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Colonial behaviour and group zooidal reactions in Bryozoa: history of research

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1. Introduction

Investigations of modular systems encompass many colonial organisms with a high level of morphological and physiological integration. Bryozoan colonies are a very promising model in this respect, and studies of colonial behaviour are one of the approaches in evaluating the degree of colonial integration. Bryozoans demonstrate a variety of group behavioural reactions which are connected with different vital functions. Co-ordinated activities of polypides are regulated neurophysiologically, physiologically, structurally and, possibly, hormonally. Different manifestations of the regulatory mechanisms have been studied previously, and we here present a review that discusses the history of these investigations.

2. Early studies

Henry Baker was probably the first who noted in passing colonial behavioural reactions in fresh-water bryozoans (possibly, *Plumatella*).¹ Barthelemy Dumortier described retraction of all polypides in a colony of the phylactolaemate *Lophopus crystallinus* (Pallas) after a stimulus was applied to a 'coenoecium'.² Contact with a single lophophore resulted only in its retraction. The first description of synchronized polypide protrusion and retraction in colonies of marine bryozoans was published by George Johnston in 1838.

Similarly to Dumortier, he also mentioned that ‘if, when many [polypides] are expanded [in a colony], one is... touched with a sharp instrument, it alone feels an injury and retires, without any others being conscious of the danger’.³ But in spite of the intensive studies on different taxa of these colonial animals using live specimens (Hassall,⁴ Dalyell,⁵ Gosse,⁶ Busk,⁷ Allman,⁸ Smitt,^{9,10} Hyatt,¹¹ Nitsche,¹²⁻¹⁵ Vigelius,¹⁶ Kraepelin,¹⁷ Pergens,¹⁸ Oka,¹⁹ Proucho,²⁰ Calvet,²¹ Gerwerzhagen,²² Borg,²³ etc.)²⁴ there are only occasional remarks concerning group autozooidal behaviour in the literature published. For instance, Thomas Hincks²⁵ and Fritz Müller²⁶ mentioned ‘common and simultaneous movements’ of the autozooids in the ctenostome *Mimosella gracilis* Hincks.^{27, 28, 29}

3. Twentieth century studies

Folke Borg described removal of released eggs by their consecutive transference from lophophore to lophophore in a colony of the cheilostome *Electra pilosa* (Linnaeus).³⁰ Ernst Marcus made some observations on bryozoan behaviour during his experiments on several species of both marine and fresh-water bryozoans, including the cheilostome *E. pilosa*, the ctenostome *Farrella repens* (Farre), and the phylactolaemates *Cristatella mucedo* Cuvier and *Fredericella sultana* (Blumenbach).^{31,32} One of his main conclusions was that there is no colonial co-ordination in gymnolaemate Bryozoa, and that, as in the case of Johnston,³³ no autozooid responded to a stimulus applied to any other.³⁴ In contrast, the transmissions of stimuli from one member of a colony to another was demonstrated by Marcus for the phylactolaemates mentioned.³⁵ Results of Marcus’s studies were regarded as being of the greatest importance by several authors^{36,37,38} in spite of the opinion of Georges Bronstein who claimed to have observed colonial responses in the ctenostome *Bowerbankia* sp.³⁹ Also the data of Stanislaw Hiller, who described the interzooidal nervous connections in *E. pilosa* and *E. crustulenta* (Pallas) (both as *Membranipora*) and group polypide retractions after the stimulation of the frontal cystid wall,⁴⁰ were considered as insufficient to cast doubt upon the conclusions of Marcus.⁴¹ Collective movements of entire zooids and whole zoarial branches resulting in a change of their orientation were investigated in detail by Lars Silén⁴² in ctenostomes of the genera *Mimosella* and *Farrella* and the cheilostome *Kinetoskias* correspondingly.⁴³ However, Silén supported Marcus’s⁴⁴ view, stating that mechanical stimulation of a zooid does not trigger any response from adjacent zooids.^{45,46} Thus, the opinion about the absence of colonial co-ordination of zooidal activity survived for about 50 years in spite of the facts that there are momentary simultaneous polypide retractions after stimulation⁴⁷⁻⁵² as well as movements of cheilostome bryozoan vibracula that can beat in unison.⁵³⁻⁵⁹ For instance, Silén believed that synchronous action of the vibracula in the cheilostome *Caberea* is a kind of metachronal chain reaction during which very long vibracular setae inevitably touch neighbouring ones that thereupon respond.^{60, 61, 62}

Further investigations led researchers to suppose that the behaviour of Bryozoa is a very flexible and sensitive system of reactions that combines diverse individual and group

zooidal activities depending on the situation. At the present time, there are a lot of both morphological and behavioural evidences in favour of existence of the presumed colonial co-ordination in all main Recent bryozoan taxa. In addition to the anatomical data of earlier authors⁶³⁻⁷¹ many new facts that are indicative of nervous connections and transmission of nervous signals between zooids were obtained by Geneviève Lutaud,⁷²⁻⁸⁰ who supported the hypothesis of interzooidal information spreading through a colony and leading to colonial responses.⁸¹

In the phylactolaemate *Plumatella fungosa* (Pallas) George Mackie recorded the phenomenon in which 'the lophophores over wide regions become orientated by muscular action so that they point in the same direction'.⁸² He also mentioned co-ordinated withdrawal responses in *Cristatella mucedo*. Colonial behaviour and nervous responses were studied in some species of free-living cheilostome.⁸³⁻⁸⁷ Colonies under investigation showed a high degree of co-ordination of avicularian setae movement owing to which they were able to stop themselves being buried in sand, to return back to a normal position after being placed upside down, to travel across the aquarium preferably towards the light and to climb one over another.⁸⁸ A high level of co-ordination was also recorded between autozooids, and between autozooids and avicularia, when feeding periods ending in simultaneous polypide retraction are alternated with simultaneous setal cleaning movement after which the colonial feeding is resumed. Co-ordinated avicularian activity in Recent lunulitiform bryozoans (Cupuladriidae) was also noted by Ernst and Eveline Marcus,⁸⁹ Patricia Cook⁹⁰ and Ronald Greeley.⁹¹ Judith Winston and Patricia Cook recorded synchronous movements of avicularian setae in different species of Cheilostomatida.⁹²⁻⁹⁵

Collective activity of another type of bryozoan polymorphs was described by Lars Silén and Jean-Georges Harmelin who observed rocking and circular movements of the single tentacle of nanozooids in cyclostomes of the genera *Plagioecia* and *Diplosolen*.⁹⁶ These movements were not synchronized but were simultaneous, and cleaned a colony surface after induced obstruction by silt. It was noted that the tentacles of nanozooids were the first to appear in the colony after strong disturbance, whereas autozooids expanded their lophophores much later. Similar 'sentry' behaviour performed solely by autozooids was also recorded in several cheilostomates.⁹⁷

Some neurophysiological aspects of intra- and intercolonial co-ordination of behavioural responses were investigated in *Membranipora membranacea* (Linnaeus), *Electra pilosa*, *Selenaria maculata* (Busk) and *Flustrellidra hispida* (Fabricius).⁹⁸⁻¹⁰¹ The long-term controversy (see above) was rejected at last. It was found in experiments that 'mechanical [as well as electrical] stimulation of an extended lophophore...resulted solely in the retraction of that polypide'.¹⁰² In contrast, stimulation of the frontal membrane triggers 'the immediate rapid withdrawal of all the extended lophophores within some distance of the zooid stimulated'.^{103, 104, 105} This is in good agreement with observations of Winston

who described group retractions during removal of large particles from a colony.¹⁰⁶ Conduction of nerve pulses through the colony accompanied by quick consecutive retractions of polypides was proved both within the same colony¹⁰⁷⁻¹¹⁰ and within complexes of adjoining colonies.¹¹¹ Moreover, such conduction was also shown in a representative of carnosan ctenostomes (*F. hispida*),¹¹² although interzooidal nervous connections were not discovered by Lutaud who investigated *Alcyonidium polyoum* (Hassall).¹¹³ Michael Berry and Peter Hayward suggested that ‘the nervous activity responsible for co-ordinating locomotion would spread throughout the entire colony’ after their experiments with free-living *S. maculata* where strong illumination caused the colonies to start moving.¹¹⁴ Noticeably, in contrast with earlier observations^{115, 116, 117} John Thorpe found no obvious evidence for co-ordinated lophophore retractions in phylactolaemates.¹¹⁸

However, it has been found that co-ordinated autozooidal behaviour in Bryozoa is not limited to simultaneous protrusion-retraction excursions. Bryozoans are colonial organisms and, therefore, the effects of large numbers of individual lophophores may be readily seen. Collective feeding leads to several problems, e.g. how to prevent a repeated water filtration, and how to remove filtered water, sediment and wastes from a colony where an area with incurrent flow is many times larger than the excurrent area. This inequality potentially must result in an appearance of zones with high water pressure where normal zooidal functioning might be hampered. In such conditions it is conceivable that autozooids will somehow react in groups to alleviate the problems, and this might be considered as a consequence of colonial regulation. Colonial effects on feeding and behaviour of marine bryozoans have been intensively studied since the work of William Banta, Ken McKinney and Russell Zimmer who observed colonies of the cheilostome *Membranipora* sp. and noted that most of the colony was covered by extended polypides, but that there were numerous blank spaces (‘chimneys’).¹¹⁹ In these areas lophophores were not extended, while those around the edge of the chimney leaned away from its centre having the obliquely-truncated tentacle crowns with the longest tentacles bordering a chimney. The authors concluded that the incurrent water passed through the tentacles and down between the zooids exiting via the colony edge or a chimney. They also suggested that a formation of excurrent water outlets was connected with a colony size. In their opinion, in large colonies ‘lophophores...interfere with each other unless excurrent channels such as chimneys are present’.¹²⁰ These researchers proposed that the monticules (maculae) known in some fossil stenolaemates might be such chimneys reflected in a skeleton, and this idea was supported and exploited by many researchers.¹²¹⁻¹³²

Removal of filtered water from the colonies and co-ordinated autozooidal activity was further studied in detail by Patricia Cook and Jim Chimonides,^{133, 134} who examined 17 different species of the Recent marine bryozoans. For multiserial encrusting colonies they noted three patterns of excurrent flow: (1) active centripetal and centrifugal colony-wide flows, (2) “active” local excurrent flows from chimneys ringed by functioning autozooids with obliquely-truncated lophophores and (3) ‘passive’ chimneys or local exhalant flows

over areas devoid of actively feeding zooids. Their observations on *M. membranacea* led them to the opinion that both the position of chimneys in a colony and the position of obliquely-truncated lophophores in a chimney are astogenetically determined. In general, these researchers supposed that both astogenetic and ontogenetic (connected with a polypide recycling) changes are involved in production of various forms of filtered water outflows, and agreed with previous authors^{135, 136} that some reproductive processes might take part in chimney formation.¹³⁷ Cook was the first to describe chimneys bordered by obliquely-truncated polypides that were tilted towards the chimney centre.¹³⁸ Scott Lidgard, who conducted his experiments on *Membranipora villosa* Hincks, concluded that chimneys are an adaptation which allows colonies to minimise the recirculation of previously filtered water, making the colony more efficient.¹³⁹ Matthew Dick proposed a hypothetical mechanism for chimney formation, suggesting that this process may involve both hydrodynamic and astogenetic control as well as their combination.¹⁴⁰ He also showed the ways of transformation from obliquely-truncated lophophore to equitentacled one, and vice versa, in his study on *Holoporella brunnea* (Hincks) and *M. serrilamella* Osburn, and connected the reason for this transformation with lophophore position respectively to excurrent flow. Some problems of the spatial arrangement of feeding zooids and their interference in encrusting colonies were also investigated and discussed by John Thorpe and John Ryland¹⁴¹ and later by Daniel Grünbaum.¹⁴²

Judith Winston investigated 79 species of Recent marine bryozoans and recognized six patterns of bryozoan colonial behaviour in relation to the morphology of polypides, their grouping, colony form and structure, and water currents produced.^{143, 144, 145} She distinguished species where colonies were characterized by (1) predominantly individualized polypide behaviour,¹⁴⁶ (2) separated polypides whose orientation is controlled by the colony skeleton, (3) polypides forming temporary clusters, (4) polypides forming fixed clusters unreflected in the colony skeleton, (5) polypides forming fixed clusters enhanced by irregular skeletal patterning, (6) polypides forming fixed clusters enhanced by regular patterning of the colony skeleton. She also observed several earlier unknown manifestations of group autozooidal behaviour, and supported the hypothesis of Banta, McKinney and Zimmer¹⁴⁷ recording an excurrent flow of filtered water above raised areas (knobs or monticules) in the skeleton of some cheilostomes.^{148, 149} This and subsequent work was reviewed by Frank McKinney^{150, 151, 152} who classified the feeding of 91 species of Bryozoa into four main categories. The first category includes those bryozoans that behave essentially as individuals when they feed. This often occurs when lophophores are sufficiently separated and do not act together with neighbours. Typically such lophophores are supported on long introverts (or elevated by tubular and erect distal ends of the cystids), radially symmetrical and equitentacled. The second category includes species where lophophores form temporary feeding clusters. In such cases only a fraction of the colony feeds at any time and clusters of lophophores form around an initially emerging lophophore. Alternatively, in the third category, lophophores are in fixed groups across a continuous colony surface, and in such colonies there is usually a high degree of

integrated behaviour. Invariably in such designs there are areas of outflow from the colony and in this category of Bryozoa there are often asymmetric lophophores found in these regions. The last category in which bryozoan colonies may be considered is that of skeletally separated lophophores, where a branching structure facilitates unidirectional flow towards the colony and between the branches. The lophophores may cover the area between the branches and lean over the space. There may also be a high degree of asymmetry in these lophophores and all of them typically have short introverts.

In her book, published in 1985, Patricia Cook mentioned the colonial behaviour in several cheilostomates. She was the first to describe the ‘colony-wide episodes of tentacle ‘reversal’’, when ‘the tentacle crowns were widely extended and the tips directed towards the colony surface’.¹⁵³ Cook suggested that this behaviour pattern might be a colonial rejection, ‘correlated with reversal of ciliary movement, and may be associated with cleaning of detritus,¹⁵⁴ sperm release or other, at present unknown functions’.¹⁵⁵

Natalia Shunatova and Andrew Ostrovsky recorded group autozooidal reactions and colonial behaviour in 13 species and subspecies of marine bryozoans.¹⁵⁶ Several collective reactions (synchronized scanning behaviour, repeated particle transference by circular water currents, feeding and cleaning of the colony surface by ‘chains’ of inclined lophophores) were described for the first time. In large colonies of *Tegella armifera* (Hincks) a new type of chimney was discovered. Chimneys are formed by temporary retraction of 10-12 neighbouring polypides, and the blank space is surrounded by equitentacled lophophores standing vertically. Chimneys associated with elevated areas on the colony surface (monticules) were found in *Porella smitti* (Kluge) and *Schizomavella lineata* (Nordgaard). But, in contrast to all previously published speculations and observations, the monticules were often places of incurrent rather than excurrent flow, and water outlets were formed in depressions between monticules. In *S. lineata*, monticules change their function from incurrent to excurrent after polypide degeneration. Shunatova and Ostrovsky suggested that elevated areas formed by frontal budding can probably change their function at least four times: (1) they can probably work as excurrent zones during the initial stages of formation when young monticules consist of only incipient zooids with non-functional polypides, (2) later they start to function as incurrent zones, (3) after polypide degeneration, they become excurrent zones, and (4) after polypide regeneration they function as incurrent zones again. The depressions between monticules would probably follow exactly the opposite succession. Thus, the hypothesis of Robert Anstey,¹⁵⁷ who speculated that in some Palaeozoic stenolaemates the hydrodynamical regime around the monticules could change, was made more plausible.

Colony-wide water currents in relation to ambient flow, colony growth form and polypide morphology, distribution and behaviour were also intensively studied by Frank McKinney with co-authors in some Recent marine Bryozoa.¹⁵⁸⁻¹⁶³ The results fit well with previously proposed theoretical speculations concerning the interrelationship of the

ambient and cilia-generated water currents and growth forms in different fossil bryozoans.¹⁶⁴⁻¹⁷⁰ It was accepted that feeding was a ‘major sculptor of bryozoan form’.^{171, 172} Colony-wide water currents have been also considered to be very important in intra and interspecific competition.^{173, 174, 175}

Beth Okamura and Julian Partridge supported Dick’s hypothesis¹⁷⁶ of pressure build-up under the lophophore sheet in experiments with *Membranipora membranacea*. They showed “a trend towards [lophophore] miniaturization with increased flow: the zooids were less elongate, the lophophores were smaller in diameter and had fewer tentacles, and the distances between excurrent jets were shorter”.¹⁷⁷

Colonial effects on feeding of some phylactolaemates have been studied by George Mackie,¹⁷⁸ John Bishop and Leonard Bahr,¹⁷⁹ Beth Okamura and Lita Doolan¹⁸⁰ and Irina Antipenko.^{181, 182}

4. Conclusions

In spite of many investigations, the only attempt to quantitatively estimate the degree of integration in bryozoan colonies was made by Frank McKinney.¹⁸³ He used the extent of the colonial feeding current interactions for this purpose. Judith Winston proposed that the data on group behaviour of autozooids could be used for such estimation, and worked up a “matrix” where “levels of morphological and behavioural integration (with respect to feeding and current producing activities)” are considered.^{184, 185} Thus, previous research showed that bryozoans are a convenient model for investigations of different aspects of integrative processes. The data accumulated at the moment can be considered as a strong background for future research, and further observations on bryozoan behaviour as well as mathematical formalization should help to make progress in this direction.

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