Individual autozooidal behaviour and feeding in marine bryozoans

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The article is devoted to individual behaviour of autozooids (mainly connected with feeding and cleaning) in 40 species and subspecies of marine bryozoans from the White Sea and the Barents Sea. We present comparative descriptions of the observations and for the first time describe some of autozooidal activities (e.g. cleaning of the colony surface by a reversal of tentacular ciliature beating, variants of testing-position, and particle capture and rejection). Non-contradictory aspects from the main hypotheses on bryozoan feeding have been used to create a model of feeding mechanism. Flicking activity in the absence of previous mechanical contact between tentacle and particle leads to the inference that polypides in some species can detect particles at some distance. The discussion deals with both normal and "spontaneous" reactions, as well as differences and similarities in autozooidal behaviour and their probable causes. Approaches to classification of the diversity of bryozoan behaviour (functional and morphological) are considered. Behavioural reactions recorded are classified using a morphological approach based on the structure (tentacular ciliature, tentacles and entire polypide) performing the reaction. We suggest that polypide protrusion and retraction might be the basis of the origin of some other individual activities. Individual autozooidal behaviour is considered to be a flexible and sensitive system of reactions in which the activities can be performed in different combinations and successions and can be switched depending on the situation.

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INTRODUCTION

Bryozoans are a group of sessile colonial suspension-feeders (Hunt 1925) – active filterers whose feeding apparatus is represented by a ciliated tentacle crown or lophophore. According to Werner (1959) the entire process of active suspension feeding consists of (1) producing a current, (2) filtering or clearing particles from it, (3) transporting the particles to the mouth, and (4) ingesting them. The work of lateral ciliated bands of bryozoan tentacles, with effective strokes of the beating cilia directed outwards in combination with a funnel-like design of the lophophore, generates a descending water current providing a transference of suspended food particles into the tentacle crown. The particles are caught there by different ways (see Gordon & al. 1987, McKinney 1990, Riisgård & Manríquez 1997, Nielsen & Riisgård 1998 for reviews), and filtered water leaves the lophophore between the tentacles. Recently, Grünbaum (1995) both observed and mathematically justified permanent circular currents surrounding the tentacle crown in still water and providing a refiltering mechanism that resulted in repeated recycling of parti-

cles. Filtration is often accompanied by different movements of the tentacles and introvert (summarized in Borg 1926; Hyman 1959; Ryland 1970, 1976; Winston 1977, 1978, 1981; McKinney & Jackson 1989; McKinney 1990).

Bryozoans demonstrate various individual as well as group zooidal activities mainly connected with transfer of water bearing suspended particles (food, wastes, and gametes) through the lophophore and entire colony. Hence it is generally accepted that the behaviour of autozooids includes feeding, cleaning and gamete manipulation. Behaviour depends on various intrinsic and extrinsic factors and reactions may be switched (Okamura 1987a, 1987b).

In general, all behavioural reactions of bryozoans may be divided into two groups. Individual activity includes the work of cilia (excepting the cases when cilia are absent in male autozooidal polymorphs) together with different movements of tentacles and entire polypide of the zooid performed independently of the activities of other colony members. They can be connected either with feeding and cleaning (Bullivant 1968a; Winston 1977, 1978; Strathmann 1973, 1982a; Dick

1984; Riisgård & Manríquez 1997; Nielsen & Riisgård 1998; etc.), including fecal pellet removal (Best & Thorpe 1987; McKinney 1997), or with different aspects of reproduction: gametes and larval release (Borg 1926; Marcus 1926a; Silén 1945, 1966, 1972; Bullivant 1967; Cook 1968; Gordon 1968; Ström 1969; Chimonides & Cook 1981; Cancino & Hughes 1988; Temkin 1994, 1996) and oviposition (Gerwerzhagen 1913; Silén 1945; Corrêa 1948; Nielsen 1981; Dyrynda & King 1983) (see Reed 1991 for review). Group behaviour includes collective activities of several neighbouring or all autozooids in a colony to intensify feeding and cleaning by creating local and colony-wide water currents (Cook 1977; Winston 1978, 1979; Cook & Chimonides 1980; etc.), or occasionally is involved in processes connected with reproduction (Borg 1926; Silén 1966) (see also above). Group reactions are mainly beyond the scope of the current paper as well as movements of entire zooids known in some marine bryozoans (reviewed in Silén 1950 and Hyman 1959). The principal goals of this paper are to (1) describe comparatively the variety of individual zooidal activities in marine ectoprocts, (2) discuss possible ways of classifying these activities, and (3) create a model of feeding mechanism, using non-contradictory aspects from the main hypotheses on bryozoan feeding. We believe that further enhancement of our knowledge of individual autozooidal behaviour will greatly assist in understanding the origin and function of group activities which, in turn, will give additional opportunities to investigate the bryozoan colonies as integral systems.

MATERIAL AND METHODS

The present study deals with 40 species and subspecies of boreal marine bryozoans (see Tables 1 & 2). 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 dredging and SCUBA diving from 0-20 m depth in the Chupa Inlet (Kandalaksha Bay, White Sea) and the Yarnjishnaja and Dalnezelenetskaja Inlets (Barents Sea). Bryozoans were found on stones, fronds of algae (*Fucus serratus*, *F. vesiculosus*, *Ascophillum nodosum*, *Laminaria saccharina*, *Phycodris rubens*, *Ptilota plumos[*, *Odonthalia dentata*, *Phillophora brodeui*, *Ahnfeltia plicata*), hydroids (*Obelia geniculata*, *O. longissima*), ascidians (*Styella rustica*), and shells of living and dead bivalves (*Mytilus edulis*, *Modiolus modiolus*, *Chlamys islandicus*, *Arctica islandica*) and gastropods (*Neptunea despecta*). Upon arrival in the laboratory the colonies were cleaned and placed in plastic and glass containers with aerated seawater (from 7 to 15 °C depending on the season). Observations were made mainly in still water; slow local currents were also created by a pipette in close vicinity to colonies. The observations were generally started on the day of sampling and were sometimes continued for three weeks with the same colonies. Colonies were starved by keeping them in containers with filtered seawater for three 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*). Particles with a diameter about 5 μm are denoted as "small", about 10 μm as "middle-sized", and more than 25 μm as "large" in this paper. Measurements of polypides as well as cystids were taken in the course of study (see Table 1).

Only six species (*Flustrellidra hispida* (Fabricius), *Buskia nitens* Alder, *Alcyonidium mytili* Dalyell, *Electra pilosa* (Linnaeus), *Cribrilina punctata* (Hassall), *Celleporella hyalina* (Linnaeus)) were studied from the Barents Sea localities, and all of these were also present in the White Sea samples. Particular emphasis was given to the comparison of the behaviour of the same species collected from different localities and, sometimes, different seas, as well as to the behaviour of different species from the same localities.

RESULTS

Polypide activity consists of three successively alternating phases: I) protrusion, including pausing in a testing-position in some species; II) feeding, cleaning or reproductive activities properly; III) retraction (see Winston 1978 and Dick 1984 for terminology).

I & III. Polypide protrusion and retraction

Both phases, noted for the first time by Cavolini (1785:241) and described in details by Farre (1837:399, 411), are the "mirror-image" halves of the process that leads to change of coelomic fluid pressure by muscular contraction (summarized in Borg 1926; Ryland 1970; Kluge 1975; Taylor 1981; Mukai & al. 1997; Taylor 1999) and results in the tentacle crown displacement in respect to the zooid orifice and tentacle sheath (see also Johnston 1838, Dalyell 1847-1848, Hincks 1880, Winston 1978). Therefore, we consider them together. In most species studied polypide protrusion (or retraction) is normally accompanied by a gradual, but not slow, expansion (or closure) of the lophophore, starting when an introvert is half or completely everted (the last case was observed in *Tegella armifera* (Hincks), *Cribrilina annulata* (Fabricius) and, sometimes, *Electra pilosa*). In some species (*Cauloramphus spiniferum* (Johnston), *Schizomavella lineata* (Nordgaard), *Elec-*

Table 1. Dimensions of several polypide and zooidal characters of the White Sea bryozoans (in mm).

Species	Lophophore diameter	Tentacle length	Introvert length	Zooid length	Zooid width	Orifice length	Orifice width	Tentacle number	Lophophore shape	Colony growth form
Cheilostomatida										
Electra pilosa +										
E. pilosa var. *dentata*										
E. crustulenta var. *baltica*	0.5-0.55	0.35-0.5	0.2-0.4	0.5-0.65	0.3-0.45	0.3-0.5	0.25-0.4	10-12	ET	EN
Tegella armifera	0.5-0.65	0.5-0.6	0.15-0.4	0.45-0.55	0.25-0.3	0.25-0.4	0.15-0.25	12-16	ET, SOT	EN
*	0.5-0.8	0.5-0.7								
Callopora aurita	0.5	0.35-0.5	0.3	0.4-0.5	0.25	0.35-0.45	0.2	14	ET	EN
C. lineata	0.4	0.45	0.3	0.4	0.25	0.2	0.15	12	ET	EN
C. craticula	0.3-0.4	0.3-0.35	0.2-0.3	0.25-0.3	0.15	0.15	0.1	10-12	ET	EN
Cauloramphus spiniferum	0.75-0.8	0.6-0.75	0.35-0.4	0.45-0.65	0.3-0.35	0.4-0.55	0.25	16-18	ET	EN
Cribrilina annulata	0.65-0.7	0.45-0.5	0.25	0.55-0.6	0.3-0.4	0.1-0.15	0.1-0.15	12	SOT	EN
C. punctata	0.6-0.75	0.3-0.55	0.35-0.45	0.4-0.55	0.3-0.35	0.1-0.15	0.15-0.2	14	ET	EN
*	0.6-0.8	0.45-0.8								
Escharella immersa	0.5-0.65	0.4-0.55	0.1-0.2	0.5-0.85	0.3-0.35	0.1-0.15	0.1-0.2	12	SOT	EN
*	0.45-0.75	0.3-0.65								
Porella compressa	0.6	0.4-0.6	0.15-0.2	0.4	0.35	0.2	0.15-0.2	16	SOT	EN
P. smitti	0.55-0.7	0.5-0.6	0.1-0.2	0.4-0.6	0.3-0.4	0.15-0.2	0.15-0.2	14	SOT	EN
*	0.5-0.8	0.4-0.95								
Schizomavella lineata	0.4-0.75	0.65	0.1-0.3	0.35-0.6	0.25-0.45	0.1-0.15	0.1-0.15	12; 14	SOT	EN
*	0.5-0.8	0.7-1.1								
Hippoporina ussowi	0.7-0.8	0.6-0.7	0.25-0.4	0.5-0.8	0.35-0.6	0.15-0.25	0.15-0.2	14; 16;18	SOT	EN
*	0.7-0.9	0.7-1.05								
H. reticulatopunctata	0.7	0.5-0.6	0.15-0.25	0.55-0.7	0.4-0.45	0.2-0.25	0.2	14-16	SOT	EN
*	0.7-0.9	0.55-1.0								
H. harmsworthi	0.85-0.9	0.5-0.6	0.35	0.5-0.7	0.3-0.55	0.15-0.25	0.15-0.2	14-16	SOT	EN
*	0.9-1.05	0.7-1.1								
H. propinqua	0.55-0.7	0.5	0.2-0.35	0.4-0.6	0.35 -0.5	0.1-0.15	0.15-0.2	12	SOT	EN
*	0.7-0.85	0.45-0.8								
Rhamphostomella ovata	0.5-0.7	0.4-0.45	0.1-0.2	0.4-0.7	0.3-0.45	0.15-0.25	0.15-0.2	14	SOT	EN
*	0.5-0.8	0.5-0.85								
R. bilaminata	0.6-0.8	0.45- 0.7	0.25-0.3	0.4-0.5	0.4-0.45	0.15	0.15	12	SOT	EN
*	0.6 -0.85	0.5-0.8								
Celleporella hyalina	0.35-0.4	0.35	0.25	0.4-0.45	0.2-0.25	0.1	0.1	12	ET	EN
Stomachetosella cruenta	0.4	0.5-0.7	0.05-0.15	0.4-0.65	0.35-0.5	0.1-0.2	0.15-0.2	12; 14	SOT	EN
*	0.4-0.6	0.5-0.9								
Cylindroporella tubulosa	0.55-0.7	0.25-0.45	0.05-0.1	0.35-0.5	0.2-0.3	0.1	0.1	10	SOT	EN
*	0.5-0.7	0.25-0.4								
Scrupocellaria scabra +										
S. elongata	0.5-0.6	0.5-0.6	0.15-0.4	* *	* *	* *	* *	12-16	SOT	ER
Eucratea loricata	0.35-0.4	0.2-0.25	0.1-0.2	0.65-0.7	0.15-0.2	0.3-0.35	0.1	10	ET	ER
Tricellaria gracilis	0.6	0.55	0.2-0.25	0.6	0.25	0.25-0.3	0.15-0.2	14	ET	ER
Ctenostomatida										
Alcyonidium mytili	0.7	0.5	0.4	0.4-0.65	0.25-0.3	0.05	0.05-0.1	14	ET	EN
Buskia nitens	0.35	0.25	0.15-0.2	0.35-0.4	0.2	**	**	8	ET	EN
Bowerbankia sp.	0.5-0.65	0.45-0.5	0.25-0.3	0.8-1.3	0.25-0.3	**	**	8; 10	ET	EN
Flustrellidra hispida	1.0-1.15	0.55-0.9	0.25-0.4	0.9-1.1	0.5-0.7	**	**	26; 28	ET	EN
Cyclostomatida										
Crisia sp.+ *Crisiella producta*	0.3-0.5	0.3-0.35	0	**	**	**	**	8	ET	ER
Lichenopora verrucaria *	0.3-0.8	0.1-1.1	0	**	**	**	**	8	AOT	EN
Disporella hispida *	0.3-0.8	0.1-1.1	0	**	**	**	**	8	AOT	EN

* measurements were made for obliquely truncated lophophores.

** insufficient data.

Lophophore shape: ET-all polypides in the colony have equally tentacled lophophores; SOT-some polypides in the colony have obliquely truncated lophophores; AOT-all polypides in the colony with obliquely truncated lophophores.

Colony growth form: EN-encrusting; ER-erect.

Data are absent for 5 species: *Porella proboscidea*, *Rhamphostomella scabra*, *R. spinigera*, *Arctonula arctica*, *Tubulipora flabellaris*.
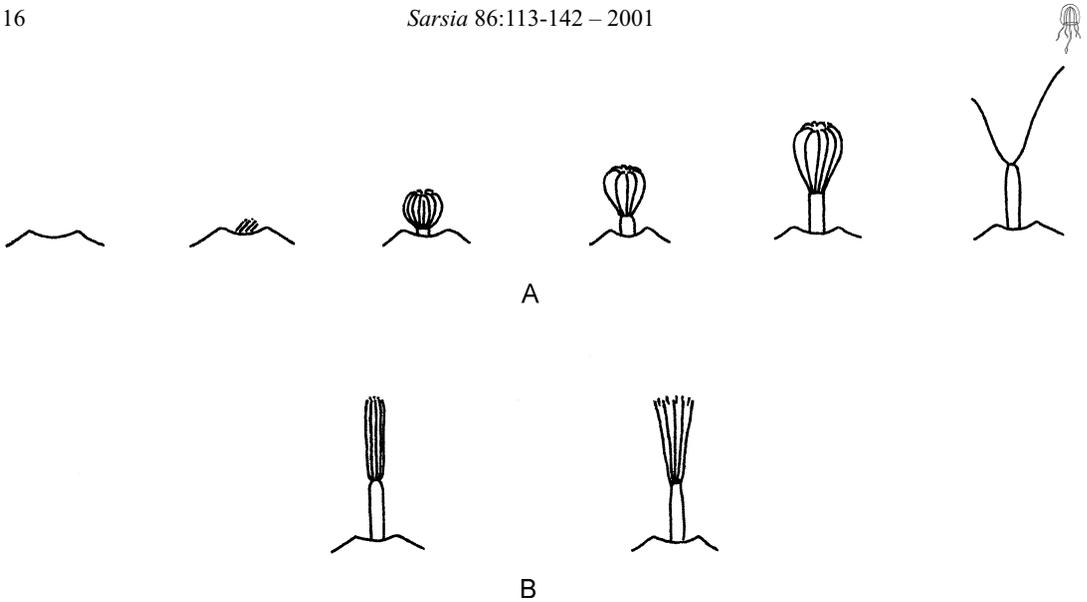
Fig. 1. A, polypide protrusion in *Schizomavella lineata*; B, variants of testing-position.

tra crustulenta var. *baltica* Borg, and, sometimes, *E. pilosa*) both these processes are usually accompanied by a sharp, energetic expansion or closing of the tentacle crown respectively. In contrast, very slow expansion (comparable with testing behaviour, see below) was sometimes observed in *Hippoporina reticulatopunctata* (Hincks) and in *Escharella immersa* (Fleming). So, there are at least three patterns of polypide movement, differing from each other in speed (see also Thorpe 1975, Thorpe & al. 1975). In *Schizomavella lineata* the lophophore sometimes spreads out through the stage of an "opening bud": during the slow protrusion the tentacles curve in such a manner that their tips stay near the mouth region. Later on the tentacles gradually straighten and expand (Fig. 1A). In *Tegella armifera* and *Stomachetosella cruenta* (Busk) the polypides bring the tips of their tentacles together, forming a tube, and twist them by 30-40 degrees before the retraction, and untwist them just after the protrusion (see also Winston 1978).

Testing-position (illustrated first in Farre 1837, pl. XX, fig. 2, pl. XXII, fig. 2, pl. XXIII, fig. 3, pl. XXV, fig. 2; see also Borg 1926, Winston 1978) was observed in eight species: *Cribrilina punctata*, *Callopora craticula* (Alder), *C. aurita* (Hincks), *C. lineata* (Linnaeus), *Rhamphostomella bilaminata* (Hincks), *Celleporella hyalina*, *Eucratea loricata* (Linnaeus), and *Alcyonidium mytili*. Polypides perform a partial protrusion in this case: either only the tips of the tentacles are protruded, or the entire crown (with tentacles brought together like a narrow tube or, sometimes expanded a little) and a small part of the introvert are everted (Fig. 1B). The polypide can stay in both positions from several sec-

onds to several minutes. The polypide can also linger in a position resembling testing during retraction (see also Thorpe 1975, Thorpe & al. 1975, Winston 1978). For all eight species both modes of testing were recorded.

A reaction that may be considered as a variant of the testing-position was observed in *Scrupocellaria elongata* (Smitt), *S. scabra* (van Beneden), and *Schizomavella lineata*. During protrusion tentacles bend their tips slightly inside the lophophore. Once completely everted, the polypide stays in this position for some time and then expands.

II. FEEDING AND CLEANING

Protrusion results in the polypide feeding position. Polypide lophophores may have different shapes and sizes (summarized in Winston 1977, 1978; McKinney 1990; see also Farre 1837, Hincks 1880, Ryland 1975, Cook 1977) varying both among taxa (see Table 1) and often within the colony.

In most species studied, observed filtering polypides were usually motionless. Some of the suspended particles that are carried to the lower part of the lophophore by descending currents pass directly to the mouth, which is permanently open, but periodically slightly contracts. Contractions of stomodaeum muscle are aided by both the activity of pharyngeal cilia and pharyngeal musculature (see above). Particles are concentrated in the pharynx and passed in parcels to the oesophagus. All species studied possess this basic mode of feeding (summarized in Winston 1977, 1978, 1981; see also Borg 1926, Atkins 1932, Silén 1944, Bullivant 1968b,

Strathmann 1973, Gordon 1974, Gilmour 1978, Best & Thorpe 1983, Riisgård & Manríques 1997, Nielsen & Riisgård 1998). In contrast to Winston (1978, 1979), we call it here "active filtration" to emphasize the active nature of bryozoan suspension feeding that differs from passive filtration in deposit-feeders (see Jumars & al. 1982).

In cyclostomatide species uncaptured particles mainly escape in the upper part of the lophophore. In the ctenostomatide and cheilostomatide species studied the particles often leave the tentacle crown not only near their tips but also in the middle and lower parts of the lophophore and it varies in different species depending on situation. In obliquely truncate lophophores particle removal mainly occurs between the bases of the two longest tentacles or between the group of longest tentacles, and this may be connected, in contrast with equitentacled crown, with a bilaterally symmetrical lophophore shape resulting in different current velocities at the opposite sides inside the lophophore (see Best & Thorpe 1983). Some of the escaping particles are involved in the process of refiltering (or repeated particle transference to the lophophore) by circular currents (Fig. 2A). Such particle recirculation was found in different species, but additional research is needed to clarify its relationship to bryozoan feeding. We suggest, however, that bryozoans avoid the refiltering in natural conditions, since they normally live in a flow (see Grünbaum 1995 and Lidgard 1981 for discussion).

Bryozoans in our experiments were not highly selective in relation to the qualitative characteristics of suspended particles. They swallowed particles of different composition in similar manner and their behavioural reactions were the same when we added either organic or inorganic particles in the water.

The response to contact with large particles was almost always negative and polypides, if not starving, tried to escape from them in various ways up to retraction (discussed in Best & Thorpe 1996). In contrast, small and middle-size particles triggered a whole spectrum of different reactions.

Absence of particles leads to an increase in the activity of polypides, and after a certain period they start to turn and bend, scanning space around them. The addition of a small amount of small and middle-sized particles results in a gradual decrease of scanning, and polypides become almost motionless. The velocity of active filtration seemingly stays constant, as estimated by watching particles transported by the feeding current, and equals some average value characteristic for each species. Further increase of particle concentration in our experiments led to increased water current velocity. Polypides often do not perform any more activity. On the other hand, many species show different
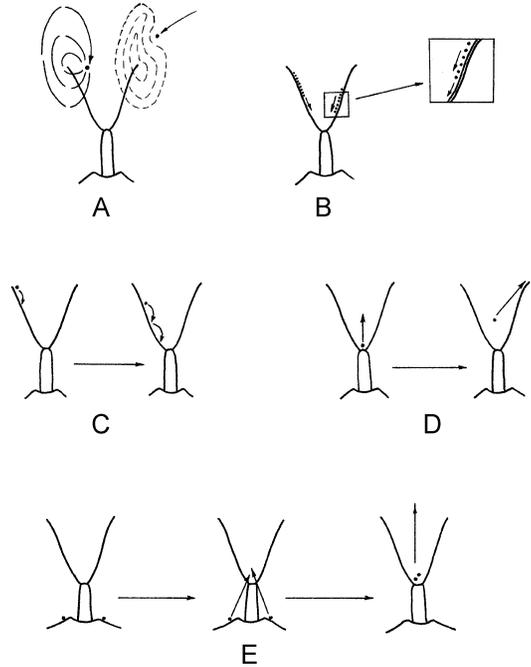

Fig. 2. A, water refiltering, and disturbances of water that arise from a particle entering into "circular" water currents (shown by interrupted and stippled lines) (arrows: direction of particle movement); B, frontal particle transport in the form of "laces"; C, frontal particle transport by means of jumps in *Schizomavella lineata* and *Escharella immersa*; D, particle rejection by lateral ciliary reversal in *Cauloramphus spiniferum*; E, cleaning of colony surface by ascending current (created by lateral ciliature reversal).

movements of tentacles and the entire lophophore as particle concentration increases. Redundant particle concentration causes more or less fast retraction of polypides.

Active filtration is a background for almost all other individual activities of polypides (summarized in Table 2). Two groups of behavioural (mainly, particle-handling) reactions were recorded (see below), and they may be considered separately (if the reaction was already described, we give some references in brackets without mentioning species). These reactions may be arbitrarily treated as "basic" or "elementary". Working often together or successively, they form more complex reactions.

The first group includes all the activities that are carried out exclusively by tentacle cilia with motionless polypide (numbered according to Table 2):
1. Collection of particles in a group inside the expanded lophophore near, or sometimes a little above, the mouth

Table 2. Occurence of the behavioral reactions in bryozoans from the White Sea.

Species								Reactions									
	1	2	3a	3b	4	5	6	7a	7b	8a	8b	9	10	11	12	13a	13b
Cheilostomatida																	
Electra pilosa + *E. p.* var. *dentata*	-	-	+	+	-	-	++	+	-	+	+	-	+	-	-	+	+
Electra crustulenta var. *baltica*	-	-	+	+	-	-	++	+	-	+	+	-	+	-	-	+	+
Tegella armifera	+	+	+	+	-	-	++	+	-	+	+	-	-	-	+	+	+
Callopora aurita + *C.lineata*	+	-	+	+	-	+	+	+	+	-	-	-	-	-	+	+	-
C. craticula	-	-	+	-	-	+	+	+	+	-	-	-	-	-	+	+	-
Cauloramphus spiniferum	+	-	*	-	-	-	++	+	-	-	-	-	-	-	+	+	+
Cribrilina annulata	-	+	-	-	-	-	++	+	-	+	-	-	-	-	-	-	-
C. punctata	-	+	-	-	-	+	++	+	+	-	-	-	-	-	-	-	-
Escharella immersa	+	*	+	-	-	*	+	+	-	+	-	-	-	-	+	+	-
Porella compressa	+	-	-	-	-	-	+	+	-	-	-	-	-	-	-	+	+
P. proboscidea	-	+	-	-	-	-	+	+	-	-	-	-	-	-	+	+	-
P. smitti	-	+	-	-	-	-	+	+	+	-	-	-	-	-	-	-	-
Schizomavella lineata	-	*	-	-	-	*	+	+	+	+	-	-	-	-	+	+	+
Hippoporina harmsworthi	+	-	+	-	-	-	+	+	-	-	-	-	-	-	+	+	-
H. reticulatopunctata	-	-	+	+	-	*	+	+	-	+	-	-	-	-	+	+	-
H. ussowi	-	-	-	-	-	-	+	+	+	+	+	-	-	-	-	+	-
H. propinqua	-	-	+	-	-	-	+	+	-	+	-	-	-	-	+	+	-
Rhamphostomella bilaminata	-	+	+	+	+	+	+	+	-	+	-	-	-	-	+	+	-
R. ovata	-	+	+	+	-	-	+	+	-	+	-	-	-	-	+	+	-
R. scabra	-	+	+	+	-	-	+	+	-	+	-	-	-	-	+	-	-
R. spinigera	-	+	+	+	-	-	+	+	-	+	-	-	-	-	-	-	-
Celleporella hyalina (White Sea)	-	+	-	-	-	+	+	+	-	-	-	+	-	-	-	+	+
C. hyalina (Barents Sea)	+	-	-	-	-	+	+	+	-	-	-	-	-	-	-	+	+
Scrupocellaria scabra + *S. elongata*	+	-	+	+	+	*	+	+	-	-	-	-	-	+	-	-	-
Arctonula arctica	+	+	-	+	+	-	-	+	+	+	+	-	-	-	-	-	-
Stomachetosella cruenta	+	+	+	+	-	-	-	+	+	+	+	-	-	-	-	+	+
Cylindroporella tubulosa	-	+	-	-	-	-	+	+	-	+	-	-	-	-	-	-	+
Eucratea loricata	-	-	-	-	-	+	+	+	-	-	-	-	-	-	+	+	-
Tricellaria gracilis	-	-	-	-	-	-	+	+	-	-	-	-	-	-	+	+	-
Ctenostomatida																	
Alcyonidium mytili	-	-	-	-	-	+	+	+	+	+	-	-	-	-	+	+	-
Buskia nitens	-	-	-	-	-	+	+	+	-	+	+	-	-	-	+	+	-
Bowerbankia sp.	-	-	+	-	-	-	++	+	+	-	-	-	-	-	+	+	-
Flustrellidra hispida	+	+	+	-	-	-	+	+	-	+	+	-	-	-	+	+	-
Cyclostomatida																	
Crisia sp.	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	+	-
Crisiella producta	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+	+	-
Lichenopora verrucaria	-	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-
Disporella hispida	-	-	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-
Tubulipora flabellaris	+	-	+	-	-	-	-	+	-	+	-	-	-	-	+	+	-

COMMENTS TO TABLE 2 (names of the reactions)

(1) collection of particles in a group inside the expanded lophophore by the lateral cilia work; (2) transport of particles downward along the surface of tentacles by the frontal cilia; (3) rejection of particles by ciliary reversal on all tentacles: (a) particles are lifted by an ascending current in the centre of lophophore by the reversal of lateral cilia, (b) particles are removed along the tentacle frontal surface by reversal of beat of the frontal cilia; (4) cleaning of the colony surface using an ascending current created by the reversal of lateral cilia; (5) testing-position; (6) scanning activity; (7) flicking activity: (a) flicks without any particles inside the lophophore, (b) particle transfer to the central current by tentacle flick; (8) bending of a single or 2-3 tentacles deep inside the lophophore: (a) in absence of any particles, (b) when tentacle placed a particle directly to the mouth; (9) retaining particles inside lophophore and cramming them into the mouth by synchronous work of several tentacles; (10) waving; (11) pushing away the particles by tips of tentacles; (12) single lophophore expansion; (13) single lophophore contraction: (a) sharp contraction with small amplitude, (b) contraction with a nod-inclination or partial retraction of the polypide; (14) repeated expansions and contrac-

Table 2. (continued)

Species	Reactions														
	14a	14b	15	16	17	18	19	20	21	22a	22b	23a	23b	24a	24b
Cheilostomatida															
Electra pilosa + *E. p.* var. *dentata*	+	-	+	+	-	-	-	-	-	-	-	*	-	-	+
Electra crustulenta var. *baltica*	+	-	+	+	-	-	-	-	-	-	-	*	-	-	+
Tegella armifera	+	-	+	+	+	-	+	-	+	+	+	-	-	-	+
Callopora aurita + *C.lineata*	-	-	-	+	-	-	-	-	-	-	-	-	-	-	+
C. craticula	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+
Cauloramphus spiniferum	-	+	-	-	-	+	+	-	-	+	+	-	-	-	-
Cribrilina annulata	+	-	-	-	-	+	-	-	-	+	+	+	-	-	+
C. punctata	+	-	+	+	-	-	+	-	-	+	+	-	-	-	-
Escharella immersa	+	-	+	+	-	-	-	-	-	-	-	-	-	-	+
Porella compressa	+	-	+	-	+	+	-	-	+	-	-	-	-	-	+
P. proboscidea	+	-	+	-	-	+	-	-	+	-	-	-	-	-	+
P. smitti	+	-	-	+	-	+	-	-	+	-	-	+	-	-	+
Schizomavella lineata	+	-	-	-	-	+	+	-	-	-	-	-	-	-	-
Hippoporina harmsworthi	+	-	+	+	-	+	-	+	+	-	-	+	-	-	-
H. reticulatopunctata	+	-	-	+	-	+	-	-	-	-	-	+	-	-	-
H. ussowi	+	+	-	+	+	+	-	-	+	-	-	+	-	-	-
H. propinqua	+	-	-	+	-	+	-	-	-	-	-	+	-	-	-
Rhamphostomella bilaminata	-	-	-	+	-	-	-	-	+	-	-	-	-	-	+
R. ovata	+	-	-	+	+	-	-	-	-	+	-	-	-	-	+
R. scabra	+	-	-	+	+	-	-	+	-	-	-	-	-	-	+
R. spinigera	+	-	+	+	-	-	-	+	-	-	-	+	+	-	+
Celleporella hyalina (White Sea)	+	-	+	-	-	+	-	+	-	-	-	+	+	-	+
C. hyalina (Barents Sea)	+	-	+	+	-	-	+	+	-	-	-	+	-	-	+
Scrupocellaria scabra + *S. elongata*	+	-	-	+	+	-	-	+	+	-	-	-	+	-	+
Arctonula arctica	+	-	-	+	+	+	-	-	+	-	-	+	-	-	+
Stomachetosella cruenta	+	-	+	-	+	-	-	+	+	-	-	-	+	-	+
Cylindroporella tubulosa	+	-	-	+	-	-	-	-	-	-	+	-	-	-	+
Eucratea loricata	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+
Tricellaria gracilis	-	+	+	-	-	-	+	-	-	-	-	+	-	-	+
Ctenostomatida															
Alcyonidium mytili	+	-	-	+	-	-	+	-	-	+	-	-	-	-	-
Buskia nitens	-	-	-	+	-	-	-	-	-	+	+	-	-	-	+
Bowerbankia sp.	+	-	-	-	-	-	-	-	-	+	+	-	-	-	+
Flustrellidra hispida	+	-	+	-	-	-	-	-	+	-	-	-	-	-	+
Cyclostomatida															
Crisia sp.	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+
Crisiella producta	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+
Lichenopora verrucaria	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+
Disporella hispida	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+
Tubulipora flabellaris	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+

The numbers of reactions are the same as in the text. "+" - the reaction is typical for this species; "-" - the reaction was not observed in this species. For the reaction number 6: "++" - the reaction is used very often, "+" - the reaction is typical but it is used rather rarely. "*" (in reactions 2, 3, 5) - these species have some pecularities (for detailed description see the text).

COMMENTS TO TABLE 2 (continued)

tions of lophophore with straight tentacles (pulsation): (a) in absence of any particles, (b) as brief series of pulsating movements during rejection; (15) bringing together only tips of the tentacles; (16) bringing straight tentacles together; (17) bending of all tentacle tips inside and/or outside of the lophophore; (18) bending of all tentacles when their tips are placed near the mouth; (19) cagemaking; (20) twisting activity; (21) writhing; (22) sharp nods-inclinations of polypide with large amplitude: (a) in absence of any particles, (b) particle flinging; (23) partial retraction of polypide connected with particle rejection: (a) without any changes in lophophore shape, (b) with simultaneous bringing tentacles together and their twisting; (24) polypide retraction: (a) accompanied by particle swallowing, (b) accompanied by particle rejection.

area (Fig. 5:8). Later on the particles can be either swallowed or rejected (see also Winston 1978).

2. Slow transport of particles downward along the frontal surface of one or several tentacles, sometimes almost from tips to their bases (but usually the distance is shorter) (described first in Lister 1834:384; see also Dalyell 1847-1848; Borg 1926; Atkins 1932; Cori 1941; Bullivant 1968a; Strathmann 1973, 1982a; Best & Thorpe 1983; Riisgård & Manríques 1997). When the trapped particles are sufficiently numerous, they look like moving "laces" on the tentacles (Fig. 2B). In *Escharella immersa* and *Schizomavella lineata* particle transport may be performed by means of jumps. It takes a particle 7-8 jumps to travel along the tentacle (Fig. 2C) (see also Strathmann 1973, Riisgård & Manríques 1997).

3. Rejection or removal of particles from the lophophore by cilia reversal on all of the tentacles (see also Becker 1938, Bullivant 1968b). Some variants were observed:

a. particles were lifted by an ascending water current in the centre of the expanded lophophore (Fig. 4:14) by active beat reversal of the lateral cilia;

b. particles were removed along the tentacle frontal surface (Fig. 4:15) apparently by the reversal of frontal ciliature (described first by Gilmour 1978:2150).

An "intermediate" variant was found in *Cauloramphus spiniferum*: particles, raised a little from the mouth region, were transported by water current first to the tips of tentacles and then upwards (Fig. 2D).

4. Cleaning of the colony surface using an ascending water current created by the reversal of lateral cilia (Fig. 2E). Particles are transferred from the colony surface into the tentacle crown between the bases of tentacles and then removed upward by the rejection current.

Cleaning of the colony can also be performed by a motionless polypide that stays in inclined position for some time, touching the colony surface by tentacles (observed in *Cribrilina punctata*). In this case particles are sucked into the tentacle crown and then removed towards the colony periphery.

The second group of activities includes the reactions which are represented by tentacle movements and/or that of the entire polypide (see Table 2) and are used separately or in different combinations:

5. Testing-position (see above) is generally thought to serve for testing a surrounding space nearby a polypide. It is the only activity in which ciliary activity may be neglected.

6. Scanning activity. Frequent rotations of polypides from side to side were first described and illustrated by Farre (1837:399, pl. XXIV, fig. 2; see also Dalyell 1847-1848; Calvet 1900; Borg 1926; Marcus 1926b; Cori 1941; Gordon 1974; Winston 1978, 1979). Polypides

perform inclined nods, circular motions and slight rockings with widely varying rates, amplitudes and frequencies (Fig. 4:6), and these movements may be presumably considered as simultaneous environmental testing and food searching. From time to time polypides pause in some position and then resume moving. Sometimes, the tentacle tips start stirring slightly (see also below). Species-scanners (according to Winston 1978) demonstrate this type of polypide activity most of the time (*Bowerbankia* sp., *Cauloramphus spiniferum*, *Cribrilina annulata*, *C. punctata*, *Electra pilosa*, *E. crustulenta* var. *baltica*, *Tegella armifera*), whereas it is less usual in others. In the latter four species the polypides nod from one to several times just after protrusion and before lophophore expansion, which may be considered a kind of testing activity. In the wake of tentacle expansion, zooids sometimes start to feed with the polypide tilted, as if the polypide would first choose an "advantageous" position for feeding. This bent position was also observed when polypides formed "chimneys" and temporary feeding clusters (see also Banta & al. 1974; Cook 1977; Winston 1978, 1979; McKinney 1990; etc.).

We do not differentiate modes of scanning, as done by Winston (1978), because of a lack of good criteria: the same species can show varied activity, differing mainly in frequency and amplitude.

7. Flicking activity. This activity is represented mainly by individual tentacles, although from time to time, rapid movements of groups of tentacles towards the inside of the lophophore and back may also occur (Fig. 4:8) (see also Grant 1827; Dalyell 1847-1848; Hincks 1880; Borg 1926; Bullivant 1968a; Gordon 1974; Winston 1978, 1979; Strathmann 1973; 1982a; Riisgård & Manríques 1997; Mukai & al. 1997; Nielsen & Riisgård 1998). Frequency, amplitude and length of the tentacle part performing flicking strongly vary, as well as the number of tentacles simultaneously involved in this process. An increase of particle concentration often results in increased flicking that looks like a lively stirring and, probably, may correlate with the part of tentacle involved: the very tips of tentacles move in this case. Two variants of the reaction were observed:

a. flicks performed without any particles inside the lophophore (or such particles were "invisible");

b. tentacles forwarded particles to the central water current or, sometimes, to the close vicinity of mouth (see also Borg 1926, Winston 1978). Flicks may be triggered by direct impact of a particle, but tentacles can also push particles inwardly without previous contact with them.

8. Bending of a single or 2-3 tentacles deep into the lophophore (see also Cavolini 1785, Farre 1837, Hincks 1880, Borg 1926, Gordon 1974, Winston 1978). These movements are more or less slow and are observed:

a. in the absence of any particles (or with particles too small to be seen) (Fig. 4:4a);

b. when a tentacle placed a particle directly to the mouth (Fig. 4:5).

Curling of tentacles (Fig. 7:8a-b) (mentioned first in Farre 1837:406; see also Hincks 1880, Gordon 1974) may be considered as a similar reaction.

9. Several tentacles can retain particles inside the lophophore and cram them into the mouth in some species. For instance, in *Celleporella hyalina* some non-neighbouring tentacles bent deep inside the lophophore and formed a sort of a "lid" whereas other tentacles remained straight (Fig. 6:9). As a result, a large particle, that had been situated inside the tentacle crown, was placed into the mouth and swallowed (see also Hunter & Hughes 1993).

10. Waving movements of either a single or 2-3 neighbouring tentacles forwarding a water current with particles directly to the mouth (Fig. 4:1) (mentioned first in Cavolini 1785:241, see also Winston 1977, 1978). We only observed the reaction in *Electra* species.

11. Pushing away particles using tentacle tips (Fig. 7:11) was recorded in *Scrupocellaria* species only. In all cases observed, the particles were placed outside the lophophore and a little below the tentacle tips (see also Cori 1941, Winston 1978).

12. Single expansion of the lophophore (first described in Cavolini 1785:242). The reaction may be performed without any particles within the lophophore or it may accompany particle rejection in some species (Fig. 5:18) (see also Dick 1984). In *Escharella immersa* moderate tentacle expansion resulted in particles being sucked into the lophophore from a distance up to two tentacle lengths away (Fig. 3A);

In *Tegella armifera* polypide can expand tentacles as wide as possible assuming the shape of disk (Fig. 5:3c). Flattening of the lophophore when the tentacles are almost perpendicular to the introvert was first described by Farre (1837:401), and redescribed in Winston (1978:15) (see also Winston 1977, 1979; Dick 1984).

13. Single lophophore contraction looking like a "hand clap" (Fig. 4:10-12) (described first in Borg 1926:249; see also Winston 1978, Dick 1984):

a. sharp contraction with small amplitude;

b. tentacle crown contraction may be accompanied by an inclined nod (first described as "flinging" in Dick 1984:200, fig. 6) or partial retraction of the polypide (Fig. 4:12).

When a particle was inside the lophophore the contraction resulted in particle rejection. If the first attempt was unsuccessful, this reaction could be repeated later. In some cases lophophore expansion occurred before the clap.

14. Repeated expansions and contractions of lopho-

phore with straight tentacles resembling pulsation (mentioned first in Calvet 1900:64), sometimes rather prolonged. Frequency and amplitude of these movements is variable, but they are smooth and not very fast in most cases. Two variants of the reaction were observed:

a. in absence of any particles both inside and outside the lophophore (Fig. 4:2);

b. as brief series of pulsating movements during rejection of particles (Fig. 3B) (described first in Borg 1926:250, see also Winston 1978, Dick 1984).

In *Scrupocellaria* species pulsating polypides bring tentacles together within the lower 2/3 of the crown. Hence, the ends of tentacles are curved outwards and the entire lophophore becomes bell-shaped for a moment (Fig. 7:6).

15. Bringing together only tips of the tentacles (Fig. 4:3) (described first by Borg 1926:249; see also Winston 1977). In most cases, no particles were observed inside the lophophore during this reaction, but sometimes it was accompanied by swallowing of particles in portions that had accumulated near the mouth (Fig. 5:9). Borg (1926) observed particle rejection between the bases of tentacles during this reaction.

16. Bringing straight tentacles together. The lophophore is shaped into a tube and stays in this position for some time (mentioned first in Cavolini 1785:244). This reaction sometimes accompanies swallowing. In contrast, it results in particle rejection from the tentacle tube in *Electra pilosa* and *Escharella immersa* (Fig. 4:13).

17. Inward and outward bending of all tentacle tips. This activity is represented mainly by single, sometimes repeated, movements in the absence of particles inside the tentacle crown (Figs 5:4 & 5:5). In contrast, Winston (1978) described this reaction as being used for rejection at high particle concentrations (see also Dick 1984).

18. Bending of all tentacles in such a manner that their tips are placed near the mouth (Fig. 3C:1) (illustrated first by Hassall 1841, pl. VI, fig. 1 and described and illustrated by Dalyell 1847-1848, Vol. II: 7, pl. II). In obliquely truncate lophophores the longest tentacles remained straight, whereas in all others they are curved to a greater or smaller degree (Fig. 3C:2-3). We were unable to see any particles inside the lophophore in this case.

19. Cagemaking. This or a similar reaction was described first by Dalyell (1847-1848, Vol. II:30), and more recently was described by Winston (1978, 1979) (see also Okamura 1987b). The tentacles are brought together with successive twisting and sometimes weaving of their ends in the upper quarter of the lophophore (Fig. 5:7). Particles were sometimes seen inside the cage, but many cages were empty (see also Winston 1978). A similar reaction was probably described by Hunt (1925), Bullivant (1968a) and Strathmann (1973),
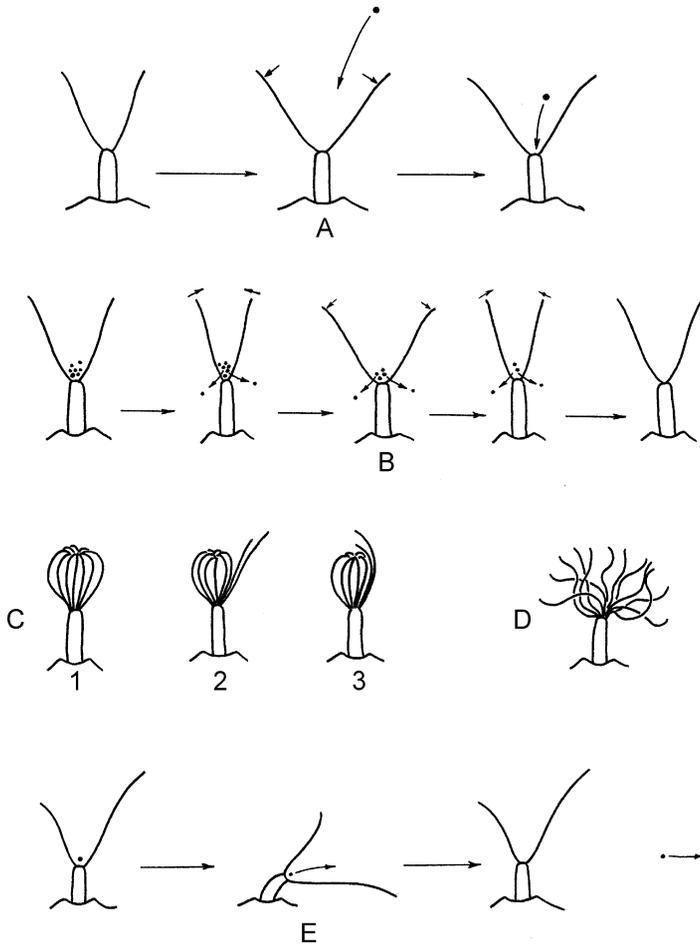
Fig. 3. A, lophophore expansion resulting in particle sucking into tentacle crown in *Escharella immersa*; B, particle rejection by repeated lophophore expansions and contractions; C, bending of all tentacles when their tips are placed near the mouth in (1) equally tentacled lophophore, (2-3) obliquely truncated lophophore; D, writhing; E, particle flinging.

who recorded the capture of large motile protozoans.
20. Twisting activity (Winston 1978). A similar reaction to cagemaking, but the tentacles are brought together and twisted for half or more of their length (Fig. 7:7a). Twisting also occurs before polypide retraction in some species (see above).
21. Writhing (illustrated first by Farre 1837, pl. XXVII, fig. 9; see also Borg 1926; Winston 1978, 1979). A strong increase of particle concentration and temperature rise leads to chaotic bending, rolling and downswing of the tentacles (Fig. 3D). In some cases it was possible to see rejected particles leaving the lophophore between the writhing tentacles (Fig. 5:20). Sometimes, before writhing starts, the entire lophophore suddenly flattens, assuming the shape of a disk. Sharp lophophore

flattening was described by Winston (1979) and Dick (1984) in a connection with a rejection of large particles (see also above).
22. Sharp nodding inclinations of the polypide with large amplitude. Two variants were recorded:
a. bending of polypides without particles in the tentacle crown (Fig. 5:6);
b. particle flinging without any changes in the lophophore shape (Fig. 3E) (see also Dick 1984). In most cases this was performed towards the longest tentacles in obliquely truncate lophophores, and/or towards the growing edge of the colony.
23. Partial retraction of polypide comparable with the "avoidance" retractions described by Winston (1978, 1979; see also Borg 1926). This was always connected

with particle rejection, and could occur:

a. without any changes in lophophore shape;

b. with simultaneous bringing together and twisting of the tentacles (Figs 6:7, 7:7b).

In *Celleporella hyalina* partial retraction of polypide was sometimes accompanied by a pharyngeal rejection (see also Dick 1984).

In *Electra* species slight retraction is accompanied by a brief series of pulsating movements (Fig. 4:11).

24. Polypide retraction taking part in feeding or cleaning processes:

a. swallowing of particles is sometimes accompanied or quickly followed by polypide retraction (described first in Calvet 1900:64);

b. the polypide can retract beneath a large particle or several smaller particles in order to reject them (Figs 5:14, 6:13a). Normally a polypide uses some of the rejection methods described above, but if these attempts are unsuccessful it simply retracts, and particles are carried away by the current (see also Winston 1978, Dick 1984, Best & Thorpe 1996).

In cyclostomatides, polypides may reject particles from the tentacle crown in groups by a series of repeated retractions and protrusions.

Reactions entailing simultaneous movements of all tentacles together are often accompanied by synchronous activity of the mouth and pharyngeal musculature. This normally results in a rejection or sucking of the particles (see Winston 1978, Dick 1984). Also pharyngeal contractions accompanied by rejection may be performed in motionless polypides (described first in Cavolini 1785:232, see also Lister 1834, Farre 1837, Borg 1926, Atkins 1932, Silén 1944, Bullivant 1968a, Ryland 1976, Dick 1984).

To create a coherent picture of polypide activities, we present descriptions of autozooidal behaviour in some species from the three orders of marine bryozoans.

Cheilostomatida

Electra pilosa, *E. pilosa* var. *dentata*, *E. crustulenta* var. *baltica*

Colonies are encrusting, often with their characteristic star-like shape varying mainly according to substratum type. Uniserial or multiserial rows of zooids radiate from the ancestrula. In older colonies the area surrounding the ancestrula consists of non-functional autozooids and is often covered by detritus. Polypides in peripheral zooids were often tilted a little towards the colony edge, and were more active in comparison with those around the colony centre. Filtered water was removed towards the periphery and in old colonies also towards the colony

centre between the zooidal rows. Temporary groups of 3-5 feeding neighbouring zooids tilting towards each other, are sometimes formed.

Polypides possess a long introvert and an equitentacled lophophore. The lophophore expands abruptly, never lingering in the testing-position. Tentacles may wave smoothly, either in turn or 2-3 simultaneously, accelerating the fall of particles into the lophophore (Fig. 4:1). The tentacle crown may pulsate, slightly expanding and contracting (Fig. 4:2). Then it either returns to a normal position or brings the tentacles together in a tube. Zooids often put the ends of all tentacles closely together for a period (Fig. 4:3), sometimes slightly stirring them. After several such contractions polypides can bend one or all of the tentacles towards the mouth (Fig. 4:4a-b) and then straighten them. This bending may accompany a feeding process when from one to 2-3 tentacles push particles into the mouth (Fig. 4:5).

From time to time a polypide may perform scanning in the form of rotations with small amplitudes or rocking (Fig. 4:6). Tilted in a particular direction, it starts to stir the tentacles actively, perhaps as a consequence of particle finding (see also the *Discussion*). If a particle is present at any distance up to a tentacle length from the tilted lophophore, it may either approach the tentacle crown and go back again several times, or remain almost still, trembling intermittently, before starting to move rapidly towards the polypide and entering the lophophore (Fig. 4:7). The polypide then brings the ends of the tentacles together and retracts. We also observed polypides responding to a particle at a distance at least twice tentacle length. If the particle was situated a little to the side of the medial lophophoral axis, the polypide tilted towards it. After some time the particle started to vibrate chaotically and then suddenly moved and was quickly transferred into the lophophore.

Both *Electra* species studied are tentacle-feeders (Winston 1978). Tentacle flicks (Fig. 4:8) were observed even with no particles in close vicinity of the lophophore. If particles were present, the flicks were either triggered by direct impact with them or tentacles batted particles from the ambient flow without previous contact.

Both species selected particles by size: large and middle-sized particles were always rejected, whereas small ones were swallowed. Rejection of large particles commonly occurred between the bases of the tentacles (Fig. 4:9), or by lophophore contraction resulting in the rapid lifting of the particles upwards (Fig. 4:10). To reject medium-sized particles, the polypide slightly retracted, contracting the lophophore (Fig. 4:11) and sometimes also tilting a little (Fig. 4:12). All three reactions may occur independently as well as almost simultaneously and in different combinations. If the first attempt to re-
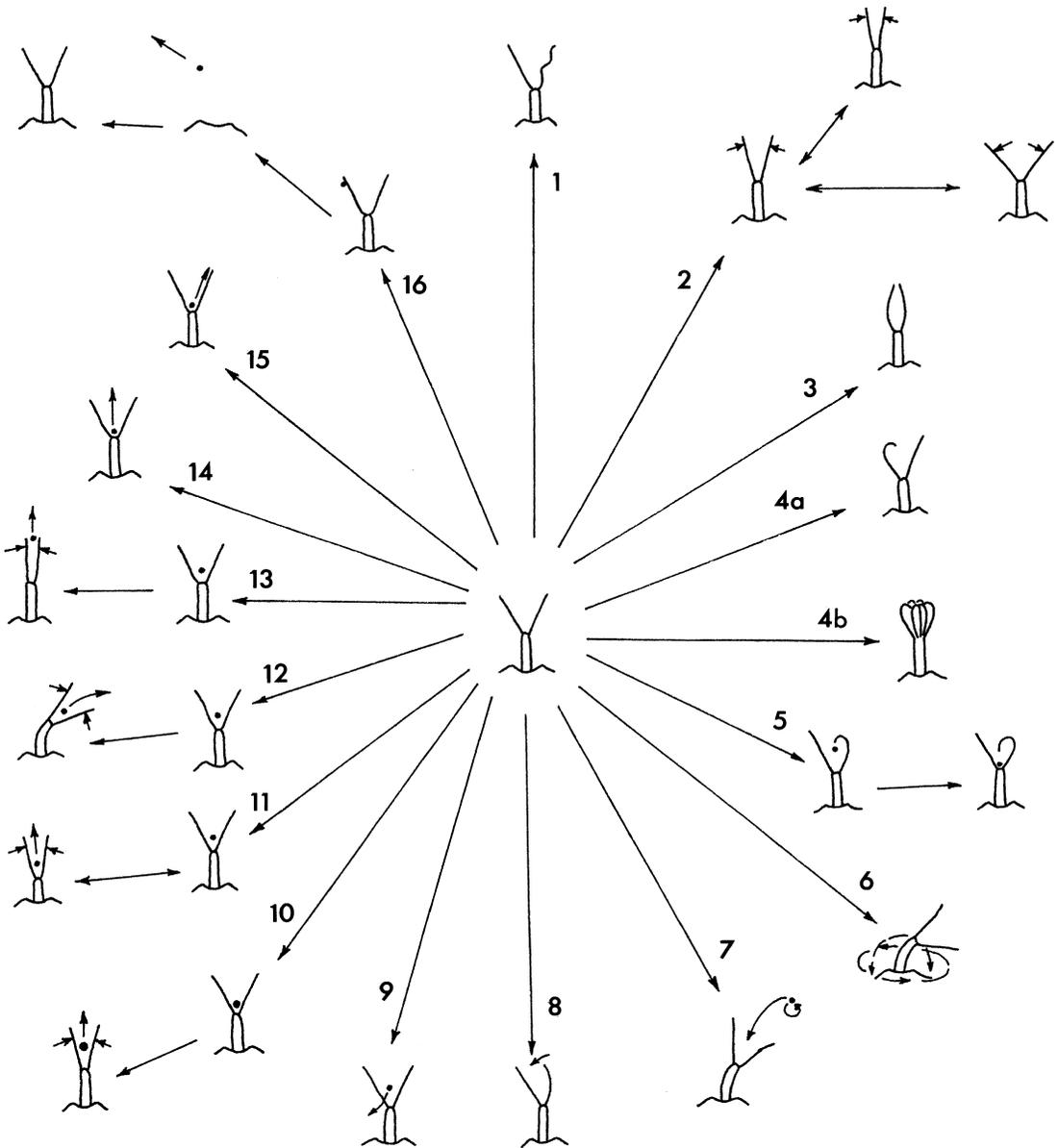
Fig. 4. Behavioural reactions recorded in *Electra* species: (1) waving; (2) repeated lophophore expansions and contractions (pulsation); (3) bringing together ends of the tentacles; (4a-b) tentacle bending inside the lophophore; (5) particle pushing into the mouth; (6) scanning activity; (7) search and dragging of distant particle by ciliary current; (8) flicking; (9) removal of large particles between the bases of tentacles; (10) rejection of large particle by single lophophore contraction; (11) rejection of middle-sized particle by brief series of pulsating movements of lophophore with slight retraction; (12) lophophore tilting during particle rejection; (13) particle rejection by bringing all the tentacles together in a tube; (14) rejection by lateral ciliary reversal; (15) rejection by frontal cilia reversal; (16) polypide retraction triggered by a particle sticking.

move the particle was unsuccessful, the polypide repeated it again and again. Particles could be removed by bringing all the tentacles together to form a tube (Fig. 4:13). Often a particle already at mouth level started to lift upward in the tentacle crown centre along the medial lophophoral axis (Fig. 4:14), or was rejected by moving along the frontal surface of one of the tentacles (Fig. 4:15). In both cases the polypide was motionless

and apparently performed the rejection by a reversal of ciliary beat (see above). Refiltering was also observed when particles left the lophophore near the ends of the tentacles before re-entering the tentacle crown. Sometimes particles stick to the abfrontal tentacle surfaces, mainly near their tips. Then the polypide sharply retracts, and the particle stays suspended in water and is later removed by a current (Fig. 4:16). Polypide protrusion occurs approximately 40-60 seconds later. An increase in particle concentration always resulted in a corresponding rise in the filtration rate in these species (see also above).

Tegella armifera

Colonies are encrusting and often circular, with a distinctive astogenetical zonation. In older colonies the area around the ancestrula consists of non-functional zooids containing brown bodies. This surrounded by a wide ring of feeding polypides and a narrow budding zone at the periphery of the colony. In small colonies all polypides possessed equitentacled lophophores; in large colonies there were 2-3 peripheral autozooidal generations with obliquely truncate lophophores. These polypides were always larger than others, and their longest tentacles were situated at the colony periphery. In old colonies filtered water was removed both towards the periphery and towards the colony centre, below and between the lophophores.

Protrusion of the polypide is gradual, but not slow. It is accompanied by an untwisting of the tentacles and is never interrupted in the testing-position. When a colony is undisturbed the lophophores are normally expanded only in some polypides, whereas in others they may be semi-expanded or have their tentacles brought together (Fig. 5:1a-b). Everted polypides may stay for a long time in any of these positions. An actively filtering polypide is motionless most of the time, sometimes flicking the tentacles (Fig. 5:2), closing and expanding the lophophore with straight tentacles (Fig. 5:3a-b), expanding tentacles assuming the shape of disk (Fig. 5:3c), curving the ends of the tentacles inwardly and outwardly (Fig. 5:4-5), or scanning (Fig. 5:19). From time to time the polypide performs a sharp sideway nod, so that the tentacles contact the colony surface (Fig. 5:6). During these reactions, we often did not see any particles within the lophophore or in its vicinity. Though most of the polypides are motionless, scanning polypides are always seen in colonies of *T. armifera*. This species may be considered as a "scanner". Sometimes polypides use cagemaking to catch and retain a particle in the lophophore (Fig. 5:7), although we did not see any particles in some "cages".

Polypides can concentrate small and middle-sized particles near the mouth (Fig. 5:8). After this, the lophophore starts to bring the tentacle ends together repeatedly. At every such movement some particles enter the mouth until all of them are swallowed (Fig. 5:9). If there is only one particle in the lophophore the polypide may bring the tentacles together and retract just after swallowing (Fig. 5:10), usually everting 1-2 minutes later, though sometimes protrusion was postponed for a longer time. Polypides may also concentrate particles to reject them. In this case the particles first accumulate in the lophophore centre, oscillating slightly, then start to move slowly towards the mouth and are rejected in clumps between the tentacle bases (Fig. 5:11). The same sequence was observed in the case of a single particle, but this sometimes culminated in swallowing. The clump of particles may be also rejected by lophophore contraction (Fig. 5:12a), sometimes with a simultaneous inclination ("flinging" of Dick 1984) during which a polypide tilts towards either the colony periphery or centre accordingly its location (Fig. 5:12b). The first attempt at rejection is as a rule unsuccessful and the polypide normally repeats the contractions. Rejected particles enter a neighbouring lophophore or are carried away by the current (Fig. 5:13). If the rejection fails the polypide sharply retracts and the aggregation of particles remains outside (Fig. 5:14).

Particles which escaped from the tentacle crown between the bases of the tentacles sometimes were lifted to a height of 1-2 tentacle lengths by a circular current and dragged into the same or a neighbouring lophophore (Fig. 5:15). Cycling movements were also observed inside the lophophore of motionless polypides: particles that almost reach the mouth start suddenly to move upwards to the ends of the tentacles where they either escape from the lophophore or sink again, sometimes performing several such cycles (Fig. 5:16).

Large particles were rejected either between the bases of all of the tentacles (Fig. 5:17a) or were first lifted halfway on the tentacle along the frontal surface and then left the lophophore (Fig. 5:17b). A single expansion of the tentacle crown may also result in particle rejection along the medial lophophore axis (Fig. 5:18).

When the concentration of particles was experimentally increased to a high level, particles settled on the frontal surface of all of the tentacles. Particle settlement triggered writhing and non-regular twisting during which polypides often pulled their tentacles down, touching the colony surface. Then the polypides expanded their lophophores and continued to writhe, and only occasional polypides were retracted. After each "series" of these convulsions the number of particles inside the lophophore was reduced. Some particles were rejected between the tentacles, but others were probably swallowed (Fig. 5:20).
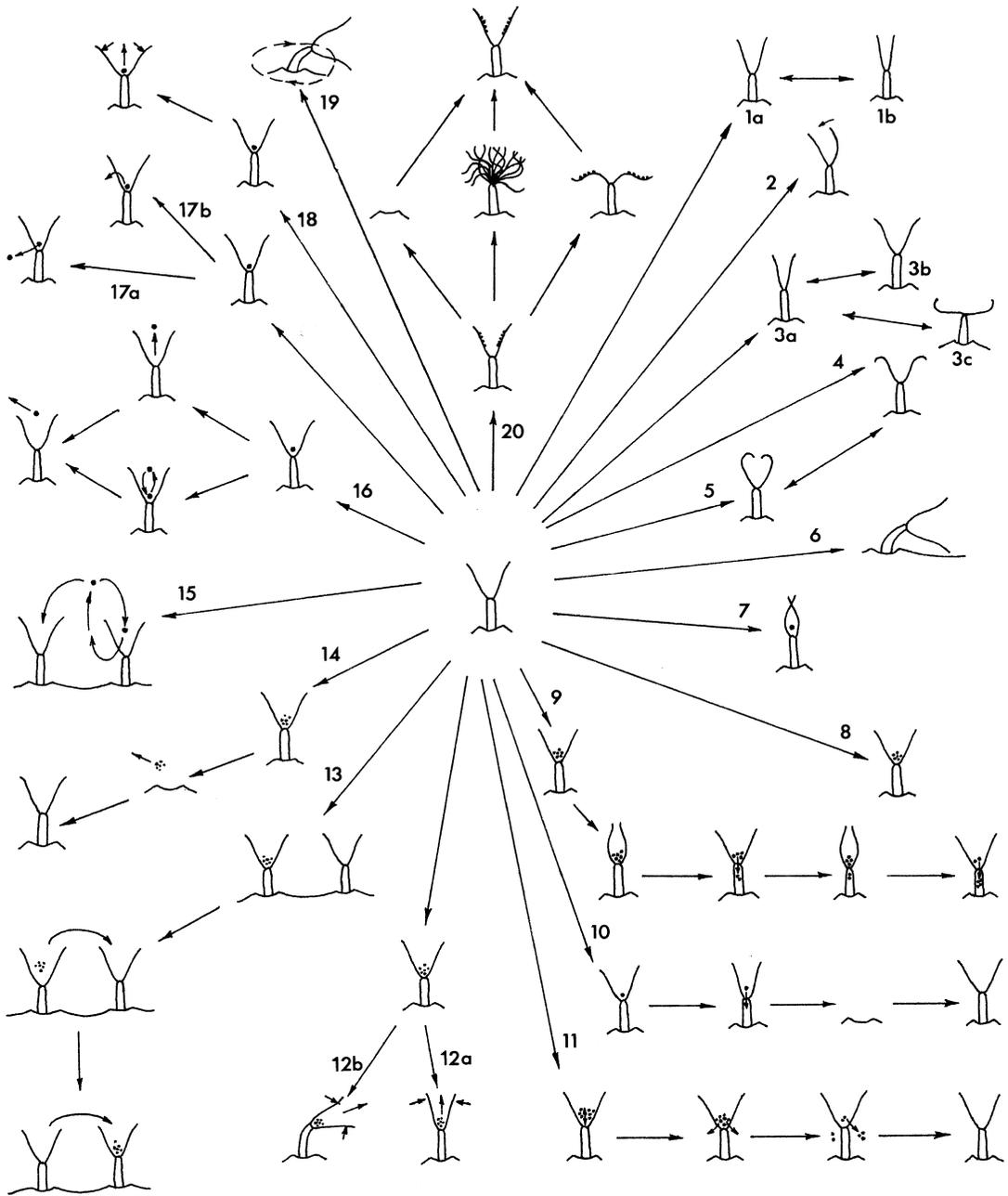
Fig. 5. Behavioural reactions recorded in *Tegella armifera*: (1) expanded (a) and semi-expanded (b) tentacle crown; (2) flicking; (3) lophophore expansion and contraction; (4) curving the ends of tentacles outwards; (5) curving the ends of tentacles inwards; (6) sharp nod with tentacle touching the colony surface; (7) cagemaking; (8) concentrating particles near the mouth; (9) swallowing of concentrated particles accompanied by repeated bringing of ends of tentacles together; (10) swallowing followed by polypide retraction; (11) rejection of concentrated in the lophophore particles between the bases of tentacles; (12a) particle rejection by lophophore contraction, (12b) the same accompanied by sharp nod of polypide; (13) transfer of rejected particles to neighbouring lophophore; (14) polypide retraction from under a group of particles; (15) repeated particle dragging into the same or neighbouring lophophore; (16) cycling movements of particle inside the lophophore; (17) rejection of large particle (a) between bases of tentacles, (b) between the tentacles with previous lifting along frontal tentacle surface; (18) particle rejection by single lophophore expansion; (19) scanning activity; (20) writhing and accompanied activities.

Celleporella hyalina

Colonies are encrusting, "two-layered" with autozooids forming the basal layer and female and male dwarf polymorphs budding frontally. Filtered water is removed between zooids towards the colony periphery.

Polypides evert with a pause in the testing-position. Lophophore expansion is gradual, but not slow. Even a minor addition of particles results in a momentary retraction of all polypides. Soon, after 10-15 seconds only, they evert again and increase the rate of filtration. But some of them often retract again and many others stay in the testing-position for a long time. Total retraction of polypides was also triggered by some experimental disturbances: a rapid rise in temperature, strong water currents, touching by a needle, or the presence of a large moving object. However, some polypides everted almost immediately after retraction and stayed expanded throughout the period of disturbance. Some of these "sentry" zooids can retract again and can be replaced by others until the source of disturbance disappears and most remaining polypides protrude. We suggest that sentry zooids undertake an additional sensory function during this period and their behaviour may be comparable with the activity of nanozooids of some cyclostomatids (Silén & Harmelin 1974).

Celleporella hyalina is one of the species where behavioural differences between starving and replete colonies are strongly pronounced in relation to reaction velocity. Normally polypides are not very motile, demonstrating smooth and unhurried movements. After some days of starvation they become "nervous", following the same pattern but reacting more quickly.

Colonies from both the White and the Barents seas demonstrated a basic set of individual polypide activities, for instance, scanning accompanied by inclinations and rockings with limited amplitude (Fig. 6:1), lophophore expansions and contractions (Fig. 6:2), tentacle flickings (Fig. 6:3) and bending of one (Fig. 6:4) or all of the tentacles simultaneously (Fig. 6:5) towards the mouth, particle rejection by lophophore contractions (Fig. 6:6a) sometimes accompanied by a partial retraction of the polypide (Fig. 6:6b) and pharyngeal contraction. A polypide may bring the ends of the tentacles together, sometimes slightly contracting the introvert at the same time, and twisting them approximately 30 degrees clockwise (Fig. 6:7). However, it never twists the tentacles before retraction. Also a polypide sometimes brings together the ends of the tentacles when it swallows a particle (Fig. 6:8), staying in that position for 5-7 seconds. *Celleporella hyalina* was found to be the least selective of all species studied, swallowing all particles in succession from small to very large. Polypides can concentrate small and middle-sized particles along the frontal surface of the tentacles in the form of moving "laces" (Fig. 6:10), slipping down towards the mouth. Some particles are swallowed and the rest escape between the bases of the tentacles.

There are also marked distinctions in autozooidal behaviour between the colonies studied from two different seas. The following behavioural responses were recorded in the White Sea colonies only. On one occasion the polypide was observed to bend two tentacles from one side of the lophophore and three from the opposite side towards the mouth and press them closely when a large particle fell into the lophophore. A sort of lid was created by this activity, though other tentacles were expanded (Fig. 6:9). The polypide spent about 4-5 minutes in this position, while the water current generated by the cilia of the expanded tentacles passed through the lophophore in the usual direction. Then the polypide started to straighten the bent tentacles very slowly, and it could be seen that the particle had entered the pharynx. We infer that the reaction described resulted in the particle being "pushed through" the mouth.

In contrast, the following responses were observed only in colonies from the Barents Sea: collection of particles in a group inside the expanded lophophore near or, sometimes, a little above the mouth area (Fig. 6:11), cagemaking (Fig. 6:12), and rejection of particles by a single expansion of the lophophore (Fig. 6:13a) or by polypide retraction (Fig. 6:13b).

Scrupocellaria scabra, S. elongata

Colonies are erect, jointed, with dense branching and a biserial arrangement of autozooids. Filtered water is expelled towards the substratum, sometimes passing around the branch.

During polypide protrusion the tips of the straight tentacles are slightly bent inside the lophophore. Once completely everted, the lophophore keeps this shape for some time before expanding; this may be a variant of the testing-position. Protruded polypides are perpetually active, slightly bending (Fig. 7:1), flicking only the tips of the tentacles (Fig. 7:2), and contracting and expanding the lophophore a little (Fig. 7:3a-b). In some polypides the tentacles are brought together, and their ends are bent inwards (Fig. 7:4). Sometimes, polypides bring together only the middle parts of the tentacles, leaving their ends expanded (Fig. 7:5). Polypides also bring tentacles together within the lower two-thirds of the crown; the ends of the tentacles stay curved outwards and the entire lophophore becomes bell-shaped for a moment (Fig. 7:6). A polypide may twist its tentacles suddenly (Fig. 7:7a), sometimes accompanying the twisting by a partial retraction (Fig. 7:7b). Then it ex-
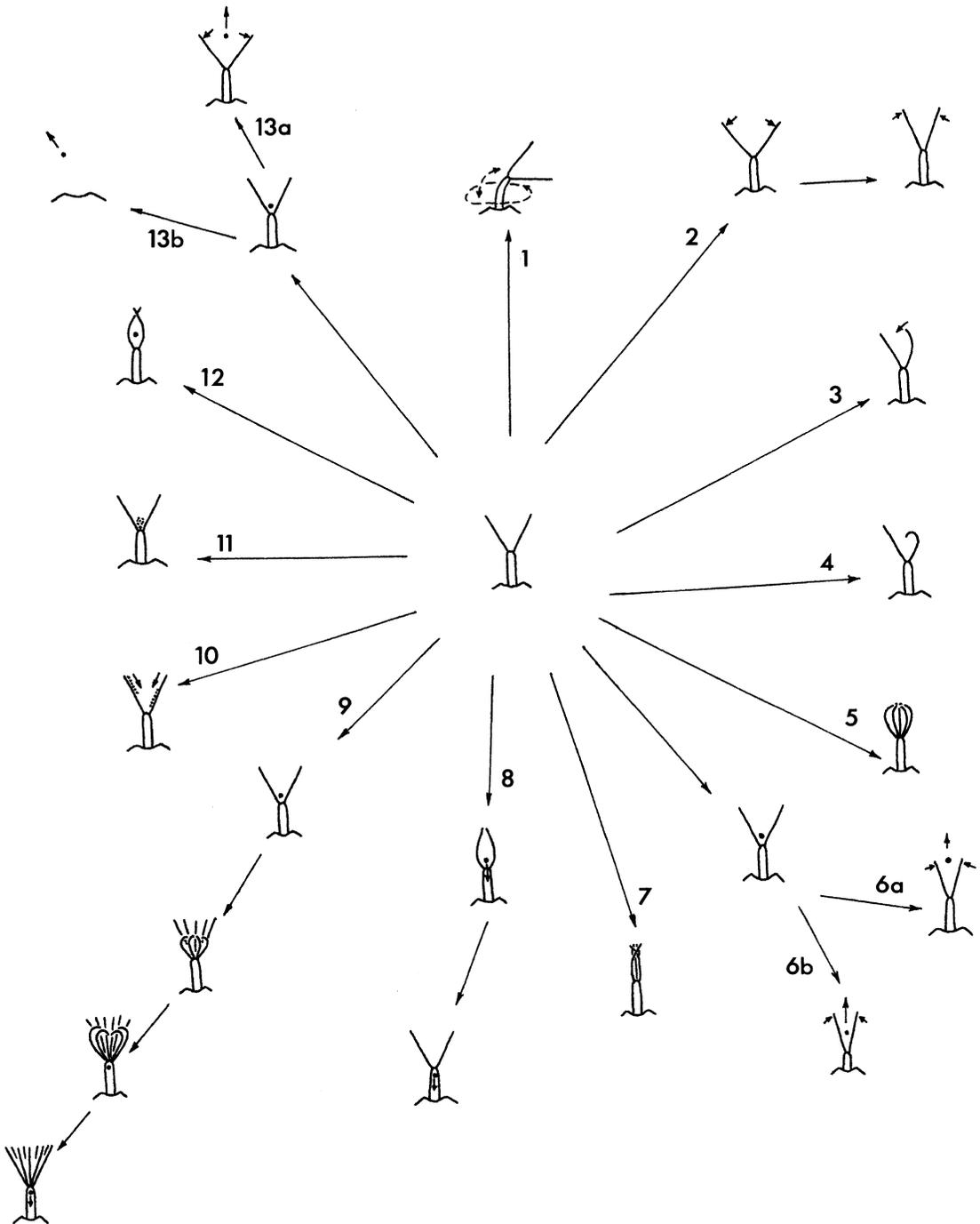
Fig. 6. Behavioural reactions recorded in *Celleporella hyalina*: (1) scanning activity; (2) lophophore expansion and contraction; (3) flicking; (4) bending of tentacle inside the lophophore; (5) bending of all tentacles when their tips are placed near the mouth; (6a) particle rejection by lophophore contraction, (6b) the same accompanied by partial polypide retraction; (7) twisting; (8) particle swallowing accompanied by bringing the ends of tentacles together; (9) swallowing accompanied by a formation of "lid" of tentacles; (10) frontal particle transport in form of "laces"; (11) collecting of particles near the mouth; (12) cagemaking; (13) particle rejection by (a) lophophore expansion and (b) polypide retraction.
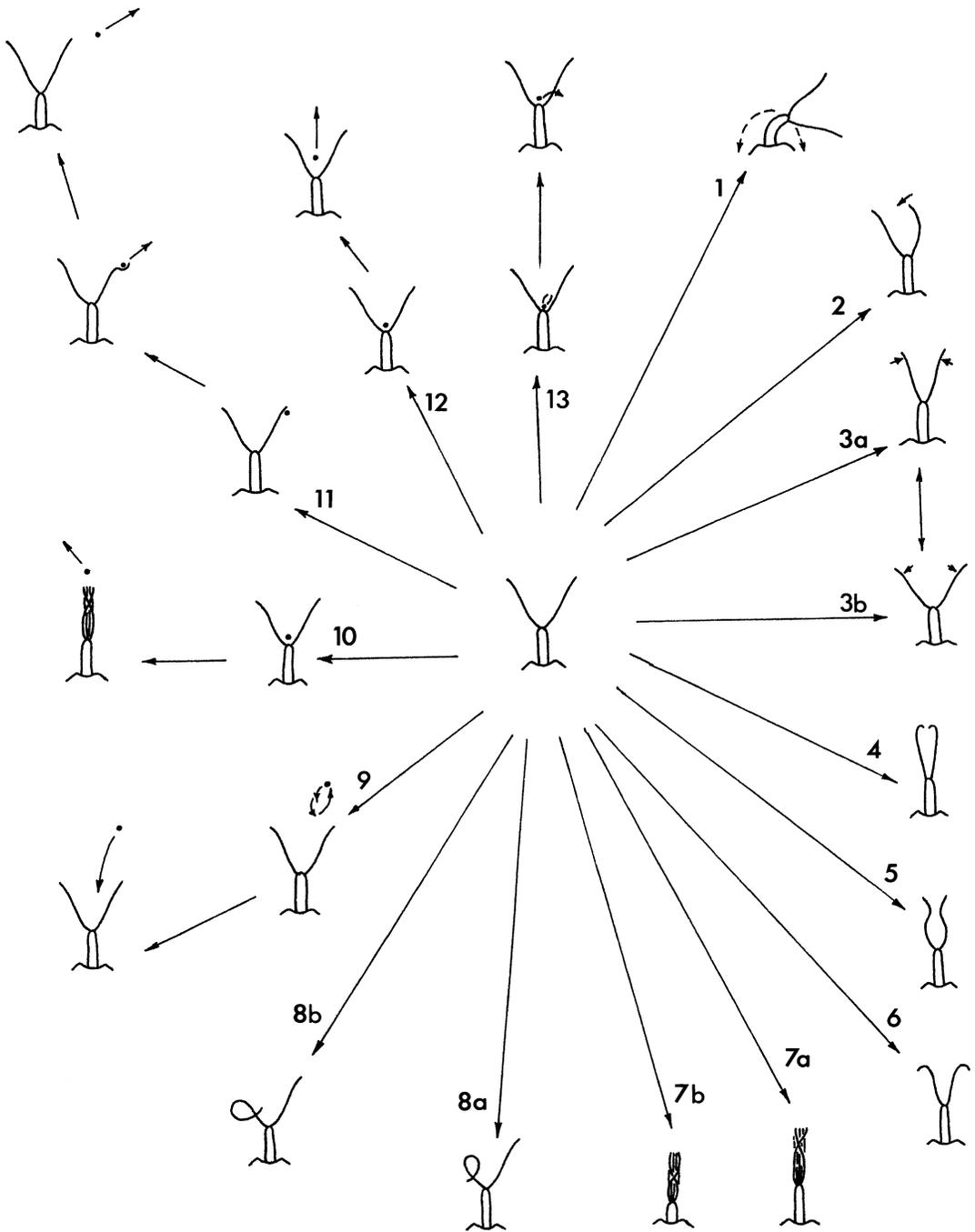
Fig. 7. Behavioural reactions recorded in *Scrupocellaria* species: (1) polypide nods; (2) flicking; (3a-b) lophophore contraction and expansion; (4) bringing the tentacles together accompanied by bending their tips inwards the tentacle crown; (5) bringing the middle parts of tentacles together; (6) bringing the tentacles together with their ends curved outwards; (7a) twisting, (7b) twisting accompanied by partial polypide retraction; (8) curling of tentacles (a) inwards and (b) outwards of lophophore; (9) dragging of the distant particle to the lophophore by ciliary current; (10) particle rejection accompanied by tentacle twisting; (11) pushing out the particle by tentacle tip; (12) particle rejection by lateral ciliature reversal; (13) cycling movements of particle inside the lophophore.
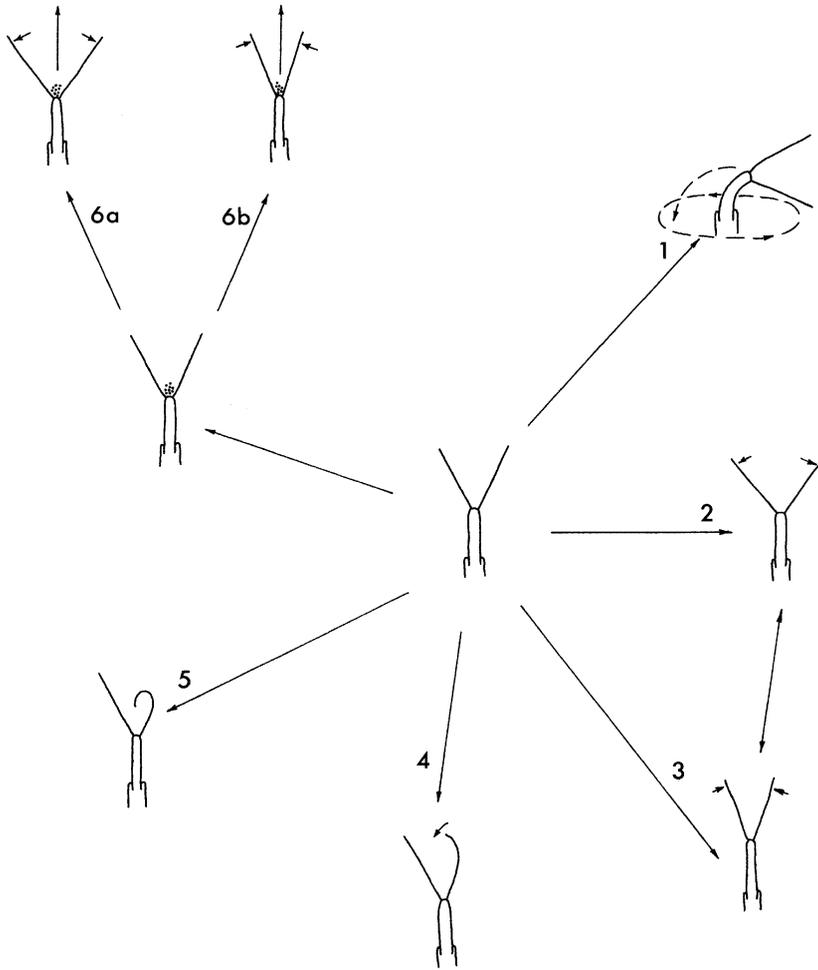
Fig. 8. Behavioural reactions recorded in *Bowerbankia* sp.: (1) scanning activity; (2) lophophore expansion; (3) lophophore contraction; (4) flicking; (5) bending of tentacle inward from the tentacle crown; (6) particle rejection by lophophore (a) expansion and (b) contraction.

pands again, but with the tentacles still together and their tips bent inside the lophophore, as in the testing-position. In normally expanded lophophores the tentacles may curl inwards (Fig. 7:8a) and outwards (Fig. 7:8b) by turns. We were unable to detect any particles during many of these reactions. In contrast, some of the reactions and their consequences were observed only due to the presence of particles, for example, concentration of particles in a group inside the expanded lophophore, and refiltering. We often observed that a particle placed at a distance up to one tentacle length above the expanded lophophore first moved half a distance in jerks towards it and then jumped back to the same position. After several such cycles the particle started to move evenly and was dragged swiftly into

the motionless lophophore (Fig. 7:9).

During the rejection of one large or several middle-sized particles, polypides use fast but incomplete retraction accompanied by tentacle twisting (Fig. 7:10). If such a particle is outside but close to the lophophore, the tentacle may push it further out (Fig. 7:11). Small and middle-sized particles are rejected by reversal of the lateral cilia that generates an exhalant current in the tentacle crown centre (Fig. 7:12). Sometimes, after sinking in the lophophore a particle may be lifted along the frontal tentacle surface apparently by ciliary reversal up to $1/5 – 1/4$ part of the tentacle length, after which it sinks down once more and then is lifted by the reversal again until at last it is rejected between the tentacles (Fig. 7:13).

Ctenostomatida

Bowerbankia sp.

Colonies are creeping, with branching stolons from which zooids originate in pairs or groups.

Protrusion of the polypide is rather fast, and it is never interrupted by halting in a testing-position. Polypides are normally very active and give the impression of searching for particles all of the time. The polypides perpetually scan the surrounding space (Fig. 8:1) and often perform different lophophore movements, for instance, expansions (Fig. 8:2) and contractions (Fig. 8:3), and tentacle movements, e. g. various flicks (Fig. 8:4) and bendings (Fig. 8:5). They appear purposefully to orient their lophophores in the direction where the suspended particles are concentrated or from which a current arrives. The tentacles draw particles by flicking them from the current and transferring them into the lophophore. As with the *Electra* species, tentacle movement followed by particle removal from the slow ambient current sometimes occurred without previous contact with the particle. If the particle moves rather far from the tentacle crown the polypide can bend markedly in order to reach it before it escapes. An increase in particle concentration triggers a momentary rise of both filtration rate and flicking activity. Polypides swallow every particle available rapidly and in great quantities. They reject particles only when they are too numerous. In this case the lophophore sharply expands (Fig. 8:6a) or contracts (Fig. 8:6b), and the particle(s) is tossed up. The first attempt at such rejection is almost always unsuccessful, but the polypide attempts it again and again until the unsuitable particles are removed. If all attempts are unsuccessful the polypide finally retracts. We also observed particle rejection by flinging.

Cyclostomatida

Crisia sp., *Crisiella producta* (Smitt), *Tubulipora flabellaris* (Fabricius), *Lichenopora verrucaria* (Fabricius), *Disporela hispida* Gray

In branching jointed colonies of crisiids with a mature or developing gonozooid, only the 2-3 youngest zooidal generations feed, and the other zooids do not protrude. This resembles behaviour described in some cheilostomatides and cyclostomatides (see Cook 1977; Okamura 1984; McKinney 1989, 1991a, 1991b). In contrast, in sterile colonies all, or almost all, polypides feed. Filtered water is directed towards the substratum. In the fan-like encrusting colonies of *Tubulipora flabellaris* zooids are arranged in linear series, and filtered water
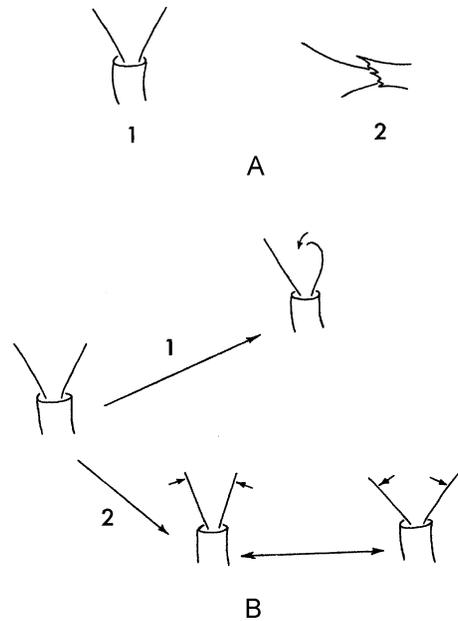

Fig. 9. Behavioural reactions recorded in Cyclostomatida: A, working position of lophophore during normal filtration in (1) crisiids and (2) in lichenoporids; B(1) flicking, B(2) lophophore contraction and expansion.

is removed from the middle and the down part of each series towards the ancestral zone between the series. In the radially "symmetrical" dome-shaped colonies of *Lichenopora verrucaria* and *Disporela hispida*, 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. Largest zooids are placed around the colony centre. Filtered water is removed between radial rows of zooids towards the colony centre (Cook 1977; Winston 1978; Taylor 1991).

During polypide protrusion straight tentacles are brought together in a sort of tube. Lophophore expansion is markedly slow. Only the tentacles are seen to be protruded from the peristome, and the mouth of the everted lophophore remains at the level or inside the skeletal aperture (Fig. 9A:1-2). The possibility for lophophore eversion is restricted in cyclostomatides and depends upon the inner structure of zooids (Taylor 1981; McKinney & Boardman 1985; summarized in McKinney 1988). Most of the time the polypides are motionless, occasionally performing flicking movements by one (Figs 9B:1 & 10:1) or some tentacles together, and slight lophophore contractions and expansions (Figs 9B:2 & 10:2). In *Tubulipora flabellaris* polypides are able to concentrate particles in a group near the mouth (Fig. 10:3) and also bend tentacles into the lophophore
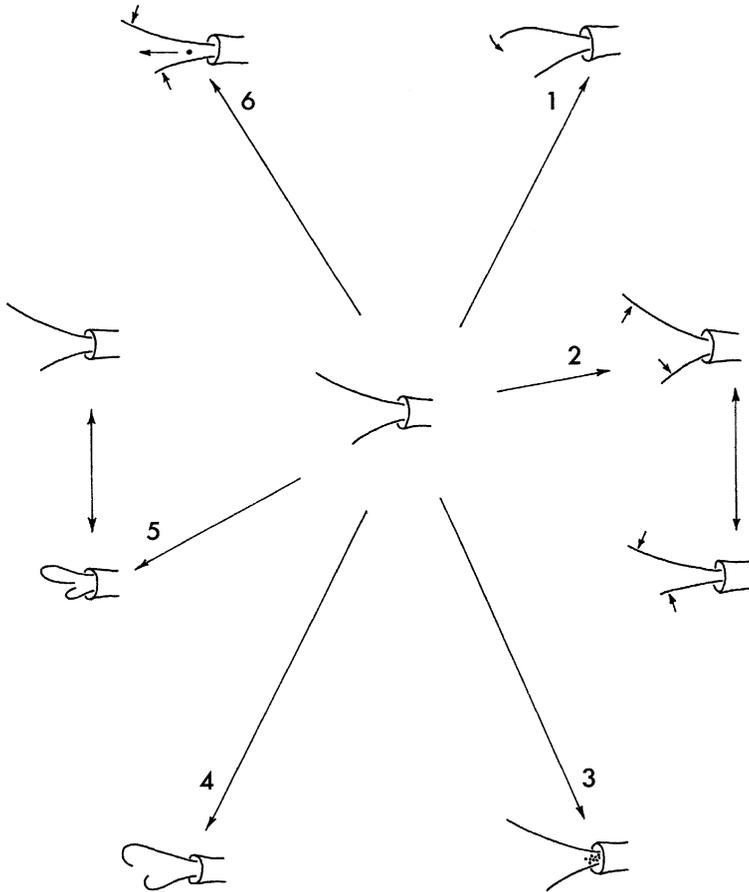
Fig. 10. Behavioural reactions recorded in *Tubulipora flabellaris*: (1) flicking; (2) lophophore expansion and contraction; (3) collecting of particles in group near the mouth; (4) bending tentacles into lophophore; (5) bending of all tentacles when their tips are placed near the mouth; (6) particle rejection by lophophore contraction.

(Fig. 10:4). From time to time some polypides bring the tentacles together and place their tips near the mouth for 30-40 seconds. Then such a polypide expands the lophophore for 1-2 seconds and brings the tentacles together again. Afterwards it keeps the tentacles in this "bud" position longer, up to 2 minutes and then expands (Fig. 10:5).

In cyclostomatides most of the rejected particles leave the lophophore between the tentacles (see above). In *T. flabellaris,* where the mouth is positioned below the peristome rim, even the particles that reached the mouth were often rejected in such a way. In this species the particles were sometimes removed by a single slight contraction of the lophophore (Fig. 10:6). In *Lichenopora verrucaria* and *Disporella hispida* the rejection method was as follows: polypides abruptly retracted from under the particle, sometimes preceded by a slow

particle lifting inside the lophophore. Particle could also be rejected by the lifting only. In this case the polypide was motionless, and the particle was removed closer to the longest tentacles. Sometimes the polypides reject particles from the tentacle crown in clumps by a number of repeated retractions and protrusions.

DISCUSSION

During our observations of marine bryozoans from the White and Barents seas almost all behavioural reactions previously recorded in the literature were found. In most species great similarity and often identical behaviour in the same species from different localities was recorded (both direct comparison of the White and the Barents seas bryozoans and the analysis of published descriptions). In addition, the present work demonstrates

that the basic behaviour seen in temperate bryozoans (Winston 1977, 1978, 1979) is also found in cold-water taxa, which previously could only be presumed. We conclude that these similarities may indicate the adequacy of the reactions observed in experiments to those occurring in nature. However, experimental data should be always treated with caution (see Cook 1977, Cook & Chimonides 1978, McKinney 1990, Riisgård & Manríques 1997) since no direct comparison of behaviour in experimental and natural conditions has been as yet performed.

Some activities were recorded for the first time (cleaning of the colony surface using ascending water current created by reversal of the lateral cilia; bending of the tentacle tips inside the lophophore during polypide protrusion; particle capture by tentacle expansion; pulsation of polypides bringing tentacles together within a lower part of the crown; particle rejection by bringing straight tentacles together; particle rejection in clumps by a series of repeated retractions and protrusions of polypide; cleaning of the colony surface by the inclined polypide), and thus the list of the known reactions was supplemented. On the other hand, we were not able to find, in the species we observed, any confirmation of particle rejection by ventral rejection tracts or by special "motions of the rejection tentacles" mentioned by some authors (Atkins 1932; Bullivant 1968a; Ryland 1976; Winston 1978; Dick 1984:200). We also never observed the method of feeding by a ciliary reversal described in Borg (1926:248) when "the direction of movement can be altered, whereby a particle which would otherwise have been carried away, can reach instead the mouth". A similar feeding method was also recorded by Hunter & Hughes (1993). It is obvious from the texts that Borg (1926) and Hunter & Hughes (1993) meant a reversal of entire lateral ciliature, but not the local reversal suggested by Strathmann (1973, 1982a). Marcus (1926b) considered the reversal of entire ciliature to be a method for sorting particles. We did not observe the ciliary cessation as described first by Farre (1837:406), who believed this to be entirely under polypide control (see also Borg 1926, Cori 1941, Dick 1984).

FEEDING MECHANISM AND EFFICIENCY OF PARTICLE RETENTION

General uniformity of the polypide and tentaculate structure in bryozoans implies common feeding mechanisms. Bryozoans probably use several mechanisms depending on structural constraints within different taxa (including size of the polypide), and changes of environment (mainly, characteristics of ambient flow and suspended matter) (Winston 1978; Okamura 1987b; McKinney 1990; Riisgård & Manríques 1997). Some

mechanisms can apparently be used simultaneously, but their importance for feeding may be different. Also Winston stressed (1978:29) that polypides could "utilize a combination of methods depending on the size and concentration of the particles" during particle rejection.

At present the most well-balanced hypothesis was proposed in the papers of Riisgård & Manríques (1997:237) and Nielsen & Riisgård (1998), suggesting that "within the ectoprocts, which all use a common basic lophophore filter-feeding principle, several mechanisms may have evolved for transporting the 'mechanical-filter' trapped particles to the mouth". Some mechanisms proposed earlier must be also considered (Borg 1926; Atkins 1932; Cori 1941; Strathmann 1973; Ryland 1975, 1976; Winston 1978; Best & Thorpe 1983; see also McKinney 1990). In undisturbed water, or when the influence of the external flow may be neglected, the process of bryozoan feeding can be imagined as follows:

• lateral tentacular ciliature of the funnel-like lophophore creates a descending water current which is the strongest in the central area (long frontal cilia at the bases of the tentacles are used to direct the main current to the mouth in gymnolaemates);

• the particles that are drawn in the central current directly hit the mouth;

• the water is sieved by the lattice of latero-frontal cilia in the lower part of the tentacle crown, and the particles filtered there are transported to the mouth by tentacle flicks, presumably triggered by the contact of particles with sensory latero-frontal cilia and, less often, by frontal cilia (in the case when the particle strikes the tentacle frontal surface);

• in the upper part of the lophophore tentacle flicking tosses the particles to the main current;

• the delivery of captured particles to the mouth proper is performed by the ciliature of the area around the mouth, stomodaeum, and pharynx accompanied by pumping action of these organs.

The upper part of the lophophore is much less effective as a filter, but plays an important role in the particle capture by flicking (see also below). Local reversals suggested by Strathmann (1973, 1982a, 1982b; Strathmann & al. 1972) can be used as a supplementary mechanism for particle capture and downward transport, simultaneously with mechanical filtering (see also McKinney 1990; Markham & Ryland 1991; Hart 1991, 1996; Hart & Strathmann 1995; Sanderson & al. 2000 for further discussion). Frontal cilia were not found in five cyclostomatides studied by transmission microscopy (Nielsen 1987; Nielsen & Riisgård 1998), hence frontal transport of particles cannot occur in these species. Additional re-

search is necessary to find out whether frontal cilia are present in other Cyclostomatida. Changes of external conditions (velocity of ambient flow, particle concentration) may lead to a switch of feeding method, which appears to be a common occurrence in benthic organisms (as summarized in Okamura 1987b; see also Hunter & Hughes 1993). At high particle concentrations most of the swallowed particles may be transported to the mouth by the central axial current, and the filtering and flicking mechanisms may play a subordinate role (see Best & Thorpe 1983). At the low concentrations presumably much more common in nature, the filtering-flicking method may dominate (Riisgård & Manríques 1997).

In the process of active filtration many of the small and middle-sized particles are not captured (see also Borg 1926; Strathmann 1982a), and it was recently suggested that retention mechanisms are not very efficient in bryozoans (Gilmour 1978; Riisgård & Manríques 1997). Several conditions may be the cause of this. Gilmour (1978:2154) suggested in general "that the inefficiency of lophophorate feeding systems results from the unseparable combination of functions [producing water currents, retention, transport and rejection of particles] which are usually separated in suspension feeding animals". Mainly it seems to happen because the majority of pumped water escapes through the laterofrontal ciliary filter since leaves the tentacle crown in its upper half (Riisgård & Manríques 1997; Riisgård & Goldson 1997; see also Ryland 1975, 1976; Markham & Ryland 1991). It was also shown (Riisgård & Goldson 1997; Riisgård & Manríques 1997) that efficiency of particle retention strongly decreases if particle size is smaller than a certain value (for instance, 4 µm for *Electra* species and 5 µm in a case of *Celleporella hyalina* and *Flustrellidra hispida*), and our observations confirm these data in general (but see Okamura 1987a, 1990). Some authors (Strathmann 1973, 1982a; Best & Thorpe 1994; Sanderson & al. 1994) reported a drop of efficiency of particle capture in time despite the fact that zooids continued to be in working position and created water currents. Since this drop is followed by a period of active feeding, Best & Thorpe (1994) and Riisgård & Manríques (1997) suggested that it might be a result of satiation (see also Winston 1978; Hunter & Hughes 1993), but any changing of the experimental conditions may be taken into consideration as mentioned by Strathmann (1973) and Best & Thorpe (1994) (for further discussion see also Menon 1974 and Sanderson & al. 1994). Riisgård & Goldson (1997) believed that there was no physiological regulation of the filter-pump in bryozoans.

An interesting question arises, does the efficiency of particle capture depend on the qualitative characteristics of these particles? In other words, can bryozoans differentiate and sort their food depending on its taste? In our experiments, bryozoans collected and swallowed particles of different composition in a similar manner (see also Ries 1936; Bullivant 1968a; Dudley 1970; Okamura 1984, 1985, 1987a, 1990), and their behaviour did not depend on their manipulation with either organic or non-organic particles (but see Borg 1926; Jebram 1973, 1975, 1979; Winston 1977; Gilmour 1978). Jørgensen (1966:134) considered suspension feeders as "typically non-selective feeders". Contradictory opinions of the authors mentioned above are not necessarily incompatible because different species may be characterized by different selectivity in relation to particles of various types (see Winston 1977 for further discussion). Similar behaviour was shown for other groups of suspension feeders (Jørgensen 1966). Differences in size and concentration of suspended particles in water as well as velocity of ambient flow and physiological state of the colony are likely to be of major importance for bryozoan feeding and behaviour as a whole (Winston 1977; Okamura 1984, 1985, 1987b, 1988; Best & Thorpe 1994; Riisgård & Goldson 1997). Jørgensen (1966) stated that the rate of the filtration is independent of the concentration of the particles below certain levels in suspension feeders. Indeed, experiments showed that at low particle concentrations the velocity of filtration seems to stay constant, as estimated by observing the feeding currents (our data, see also Bullivant 1968b). However, measurements show that the average rate of filtration varies markedly (Menon 1974) and there are slight oscillatory fluctuations in feeding-current velocity in time (Best & Thorpe 1983; Sanderson & al. 1994). In good agreement with the data of Best & Thorpe (1983, 1986a) and Sanderson & al. (1994), an increase in particle concentration resulted in the rise of the water-current velocity in our experiments. This is apparently caused by a faster ciliary beat (McKinney 1990), and was described first by Dalyell (1847-1848) in phylactolaemates. Best & Thorpe (1994) showed also that the velocity of the feeding current depends on particle size: bryozoans fed more quickly on large food particles in experiments. Too high particle concentrations lead to an obstruction of the lophophores resulting in a retraction of polypides (see also Winston 1978, Gilmour 1978, Riisgård & Goldson 1997, our data) or ciliary reversal, disorganized flickings, frequent contractions of the lophophore and pharyngeal expulsions (Best & Thorpe 1996; Riisgård & Manríques 1997; our data). It was also shown in experiments of Best & Thorpe (1996) that "increasing overall silt loads progressively inhibit feeding", and "smaller particles", clogging the lophophores, "reduce feeding far more than larger particles" that, apparently, "drop out of suspension more rapidly" (p. 44).

FLICKING ACTIVITY

Grant (1827) was apparently the first to observe tentacle flicks, attributing them to particle impacts. Number of flicks increases with particle concentration (Hunter & Hughes 1993; Riisgård & Manríques 1997; Nielsen & Riisgård 1998; our data). However, many authors (Baker 1753; Johnston 1847; Dalyell 1847-1848; Calvet 1900, etc.) reported that bryozoans actively grabbed the particles by the tentacles, implying an absence of the previous mechanical contact between the tentacle and the particle. Winston (1978) introduced the term "tentacle feeder" for bryozoans that used this feeding method. Hunter & Hughes (1993) recorded it in *Celleporella hyalina* fed at low concentrations of the particles. Our observations support the existence of this method. Indeed, among the species observed there were some (*Electra* spp. and *Bowerbankia*) that could extract the particles from the ambient flow by tentacle flicking before their contact with tentacles or before they were dragged into the lophophore by the cilia generated current. Similarly, *Scrupocellaria scabra* pushed away particles, that did not touch yet the polypide using tips of tentacles (see above). The cases of the "intentional" search of particles in still water (e. g. in *Electra pilosa* when the polypide stayed directed toward the distant particle until it was dragged in by the cilia current) show an ability to detect particles at some distance. Winston (1978) reported that in many species which she studied an addition of food particles to the water led to rapid emergence of polypides to the testing-position and then to their expansion. Unfortunately, little is known about sensory structures and their functioning in bryozoans (summarized in Winston 1978, Mukai & al. 1997, Nielsen & Riisgård 1998). The position of the tentacle nerves implies that latero-frontal, abfrontal and, perhaps, terminal rigid cilia might be sensors in marine Bryozoa. But we can only speculate that polypides can sense weak water movements (see also McKinney & al. 1986, and our observations of *Bowerbankia* sp.). We suggest that, in some circumstances, the disturbances of water may arise from a particle entering into the "circular" water currents surrounding the lophophore and created by its ciliature (Fig. 2A), and that these disturbances might trigger a response, either capture of the particle or pushing away.

BEHAVIOURAL REACTIONS: NORMAL AND "SPONTANEOUS"

In metazoans simple behavioural reactions manifesting themselves in different motions are considered as a final stage of reflexes and may be called responses (Jennings 1906; Busnel 1963; Bullock & Horridge 1965; Hinde 1970). A reflex is characterized by a certain threshold value (Brown 1975) which correlates with a physiological state of an organism (or colony). In turn, the internal state is influenced by past irritants (stimuli) received and past reactions given (Jennings 1906). A stimulus of a certain strength and duration corresponding to the certain threshold value triggers the reflex. Thus the response depends both on the threshold value and that of the stimulus. In the case of bryozoan autozooids, size and number of suspended particles are mainly responsible for the strength and duration of the stimulus. Switch of the response occurs either because the stimulus changed its value in such a manner that the threshold limits were exceeded or because of the recurring action of the same stimulus. For instance, the writhing caused by high concentration of particles is normally followed by polypide retraction, and repetitive (and unsuccessful) attempts to reject a particle by the lophophore contraction usually finish by retraction as well. The physiological state of the colony determines the value of the threshold and reflex quickness. One and the same stimulus may cause different responses and, vice versa, the same response may be triggered by various stimuli (see Jennings 1906, Thorpe & al. 1975). For instance, hungry bryozoans are "nervous" (Braem 1940; our data), performing all the reactions much more actively. Despite the fact that a strong irritant, regardless of its nature, normally causes a negative reaction (Jennings 1906), and large particles are normally rejected by polypides or cause polypide retraction (Best & Thorpe 1996), hungry bryozoans do not try to get rid of such a particle, but actively push it into the mouth by tentacles (for instance, in *Celleporella hyalina, Electra pilosa* and some others). In contrast, both diversity and frequency of reactions, and efficiency of particle capturing are much less in replete colonies.

The function of some of the bryozoan reactions is still unknown ("spontaneous" or "random" reactions of Jennings 1906). This is the case when polypides perform actions, but particles inside or nearby the lophophore are absent (Winston 1978; our data). It is also not inconceivable that sometimes particles are transparent or too small to be seen. So, if the polypide responds to contact with an "invisible" particle, it looks like a "senseless" reaction for an observer. Some of the "spontaneous" reactions, for instance, twisting of tentacles may be a consequence of an interruption of the polypide contraction: in several species retraction is preceded by tentacle twisting which seems to produce a more compact arrangement of tentacles in the tentacle sheath. If the whole process was not completed for some reasons, twisting might be its first phase that was not followed by the retraction. Some of the simple activities may be united in groups of successively alternating actions, and carrying out one of the activities may lead to the performance of the whole complex like in a chain-reaction, even if the stimulus which triggered it is no longer

present (see Dick 1984 for discussion). In this case one may decide that he observes a "senseless" reaction.

It is also necessary to keep in mind that stimuli triggering some reactions may have endogenous origin. Jennings (1906:283, 285) stated that "activity does not require present external stimulation" in some cases and "activity may change without external cause". Our knowledge of bryozoan physiology is still not adequate to estimate the importance of the endogenous stimuli for their behaviour, but there is no doubt that such relationships exist. For instance, regular retractions of the polypides in undisturbed colonies of some species can be explained by respiration and by the need of circulation of the oxygen enriched coelomic fluid inside the zooid (von Buddenbrock 1912; Mangum & Schopf 1967). It is obvious that internal reasons are also responsible for the activities connected with reproduction (see *Introduction*).

In *Results* we stressed that there are various patterns of polypide excursions and expansion, differing from each other by the rate. The same may be said of entire zooidal behaviour, and we suggest that some of these differences may be species specific. It was already recorded by Farre (1837) that some species may be more active in comparison with others. Indeed, there are "brave and cheeky" species (for instance, *Tegella armifera*, *Rhamphostomella bilaminata*, *Electra* species), performing various movements most of the time and "scornfully" regarding the disturbances, and "cowardly and shy" ones (*Cribrilina annulata*, *Celleporella hyalina*, all cyclostomatides) that are very careful in every way. It is interesting that there are such differences within the same genus: *Cribrilina punctata*, for instance, must be assigned to the first group whereas *Cribrilina annulata* to the second one. At the same time, most species usually demonstrate non-extreme manifestations of their activity. This specific norm of behaviour changes according to the physiological state of the colony: zooids are much more active in starving colonies. Thorpe (1975) and Thorpe & al. (1975) showed that the speed of the polypide protrusion and withdrawal may vary even within one and the same colony, depending apparently on its physiological state (see also our observations on *Electra pilosa)*. Also Winston (1978:14) noted that the rate of the eversion-retraction process "depends on how well the animals are adapted to the [experimental] conditions".

DIFFERENCES AND SIMILARITIES IN AUTOZOOIDAL BEHAVIOUR

The distribution of the individual behavioural reactions among different bryozoan species (see Table 2) suggests that some of the autozooidal reactions are basic, necessary for normal feeding, and determined by common bryozoan ancestry. In contrast, other reactions are "specific", and their existence is determined by belonging to a particular taxon and dependent on intrinsic factors including zooidal morphology. Sanderson & al. (2000:362) noted that in Bryozoa "structure as well as behaviour may indicate differing feeding strategies, food particle preferences and capture methods between species … adapted to differing feeding niches". For instance, behavioural uniformity and low diversity are dictated by zooidal morphology in stenolaemates (see Taylor 1981, McKinney & Boardman 1985, McKinney 1988). An absence of projecting introvert in most cyclostomatides is probably one of the main reasons for the scarcity of behavioural reactions within the group (Farmer 1979; Taylor 1981). Notably, McKinney (1988) described slightly projecting introverts in two cyclostomatides from the Mediterranean (see also pers. commn of J.R.P. Ross in Taylor 1981), including *Disporella hispida.* He suggested that the species mentioned might be actually a species complex. Indeed, we have never observed projecting introverts in what is considered to be the same species from the White Sea.

However, zooidal behaviour may be different even within the same colony: in gymnolaemates with polypides with equitentacled and obliquely truncate lophophores some differences in the rejection process are always present (see also Dick 1987). Differences in behaviour can be also caused by differences in size (discussed in Bullivant 1968b, Dudley 1970, Ryland 1975, Winston 1977) and colony structure (Winston 1978, 1979; McKinney 1990). Hence bryozoans that are close in size, but belong to distant groups may possess a greater number of reactions in common with each other than with their smaller relatives. However, it is logical to suggest that closely related species, for instance, congeneric species should possess the same or very similar behaviour, and this was observed within genera the *Electra*, *Scrupocellaria*, and *Callopora.* But relatives are often characterized by different zooidal arrangement within a colony, and behavioural diversity may be restricted by the colony structure (Winston 1978, 1979). Even among the colonies of one and the same species, colonies of different age and on different substrata (and therefore having different colony structure) showed behavioural differences. Such cases show behavioural diversity. For instance, the number of the reactions recorded in the colonies of *Porella smitti* studied, growing on some red algae (small cylindrical muff-like colonies overgrowing the thallomes) and rhizoids (small flat colonies) and fronds (large old colonies with areas of frontal budding) of *Laminaria saccharina,* was different. The diversity of reactions was somewhat greater in "cylindrical" colonies, than in "small flat" colonies where polypides were placed very close to each other. The last condition may be considered as a factor re-

stricting some reactions (see also Dick 1987, Thorpe & Ryland 1987, Grünbaum 1995). Behaviour of polypides in large colonies was also more diverse than in small colonies. Both a complicated relief of the colony surface presented by monticules and depressions between them and widespread polypide recycling were responsible for a less compact arrangement of polypides.

Scanning activity also may be restricted both by polypide and colony structure. Introvert length directly affects the possibilities of scanning, and polypides with short introverts are strongly limited in their scanning activities. At the same time even polypides with long introverts in some species do not demonstrate scanning or perform it very rarely. This situation occurs in the colonies of species in which water currents are strictly channelled (Winston 1978, 1979).

We also recorded marked differences in the behaviour of *Celleporella hyalina* from the White and the Barents seas. The spectrum of the reactions observed in the colonies from the Barents Sea was much closer to these observed in the colonies of *Tegella armifera*, than to *Celleporella hyalina* from the White Sea (Table 2), and we suggest that this species may be actually a sibling species complex.

CLASSIFICATION OF THE BEHAVIOURAL REACTIONS

As mentioned above, a period of a polypide activity consists of three successively alternating phases: protrusion, activity proper and retraction. Three different approaches have been used in the literature to classify individual polypide reactions performed during the second stage. A "functional" approach is applied to reflect the functional importance of the activities, and the reactions connected with feeding, cleaning of the lophophore (that may be considered as equivalent of rejection) or the colony, removal of the fecal pellets and reproduction may be distinguished (Atkins 1932; Winston 1978; Dick 1984; McKinney 1997). In this case different reactions are united according to the final result only. The main problem is that the function of some of the reactions described is unknown (see above).

The second approach is based on the superficial resemblance of the behavioural reactions without considering their functional role. For instance, a single expansion of the lophophore may serve opposite purposes (particle rejection and capture) in different species. Similarly, Winston (1978) marked out a conventional group of the "flicking activity" in which reactions different by their function were included. But the diversity of bryozoan activities is too high to use this approach, and Winston was forced to unite some of the encountered reactions in "other individual actions".

Working with the ejection mechanisms, Dick (1984) applied what we call here the "morphological" approach

in accordance with functioning part of feeding apparatus. We also used a similar method to classify the reactions and suggest that it has the greatest practical utility. Thus in bryozoan behaviour four categories of reactions may be distinguished that are carried out by: (I) lateral and frontal ciliature of tentacles (activities No 1-4 in the list in Chapter Results and Table 2); (II) mouth and pharynx (in motionless polypide or in connection with some other reactions); (III) tentacles: (a) single or several tentacles (No 7-11), (b) all tentacles of lophophore together (No 12-21); (IV) entire polypide (No 5-6, 22-24). It should be kept in mind that ciliary work is also the basis for the last three groups of activities, but it often plays a subordinate role in these cases. Some of the reactions that are carried out by an entire polypide may be considered as complex. For instance, in *Celleporella hyalina* partial retraction of the polypide is accompanied by lophophore contraction and pharyngeal rejection.

ORIGIN AND EVOLUTION OF DIFFERENT GROUPS OF BEHAVIOURAL REACTIONS: SOME REMARKS

We consider polypide protrusion-retraction as one of the initial bryozoan activities that might be basic for the origin of some others, for instance, of all the reactions connected with tentacle crown expansion and contraction, including twisting, bringing the ends of tentacles together, partial retraction, retraction with ingestion, etc. This diversity might originate by both modification and falling out of some of the phases of the protrusion-retraction activity. Some of the reactions might have evolved as the most efficient (in terms of expenditure of time and energy) response to stimulus. Action of only one tentacle (during flicking, for instance) may be considered as more effective in some cases since the filtration work of the entire lophophore is not interrupted. Similarly, sharp nods with flinging might substitute for "rejecting" retraction of the polypide in some forms. Dick (1984:205) suggested that an initial rejection activity of a polypide might be "tentacular downswing probably coordinated with a strong upward current produced by ciliary reversal" and the polypide retraction "from under a particle" in ancestral forms. The author assumed the correlation between the complication of autozooidal behaviour and the suggested increase of zooidal (and polypide) size in evolution of marine Bryozoa. Also Winston (1978) recorded that the behaviour of bryozoans with large polypides is more diverse in general. In turn, the reason of the increase mentioned might be connected with a rise of the feeding efficiency since the increase of the polypide size correlates with an increase of velocity (and efficiency) of the feeding current (Best & Thorpe 1983, 1986b). At the same time new behavioural reactions, for instance, those connected

with cleaning, might have evolved because the amount of captured particles was increased too. If so, the methods of cleaning a lophophore might have originated first, followed by the methods of cleaning a colony surface (Dick 1984; our data).

CONCLUSIONS

Following the works of Winston (1977, 1978, 1979) and McKinney (1990), the paper presented is an attempt to discuss from different angles the phenomenon of feeding behaviour in marine bryozoans. Using non-contradictory aspects from different hypotheses, we aimed the creation a model of bryozoan feeding mechanism. We also tried to show a variety of behavioural reactions in these sessile animals. Our observations and analysis of the descriptions published lead us to the conclusion that bryozoan individual autozooidal behaviour is much more diverse than in any other groups of colonial epibionts (see Boardman & al. 1973, Chamberlain & Graus 1975, Larwood & Rosen 1979, Marphenin 1995). In some ways it may be only compared to the behaviour of entoprocts (Atkins 1932; Nielsen 1987, 1989). The variety of the reactions shows that bryozoans possess a wide range of behavioural adaptations for feeding on suspended matter. We believe that a morphological approach based on the structure performing the reaction, is the most useful to classify the behavioural reactions recorded. The data discussed allow to consider individual autozooidal behaviour of Bryozoa as a complicated process that is characterized by diverse combinations of ciliature, tentacles and entire polypide activities. Active filtration is a background for almost all other activities. It is based on a filter-feeding principle (Riisgård & Manríques 1997; Nielsen & Riisgård 1998), but supplementary mechanisms (Borg 1926; Atkins 1932; Cori 1941; Strathmann 1973; Ryland 1975; 1976; Winston 1978; Best & Thorpe 1983; see also McKinney 1990) can be also used (summarized above). Our data are in a good agreement with this model.

In terms of neurophysiology autozooidal behaviour may also be considered to be a very flexible and sensitive system of reactions in which the activities can be performed in different combinations and successions and can be switched depending on the situation. Interacting exogenous and endogenous factors are responsible for it. Exogenous factors include, among others, the physical and chemical characteristics of water (mainly, temperature) and suspended particles (size, weight, taste (?), concentration, motility), substratum and its microrelief, neighbouring epibionts, and ambient flow (its form and velocity). Endogenous factors are zooidal size and morphology, specific behavioural features, physiological state of colony, colony shape and size, zooidal arrangement, and position of zooid relatively to external current. In a feeding colony autozooids perform different activities at the same time. And the mode of the activity of each zooid depends on particular conditions reflecting the state of the entire colony, the zooid and an environment. It is clear that data on individual behaviour of modules in colonial organisms are insufficient to understand all their vital functions. However, without knowledge of individual zooidal activities it is often impossible to explain the origin of group behavioural reactions in particular and main trends in evolution of bryozoan coloniality in general.

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