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Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences,
Volume 313, Issue 1159, The Growth and Form of Modular Organisms (Aug. 14, 1986),
175-196.

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Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences
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Sat Apr 26 09:50:34 2003

From aggregates to integrates: physiological aspects of modularity in colonial animals

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[Plate 1]

Physiological adaptations of colonies in the areas of resource-sharing, defensive behaviour and locomotion are reviewed and discussed.

Exchange of nutrients between zooids is a fundamental attribute of true colonies, although the transport systems involved vary and, in some cases, complex junctional structures appear to regulate passage of materials between zooids, as in the parallel case of interconnected cell systems. It is not known if regulatory molecules, as well as nutrients, pass via these interzooidal pathways.

Almost all colonies show some form of behavioural coordination but, again, the pathways employed vary considerably. Examples of coordination by nerves, by conducting epithelia and by photic signals, are given. Zooids typically retain a high degree of local autonomy and the interzooidal pathways serve more as labile links between the action systems of the zooids than as centres where behaviour is initiated. Siphonophores are exceptional in having nerves, in their stems, which initiate as well as relay behaviour.

Defensive responses are the commonest form of coordinated activity in colonies, but some colonies show coordinated locomotion. The most striking examples are those salps and siphonophores that regulate the activity of their locomotory modules either in terms of frequency of pulsation or in terms of direction of locomotion, or both. Modularity has theoretical mechanical advantages in animals swimming by jet propulsion.

The requirements of pelagic locomotion have led planktonic colonies to diverge markedly from the pattern seen in sessile colonies. Pelagic colonies, unlike sessile ones, are typically linear and unbranched, show an anterior–posterior axis, are determinate in form, at least at the anterior pole, and lack much of the plasticity and regenerative ability that characterize sessile colonies.

The significance of coloniality has been much discussed in the past and is once again the focus for research and debate, chiefly among population biologists. A new way of looking at clones and colonies has emerged, and along with it a new language, and those of us who participated in the earlier debate must come to terms with these developments. I will approach the topic, therefore, by reviewing some of the prevailing ideas from my standpoint as a classically trained zoologist and as a behavioural physiologist with a special interest in gelatinous marine macroplankton.

1. THE NATURE OF COLONIES: OLD AND NEW IDEAS

(a) *Individuals and modules*

Where now we speak of modules, the operative word used to be ‘individuals’, and discussions of coloniality often centred around levels and degrees of individuality (see, for example, Beklemishev 1969). Going up the scale of complexity from cell to tissue to multicellular

organism to colony or society we find individuality expressed at each successive level, along with a tendency for the individualities of the lower order units to be suppressed or submerged. The cell (itself probably derived from a symbiotic association of microorganisms) tends to lose its individuality in multicellular associations, just as the individuality of the zooid is subordinated to that of the colony of which it forms a part, or that of the unitary animal to that of the society.

These ideas go back at least to the time of Haeckel, who recognized six levels of morphological integration (see White 1984). Most writers have couched the argument in terms of an evolutionary progression from lower to higher organizational levels. As Dendy (1924), for instance, expressed it 'evolution consists to a very large extent, if not mainly, in the progressive merging of individualities of a lower order in others of a higher order'. One might quibble about 'if not mainly', but most people would probably accept Dendy's comment as a valid expression of an important biological truth. The idea is useful also because it encourages comparison of processes occurring at different organizational levels, a point touched upon below (§3) in reference to intercellular and interzooidal communication.

If, then, as aggregates progressed along the road toward integration they began to acquire a new individuality of their own, we must still agree with Herbert Spencer (1898) who remarked that 'it would be impossible to say where the lower individualities ceased and the higher individualities commenced', and that 'there is no definition of individuality that is unobjectionable' (he went on to define it anyway!). Attempts to classify animals in order of structural complexity according to their supposed level of individuality can produce bizarre results. In Cattaneo's (1879) scheme, for example, tapeworms are put above molluscs. Many other difficulties surround use of the word 'individual' (Mackie 1963), not least its failure to distinguish between the products of replicative growth and the products of sexual reproduction (Harper & Bell 1979). Thus, while the general concept (individuality) is useful, we run into problems when it comes to calling specific objects individuals.

The same is true with modularity and modules. A module is a product of iterative growth. The term is happily free of evolutionary and metaphysical overtones. Originally used in a restricted sense to describe the products of a plant apical meristem, it has now acquired a much broader range of possible meanings, especially in reference to animals. 'Module' could be used to describe cells, developmental compartments, segments, metamers, tagmata, cormidia, cyclosystems, chimney systems and members of clones, colonies and societies. Modules need not be attached to one another physically and they need not even be genetically identical. Rosen (1979), for instance, regards insect colonies as 'discontinuous modular societies'. Thus, while modularity is valuable as an expression of a mode of growth, use of 'module' itself is hazardous unless the identity of the particular module under discussion is made unmistakably clear. White (1984) would like to see a return to a more restrictive definition of the word. This seems a forlorn hope. 'Module' is firmly established in a general sense and cannot now be used to replace any of the old descriptive terms applying to specific morphological entities.

The modules I will be referring to in this article are the zooids in animal colonies. Zooids have these characteristics:

(i) They arise by budding from single oozoids and are therefore parts of single genets. Fusion of colonies representing different genets may subsequently occur producing a chimeric colony, no different in principle from a chimera made by combining blastomeres from sheep and goat embryos (Fehilly *et al.* 1984).

(ii) Zooids are organically linked in such a way that direct exchange of metabolites can occur. A problem here is lack of information about exactly what if any exchange takes place in specific cases. Some compound acidians (for example, *Botryllus*, *Perophora*) are truly colonial, being linked by a common blood vascular system. Others show no such obvious pathways of metabolic exchange and might better be regarded as mere aggregates of unitary organisms.

(iii) With few exceptions, zooids in colonies are coordinated behaviourally by nerves, conducting epithelia, or both.

(iv) Zooids evolved from single unitary organisms and are equivalent to them in terms of primary individuality, however specialized they may have become, and however subordinate to the emergent colonial individuality. Thus 'zooid' has a strong evolutionary connotation. It is not always possible to decide if a particular structure is a true zooid. Bracts and pneumatophores in siphonophores and spines in bryozoans may be colonial neomorphs, but are often regarded as zooids.

Metamerically segmented animals are probably not colonies or the derivatives of colonies, and it is doubtful if metamers are or ever were zooids in the sense defined above, unless the corm theory of annelid evolution is correct. Accordingly, this discussion will not cover metamerically segmented animals. Though still problematical in botany (White 1984) the term metamer has found a stable niche in zoological usage meaning essentially the same as 'segment'. Little is to be gained by thinking of zooids as metamers, and we must hope that Harper's dalliance with this idea (Harper 1984) fails to develop into a full-blown affair.

(b) *Benthic versus pelagic colonies: do the same rules apply?*

An important literature has grown up on the adaptive significance of animal modularity, which is concerned almost exclusively with plant-like sessile colonies: sponges, cnidarians, bryozoans and ascidians in particular (see, for instance, Buss 1979; Chapman & Stebbing 1980; Hughes & Jackson 1985; Jackson 1977, 1979). These colonies share a number of common characteristics, which distinguish them from solitary forms.

(i) They often show indeterminate growth, with the potential for exponential increase in numbers of modules, and hence for rapid expansion over available substrates. Rapid exploitation of substrate is also presumably the rationale for coloniality in various parasitic worms (*Echinococcus granulosus*, *Taenia crassiceps*, etc.) as discussed by Beklemishev (1969). The phenomenon of polyembryony in parasites comes in the same category, along with such oddities as *Thompsonia*, the colony-forming parasitic barnacle.

(ii) Following from (i), many colonial genets achieve large size, wide dispersal and extreme longevity. Corals, for example, can be far larger than solitary anthozoans. They have a high surface area : volume ratio, as they consist of many small zooids covering a skeleton which they secrete. Size increase is not accompanied by changes in this ratio as would be the case, along with various attendant problems (see Strathmann & Chaffee 1984) in solitary forms. The ability of corals and other sessile colonies to fragment and for the fragments to fuse and/or regenerate imparts the potential for extensive dispersal and for indefinite survival. Some corals living today may be over 1000 years old, and corals living in the past when sea levels were more stable may have lived many times longer (Potts 1984).

(iii) Modular growth typically produces a branching colony structure. Branching ensures that the modules are spaced out or packed together in some way that automatically 'regulates competition between zooids' (Knight-Jones & Moyse 1961), and is presumably 'the most

effective arrangement for feeding' (Bayer 1973). This may of course be assisted by active orientation movements of the zooids, rather than being merely a product of patterned or tropistic growth processes.

(iv) Plasticity is an obvious characteristic of many sessile colonies. They can assume a variety of sizes and shapes depending on spatial and temporal variations in the substrate. The ectoproct *Stomatopora*, when displaced from its original substrate by a bivalve, grows up and over the shell of the bivalve (Jackson 1977). *Electra pilosa*, which grows on *Fucus* fronds, finds refuge at the tip of the frond, keeping up with the latter's growth by extending runners in that direction (Stebbing 1973).

Not only size and shape vary, but the disposition of different zooids can sometimes be adjusted to local conditions, as in *Hydractinia*, where spiral zooids are produced only around the opening of the shell it lives on. Some ascidian colonies and calyptoblastic hydroids resorb and replace their zooids according to a regular cycle, a process of continual rejuvenation (Gordon 1977) which also permits rapid changes in zooid numbers and distribution (Sabbadin 1979).

If a sessile colony hits hard times or suffers partial predation it can contract, expand again in new directions, replace missing modules or pursue a number of other strategies made possible by its plastic properties. Degenerate zooids are not wasted, but provide nutrients for new growth (Werner 1979).

(v) The existence of tissue connections between the zooids in colonies nearly always allows transmission of behavioural signals warning of danger or disturbance. Thus, zooids far from the site of impact can protect themselves in advance.

When we come to look at pelagic colonies we find a somewhat different picture. As with sessile colonies, defensive reactions are highly developed in pyrosomes, salps and siphonophores but these often take the form of escape locomotion, because all pelagic colonies (cystonectid siphonophores excepted) are highly specialized for swimming by jet propulsion. In keeping with their locomotory style of existence, pelagic colonies are linear and polarized. Branching is minimal (doliolids, siphonophores) or absent (salps, pyrosomes). Doliolid chains are budded from the rear end of the oozoid ('nurse') stage, salp blastozooids from a stolon produced by the oozoid; siphonophores bud their nectophores from one budding zone and their other appendages from another, but both budding zones are incorporated into a single linear stem, which is derived from the oozoid (figure 1). Pyrosomes are cylinders closed at one end, open at the other. Streamlining sometimes reaches a high pitch of perfection, as in diphyid siphonophores. Some salp chains and siphonophores show bilateral symmetry. There is always a front and a back end.

Thus we find that one end of the colony has a well-defined shape and may consist of one or a fixed number of specialized zooids. Indeterminate growth, to the extent that it occurs, is seen at the other (posterior) end where modules are added progressively. Even here, however, detachment of modules may be balanced by production of new ones so that overall body form is maintained. The body proportions of most siphonophores change little as the animal grows even where stem groups detach to become free eudoxids. Calycophores and physonects seem to reach and maintain a certain size, characteristic for each species. Physonects cannot really be said to show indeterminate growth at either end, except possibly in some poorly understood cases (for example, *Apolemia*, which may be over 10 m long).

Pelagic colonies show little plasticity. Siphonophores, doliolids and salps can bud new modules only from their one or two localized budding zones. The only fragment of a physonectid

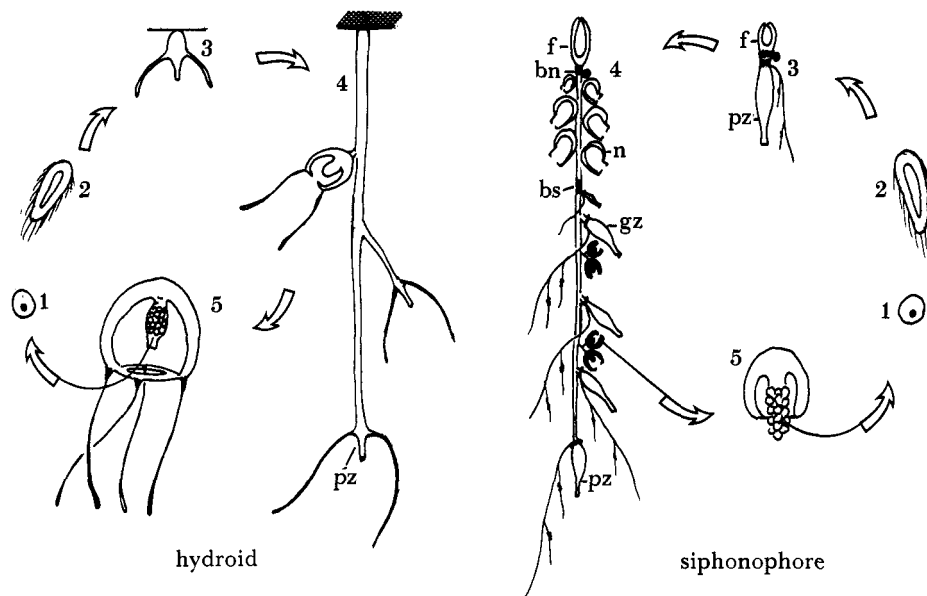


FIGURE 1. Comparison of the life cycle of an agalmid siphonophore with that of an athecate hydroid. In the hydroid cycle, following the egg (1) and planula (2) stages the larva becomes a tentaculated actinula (3) which settles by its aboral pole. The actinula forms the primary polyp or protozoid (pz) of the hydroid colony (4), from whose elongated base secondary polyps and medusae are budded. The medusae (5) are retained in some species, set free in others, as here. They produce and release the gametes. In the siphonophore cycle, the siphonula larva (3) can be regarded as a type of actinula but it forms a protozoid with only one tentacle, and the aboral end, instead of attaching to a substrate, becomes invaginated as a float (f). Elongation of the middle section of the larva produces a long stolon, the stem of the siphonophore colony (4), with the protozoid at its distal tip. The stem buds off sexual medusae (5) (which are usually retained, but are sometimes set free) and sterile locomotory medusoids, or nectophores (n). Several sorts of polyp are also budded off, of which only gastrozooids (gz) are shown. The stem elongates and buds from two blastogenic zones, one for the nectophores (bn) and one for the gastrozooids and other siphosomal appendages (bs). Most specialists now regard the float as a neomorphic structure, not as zooid of medusoid origin. Tentacles in siphonophores are parts of gastrozooids or palpons, not separate 'dactylozooids'.

siphonophore that could regenerate to produce a perfect colony would be a piece of stem containing both budding zones as well as the float. Isolated zooids cannot produce new colonies. Pelagic colonies do not fuse, vary their shapes, shrink and re-expand or switch their zooids around.

Salps and certain pelagic polychaetes (for example, *Trypanosyllis*) come closest to fitting the paradigm established for benthic colonies. In both cases, though linear and unbranched, they show unipolar indeterminate growth, producing chains of zooids which separate either as shorter chains or as solitary zooids. Phenomenal rates of increase are reported for salps under phytoplankton bloom conditions (Heron 1972). The Portuguese man-of-war 'is distinguished from every other siphonophore by the complexity of branching by budding of the cormidia' (Totton 1960). It thus somewhat resembles sessile, benthic colonies. However, it is not truly pelagic, and cannot swim. It lives at the air-water interface and can be regarded as sessile at the surface. Thus, its resemblance to sessile benthic colonies is not so surprising. The peculiar branching syllid, *Syllis ramosa*, likewise is not truly pelagic, but parasitizes sponges.

2. PHYSIOLOGICAL ASPECTS OF COLONIALITY

It seems likely that most colonies evolved from clone-forming solitary ancestors (see, however, Silén (1944) on bryozoan origins). Where the rate of bud production exceeded the rate of bud separation, temporary colonies would have been formed, much as in *Hydra*, *Loxosoma* and *Cephalodiscus* today. Having thus stumbled upon coloniality, the ancestral forms would have found advantages in remaining interconnected, perhaps to monopolize the substrate. The retention of primary tissue connections between the zooids must have had important consequences. By making possible transfer of metabolites between the zooids it would have allowed some colonies to evolve non-feeding zooids which could become specialized for other tasks. Secondly, it would have provided pathways for the direct transmission of behavioural responses, so that certain functions, particularly defensive responses, could spread across the colony. Even in highly polymorphic colonies such as siphonophores, where the physiological functions are distributed among several different zooid types, we still see a high degree of behavioural coordination in the colony as a whole, thanks to the presence of a colony-wide network of nervous connections.

Beyond this point, it is hard to generalize about colonial evolution. The picture is not a tidy one. Each group has gone its own way. Not all colonies became polymorphic, and of those that did, not all are strikingly well integrated. The most dramatic examples of behavioural integration are to be found in certain free-swimming pelagic colonies, but the actual mechanisms of coordination involved differ from group to group. We can only review the facts as they apply to different present-day colonies and consider how their zooids share resources, communicate with one another and collaborate in common tasks.¹

(a) *Sharing of resources*

Feeding may be carried on independently by individual zooids or be organized on the colonial level, for instance in the formation of chimneys in ectoproct bryozoans (Lidgard 1981) and in the collaborative activity of several different sorts of zooid in stylasterine cyclosystems (de Kruijf 1977). The mere ability to deploy large numbers of relatively small feeding zooids within a confined space may enable predatory colonies to capture very large prey. This is seen in the Portuguese man-of-war, which can capture and digest whole mackerel. Although it cannot ingest the fish in the usual sense, it can envelop it completely in the expanded mouths of numerous gastrozooids, which press up tightly to one another, thus creating an improvised external stomach wherein extracellular digestion takes place (Hardy 1956) (figure 2). Biggs (1977) reports similar observations for *Rhizophysa*.

In cnidarian colonies the gut cavity is continuous throughout the colony and transport of nutrients is simple and rapid. Rees (1971) found that ¹⁴C-labelled food spread through small *Pennaria* colonies within 30 min. Rinkevitch & Loya (1983) showed that labelled metabolites underwent translocation from a donor branch of the coral *Stylophora* to a recipient branch after fusion of the two. The label appeared in highest concentrations at the tips of the recipient branches, presumably the most metabolically active sites.

In siphonophores, only the gastrozooids feed, and all nutrients must therefore be transported to the other regions, sometimes over distances of many centimetres or even metres (*Physalia* has tentacles over 6 m long). Mackie & Boag (1963) used carmine-infiltrated food to trace movement of digested material in a siphonophore. Five minutes after feeding, carmine appeared

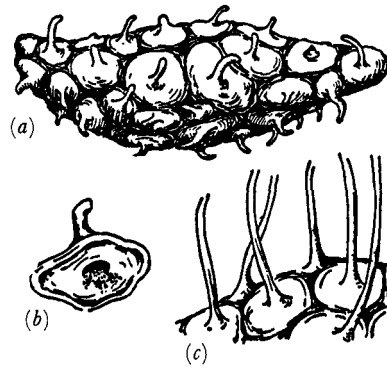


FIGURE 2. Evidence of collaborative feeding in the Portuguese man-of-war (from Hardy 1956). A partly digested fish, forcibly removed from the siphonophore, is shown in (a), from a preserved specimen. The gastrozooids have broken off near their distal ends, but their expanded mouths still envelop the prey. A single such expanded 'mouth' is shown in (b). The condition in life approximates to (c).

in the stem canal and was flushed up and down the stem by rhythmic pumping movements of the gastrozooids and palpons. Cilia lining the canal assist the process. Valves at the bases of the zooids regulate exchange of fluids with the stem. Peristaltic pumping movements assist food dispersal in many hydrozoan colonies (reviewed by Mackie 1973).

Colonial styelid ascidians and *Perophora* have common colonial blood-vascular systems, which presumably serve for metabolite exchange. Pumping structures (ampullae) are present in the styelids. Their contractions are coordinated over large areas by propagated electrical signals (Mackie & Singla 1983a). When two colonies fuse, one of the first indications of fusion is that the ampullary rhythms come into synchrony.

Interzooidal communication in ectoprocts is less straightforward than in the above cases. The polypides of phylactolaemates arise as buds within a common coelom initially, but partitions develop later in some species; the common coelom presumably guarantees dispersal of food metabolites. In some fossil stenolaemates the zooids were entirely walled off from one another but in existing cyclostomes the zooids communicate via holes in the septal walls. The funicular system does not pass through these pores, but it is thought that coelomic fluid can be exchanged. In gymnolaemates pores are again present, but they are plugged by funicular and other tissues. Bobin's (1977) histological studies on *Bowerbankia* show evidence of lipid transport from degenerating autozooids to the stolon, from which new zooids are budded. There are few experimental studies on interzooidal transport in bryozoans, but Best & Thorpe (1985) recently fed ^{14}C -labelled flagellates to *Membranipora* and found spread of the label to adjacent zooids within 15 min. Spread to a distance of 9 cm (equivalent to about 90 zooids) took place over 24 h. The label accumulated at the growing edge of the colony. It seems likely that the funicular system is the transport pathway.

(b) Distant early warning systems

A solitary organism can receive warning of the approach of a predator or the presence of some other threat only if it has sense organs capable of detecting the danger at a distance; otherwise, it may be mortally injured before it has had time to protect itself. Most marine invertebrates are poorly equipped with respect to such sense organs. Colonies, on the other hand, frequently have built-in signalling systems that allow the zooids to react in anticipation.

Damage at one point may wipe out several modules but the others protect themselves and the genet survives, often to regain the lost modules.

Highly polymorphic colonies have, in addition, special defensive zooids (for example, avicularia). Solitary animals have similar devices (for example, pedicellaria) and possession of defensive structures cannot be regarded as a characteristic of coloniality *per se*. In at least one case, however, the ectoproct *Membranipora*, development of defensive structures (spines) appears to be organized on a colonial basis by some sort of signal transmitted within the colony following attack. Harvell (1984) shows that spines are produced all the way around the periphery even following strictly local attack by a nudibranch. The evidence is most readily explained on the assumption of internal signalling within the colony, but the precise mechanism has not been determined.

In the remaining cases, to be discussed below, we are dealing with behavioural responses involving conventional neuromuscular or other neuroeffector actions transmitted through colonies by electrical impulses in nerves or excitable epithelia. A range of examples illustrating the variety of such responses is provided in table 1.

TABLE 1. EXAMPLES OF PROPAGATED DEFENSIVE RESPONSES IN MODULAR ORGANISMS

| organism | response | conduction system | conduction velocity | source |
|---|--------------------------------------|--|---------------------|--|
| | | | mm s ⁻¹ | |
| <i>Rhabdocalyptus</i> (hexactinellid sponge) | ciliary arrest | trabecular tissue | 3 | Mackie & Singla 1983 <i>b</i> |
| <i>Mimosa</i> (vascular plant) | leaves fold up | vascular tissue | 10 | Sibaoka 1966 |
| <i>Membranipora</i> (ectoproct) | lophophore retraction | nerve net | 10 | Thorpe <i>et al.</i> 1975 |
| <i>Botrylloides</i> (ascidian) | siphon closure, ciliary arrest | vascular epithelium | 20 | Mackie & Singla 1983 <i>a</i> |
| <i>Cordylophora</i> (hydroid) | polyp retraction | stolon epithelium | 30 | Josephson 1961 |
| <i>Renilla</i> (pennatulid) | bioluminescence, polyp withdrawal | nerve net | 60 | Anderson & Case 1975 |
| <i>Pegea</i> (young salp chain) | change in direction of locomotion | nerves and epithelia in alternation | 125 | Mackie & Bone 1977 Anderson & Bone 1980 |
| <i>Chelophyes</i> (siphonophore) | stem contraction epithelium | exumbrellar | 500 | Mackie & Carré 1983 |
| <i>Forskalia</i> (siphonophore) | escape locomotion | giant nerve axon | 4000 | Mackie 1978 |

(1) *Muscular evasive actions*

With few exceptions (for example, *Syncoryne*) both thecate and athecate hydroids show hydranth retraction responses after strong stimulation of the stolon or of other hydranths. Neuronal mediation has been demonstrated in several cases (reviewed by Spencer & Schwab 1982).

In siphonophores, the most obvious propagated defensive response is escape swimming (see below) which is mediated by the twin nerve nets of the central stem of the colony. The reaction can, however, be set off by tactile stimulation of certain areas lacking nerves, such as the epithelia covering the bracts and nectophores. It was this observation that led to recognition of the important role of conducting epithelia in the mediation of protective reactions in colonial hydrozoans and pelagic tunicates (reviewed by Anderson 1980).

Siphonophores also show protective contractions of their zooids, shortening of the stem, elimination of gas bubbles from the float (causing sinking) and involution of the velum and bell margin (in hippopodiids). These responses spread for varying distances depending on the strength and duration of stimulation. Labile neural or epithelioneural couplings link the stem and its attached zooids (figure 11*a*). Habituation is rapid. Thus the colony as a whole is not obliged to maintain a defensive posture if the warning signals are not of exceptional duration and magnitude. Giant axons in the stems of many siphonophores enable them to respond with lightning speed to damaging stimuli.

Coordinated retractions of coral polyps have been thoroughly studied and are reviewed elsewhere by Horridge (1957) and Shelton (1979, 1982). Local stimulation may cause responses only in the immediate vicinity (*Porites*) or the response may spread through the whole colony (*Tubipora*). In *Porites*, repeated stimuli may be needed to procure maximum spread of the response. In most cases, spread is thought to be mediated by the colonial nerve net.

It is worth stressing that polyp retraction responses in cnidarian colonies operate on a similar basis to retractions in solitary species. Similar muscles and nerve pathways are involved. The colony provides interzooidal conducting pathways that determine *how* the response spreads: locally, generally, incrementally, decrementally, at what threshold, with what fatigue properties, etc. Only in the siphonophores do we find completely new coordinating elements introduced at the colonial level, such as giant nerve axons. The capacity for autotomy has also been evolved, apparently *de nouveau*, as a defensive measure in physonectid siphonophores. Bracts and nectophores have autotomy joints at their junctions with the stem and shed themselves when strongly stimulated.

A colony-wide nerve plexus (Hiller's plexus) is present in cheilostome ectoprocts, confirmed in recent work on *Electra*, summarized by Lutaud (1977), but is absent in the ctenostome *Alcyonidium* (Lutaud 1981). Information is lacking on cyclostomes. Phylactolaemates have long been known to have a colonial nervous system.

The system in cheilostomes consists of fine neurites which run from zooid to zooid via the mural pores, connecting the cerebral ganglia of each zooid. In *Membranipora*, stimulation elicits bursts of electrical events, presumably action potentials in the colonial nerve net (see Thorpe 1982). Giant axons are thought to mediate lophophore retraction and associated muscular events. Lophophore retraction is a very rapid process, and Thorpe's data suggest that the retractor may be one of the fastest contracting muscles known. Surprisingly, it is said to be a smooth muscle, but I have observed the retractors of *Plumatella* and *Fredericella* to be striated. Operculate forms close the operculum as the lophophore is pulled in.

Contrary to earlier reports, Thorpe (1982) finds no good evidence for coordinated lophophore retractions in phylactolaemates. The colonial nerve net might be concerned with other functions, for example, locomotion in the case of *Cristatella*.

Interzooidal communication has been proposed to explain the apparent coordination of vibracular sweeping movements in the cheilostomes *Caberea* and *Cupuladria*. The phenomenal *Selenaria* can uncover itself when covered with sand, and right itself when overturned, by seemingly coordinated movements of its vibracular setae (Cook & Chimonides 1978). The animals are sensitive to light in the blue-green range of the spectrum and move towards it (Cook & Chimonides 1981). Light increases the frequency of small electrical signals resembling nerve impulses, which spread over the surface of the colony, and may be indirectly responsible for the setal movements of locomotion (Berry & Hayward 1984).

(ii) *Ciliary arrest*

Organisms that filter their food from water are generally sensitive to water quality and may arrest or reverse the flow when stimulated by 'bad' water. For a colonial animal, there are clear advantages, not open to solitary forms, in being able to signal the presence of noxious stimuli from zooid to zooid within the colony, so that zooids remote from the stimulus can protect themselves in advance.

Rhabdocalyptus and other hexactinellid sponges are well-individualized solitary animals which bud asexually, forming temporary colonies consisting of a parent and several buds in various growth stages. The buds eventually separate. While still attached to the parent the buds are physiologically integrated with it. Hexactinellids, unlike other sponges, show a rapidly propagated ciliary arrest response when stimulated. Excitation spreads through the whole sponge within a few seconds, and in the case of bud colonies, through the whole colony. Sponges are very susceptible to clogging of their canals by suspended sediments and arrest of the feeding current probably helps prevent this. Any local disturbance can set the response off (Mackie *et al.* 1983).

In *Botryllus* and related colonial styliid ascidians, the blood vessels that interconnect the zooids are lined with excitable epithelium, which provides a non-nervous conduction pathway for electrical impulses triggering ciliary arrests in the gills of the zooids (figure 3). On entering the zooid, these signals excite the normal nerve reflexes of squirting, siphon closure and ciliary arrest common to both colonial and solitary ascidians. All that has been added is an interzooidal conduction pathway (Mackie & Singla 1983*a*).

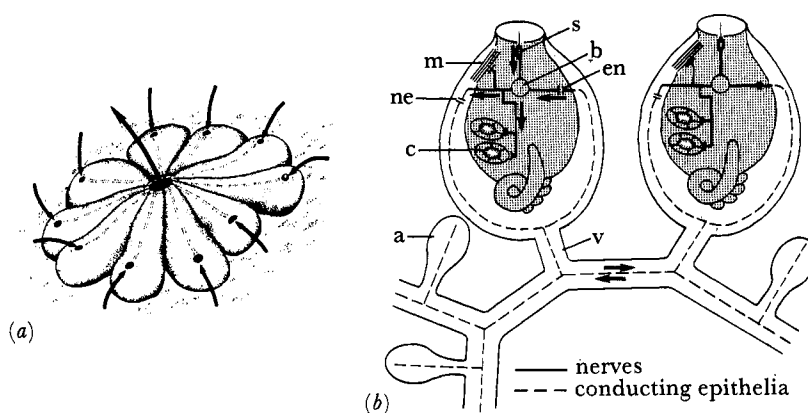


FIGURE 3. *Botryllus*. (a) Cyclosystem, with current flow indicated. The zooids share a common cloacal opening. From Vogel 1981. (b) Action systems and conduction pathways mediating defensive responses (squirting, and ciliary arrest). Nervous links within zooids are shown as solid lines, conducting epithelia between zooids as broken lines. From Mackie & Singla 1983*a*. Abbreviations: a, ampula; b, brain; c, ciliated cells of branchial basket; en, epithelioneural coupling; m, muscle of mantle wall; ne, neuroepithelia coupling; s, sensory cell; v, vascular network.

Pyrosoma (figures 4 and 7) coordinates siphon closures and ciliary arrests in a completely different and unique manner. The zooids are organized around a central cavity into which they empty their effluent water streams (figure 4*a*). The streams combine to provide the locomotory jet which propels the colony. The zooids are not linked by nerves or conducting epithelia but they are situated side by side in close proximity, as in the sessile, compound

ascidians from which they doubtless evolved. Each zooid has a light-producing organ and an eye capable of detecting flashes of light produced by the light organs of neighbours. Under adverse conditions, a zooid closes its siphons, arrests its cilia and gives off a flash of light. Neighbouring zooids detect the flash and respond in turn by ciliary arrests and flashes. In this way it is thought that a photic signal can be relayed from zooid to zooid along the colony causing them all to arrest their feeding currents (figure 4*b*). The flash is, in fact, so bright that nearby colonies could also be affected. The system only works in dim light for obvious reasons, but *Pyrosoma* lives in mesopelagic waters where light levels are low. Each zooid's flash would represent a signal saying 'beware/bad water ahead/turn off feeding current/pass message on'. An incidental effect of cessation of feeding is that locomotion also stops and the colony, being somewhat heavier than water, starts to sink and could thus enter a different, more suitable water layer (Mackie & Bone 1978; Bone & Mackie 1982).

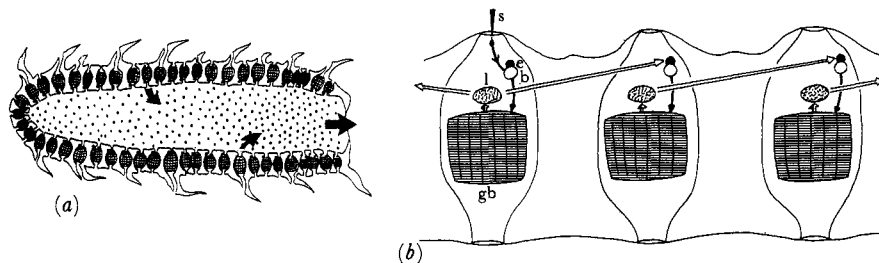


FIGURE 4. *Pyrosoma*. (a) Sagittal section of the whole colony from Barnes (1974) after Grobben. Water currents (arrows) from individual zooids enter the common cloacal cavity and are expelled as the locomotory current to the rear. (b) Scheme showing serial photic excitation of zooids following stimulation of the left hand zooid, from Bone & Mackie (1982). Abbreviations: b, brain; e, eye; gb, gill basket; l, luminous organ; s, stimulus.

(iii) Light emission

Waves of luminescence accompany spreading polyp retractions in various colonial hydroids and pennatulids (summarized in Morin 1974). The conduction system is probably an excitable epithelium in the hydroids, and a nerve net in the pennatulids. The functions of these responses have not been convincingly demonstrated but speculation favours a protective role of some sort.

In the siphonophore *Hippopodius*, following sharp or damaging stimulation, waves of luminescence spread between the nectophores, and are accompanied by protective involution of the nectophore margins. At the same time, the siphonophore, which is normally transparent, becomes opaque owing to the formation of light-scattering granules in the mesogloea (figures 5 and 6, plate 1), and endodermal secretory cells of unknown function discharge their product. Opacification by day is thought to function like luminescence at night, making the organism loom up terrifyingly out of nowhere, so discouraging molesters. The response is spread by excitable epithelia in the nectophores but passage from one nectophore to another involves a labile nervous intermediate step (Mackie & Mackie 1967; Bassot *et al.* 1978).

(iv) Locomotion

Locomotory ability has evolved in several benthic colonies, including some pennatulids, the acrobatic coral *Diaseris* (Hubbard 1972), ectoprocts such as *Cristatella* and *Selenaria* (discussed by Thorpe 1982) and various colonial ascidians (Carlisle 1961; Ryland *et al.* 1984). However, these are exceptional: the vast majority of benthic colonies are firmly attached to their

substrates. It is the pelagic colonies that most clearly illustrate the possibilities of modularity in the area of locomotion.

In brief, a serial arrangement of interconnected propulsive units can provide smoother and more economical locomotion than separate units and, provided that the modules can communicate behaviourally, there need be no lessening of the ability of the colony to execute coordinated escape movements: the colony can behave like a well-integrated unitary organism. Rapid changes in direction are possible in some cases.

(a) *The locomotion of salps*

In salps such as *Salpa fusiformis*, the blastozoids fit snugly together in streamlined chains. The zooids can also separate and live freely. Bone & Trueman (1983) show that feeding and swimming of chains is a more economical process than that of zooids operating individually. This is because the chain experiences relatively less drag than the isolated zooid. Drag depends on (i) total exposed surface area; (ii) frontal area; and (iii) greatest projected area (Alexander 1968). The last two factors will be about the same for colonies as for separate zooids in the case of linear, 'tubular' salp chains like *S. fusiformis*. Exposed surface area, however, will be proportionately less in the chain than in the single zooid because of the way the zooids fit together in the chain, with large parts of their outer surfaces pressed together. This then results in reduced drag. A salp chain can swim as fast as a solitary zooid with less effort per zooid. Only a fraction of the zooids need swim at all for the chain to achieve acceptable cruising velocities. Water passes through swimmers and non-swimmers alike, so the non-swimmers can feed without expenditure of energy in locomotion.

Unlike single zooids, which swim in jerks, filling and emptying in a regular cycle, the chain glides along in a smooth manner owing to the fact that the zooids contract asynchronously. Bone & Trueman (1983) suggest that this steady-state swimming further reduces drag owing to the establishment of stable boundary layers. In addition, smooth locomotion probably favours food capture. Salps use a mucous net to filter particles from the water. This is a delicate structure which could be disorganized by strong contractions or sudden movements.

Salps are extremely efficient swimmers in mechanical terms (Bone & Trueman 1983) and perform extensive diurnal vertical migrations. Wiebe *et al.* (1979) report that *Salpa aspersa* ascends and descends daily over a range of 800 m. To do so, it must swim at velocities of $5\text{--}10\text{ m min}^{-1}$ ($8.3\text{--}10.7\text{ cm s}^{-1}$). Fedele (1923) further demonstrated that salps can swim both forwards and backwards.

A salp blastozoid can be thought of as a contractile tube, closable by valves at either end (figure 9a). If, when the tube contracts, the front valve closes first, water will be jetted backwards, and the salp will move forwards.

Salps swim backwards by the simple expedient of changing the order in which the valves close. The brain produces the locomotory rhythm, and determines the timing of the opening and closing of the valves. In a solitary salp swimming forwards, collision or a touch at the anterior end generates impulses, in sensory nerves, which travel to the brain and cause either a brief locomotory arrest or an arrest followed by reverse locomotion. If the rear end of the swimming salp is touched, the response is an acceleration of forward swimming. Fedele (1923) showed that chains perform exactly like individual salps. The mechanism has now been worked out (Bone *et al.* 1980; Anderson & Bone 1980).

Each zooid in the salp chain is linked to each of its neighbours by a pair of attachment plaques

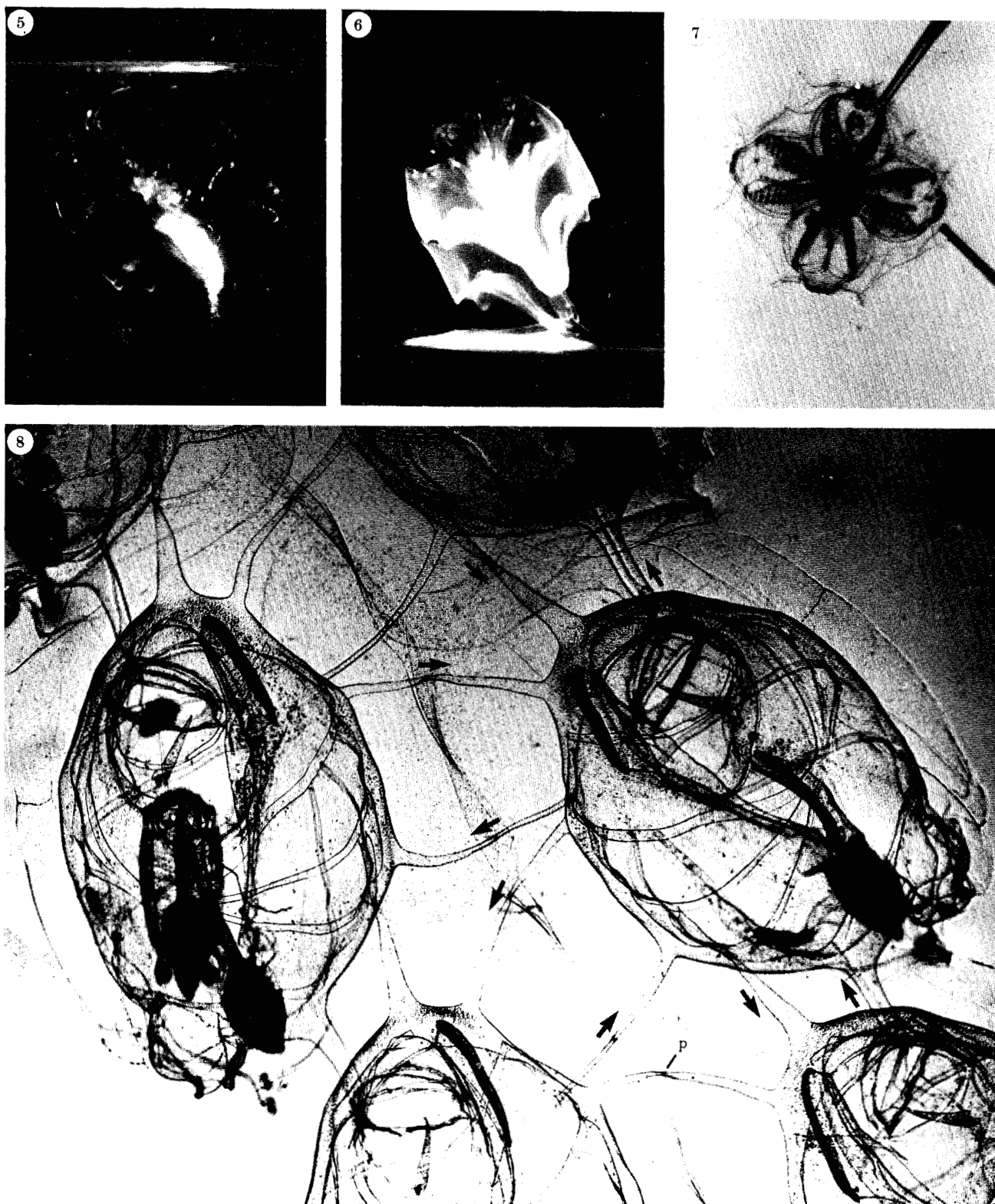


FIGURE 5. The siphonophore *Hippopodius hippopus* in its normal, transparent state (Mackie & Mackie 1967).

FIGURE 6. *Hippopodius* in opaque state following a sharp tap to one of the nectophores (Mackie & Mackie 1967).

FIGURE 7. *Pyrosoma atlanticum*, tetrazoid larva held by suction tubes which also serve as external electrodes for recording ciliary arrest potentials (Mackie & Bone 1978).

FIGURE 8. Part of a salp chain, *Thalia democratica*, (photo by Claude Carré), showing connections between blastozoids. An adhesion plaque is visible at p. Arrows show the presumed polarities of the eight plaques by which a single blastozoid is attached to its four neighbours, as in *Salpa fusiformis* (see figure 9b).

(Facing p. 186)

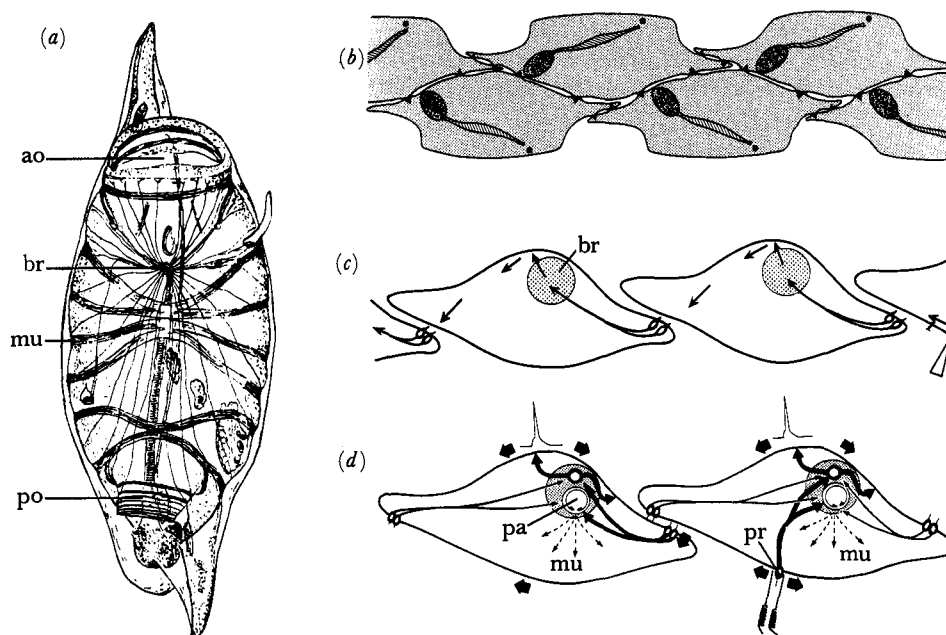


FIGURE 9. Coordination in salp chains. (a) A dorsal view of the sinistral form of a blastozooid of *Salpa maxima*. The dextral form is a mirror image of the sinistral (Fedele 1923). Abbreviations: ao, anterior opening; br, brain; mu, muscle band; po, posterior opening. (b) Positions of attachment plaques in *S. fusiformis*. Triangles indicate the innervated side of each plaque. Conduction is polarized toward that side (Bone *et al.* 1980). (c and d) Routes whereby epithelial signals (outer skin pulses) spread between zooids in the chain (Anderson & Bone 1980). (c) A simplified diagram showing generation of outer skin pulses (short arrows) at a site of mechanical or electrical stimulation (arrowhead right). Outer skin pulses enter sensory neurons at the plaque and pass as nerve impulses to brain (br) of the next salp, where they trigger outer skin pulses which pass on as before. (d) A diagram as in (c) above, but showing additional features: pacemakers (pa) in the brain which generate rhythmic output to the swimming muscles (mu); peripheral receptors (pr) in the skin which feed into the brain evoking the same responses as sensory signals arriving via the plaque receptors; and electrical traces of outer skin pulses recorded from the skin (shown above the drawing).

(figures 8 and 9*b*). Sensory neurons are located on one side of each plaque, their processes extending across to the other side. Of the two plaques joining a pair of zooids, one plaque is polarized so as to transmit forwards, the other backwards. Excitation entering the nerve at the front end of a zooid passes to the brain and causes the switch to reverse swimming. At the same time, impulses invade the skin, which is an excitable epithelium propagating impulses in all directions (Mackie & Bone 1977). These epithelial impulses travel to the plaque at the rear of the animal and are picked up by sensory processes projecting across the plaque from the salp behind. Thus, the signal to change direction is relayed through a series of neural and epithelial pathways from salp to salp down the chain (figure 9*c, d*).

Likewise, acceleration of forward swimming requires signals to be transmitted through plaques polarized in the anterior direction. The sensory nerves receiving these signals enter the brain and cause an increase in the output frequency of the locomotory pacemaker. At the same time, skin impulses are generated and pass to the front, where they are picked up by the sensory cells of the salp next in line ahead. The interposition of polarized nerve pathways in the system ensures that, even though the skin pulses are propagated to all parts of the skin, directional information is conserved, and the whole chain swims as a unit either forwards or backwards.

When no information is transmitted, the salps swim forward at their own rhythms, or coast along passively.

Strong stimulation causes the zooids to detach from one another. Fedele (1923) showed that a strong stimulus to the middle of a chain causes separation at that point. The front half then swims forwards at an accelerated rate while the back half swims backwards in the reverse response. The mechanism worked out by Bone and his colleagues is both elegant and simple. The separated zooid continues to respond exactly as it did while a member of the colony, using the same conduction pathways and brain circuitry.

Another group of pelagic tunicates, the doliolids, also alternate between free and attached stages. Free stages show a capacity for bidirectional locomotion and also for arresting their branchial cilia (Bone & Mackie 1977) but it is not known if these responses are coordinated between zooids during the colonial parts of the life cycle, when the zooids are held together by peculiar placenta-like structures.

(b) *The locomotion of siphonophores*

As shown in figure 1, siphonophores can be viewed as pelagic, athecate hydroids in which the primary medusa stage is somewhat reduced, and which have produced several polymorphically specialized secondary zooids, some derived from polyps, some from medusae. Polyps are basically designed for food capture and for budding other zooids, medusae for swimming and for gamete production. By combining within a single organism altered versions of two zooid types which originally followed in sequence in the life cycle the siphonophore has gained the advantages of both. It gets feeding modules (gastrozooids) and digestive modules (palpons) from polyps, and locomotory modules (nectophores) from medusae.

Superficial appearances notwithstanding, nectophores retain all the essential medusan locomotory features. They have lost their tentacles, mouth and gonads. They cannot feed and depend on the colony for their nutrition. They are stripped down to the bare locomotory essentials: striated swimming muscles arranged circularly in the wall of the subumbrellar cavity, a velum to direct the water jet, and marginal nerve rings containing the pacemakers driving locomotion. Their strange shapes are related to streamlining, or to articulation with other nectophores.

In a physonectid siphonophore such as *Nanomia* (figure 10) the nectophores are deployed in two rows, back to back. They fit together into a 'solid' column by means of grooves and flanges. As in a salp chain, the exposed surface area, and hence drag, is presumably greatly reduced by the packing arrangement. The frontal area is small, offering little water resistance. When swimming normally (figure 10g), *Nanomia* allows its nectophores to pulsate at their own natural frequencies, which results in smooth, gliding motion, despite some tendency to veer from side to side. Steady-state conditions, which further reduce drag, doubtless apply here, as in salps. *Nanomia* is a vertical migrator, capable of ascending and then descending through hundreds of metres every 24 h.

When abruptly stimulated at the rear end, *Nanomia* darts forward at high velocity (20–30 cm s⁻¹ compared with 8–10 cm s⁻¹ in normal swimming). The nectophores contract in unison during this response (figure 10a). The escape reaction is mediated by giant axons in the stem, which contract at velocities in the range 1.0–3.0 m s⁻¹, about an order of magnitude faster than non-giant axons in typical hydrozoans. Nerves run from the stem to the marginal nerve rings of the nectophores, coordinating the swimming contractions. These nerves, and the

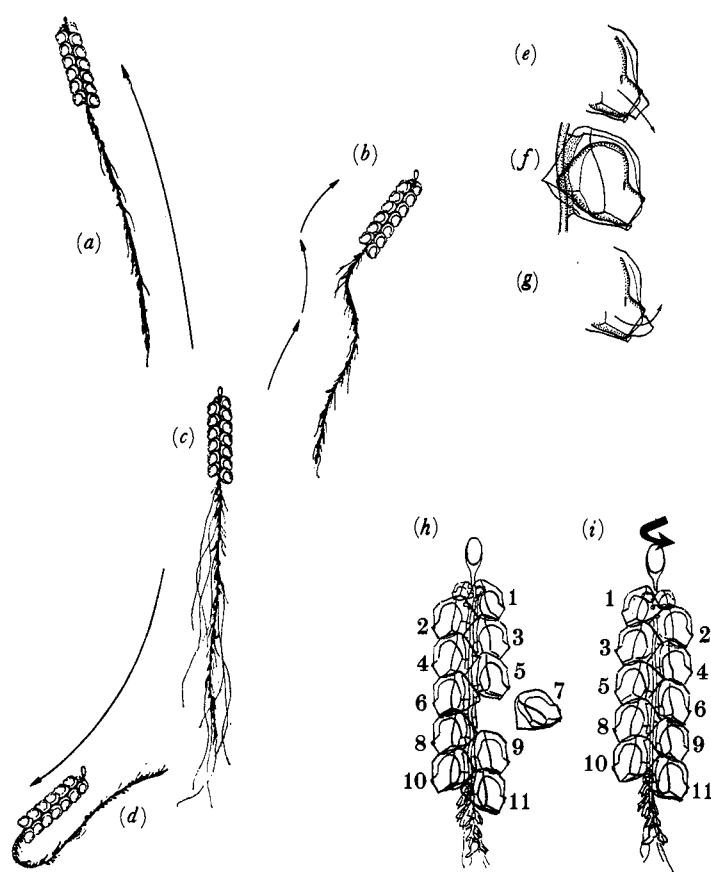


FIGURE 10. *Nanomia cara*, a physonectid siphonophore, from Mackie (1964). (a) Colony performing escape forwards swimming; (b) slower, serpentine swimming (normal locomotion); (c) colony at rest; (d) reverse escape swimming; (e) side view of nectophore showing jet direction during forward swimming; (f) the same, at rest; (g) the same, in reverse swimming; (h) following autotomy of the seventh nectophore, the upper part of the colony rotates through 180° (i) restoring symmetry.

giant axons, are clearly special components evolved for purposes of the colonial escape response (Mackie 1984).

When the anterior end of the colony is stimulated, giant axons are excited as before, but this time the colony swims backwards (figure 10d). The mechanism involves contraction of bundles of radial muscle fibres located at either side of the velar opening. These contract simultaneously with the swimming contraction and, because of their asymmetrical placement, change the direction of the water jet (figure 10e, f, g). The colony shoots violently backwards, as all the nectophores perform reverse swimming in unison. Conducting epithelia, not nerves, prove to be the peripheral pathway for colonial control over the radial muscles. A similar, indeed homologous, system mediates protective involution of the margin (crumpling) in hippopodiid siphonophores and in many free medusae. Apart from concentrating the radial muscles into bundles and preserving the primary conducting epithelial links with the stem, *Nanomia* has simply had to convert one protective response (crumpling) into another (escape locomotion).

Clearly, for effective swimming, the nectophore column must be bilaterally symmetrical. In normal growth, nectophores are inserted to left and right in an alternating pattern. Loss of nectophores from within the column would weaken the whole structure and introduce

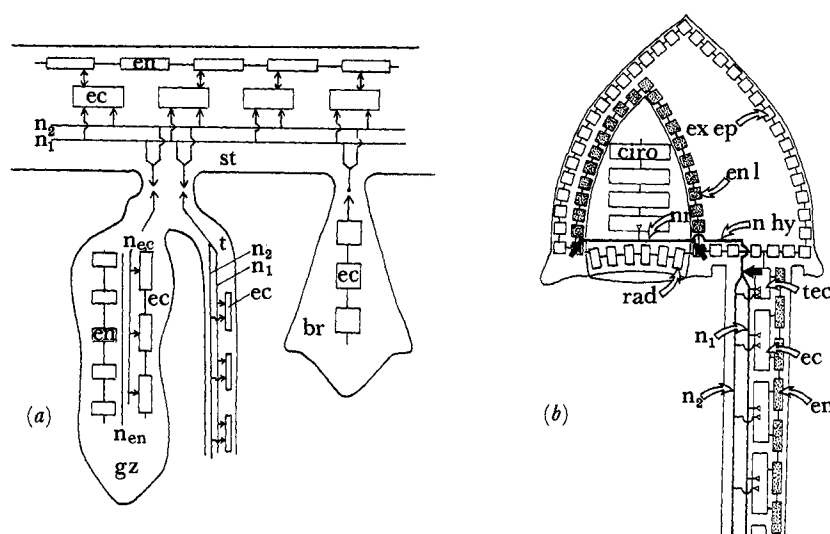


FIGURE 11. Action systems and conduction pathways in siphonophore colonies. (a) *Nanomia*, showing conducting pathways (arrows) and effector muscles (rectangles and squares) in the stem (st), in a gastrozoid (gz), a tentacle (t) and a bract (br). In the stem, the ectodermal muscle (ec) receives dual excitatory input from the two stem nerve nets (n_1 , n_2) and is electrically coupled to the endoderm (en), which is a conducting epithelium. Activated via these two routes, the stem muscles show fast and slow contractions respectively. In the gastrozoid both ectoderm and endoderm have nerve nets (n_{ec} , n_{en}). The ectodermal net is physiologically connected with the stem nervous systems by labile couplings. Contractions can spread in either direction, but habituation is rapid. The two nerve nets in the tentacle also show labile functional connections with the stem. The bract lacks nerves, but its covering epithelium is excitable, and conducts impulses to the stem, where they evoke nervous activity and resulting contractions or escape behaviour (from Mackie 1978). (b) *Chelophyes*, showing nervous and non-nervous links between a nectophore and the stem. Black arrows symbolize epithelioneural excitation, triangles show neuromuscular excitation. Lines between excitable units represent electrical coupling. Stimulation of the exumbrellar epithelium (ex ep) evokes impulses that propagate to the margin where they excite nerves in the nerve ring (nr) that excites the circular swimming muscle (circ). Epithelial impulses also propagate directly to the radial muscles (rad) of the velum, causing them to contract during swimming. On reaching the stem, epithelial impulses pass directly to ectoderm cells in a transitional zone (t ec) that has the property, when excited, of exciting the stem nervous systems (n_1 , n_2), both of which contain a giant axon. Depolarizations of the transitional ectoderm also pass directly to the endoderm (en) where they propagate as slow (s) events. Throughout the length of the stem, activity in n_1 and n_2 causes twitch depolarizations in the ectodermal muscles (ec) but impulses do not propagate within this tissue. Two-way interactions occur between the ectoderm and the endoderm. Activity in the stem nerves leads to twitch depolarizations in the transitional ectoderm that, if sufficiently large, propagate to the exumbrellar epithelium as exumbrellar impulses. On reaching the nectophore margin, they cause swimming as before. The hydroecial nerve (n hy) is implicated as an alternate, but faster, pathway mediating escape swimming responses following stem stimulation (from Mackie & Carré 1983).

asymmetries. This danger is minimized by a torsional response of the stem which takes place whenever a nectophore is lost (figure 10*h, i*).

Calycophoran siphonophores cannot swim in reverse but many of them, especially the streamlined diphyids, are extremely agile and powerful swimmers, capable of a wide range of swimming velocities. *Chelophyes*, for example, can swim at 1 cm s^{-1} using only its posterior nectophore, or at any intermediate velocity up to 30 cm s^{-1} during escape behaviour, with both nectophores active. Here too, giant axons mediate escape reactions (Bone & Trueman 1982; Mackie & Carré 1983). Figure 11*b* shows the main action systems and conduction pathways linking the nectophore of a diphyid with the stem, as established by neurophysiological investigation.

It seems clear that much of the success of siphonophores is due to their possession of highly efficient locomotory mechanisms. Swimming is a function of the colony. The individual swimming modules are subordinated to what Vogt (1853) called *la volonté commune*. Interesting parallels exist between the swimming of salps and physonectid siphonophores in the serial arrangement of their propulsive units, which interlock in configurations that minimize drag, in their ability to swim slowly and smoothly in normal forward swimming, in their ability to swim forwards rapidly in escape, and in their ability to perform escape locomotion in the reverse direction.

3. THE WISDOM OF THE COLONY: GAPS IN OUR UNDERSTANDING OF CHEMICAL COMMUNICATION

Cannon (1932) talked of the 'wisdom of the body' as the sum of its homeostatic mechanisms, which we would now consider to include mechanisms involving hormones, neuromodulators, growth factors, morphogens and other mysterious regulatory substances. Plants, which are modular organisms, also communicate internally by means of hormones, growth regulators, flowering regulators, etc. Altogether, these substances fall into some nine categories (Devlin 1975). It would therefore be surprising if animal colonies were completely devoid of any capacity for internal chemical communication but to date no evidence for this has come forth.

In considering this problem in relation to colonial forms, it is apparent that major differences exist between the two principal polymorphic, colonial groups, the cnidarians and the bryozoans. All the zooids in a cnidarian colony are in communication by open gastrovascular canals. These serve to distribute digestive products and appear quite unsuited to the more subtle forms of chemical communication now under consideration. It is hard to see how chemical gradients could be maintained in such a system. If colony morphogenesis or homeostasis does involve chemical or electrical gradients, these must be set up in the epithelia themselves, or perhaps in the nerve cells running in the intraepithelial spaces. The complete lack of gastrovascular compartmentalization in cnidarian colonies has not prevented them from becoming polymorphically specialized. The Portuguese man-of-war, for example, has at least seven, possibly eight, different zooid types.

Ryland (1979), by contrast, holds that compartmentalization was a necessary prerequisite for polymorphic specialization in ectoproct evolution. Phylactolaemates, which are the least compartmentalized, show least polymorphism, whereas cheilostomes, which are highly compartmentalized, show 'spectacular zooidal evolution and diversification'. Compartmentalization has, however, prevented bryozoans from evolving a true colonial individuality. It is in the least compartmented genus, *Cristatella*, that colonial individuality is most clearly expressed.

It would seem, then, that in the evolution of ectoprocts, if not of cnidarians, specialization of zooids for different functions could not occur in a continuum and that partial metabolic isolation by means of compartmental divisions was necessary for this to take place. A need for isolation on the one hand had to be reconciled with a need for intercommunication on the other, and the result was a set of compromises. This is all very reminiscent of a similar problem in cell biology, discussed by Loewenstein (1984). Like interzooidal communication, intercellular communication is 'a compromise between cell connectivity and cell individuality' and Loewenstein is 'inclined to view the evolution of cellular communication systems as an endless maneuvering for achieving cell orchestration without loss of cell individuality'.

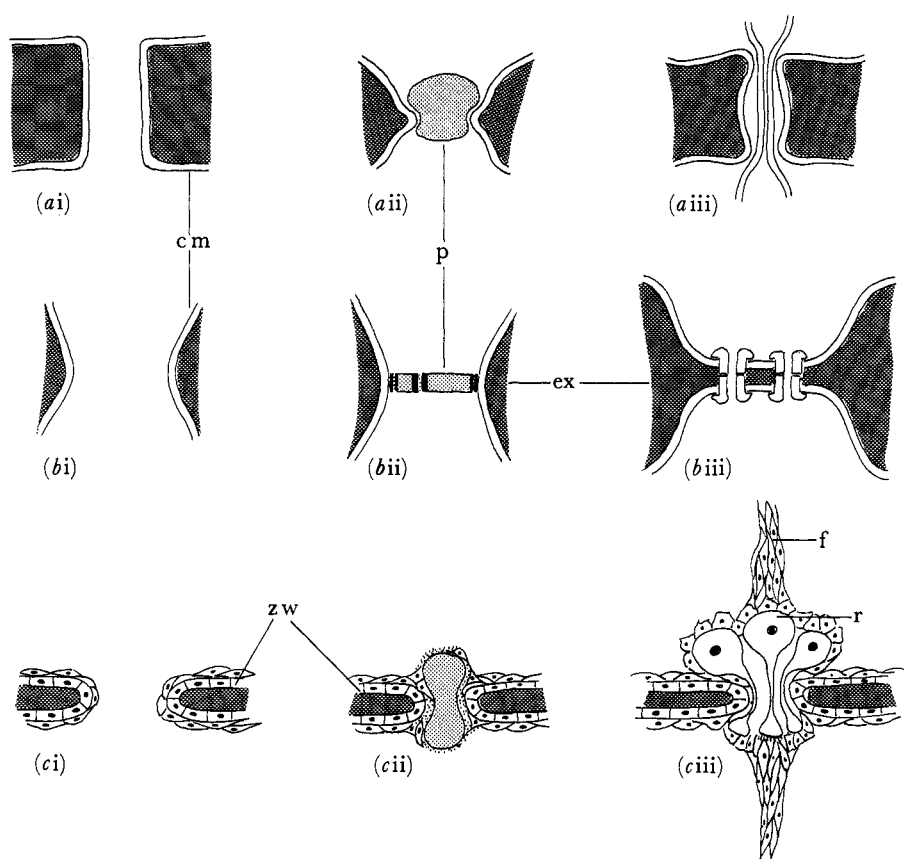


FIGURE 12. Comparison of intercellular junctions of plants (ai–a iii) and animals (bi–b iii) with interzooidal junctions in ectoproct bryozoans (ci–c iii). (ai) Simple intercellular bridge, such as a septal pore of an ascomycete. (a ii) Plugged 'transfer' connection as in *Polysiphonia*. (a iii) Plasmodesma of higher plant. (bi) Simple syncytial bridge as found between follicular nurse cells and oocytes in insects. (b ii) Plugged bridge with pores, in a hexactinellid sponge. (b iii) Gap junction of higher animal. (ci) Open mural pore between the coelomic compartments of adjacent zooids as in cyclostome stenolaemates. (cii) Immature pore with mucus plug, as in *Bowerbankia*. (c iii) Mature pore of *Bowerbankia* with rosette complex and funicular connections. The pore is polarized toward the stolon side (downwards in the drawing). Abbreviations: cm, cell membrane; ex, extracellular material (dark stipple); f, funiculus; p, plug; r, rosette cell; sw, zooid wall. Freely adapted from Bobin (1977) (cii, c iii); Mackie & Singla (1983b) (b ii); Robards (1976) (ai, a iii); Telfer (1975) and Wetherbee (1980) (a ii).

In figure 12 I show three grades of connectivity as expressed in plant cells, animal cells and bryozoan colonies. Unfortunately, bryozoologists have encountered the same sorts of difficulties as students of cellular communication when it comes to deciding what, if any, morphogenetic and regulatory substances are actually translocated via the junctions in question. Most plant physiologists assume that plasmodesmata mediate translocation of natural regulatory substances but, although experiments with fluorescent and radioactive markers show what sizes of molecules could pass, evidence for translocation of specific metabolites is still scant (Gunning & Overall 1983; Erwee & Goodwin 1985). Students of gap junctions in animals have been equally poorly placed. Now at last, with the development of antisera to the gap junction protein, the way seems open for research into what actually goes through these junctions (Warner *et al.* 1984).

In bryozoans, Ryland (1979) lists a number of forms of coordination that could be due

to movement of regulatory factors between zooids, but in no case is there clear evidence for such processes and the 'coordination' could simply be a matter of the working out of ageing rates, that is part of the built-in developmental programme. However, the progression towards complex junctional structures seen alike in cellular and colonial systems suggests that junctions such as *ciii* in figure 12 are highly selective filtering devices which allow certain molecules to pass, but block others, and are therefore potentially well suited to playing a role in the establishment of chemical gradients and for translocation of key morphogenetic and regulatory factors.

4. GENERAL CONCLUSIONS

We have looked at physiological adaptations of colonies in the areas of resource sharing, defensive behaviour, locomotion and chemical coordination.

Resource sharing can be regarded as a fundamental attribute of all true colonies, which sets them apart from mere aggregates. The pathways by which digestive products move between zooids may be blood vessels, extensions of the gut or shared portions of the body cavity. Restrictions on the free exchange of metabolites may be inferred from the complex morphology of the interzooidal connections in cheilostome bryozoans but the precise significance of these specializations is unknown. The same pathways that mediate transport of nutrients might also allow chemical regulators, morphogens, hormones, etc., to spread between zooids, but this is another unexplored area.

The possession of a colonial nervous system or of excitable epithelia functioning like nerves in conduction of electrical signals is an attribute of almost all true colonies. The parsimony principle applies here. Zooids typically show a high degree of local autonomy and use the same, or modified versions of, basic neuroeffector action systems found in unitary organisms or in the forms from which they are derived. Interzooidal pathways of behavioural communication function, so far as we know, in a rather restricted way, serving more as labile links between the action systems of the zooids than as centres where colonial behaviour is initiated. The siphonophores are exceptional in having nervous systems in their stems which not only relay responses between zooids but initiate activities such as swimming.

While defensive responses are the commonest, and often the only, known type of coordinated behaviour, some colonies show coordinated locomotion. Coordination may simply mean that the swimming modules are all active or all quiescent at the same time, but in some cases there is overall control of the frequency of the swimming contractions and even of the direction in which swimming occurs. Physonectid siphonophores and salp chains can swim either forwards or backwards in a coordinated manner.

The requirements of pelagic locomotion have led planktonic colonies to diverge from the pattern seen in the sessile colonies from which they presumably evolved. Most pelagic colonies are linear and unbranched, show an anterior-posterior polarity, are determinate in form, at least at the anterior end, and lack much of the plasticity and regenerative ability characteristic of sessile colonies.

It seems clear that the evolution of colonies occurred many times, in many different ways and according to diverse selective pressures. Beklemishev (1969) sees a progression in colonial evolution marked by increasing polymorphism, increasing zooidal physiological interdependence, reduced local autonomy, etc., culminating in the siphonophores where the emergence

of a truly colonial individuality can be recognized. Beklemishev's 'progression' is, however, essentially a pedagogical formulation and it does not necessarily reflect actual directions of evolution, certainly not in all colonial groups. Many very simple colonies have been highly successful. Aggregates have flourished as well as integrates. There is no one consistent trend in colonial evolution that would allow us to define 'higher' and 'lower'; accordingly, attempts to categorize and compare various groups in such terms are rather academic and should not be mistaken for descriptions of evolutionary processes.

Of those who have helped with the preparation of this paper I wish to express my particular thanks to Dr Drew Harvell for critically reading the manuscript and for her many valuable suggestions.

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