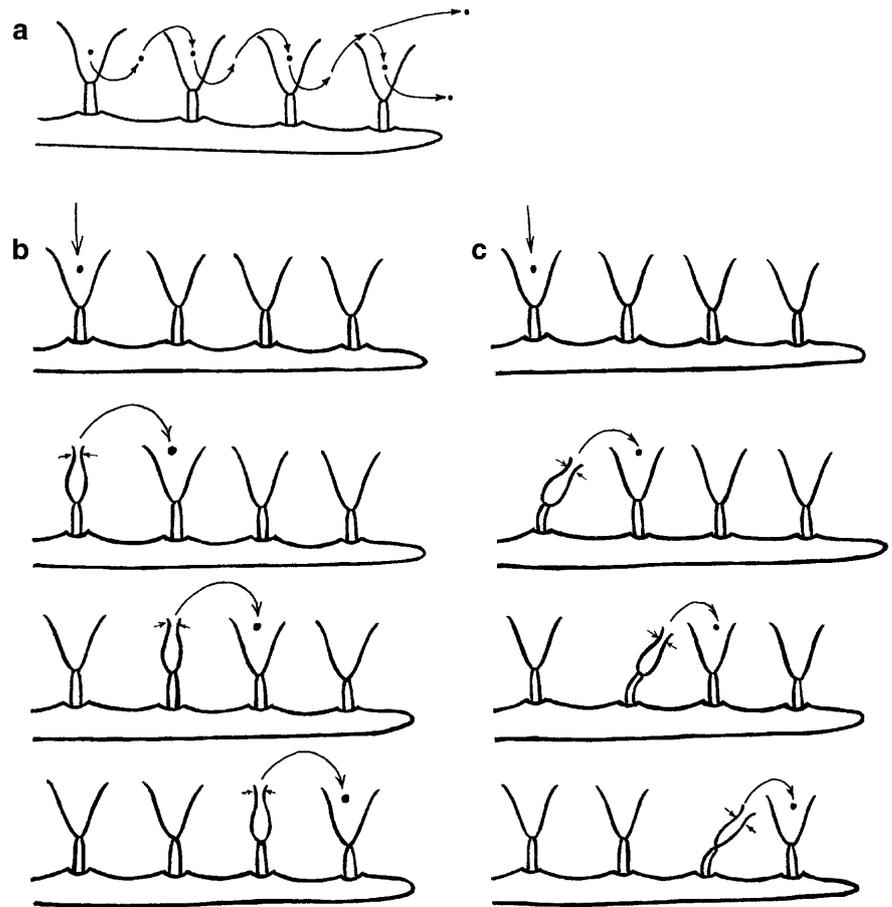
b. In *Electra pilosa, Cauloramphus spiniferum* and *Cribrilina punctata* some polypides can incline their lophophores towards the base of the neighbouring tentacle crown. Particles that escape between the tentacles of the latter are sucked into the inclined lophophore and then they are either swallowed or escape (Fig. 3a). Sometimes chains of the inclined lophophores were observed to function for 3–7 min (Fig. 3b). In *C. punctata* such polypides could reject large particles using lophophore contraction accompanied by a sharp sideways rotation towards the growing edge of a colony. The polypide performs this action while inclined. Tilted polypides may also be used for cleaning of the colony surface in this species (first mentioned in Shunatova and Ostrovsky 2001). We observed that during this action the polypide tilted towards the colony centre or aside (approximately perpendicular to the colony radius), but never towards the growing edge, touching the colony surface with the tentacle tips and filtering particles that lay on the surface or were suspended just above it. The particles sucked then escaped between the tentacles and were removed under the lophophores towards the periphery (Fig. 3c). All such polypides were recorded in the "middle" part of the
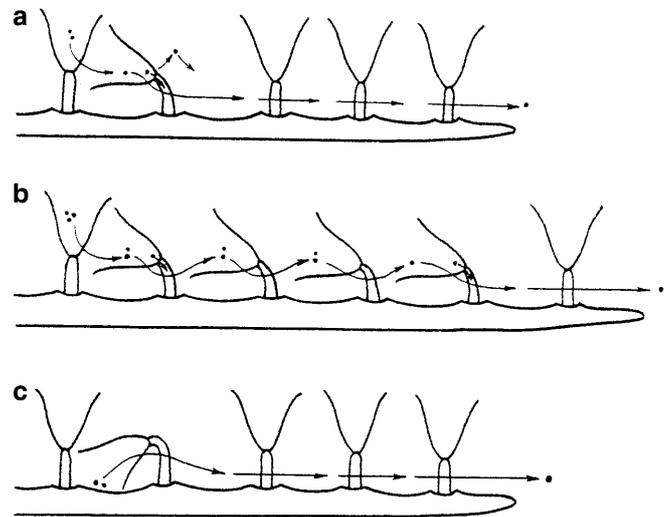
Fig. 3 a Feeding polypide inclined towards the base of the neighbouring tentacle crown, **b** chain of such inclined lophophores (*Electra pilosa, Cribrilina punctata, Cauloramphus spiniferum*) and **c** colony surface cleaning by a tilted polypide (*Cribrilina punctata*)

colony; depending on colony size, they could be from two to seven zooidal generations from the periphery. It is notable that Antipenko (1998) described similar "two-level" feeding in the colonies of the phylactolaemate *Cristatella mucedo*

Cuvier when some polypides fed while being inclined towards the base of their neighbour. Often, several inclined autozooids were seen around the central one, and sometimes there were so many inclined zooids that the whole colony could be described as being divided into two "feeding levels".

4. Local excurrent water outlets (chimneys) can be formed by the temporary retraction of a group of 10–12 neighbouring polypides (Fig. 4). The blank space formed is surrounded by polypides with equitentacled crowns standing vertically. Such chimneys were recorded in *Tegella armifera*.
5. In *Hippoporina ussowi* (Kluge) and *Porella smitti* chimneys are formed in the place where from one to two zooids possess non-functional polypides. We were not able to recognise whether they were retracted or degenerated. The blank space was surrounded by five to seven obliquely truncate lophophores, slightly tilted towards the chimney centre (see Fig. 6b). Occasionally they stood vertically. In both cases the longest tentacles of the polypides bordered the chimney. Such clustering was first described by Cook (1977) in *Flustrellidra hispida* (Fabricius).

Colony-wide water currents and colonial behaviour

Patterned transference of water through a colony ("colony-wide water currents" according to Cook 1977, p. 33) is determined by an interaction of the colony structure (growth form and zooidal arrangement) and collaborative water-pumping activities of autozooids (see also "Discussion"). In the majority of erect species with narrow unilaminate branches, which have frontal and reverse (or abfrontal) sides to the branches, filtered water passes between the tentacles of lophophores to the reverse side of the branches and then downwards to the substratum (Cook 1977; Okamura 1984; Winston 1978, 1979; McKinney 1989, 1991a,b; our observations). This statement does not hold for taxa such as *Cellaria*, *Myriapora* and others with zooids completely encircling the branches. In fenestrate (reteporiform) colonies that can be complexly folded, water passing toward the reverse side of branches may be directed laterally or even away from the substratum, depending on the orientation of the local portion of the colony (for review see McKinney and Jackson 1989; McKinney 1990; Taylor 1999). Patterning is absent in species in which polypides are distant and there is "little or no interaction of feeding currents among individuals" (Cook 1977; Winston 1978, p. 21–22, 1979). This can be encountered in both erect and encrusting forms. We also found an absence of patterning in some colonies of encrusting species in which colony-wide water currents were normally present; in all such cases this was connected with their existence on small or narrow substrata. Similar to young colonies in which patterning is also absent, filtered water was directed upward from a colony surface (Fig. 5a).

In middle-sized, encrusting, multiserial colonies with close zooidal packing, filtered water passes between the autozooids, moving beneath the lophophores towards the periphery or the colony centre when there are no functional autozooids (Fig. 5b) (see also Nielsen 1981). A similar central area with outflow was recorded in the freshwater bryozoan *Cristatella mucedo* (see Antipenko 1998).

Fig. 4 *Tegella armifera*. Formation of a chimney by the temporary retraction of the group of neighbouring polypides
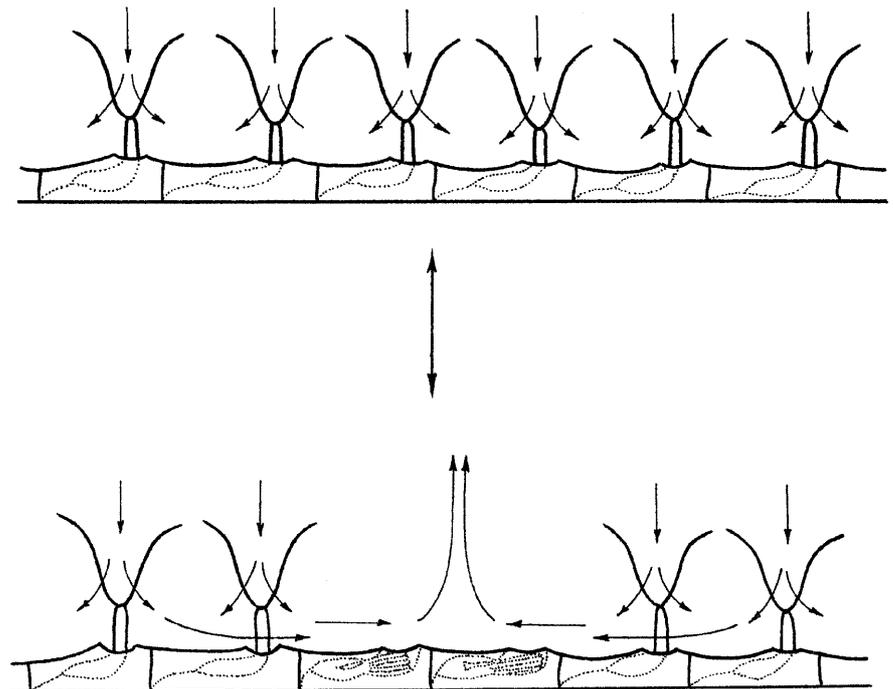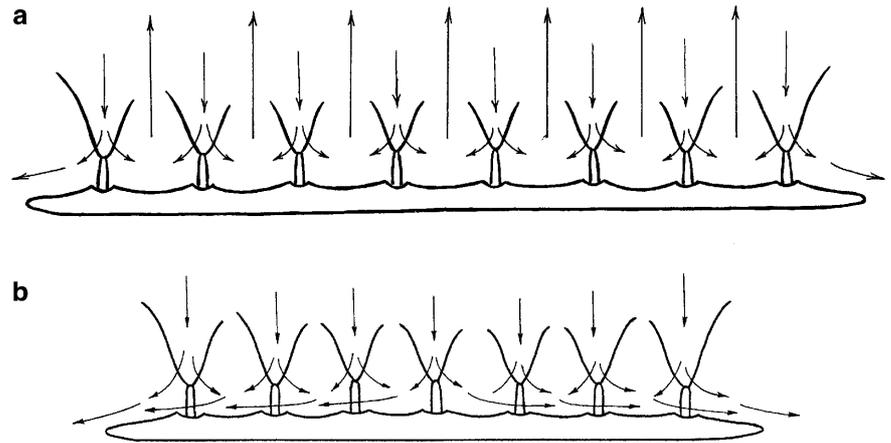
Fig. 5 Schemes of filtered water removal in: **a** encrusting colonies with distant polypides (*Schizomavella lineata, Hippoporina* species) and **b** middle-sized encrusting colonies with close zooidal packing (*Tegella armifera*)

In large, encrusting, multiserial colonies of some species, the removal of filtered water is intensified by formation of small local areas (chimneys), where either groups of autozooids temporarily do not feed or functional autozooids are absent.

In colonies of *Tegella armifera*, most of the polypides are equitentacled. Transition to obliquely truncate lophophore shape, accompanied by a slight increase in polypide size, can be easily seen in a peripheral ring zone (three to six zooidal generations counting from the growing edge), with the outermost polypides slightly tilted from the colony centre. In large colonies, where the central area with degenerated polypides has not appeared yet, from four to six approximately equidistant chimneys were observed within a "middle" ring zone around the central part of the colony. The chimneys were surrounded by polypides with equitentacled crowns standing vertically (see above). Each chimney was formed owing to the temporary retraction of polypides in 10–12 neighbouring autozooids for 10–15 min up to 1 h. During 3–4 h of observations, the chimneys alternately appeared and disappeared at the same places; in some cases, all water outlets were seen, whereas sometimes only part of them were functioning. In such chimneys the polypide retractions and protrusions were not strictly synchronised; polypides performed their excursions one after another successively and almost simultaneously. We were not able to determine how stable the limits of each chimney were. In other words, were exactly the same polypides retracted each time a chimney was formed or were some new polypides involved in chimney formation? We must stress that in species with close zooidal packing, like in *T. armifera*, all autozooids feed simultaneously only incidentally. Normally, several single (occasionally, two to three neighbouring) polypides are retracted and substituted by others. So, small blank spaces are permanently present in a lophophore sheet of the colony (see also Thorpe and Ryland 1987). The chimneys were dynamic in terms of retractions and protrusions, but the position of chimneys was constant during all observations (Fig. 4).

An increase in colony size is always connected with degeneration of the polypides at the colony centre. By this means the central excurrent area is formed, bordered by upright zooids with equitentacled lophophores. The number of chimneys can be increased up to eight, always positioned within a "middle" ring zone around the central part of the colony. The chimneys are located at approximately regular intervals, but the distance to the periphery is slightly different (see also Lidgard 1981; Dick 1987).

Except in young colonies, where all polypides other than peripheral possess equitentacled lophophores, in *Hippoporina ussowi* the shape and size difference between the polypides in the central and peripheral autozooids is much more pronounced (Fig. 6a) than in *T. armifera*. Obliquely truncate lophophores, which are always larger than equitentacled ones, border the colony and surround the chimneys that are formed in the places where one to two zooids possess non-functional polypides (see above). The lophophore gradient mentioned was even sharper in the case of chimneys (see also Cook 1977; Winston 1979, 1981), and this implies that they are long-term structures. In chimneys the obliquely truncate
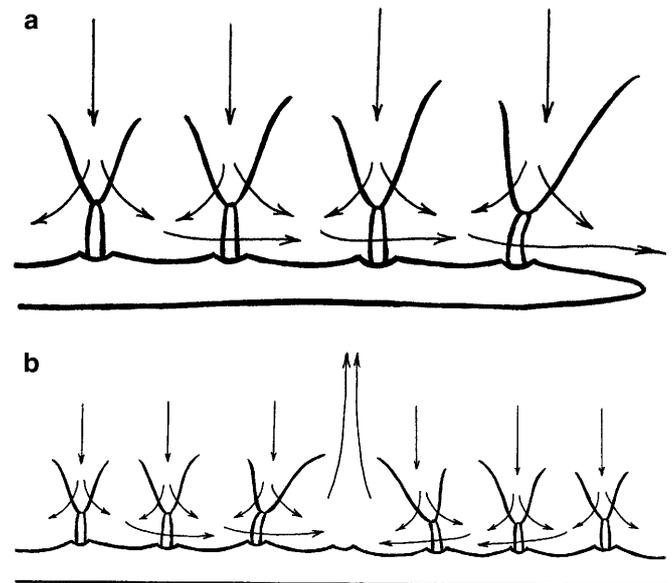

Fig. 6a, b *Hippoporina ussowi*. **a** Polypide shape and size gradient in the peripheral part of the colony and **b** chimney

lophophores were usually slightly tilted towards the chimney centre (Fig. 6b). In some colonies the peripheral polypides were slightly tilted away from the colony centre.

During our studies of *H. ussowi* we were able to observe only one chimney at a time, but, judging from the colony size there, several water outlets can function simultaneously. As in the case of *T. armifera*, the chimneys were never formed within a peripheral ring zone.

In both the latter species, the zooidal groups involved in chimney formation may be considered as "fixed clusters...without reflection by skeletal morphology" (Winston 1978, p. 23; see also Winston 1979, 1981). The same was recorded in colonies of *Porella smitti*, where frontal budding had not yet occurred. However, in large colonies of *P. smitti* and *Schizomavella lineata*, the position of chimneys was reflected in the skeleton depending on the arrangement of monticules formed by the frontal budding. However, in most colonies of these species, when monticules occurred their tops were places of incurrent, but not excurrent flow. The upper part of each monticule consisted of autozooids with upright, equitentacled polypides that actively fed, often nodding to each other. In contrast, the base of the monticules was formed of zooids with obliquely truncate lophophores with the longest tentacles faced towards the "depression" between the monticules (Fig. 7a) (for comparison see also Winston 1979). Between these two different lophophore modes the autozooids on the slopes of the monticules show a gradual change in size and tentacle crown shape: the lower position is taken by larger and more obliquely truncate lophophores. Most of the particles escaping such lophophores are left between the longest tentacles. The monticules observed were placed rather close to each other, and there were only two to five zooids with degenerated polypides in the "depressions" between them. In autozooids that formed the monticule base, the cystid position leads to a bending of their introverts towards the depression centre. An

absence of feeding polypides in the depression, which is surrounded by tilted obliquely truncate lophophores, results in chimney formation. In *P. smitti* such chimneys existed along with those not reflected in the skeleton.

In *S. lineata* we observed chimneys correlated with the monticules only. Newly formed monticules of young autozooids with actively feeding polypides are the places of incurrent flow, whereas the spaces between them are the chimneys (see above). Polypide recycling within these areas leads to a completely opposite picture. The zooids on the tops and slopes of the monticules are devoid of polypides after degeneration. In contrast, autozooids in the depressions between monticules regenerate the polypides that have started to feed. The lophophores of the zooids at the depression bottom are equitentacled and stand vertically. The polypide shape and size change towards the monticules; the largest polypides with obliquely truncate lophophores and with the longest tentacles directed to the monticule top are on the base of the monticule (Fig. 7b). By this means, an absence of the functional polypides at the monticule surrounded by obliquely truncate lophophores results in formation of the water outlet, with a centre coinciding with the monticule top. We suggest that the same can happen with monticules in the colonies of *P. smitti* after polypide recycling.

In the radially "symmetrical", dome-shaped colonies of *Lichenopora verrucaria* (Fabricius) and *Disporella hispida* Gray, all polypides possess bent-tentacled lophophores oriented laterally, so that, while the tentacles are always longer on the side of the lophophore closest to the colony centre, all lean away, or almost away (Fig. 8) (Dr. F.K. McKinney, personal communication; our observations). We note in this connection that the diagram of the lichenoporid colony published as Fig. 1B in Cook (1977) is too schematic. The largest zooids are located around the colony centre. Filtered water is removed between radial rows of zooids towards the colony centre (Cook 1977; Winston 1978; Taylor 1991), which

Fig. 7a, b *Schizomavella lineata*. Change of the incurrent–excurrent function of monticules: **a** before and **b** after polypide degeneration
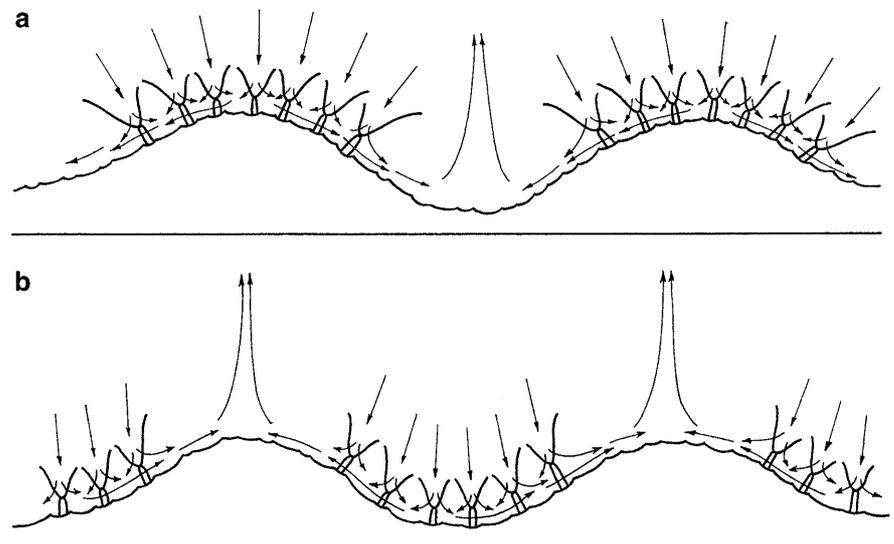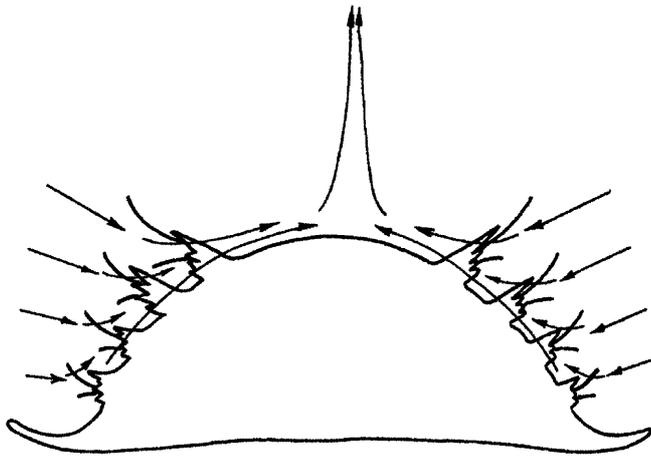
Fig. 8 Scheme of feeding lichenoporid colony

can be compared with a central area devoid of functional polypides and working as a water outlet, as is known in some cheilostomatids (see also above). In contrast with the latter, no peripheral water outflow occurs in lichenoporids (see also McKinney 1990, 1992; Viskova 1992).

In the fan-like encrusting colonies of *Tubulipora flabellaris*, zooids are arranged in linear series, and filtered water is removed from the middle proximally towards the ancestral zone between the series.

Sensory behaviour

Total retraction of polypides in a colony was triggered by different factors: a rapid rise in temperature, strong water currents, touching the colony surface (not a lophophore!) by a needle or the presence of a large, moving object. Also, even a minor addition of particles resulted in a momentary retraction of all polypides. However, in several species observed (*Celleporella hyalina*, *Cauloramphus spiniferum*, *Porella compressa*, *Escharella immersa*, *Hippoporina ussowi*) some polypides everted almost immediately after retraction and stayed expanded throughout the period of disturbance (first noted in *C. hyalina* by Shunatova and Ostrovsky 2001). Some of these "sentry" zooids can retract repeatedly and be replaced by others until the source of disturbance disappears and most remaining polypides protrude. Thus, it appeared as if sentry zooids performed a sensory function during the troubled period and their behaviour may be comparable with that of the nanozooids in some stenolaemates (Silén and Harmelin 1974).

Discussion

The existence of colonial organisms as modular systems with a high level of morphological and physiological integration is based on colonial regulation. From an ecological point of view, a colony is identical to a solitary organism (Boardman and Cheetham 1973), but it would be wrong to consider its vital functions simply as a sum of the zooidal activities. The zooids function more-or-less independently, but the colony control, in a general sense, is always present in even poorly integrated colonies. Concerning feeding activities, the colonial control is absent in such taxa as the cyclostomatide *Stomatopora*, the cheilostomatide *Aetea*, and other encrusting, uniserial forms in which lophophores are tiny compared with the distances between them (McKinney and Jackson 1989; McKinney 1990). The higher the level of colonial integration, the more dependent the zooidal activities (including behaviour) are on this control (Boardman et al. 1983). So, for instance, in bryozoans the degree of colony integration can be estimated primarily from the degree of behavioural integration in polypide activities (Winston 1978), although criteria for such evaluations are not clear (see also McKinney 1984). This section is intended to discuss the role of group zooidal actions in the life of a bryozoan colony and the sources of their regulation.

Neurophysiological and hormonal regulation

In a feeding colony, polypides of autozooids perform different activities at the same time. Some of them retract but are substituted by others; this may be a consequence of the avoidance reaction or be connected with periodical physiological "rest". The influence of a strong irritant applied to a colony surface results in uniform action, namely total or local polypide withdrawal, which is a coordinated nervous response (reviewed in Thorpe 1982). Winston (1978, p. 27) described local group retractions "when it was necessary to clear the space between the branches of a large particle", supposing that it is "one of the simplest types of unified activities". It was not mentioned in the paper if the particle touched the colony surface or not, or whether rough impact of a large, moving particle on several neighbouring polypides or any significant hinderance of normal feeding due to the particle could be considered the reason for the simultaneous retraction.

It is more difficult to judge if the sensory behaviour (see above) is or is not a consequence of coordinated neurophysiological regulation. This activity (see also Silén and Harmelin 1974) can be compared with the group scanning behaviour that was observed in *Electra pilosa*. We suggest that both behaviours might have evolved as methods of receiving information about the environment through specialised sensory structures (summarised in Winston 1978; Shunatova and Ostrovsky 2001). In turn, group scanning resembles, in some ways, synchronised avicularian activity, which is probably coordinated (for discussion see Thorpe 1982). But, the two latter cases involve adjoining zooids, the activity of which can be the result of coordinated nerve impulses travelling locally or embracing large areas. In the case of

sensory behaviour, the sentry zooids are normally distant and their actions appear to be non-coordinated. Moreover, the sentry zooids (which can be any zooids in a colony) are often substituted by others. We can only speculate that their nervous activity might somehow influence a "general nervous background", possibly existing in bryozoans via the "colonial" nervous system (Lutaud 1977; Mukai et al. 1997), and inhibit a protrusion of other polypides in a troubled period. Normal colonial "nervous background" stimulates polypides to feed. For instance, Antipenko (1998) noted that, in *Cristatella mucedo*, a polypide retracts after a disturbance, everts promptly (or after brief pause) if it has been surrounded by feeding polypides, but less quickly if it has been surrounded by retracted polypides.

The potential for joint work of polypides connected with feeding, cleaning and scanning is determined by structural and functional aspects: zooidal as well as polypide size, their structure and arrangement, and a specific spectrum of individual autozooidal reactions (Taylor 1981; Winston 1978; Cook 1985; Shunatova and Ostrovsky 2001). In Stenolaemata this potential is strongly reduced due to an absence of projecting introverts (Farmer 1979; Taylor 1981; McKinney and Boardman 1985; see also Cook 1985). In spite of the fact that McKinney (1988) described slightly projecting introverts in two cyclostomatids from the Adriatic Sea (see also personal communication of J.R.P. Ross cited in Taylor 1981), the only mode of joint activity known at the moment is the repeated particle transference in a chain succession of polypides by interaction of their circular currents, and this is not a coordinated activity (see below). In stenolaemates the colonial structure is a basic factor regulating collective zooidal activity (see also Banta et al. 1974; Anstey 1981). In contrast, in most gymnolaemates the presence of long and flexible introverts is one of the main preconditions for group behaviour (Taylor 1981). However, in the colonies with close zooidal packing, individual activity is strongly restricted and plays a subordinate role in comparison with group reactions (Winston 1978; McKinney 1990; Shunatova and Ostrovsky 2001).

It is generally accepted that synchronous, uniform, zooidal actions are neurophysiologically coordinated (for discussion see Ryland 1979; Thorpe 1982). In contrast, such coordination is not always obvious in the case of some simultaneous or successive activities, even though these are performed by neighbouring zooids. The question further arises if all joint zooidal activities other than group retractions and sensory behaviour are coordinated. Winston (1978, p. 27, 1979), who gave the first descriptions of several local group actions, suggested a high "degree of behavioural (neurophysiological) integration" in the bryozoans possessing them. It is probably correct for several such activities, for instance, a "waving or bending [of] the lophophores in the same direction at once" (Winston 1978, p. 28) and "colony-wide episodes of tentacle 'reversal'" (Cook 1985, p. 29), whereas a repeated particle (or larval) transference from one lophophore to another in a chain succession by their contractions and inclinations (Borg 1926; Winston 1979; our data) we tend to consider as a group, but not a coordinated reaction. In our opinion, repeated transference only superficially appears coordinated because of the regular arrangement of zooids, the polypides of which successively perform a rejection. In other words, it is a simple chain reaction, comparable with particle transference by interacting circular currents (see above), and the coordinating factor here depends on colony structure. Further investigation is necessary to determine whether simultaneous activities performed during formation and functioning of the temporary feeding clusters of polypides and cleaning of the colony surface by the chains of inclined lophophores are coordinated neurophysiologically. We suggest that they could have evolved, respectively, as a reaction to starvation and high particle concentration: cluster formation can intensify colony feeding and cleaning. In both cases an unfavourable situation must be reflected in the physiological state of a colony that, in turn, might result in a nervous response. However, the role of nervous regulation (and, moreover, coordination) here is still unclear, and it is quite possible that polypides in such groups act independently, taking some optimal position in accordance with a particular situation.

For several cheilostomatids and stenolaemates Silén (1966, 1972) described simultaneous autozooidal activity during sperm release that sometimes took place in large colony portions (reviewed by Ryland 1976; see also Cook 1985; Reed 1991). Chimonides and Cook (1981) reported collective activity in groups of male autozooidal polymorphs of the lunulitiform cheilostomatide *Selenaria maculata* (Busk). We can only speculate that in these cases synchronism is based on a hormonal regulation connected with a "simultaneous" maturation of testicles.

Chimneys

Colonial effects on feeding and behaviour of marine bryozoans have been intensively studied since the work of Banta et al. (1974), who observed colonies of the cheilostomatide *Membranipora* sp. and noted that most of the colony was covered by extended polypides, but that there were numerous blank spaces ("chimneys"). In these areas lophophores were not extended, whereas those around the edge of the chimney leaned away from its centre and had obliquely truncated tentacle crowns. Their longest tentacles bordered a chimney. The authors concluded that the incurrent water passed through the tentacles and down between the zooids, exiting via the colony edge or a chimney. They also suggested that formation of excurrent water outlets was connected with colony size. In their opinion, in large colonies "lophophores...interfere with each other unless excurrent channels such as chimneys are present" (Banta et al. 1974, p. 783).

Removal of filtered water from the colonies and co-ordinated autozooidal activity was further studied in detail by Cook (1977) and Cook and Chimonides (1980) (see also Cook 1985). For multiserial, encrusting colonies they noted three patterns of excurrent flow: (1) active centripetal and centrifugal colony-wide flows, (2) "active" local excurrent flows from chimneys ringed by functioning autozooids with obliquely truncated lophophores and (3) "passive" chimneys or local exhalant flows over areas devoid of actively feeding zooids. Their observations on *Membranipora membranacea* (Linnaeus) led them to the opinion that both the position of chimneys in a colony and the position of obliquely truncated lophophores in a chimney are astogenetically determined. In general, these researchers supposed that both astogenetic and ontogenetic (connected with a polypide recycling) changes are involved in production of various forms of filtered water outflows, and agreed with previous assertions (Banta et al. 1974; Taylor 1975) that some reproductive processes might take part in chimney formation (for review and discussion see Cook 1979).

Lidgard (1981), who conducted his experiments on *Membranipora villosa* Hincks, concluded that chimneys are an adaptation which allows colonies to minimise the recirculation of previously filtered water, making the colony more efficient. Dick (1987) proposed a hypothetical mechanism for chimney formation, suggesting that this process may involve both hydrodynamic and astogenetic control, as well as a combination of the two. He also showed the ways of transformation from obliquely truncated lophophore to equitentacled one, and vice versa, in his study on *Holoporella brunnea* (Hincks) and *Membranipora serrilamella* Osburn, and connected the reason for this transformation with lophophore position respective to excurrent flow. Some problems of the spatial arrangement of feeding zooids and their interference in encrusting colonies were also investigated and discussed by Thorpe and Ryland (1987) and later by Grünbaum (1995).

Winston (1978, 1979) recognised six patterns of bryozoan colonial behaviour in relation to the morphology of polypides, their grouping, colony form, and the structure and water currents produced (see also Winston 1981). She distinguished species where colonies were characterised by: (1) predominantly individualised polypide behaviour (see also Cook 1985), (2) separated polypides the orientation of which is controlled by the colony skeleton, (3) polypides forming temporary clusters, (4) polypides forming fixed clusters that are not reflected in the colony skeleton, (5) polypides forming fixed clusters enhanced by irregular skeletal patterning, and (6) polypides forming fixed clusters enhanced by regular patterning of the colony skeleton.

What factor mainly determines such group zooidal actions as the functioning of those chimneys that are not reflected in the skeleton? Functional bryozoan polypides perform feeding, cleaning, gamete release, scanning and avoidance reactions, and group behavioural effects ob-

viously give significant advantages to a colony (Mackie 1963; Silén 1966, 1972; Cook 1977; Thorpe 1982; Okamura and Eckman 1997). However, a colonial existence has some negative consequences, for instance, lophophore interference and difficulty in removal of filtered water (Dick 1987; Grünbaum 1995; see also Bishop and Bahr 1973). It is suggested that colony control of zooidal functions manifests itself in the spatial allocation of incurrent and excurrent water to intensify feeding, to prevent recirculation of previously filtered water, and to remove indigestible particles, faecal pellets and settling larvae (Cook and Chimonides 1980; Lidgard 1981; Palumbi and Jackson 1982; McKinney 1997; see also McKinney 1984). In small, encrusting cheilostomatide colonies all feeding polypides are close to the colony periphery, and filtered water can be easily removed centrifugally beneath their lophophores (Taylor 1999). As growth continues, the perimeter to surface area ratio decreases, but the potential problem with a hampering of the peripheral outflow is obviously compensated for by the formation of larger polypides at the colony edge. During initial colony growth this increase in size is connected with an increase of zooids in the zone of astogenetic change. However, in some species there is a size gradient of polypides in the zone of astogenetic repetition too: younger zooids possess larger polypides. Many encrusting gymnolaemates we observed possessed this feature (for instance, species of the genera *Schizomavella*, *Hippoporina*, *Tegella*, *Porella*), but it was absent in others (*Electra*, *Callopora*, *Cribrilina*, *Celleporella*). So, it is obvious that, being the largest in the colony, these polypides are the strongest pumps, forming a low water pressure zone at the periphery that results in a centrifugal current (see also Cook 1977). Interestingly, the situation in the colonies of lichenoporids and freshwater *Cristatella mucedo* is structurally (but not functionally!) exactly the opposite: the smallest polypides are peripheral, so the main pumping zone surrounds the colony centre, which works as an outlet, and a centripetal current is formed (Cook 1977; Winston 1978; Taylor 1991; Antipenko 1998; our observations). Notably, the peripheral water removal is absent in lichenoporids, but present in *C. mucedo*. In gymnolaemates, the directing of filtered water from the centre is obviously helped by the formation of obliquely truncate lophophores, with the longest tentacles bordering the colony edge. Judging from the measurements of water current inside the ring lophophore (Best and Thorpe 1983, 1986, 1994; Sanderson et al. 1994; Riisgård and Manríquez 1997; for review see also McKinney 1990) and from observations on the particles escaping the obliquely truncate lophophores (Winston 1978; Shunatova and Ostrovsky 2001), the strongest excurrent probably exists within the obliquely truncate lophophore sector with the long tentacles, and the greatest volume of filtered water leaves such lophophores here as well. As known from the literature, the almost obligatory presence of obliquely truncated lophophores around the long-term zones of water outflow supports this idea

(for discussion see also McKinney 1990). Dick (1987) showed in experiments that a zooidal position near the exhalant zone leads to a corresponding change in lophophore shape in some species. He suggested that this could be a physiological response to a differential water flow around the lophophore, perceived via abfrontal sensory structures (see also Winston 1978; Shunatova and Ostrovsky 2001). Dick also described that, in the peripheral zooids of *Membranipora serrilamella*, young polypides possessed equitentacled crowns, the shape of which changes to obliquely truncate during ontogeny. The same modification was recorded after the sectioning of colonies of *Holoporella brunnea*: equitentacled polypides bordering the cut soon became obliquely truncate. We suppose that the polypide-shape gradient towards the colony periphery (mentioned above) may be connected with the same reason: the larger the encrusting colony, the smaller the perimeter to surface area ratio is, the stronger the peripheral excurrent is, and the more pronounced are differences in shape between more central and peripheral polypides. Notably, in *Tegella armifera*, we never saw obliquely truncate lophophores around the central area, which was devoid of functional polypides and obviously working like an excurrent zone; the same was reported by Thorpe and Ryland (1987) for *Tegella aquilirostris* (O'Donoghue and O'Donoghue). The tilted position of peripheral polypides in encrusting gymnolaemates could be connected with interference (see also Dick 1987): the more closely spaced lophophores are, the more pronounced their bending towards the periphery could be.

Further increase in colony size is often accompanied by the polypide recycling that results in appearance of additional excurrent zones. The degeneration starts from the colony centre, where polypides often do not regenerate at all, and expands toward the periphery. Polypide regeneration follows degeneration over most of the colony area in the majority of species, and sometimes there are several successive degeneration–regeneration ring zones in a colony (for instance, two to three in *Celleporella hyalina*, see Cancino and Hughes 1987; Ostrovsky 1998). Also, we already stressed that in species with close zooidal packing (for instance, in *Tegella armifera*), single polypides often retract and are substituted by protrusion of others, which leads to formation of temporary gaps in the lophophore sheet of a colony (see above). In spite of the fact that in some species the neighbouring polypides often tilt towards these spaces (to prevent interference in the opinion of Thorpe and Ryland 1987), they can function as temporary micro-outlets, aiding the zones of peripheral and central outflow. The irregularities in zooidal arrangement, bifurcations, microenvironmental obstructions, and prominent or frontally budded separate zooids (for instance, "tower cells" in *Membranipora membranacea*, female autozooidal polymorphs in *Celleporella hyalina*, dwarf hermaphroditic autozooids in *Cribrilina annulata*), as well as kenozooids and brooding zooids with non-functional polypides, probably can be used for the

same purpose (Cook 1977; Winston 1979; Cook and Chimonides 1980; Cancino and Hughes 1988; Ostrovsky 1998). In many such cases, the existence of excurrent flow results in the obliquely truncate shape of the surrounding polypides (see, for example, Cook 1977).

However, these methods of filtered water removal are, in some cases, probably not sufficient to compensate for the total pumping activity of the polypides. Cook and Chimonides (1980) recorded 2500 lophophores feeding simultaneously in areas not exceeding 30 cm^2 in *Electra pilosa*. Using the related *M. membranacea* as a model, Grünbaum (1995) calculated the existence of strongly negative hydrodynamic interactions between zooids in large, encrusting colonies, in which tentacle crowns form "an interdigitating network above the frontal surface of zooids" (Cook 1985, p. 29). Zooidal interference results in the collision of countercurrents and leads to high water pressure in the interior part of the colony. In turn, this strongly reduces the ability of interior zooids to pump water through their lophophores (for phylactolaemates see also Bishop and Bahr 1973). This conclusion supports the earlier suggestion of Dick (1987), who hypothesised that once a limiting colony size has been reached, the lophophore sheet cannot resist the water pressure beneath, and water outlets must be formed. This author proposed a mechanism of chimney formation in accordance to which filtered water begins "to force its way out at a weak spot in the [lophophore] sheet, such as between two lophophores more widely spaced than others" (Dick 1987, p. 77). A strong excurrent leads to an obliquely truncate lophophore shape of the surrounding polypides, which then further enhances the exhalant function. This particular shape, together with the tilting position, strongly influences the hydrodynamics around the chimney and results in a corresponding shape modification of the neighbouring polypides, similar to that at the colony periphery (see above). Dick (1987) supposed that polypides bending away from the excurrent flow increase the diameter of the forming chimney. However, bordering lophophores can also tilt towards the chimney centre (see observations of Cook 1977 on *Flustrellidra hispida* and our observations on *Hippoporina ussowi*), which may be connected with a reduction in zooidal interference (see also above). In such species lophophores are so close together that their tentacles touch or overlap (Cook 1977; Winston 1979; our observations). We suggest that strong local exhalant flow that originates in the manner described can sometimes influence the bordering polypides in such a way that their feeding is hampered or even becomes impossible. These polypides can temporarily retract (variant of *Tegella armifera*) or degenerate later, which leads to an increase in chimney diameter. In the latter case, one to several zooids are "sacrificed" to increase "a whole feeding efficiency" (Lidgard 1981, p. 135). In *T. armifera*, periods of retraction alternate with feeding; this behaviour resembles the temporary polypide retraction of a central zooid in the chimneys of *M. membranacea* (see Cook and

Chimonides 1980). These outlets are short-term and, in contrast with the long-term ones described in, for instance, *H. ussowi*, the group polypide retraction does not lead to a corresponding modification in the lophophore shape of the surrounding polypides.

We suppose that the first chimney can originate in any suitable place in the interior part of the colony. Successively formed outlets normally have a regular distribution pattern (Cook 1977; Lidgard 1981; Dick 1987) that can be explained by hydromechanical principles (e.g. McKinney 1986a), but irregular distribution has also been described (Cook 1977) and could be connected with the microenvironmental conditions in which the colony was formed. We also speculate that the appearance of a central zone of polypide degeneration in *T. armifera* can lead to a corresponding shift in the location of the chimneys already formed towards the periphery.

If Dick's (1987) model is correct, it must be admitted that, in some species, the appearance, size and spacing of the chimneys are exclusively determined by a physiological response to hydrodynamical factors. In contrast, these characters are thought of as being determined astogenetically in, at least, several species of the genus *Membranipora* (Cook 1977; Cook and Chimonides 1980; Lidgard 1981; Dick 1987) when chimneys are formed at the growing edge of the colony. This may be connected with the high rate of colony growth and large size of membraniporids when the appearance (not their exact location) of chimneys is controlled genetically. However, Okamura and Partridge (1999) have thrown doubt on the astogenetical determination of chimneys in *M. membranacea*. These authors showed a trend towards miniaturisation with increased flow, whereby the zooids were less elongate, the lophophores were smaller in diameter and had fewer tentacles, and the distances between excurrent jets were shorter in experiments. But "if chimneys are astogenetically determined, interchimney distances might be expected not to vary when growth is equivalent", whereas "smaller and shorter lophophores provide less space for excurrent water below the lophophore array [and]...thus, pressure develops more quickly and excurrents must be vented sooner" (Okamura and Partridge 1999, p. 213). This conclusion is consistent with Dick's (1987) hypothesis of a pressure build-up under the lophophore sheet. Nonetheless, Cook and Chimonides (1980) described partially formed chimneys that were recognisable from four to eight zooidal generations proximal to the giant buds, and in which the distal members had not yet developed fully formed lophophores. Proximal and lateral lophophores in such groups "had elongated tentacles...and 'leaning' behaviour". These authors believe that "active chimneys [are] therefore the direct result of astogenetic changes" (Cook and Chimonides 1980, p. 396). We speculate that the appearance of partially formed chimneys, if they are not positioned too closely to the colony periphery, can also be explained by the hydrodynamical model. Judging from the description in question, the distal zooids mentioned obviously had completely formed equitenta-

cled crowns at the moment of observation (in other words, the shape of their lophophores had not changed yet). Additional research is necessary to verify this finding, and a combination of hydrodynamic and astogenetic controls (see Cook and Chimonides 1980; Dick 1987) may be at work in this case.

Often kamptozoans take part in the formation of water outlets. In the White Sea *Loxosomella* sp. lives on bryozoan colonies, preferring species with large polypides (Yakovis 1997; our observations). Being, sometimes, twice as small and situated under the bryozoan lophophores, these entoprocts use water currents generated by bryozoan polypides for their feeding. Moreover, when polypides are not closely packed in a colony, such kamptozoans create the water outlets that function like chimneys. We can only speculate that this may reflect a facultative commensal system.

Following Winston (1979), we have not used the terms "active" and "passive" chimneys, sensu Cook (1977), since her definitions do not describe all existing types of chimneys and can lead to ambiguity. For example, the water outlets described in *Tegella armifera* must be termed "passive" because of the absence of the obliquely truncate lophophores around them, whereas the chimneys formed around microenvironmental obstructions could be thought of as "active" since they are surrounded by such heteromorphs (see also Dick 1987). We think that the terms in question may be better used for describing the extent of colony control in chimney formation, but this requires further definition.

Monticules

Elevated areas on the colony surface, or monticules, are known in many fossil and Recent bryozoans (for reviews see McKinney 1986a,b; McKinney and Jackson 1989). In some cases they are formed of larger zooids that are prominent over a colony surface, in others by frontal budding; their formation could be connected with sexual reproduction (brooding and sperm dispersal) or zooidal budding (for discussion see Banta et al. 1974; Taylor 1975, 1979a; Cook 1977, 1979; Anstey 1981; McKinney and Jackson 1989). Sometimes, the microrelief of the substratum beneath the colony is responsible for the existence of such raised areas (Cook 1979; Winston 1979). An excurrent function of the monticules was first suggested by Banta et al. (1974) for fossil stenolaemate Bryozoa. These authors proposed that the raised areas on the colony surface did not resist the excurrent flow since functional lophophores were absent or modified there. This idea has been supported and exploited by many researchers (e.g. Taylor 1975, 1979a,b; McKinney 1977, 1986a,b; Anstey 1981, 1987a,b; Anstey et al. 1976; Patzkowsky 1987; McKinney and Jackson 1989). Winston (1978, 1979) was the first to record an excurrent flow of filtered water above raised areas (knobs or monticules) in the skeleton of some cheilostomatids. For the monticules consisting of kenozooids (Cook 1979) or

male autozooidal polymorphs (Cook 1968, 1979) this function is quite obvious, and, in the latter case, probably facilitates gamete dispersal (for discussion see also Banta et al. 1974). However, in the monticules formed of autozooids the exhalant function can be disputed. For instance, Anstey (1981) suggested the presence of incurrent monticules in some Paleozoic stenolaemates (see also Anstey 1987a), and our observations on the cheilostomatids *Porella smitti* and *Schizomavella lineata* demonstrate the same. Taylor (1975) and Cook (1977) showed that feeding autozooids were present in the monticules (in Jurassic cyclostomatides and Recent ctenostomatides respectively), but their numbers were much lower than in the spaces between monticules (see also Taylor 1979a). At the same time, judging from Cook's (1977) description and figure of *Alcyonidium nodosum* O'Donoghue and de Watteville, one can suggest that all autozooids had functional polypides in the newly formed monticules and that the monticules were not capable of functioning as water outlets, at least during some period of their existence. For some Paleozoic stenolaemates Anstey (1981) hypothesised that the hydrodynamical regime around their monticules could change from "bypassed" to "funnel" and, further, to excurrent, as monticules become larger during zooidal budding and as autozooidal peristomes change their orientation (see also Patzkowsky 1987). Our observations on *P. smitti* and *S. lineata* strongly support this speculation, although the functional change described in these cheilostomatids is more radical: the incurrent function is substituted for excurrent. The reason for this change is the polypide recycling that engulfs a whole monticule consisting of autozooids of approximately the same age. The position of exhalant flow determines the shape gradient (and its change) of the obliquely truncate lophophores, which are initially equitentacled. This leads us to the following suggestions. In cheilostomatid bryozoans the elevated areas formed by frontal budding can probably change their function at least four times: (1) they can probably work as excurrent zones during the initial stages of formation, when young monticules consist of only incipient zooids with non-functional polypides; (2) later they start to function as incurrent zones; (3) after polypide degeneration, they become excurrent zones; and (4) after polypide regeneration they function as incurrent zones again. The depressions between monticules would probably follow exactly the opposite succession. Thus, the suggestion of Cook (1977, p. 40) that chimney formation could be "the result of colony-controlled cycles of degeneration and regeneration" is supported for this particular case: the alternating excurrent–incurrent function of the monticules and depressions between them is determined astogenetically as well as ontogenetically. Notably, in *P. smitti*, the chimneys associated with the monticules as well as those non-associated can simultaneously exist in the same colony. It appears that until the formation of these elevated areas (or polypide degeneration in them) starts, the previously formed outlets will be functional, but we are not able to say at the moment whether or not the number of chimneys that are not reflected in the skeleton is reduced after these events.

General remarks and conclusions

The data discussed show that there may be four main types of colonial regulation in bryozoans: neurophysiological, physiological, structural (connected with colony formation, and zooidal morphology and arrangement) and, possibly, hormonal, the interactions of which determine all aspects of group autozooidal behaviour. Hormonal and neurophysiological regulation mechanisms may be responsible for simultaneous zooidal activities during sperm release and avoidance behaviour, whereas physiological and structural ones participate in regulating the colonial water balance. During colony development a genetic program dictates a sequence of astogenetical events that occur under microenvironmental pressures. This results in a potential colony size, shape and surface relief as well as a zooidal morphology, size and arrangement that, in turn, determines the colonial hydrodynamics (see also Cook 1977; Winston 1979; McKinney and Jackson 1989; McKinney 1990; Taylor 1999). Hydrodynamics results in an optimal relationship between volumes of entering and filtered water as well as in water turbulence (Winston 1978; Lidgard 1981), being intimately linked with the efficiency of the colonial energy balance. In bryozoans this efficiency is achieved, primarily, by the structural regulation of colonial behaviour when both colony and zooidal size and structure determine the optimal amount and position of simultaneously feeding lophophores "in order to separate, increase and channel feeding currents" (Winston 1978, p. 21, 1979; for discussion see also McKinney 1990). In a growing colony structural regulation influences the colony-wide water currents according to astogenetical changes and the corresponding changes in zooidal interactions (Cook and Chimonides 1980). In large, encrusting colonies this appears to compensate for the negative effects of zooidal interference (see above). However, these effects probably influence the balance in question and, by this means, can affect the physiological state of the whole colony. We suggest that in some cases the origin of the water outlets/chimneys can be a consequence of the physiological regulation that smoothes over contradictions between increasing pumping activity and restricted areas of water outflow. This is triggered by a local rise in water pressure, leading to a particular change of polypide grouping, including possibly polypide suppression, and results in a chimney formation. This local group reaction is directed towards regulation of the colonial water balance, and, as a result, colonial energetic efficiency. Accordingly, a bryozoan colony can be imagined as a self-regulating hydrodynamical system, that, being a living organism, responds to changes in extrinsic as well as intrinsic conditions through several regulatory mechanisms (see also McKinney 1986a, 1991c).

We suppose that in gymnolaemates short-term chimneys might originate first, as a consequence of physiological regulation (variant of *Tegella armifera*). The long-term chimneys could be considered as derivates of the former. Further evolution probably led to chimneys that are already formed during astogenesis (as in case of membraniporids); as previously mentioned, this might be connected with the large size and fast growth that are characteristic of the bryozoan group in question. If these conclusions are correct, membraniporids reflect an interesting combination of plesiomorphic states of morphological characters and the highest level of colonial integration, with "astogenetically" determined chimneys and a growing-edge giant bud.

In bryozoans a comparative evaluation of the degree of colonial integration is mainly based on a morphological approach (Boardman and Cheetham 1973; Cook 1977). The only attempt to estimate it quantitatively was made by McKinney (1984), who used the extent of the interactions of colonial feeding currents for this purpose. Winston (1978, 1979) proposed that the data on group autozooidal behaviour could be useful for such estimations, and worked up a preliminary "matrix", in which "levels of morphological and behavioural integration (with respect to feeding and current producing activities)" are considered (Winston 1978, p. 30). Further accumulation of data on bryozoan behaviour as well as mathematical formalisation are necessary to make progress in this direction and to contribute to a better understanding of colonies as complex living and evolving systems.

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