

# **ANIMAL COLONIES**

## **Development and Function Through Time**

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# Coordinated Behavior in Hydrozoan Colonies

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## ABSTRACT

Coordinated activities in thecate and athecate hydroid colonies and in siphonophores are reviewed. Coordination may be achieved by means of electrical impulses propagated between connected zooids in nerves or in nonnervous epithelia. In some cases behavioral coordination may result from pressure changes transmitted in the canal system or from some other purely mechanical process. Coordination by chemical means, theoretically possible, is not known to occur.

Feeding activities are generally carried on independently in hydrozoan colonies. Digestive movements may be synchronized. Protective and escape movements are almost universally found to be coordinated between the zooids in hydrozoan colonies. Some types of nonescape locomotory activity also involve coordinated activities between different zooids in the colony.

## INTRODUCTION

All invertebrate bud-colonies are integrated. Their component zooids are connected by living tissues, materials pass between them, and the whole morphology of the colony is the product of a single morphogenesis. To review the subject of integration of hydrozoan colonies would require coverage of growth, form, metabolism, physiology, and

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behavior—in short all aspects of the biology. Instead, this review will deal with one particular aspect of colonial integration: coordination of behavior.

Under the heading “behavior” we will consider only those activities involving muscular contraction. Morphogenetic movements, some of which seem to be controlled by diffusible metabolites (e.g., Rose, 1967) are excluded from the present discussion. There may, however, be a “gray area” here, for some activities such as the rhythmical extension and retraction of stolon tips in hydroids (e.g., Wyttenbach, 1968), might represent either muscular movements or nonmuscular contractile changes in the meristematic cells. Contractility is a property of cells other than muscle, and on the biophysical level the differences between muscular and other types of contractility need not be profound.

As possible mechanisms whereby behavior is coordinated, we will consider coordination by mechanical interaction, by specific chemical signals, and by spreading electrical impulses; an attempt will be made to classify the responses on this basis.

A final point in setting the terms of reference for this paper concerns the distinction between collaborative and coordinated behavior. If the zooids in the colony are active together due to their independent reception of similar stimuli originating from some source outside the colony, their behavior cannot be regarded as coordinated, even if they appear to be collaborating in the execution of a common behavioral task. Although this distinction is clear-cut in semantic terms, it is a hard one to draw in practice, as we often simply do not know enough about the behavior to be sure which phenomenon we are dealing with.

Three groups of colonial hydrozoans will be considered: the thecate and athecate hydroids and the siphonophores.

### THECATE HYDROIDS

Until recently it was considered that the polyps in thecate hydroid colonies were behaviorally isolated. Naumov (1969) stated that stimuli are not transmitted between polyps in the colony. However, Josephson (1961a) briefly noted observations to the opposite effect in the case of *Obelia*, and Morin and Cooke (1971a, 1971b, 1971c) found that stimulation evokes spreading hydranth contractions in *O. geniculata* and related campanularians. Flashes of light accompany the spread of the withdrawal response. The bioluminescent flashes are always preceded by electrical pulses (“luminescent potentials”) which are propagated singly or in bursts through the colony at a velocity of about 22 cm/sec. The spreading hydranth withdrawals can reasonably be regarded as protective behavior and, although there is no direct evidence regarding the utility of flashing, the fact that it accompanies hydranth withdrawal suggests that it may also somehow serve a defensive role.

Hydranths contract spontaneously, move their tentacles, and open their mouths and ingest food, but these activities are not coordinated among different hydranths.

### ATHECATE HYDROIDS

Because of their relatively large size and the accessibility of their hydranths for attachment of recording electrodes, athecate hydroids have received more attention than thecates.

Josephson (1961a) reviewed early evidence on coordinated responses in athecate colonies and added new findings on several species. A considerable body of work is now available, particularly on *Tubularia*. The various athecate forms show sufficiently important differences to require separate descriptions.

### *Tubularia*

Spontaneous activity cycles known as "concerts" occur in all hydranths of *Tubularia*, consisting basically of a pumping sequence by which fluids are shifted from one end of the proboscis cavity to the other, or from the stalk cavity to that of the proboscis and back (Beutler, 1925; Josephson and Mackie, 1965). Concerted tentacular flexions accompany the pumping movements.

Concerts are accompanied by a characteristic pattern of electrical events originating from or spreading within cells or groups of cells of uncertain identity, known as pacemakers (Josephson, 1961b, 1962, 1965; Josephson and Mackie, 1965). Major interacting pacemaker systems are located in the distal stalk region (neck potential system) and in the hydranth body (hydranth potential system).

Polyps which are connected by stolons containing living tissue often show synchronized concert activity, which is attributable to coupling between their neck potential pacemakers. Josephson (1965) called the coupling system the "triggering system." Josephson and Mackie (1965) attribute functional advantages to concert synchronization in terms of improved "tidal" ebb and flow of fluids between hydranths and stems,

In addition to the triggering system, the stem possesses two additional conducting systems (Josephson, 1965). One, the "slow system," controls opening of the distal tentacles, a response of unknown behavioral significance. Stimulation of the stem between connected polyps can, but does not usually, elicit the opening response of the distal tentacles in both polyps (Josephson, 1961a). The system conducts at about 15 cm/sec, compared with 17 cm/sec for the triggering system, and has a higher threshold of excitability. Continued low-frequency stimulation of the stem tends to inhibit the neck potential system in connected polyps and to suppress concerts. The inhibition is probably due to impulses traveling in the distal opener system (Josephson and Uhrich, 1969).

There is some indirect evidence that the distal opener system involves nervous pathways in the stem and polyps, but the histological identity of the three stem systems has not yet been satisfactorily established.

### *Cordylophora*

If a polyp is pinched or a stolon prodded, a wave of polyp contraction spreads across the colony (Josephson, 1961a). The response appears to resemble that described in the related form *Clava* (Föyn, 1927).

Josephson (1961b) recorded electrical signals from the stolons following stimulation. These events propagate at about 2.7 cm/sec at 22°C. Single pulses or bursts may be produced by single shocks. Repeated stimulation leads to an increase in the number of pulses in the bursts; with longer bursts the greater and faster is polyp contraction

in the vicinity. Not all pulses spread throughout the colony. Whether or not distant polyps contract and to what degree depends on the number of pulses which get through to them, and this is related to intensity of stimulation.

Fulton (1963) found that *Cordylophora* polyps undergo regular cycles of peristaltic activity, and he showed that these were roughly synchronized between connected polyps. There is no evidence of any conducting system operating to integrate the activity of different polyps other than the one described by Josephson, and this is not involved in the coordination of peristaltic activity (Mackie, 1968). Coordination might be "hydraulic," i.e., mediated by pressure changes in the fluid column itself.

### *Syncoryne*

Stimulation of the stem adjacent to a hydranth evokes some degree of polyp response but only if the stimulus is applied close to a polyp. There is little, if any, evidence for spreading responses between adjacent polyps (Josephson, 1961a). *Syncoryne* is exceptional in lacking interpolyp coordination or exhibiting it only in a rudimentary form.

### *Pennaria*

Josephson (1961a) confirms Zoja's (1891) observation that polyp contractions spread from points of strong stimulation. Spread is very slow (about 1 cm/sec). Both the magnitude of the contraction and the distance of spread vary with stimulus strength.

### *Hydractinia* and *Podocoryne*

*Hydractinia* lives on the outside of gastropod shells inhabited by hermit crabs. Presence of the crab appears to be essential for maintenance of the colony in a fully differentiated form, but the factors responsible for this dependence are unclear (Cazaux, 1958; Burnett et al., 1967). Four polyp types are present: gastrozooids, gonozooids, tentaculozooids, and dactylozooids. The medusae are not set free in most species but are reduced to sessile sporosacs.

In *H. echinata*, Josephson (1961a) found evidence of a local conducting system spreading polyp contractions over a limited area and of a second, through-conducting system activated by strong stimulation and involving the whole colony on an all-or-none basis. Stokes (1972) has recorded the electrical correlates of these two systems and of a third possible system. The local system ("incrementing system") conducts at 4.8 cm/sec, the general or "through system" at 12 cm/sec. The incrementing system mediates degrees of local activity from the single polyp up to small groups. Stokes gives unequivocal evidence for the presence of nerves within and between the polyps in the colony. The nervous system in whole or part would seem to be a likely candidate for the incrementing system.

Although the gastrozooids respond in the same way to excitation transmitted via the two systems, the dactylozooid response differs. Following stimulation received from the incrementing system the muscle response is unilateral, while after activation from the through system it takes the form of bilateral thrashing movements. In spite of this difference, responses are probably protective in both cases.

The related *Podocoryne* appears to lack a local system, showing the colony-wide response only (Josephson, 1961a).

### *Proboscidactyla*

The Limnohydrina include a number of small, often very specialized, athecate hydroids, of which *Proboscidactyla* shows the highest degree of colonial development. It lives commensally with sabellid polychaetes. Recent evidence (Strickland, 1971; Donaldson, 1971) indicates that contact with the worm's radioles is essential for the hydroid to be maintained in the differentiated state.

Spencer (1971) discovered a protective response in *Proboscidactyla* colonies in which all three polyp types (gastrozooids, dactylozooids, and gonozooids), as well as young attached medusae, contract. In nature the response is seen when the worm retracts its tentacular crown or when small invertebrates clamber over the colony. Excitation at any point can cause contraction of all members by conduction of electrical signals ("colonial pulses") through the stem. These pulses spread at about 9 cm/sec and are through-conducted to all points, like those in the *Hydractinia* through system.

The medusae of *Proboscidactyla* achieve swimming ability when about 0.5 mm in diameter and while still attached to the colony. They swim in bursts like free medusae, an activity attributable to pacemakers, presumably nerves, in the bell margin. "Crumpling," a protective closure response involving excitable epithelial tissues, is developed later. Colonial pulses reaching attached medusae elicit swimming while the medusae are small but later evoke crumpling. This remains the response to colonial excitation until the medusae, now measuring 0.8 mm, are released.

Functionally speaking, then, the medusae are "part of the colony" prior to their release, as their action systems are controlled by impulses arriving from the colony.

## SIPHONOPHORES

Siphonophores are the most complicated and highly evolved animal colonies, showing a higher degree of polymorphic differentiation and functional specialization of component zooids than any other colonial group (Mackie, 1963). They inhabit the competitive world of the plankton and have developed sophisticated response capabilities in the areas of locomotion and protective behavior. There is a fair amount of scattered information on siphonophore behavior but this account will stress recent work on a few forms which have received special study from the behavioral point of view.

The chondrophores *Porpita* and *Velella* are excluded, as they are best regarded as large, individual, tubularian hydranths and consequently have no place in discussions of coloniality (Fields and Mackie, 1971, and references therein).

Siphonophore behavior is often too complex or too little understood to be easily analyzable in terms of local versus coordinated behavior. For example, some physonectid siphonophores show a diffuse photosensitivity of the hinder parts and swim in response to sudden illumination. They also show color changes in response to light but these appear to be locally induced, and there is no correlation between the distribution of chromatophores and the distribution of light-sensitive areas for the swimming response.

These siphonophores carry out diurnal vertical migrations, presumably in response to light, but whether they do so by swimming or by density regulation is unclear. Density regulation involves muscular elimination of gas bubbles from the float and resecretion of gas in the gas gland, both seemingly local events. The float is not one of the regions showing photosensitivity as far as swimming is concerned. However, the float tissues involved in elimination and secretion of gas might be independently photosensitive. The whole complex of light-induced activities, buoyancy control, and vertical movements requires much more study.

### *Physalia*

The Portuguese Man-of-War consists of seven different zooid types (Totton, 1960). The float (part of the primary zooid) is capable of rather complex muscular movements concerned with erection of the crest and adoption of a curved sailing posture. The secondary zooids show various local activities. The only clear example of a coordinated response is the generalized, presumably protective contraction which spreads through the colony when any part is abruptly stimulated (Bigelow, 1891; Mackie, 1960). Nerves are present in the ectoderm throughout most regions, but it is not clear whether they are responsible for the through-conducted response or organize local activities. The latter appears most likely from what is known about hydrozoan conducting systems generally (Mackie, 1970).

*Physalia* can catch large fish by collaborative action of the many tentacles and gastrozooids (Wilson, 1947), but there is nothing to suggest that these activities are coordinated. Likewise, pumping movements are performed by the digestive members, distributing food around the colony, but pumping is probably locally organized.

### *Hippopodius*

In sessile hydroids and in *Physalia* the swimming activity of attached medusoids contributes nothing toward locomotion of the colony. In physonectid and calycophoran siphonophores, asexual medusoids have been evolved which serve specifically for locomotion. These nectophores or swimming bells are dependent on the colony for food, as they lack mouths and tentacles. They may be shed by autotomy but die soon after release.

*Hippopodius* has two columns of nectophores. In each column, the velar apertures of the upper nectophores open against the backs of the nectophores beneath. Thus, with the exception of the bottom two, their swimming activity has no locomotory effect. The upper ones apparently serve as a stock of replacements for ones lost from below. They also provide buoyancy for the colony as a whole (Jacobs, 1937) and enclose a sheltered central space into which the stem can be withdrawn.

Swimming is not obviously coordinated. It does not start or stop simultaneously in the different nectophores and each nectophore has its own rhythm. However, once activity begins (usually in an upper one) it tends to spread to others, probably because of the mechanical agitation set up. The marginal swimming centers in the nectophores are not connected by nerves with the stem (Mackie, 1964).

*Hippopodius* shows what is held to be a photokinetic response, aggregating in relation

to illumination (Mackie and Boag, 1963). The location of the photoreceptors is not known, but in view of the lack of swimming coordination, it seems likely that each nectophore is independently photosensitive.

When a *Hippopodius* is touched or abruptly stimulated it withdraws the stem and tentacles into the interior of the nectophore column, curls up the margins of the nectophores, becomes opaque due to formation of light-scattering granules adjacent to the covering epithelium of the nectophores, and emits a flash of light from the same epithelium (Mackie, 1965; Mackie and Mackie, 1967). This syndrome is considered to represent a complex of protective responses. Excitation spreads primarily in conducting epithelia and can be recorded in the form of electrical potentials. Epithelial or "neuroid" conduction is now known to be widespread in siphonophores and hydromedusae, functioning particularly in protective types of response (Mackie, 1970).

*Hippopodius* differs from most siphonophores in lacking an escape swimming response. The epithelial potentials transmitted through the colony do not evoke contractions in the swimming muscles but only in the radial fibers concerned with curling up the margin. Locomotion is so slow in this form that swimming would probably be ineffective in removing the colony from dangerous situations.

### *Muggiaea* and the Family Diphyidae

Typical diphyids have a pointed anterior nectophore and a smaller posterior one which fits into the back of the anterior one but not in such a way as to impede swimming activity. The stem streams out behind but can be withdrawn into the hydroecial folds of the nectophores. Diphyids dart around rapidly using the anterior or both nectophores or cruise slowly using the small posterior one. *Muggiaea* has only the anterior nectophore but is otherwise similar to the diphyids.

Locomotion serves either for escape, as when a nectophore or the stem is touched, or for spreading of the stem and tentacles ("fishing behavior"). Stimulation of a nectophore of *Chelophyes* excites the epithelial system and elicits rapid stem contraction and escape swimming. The epithelial pulses are propagated at velocities of at least 35 cm/sec (Mackie, 1965).

In addition to rapid stem contraction, a slower spreading response can be obtained by weak stimulation (Ebbecke, 1957). Fishing behavior is described in *Muggiaea* and involves a coordinated sequence of events in the stem and nectophore, wherein the colony swims in a circle, releasing the tentacles, which spread out centrifugally (Mackie and Boag, 1963).

A nerve tract connects the stem with the marginal nerves of the nectophore (Mackie, 1964), providing the potentiality for one of two possible pathways of communication between the stem and nectophore, the other being the epithelial route. It is clear that locomotion is under colonial control in diphyids, contrary to the situation in *Hippopodius*.

An interesting feature of this group from the point of view of coloniality is their ability to strobilate subcolonies from the posterior end of the stem. These "eudoxids" are fully equipped for swimming, feeding, and reproduction. Beklemischev (1958) called them "colonies within the colony."



*Nanomia*

Physonectid siphonophores such as *Nanomia* have an apical gas-filled float below which the nectophores are arranged in two regular columns on either side of the stem. The lower part of the stem bears the gastrozooids, palpons, bracts, and sexual medusoids. The food-catching tentacles are parts of either palpons or gastrozooids and are not separate zooids, although their behavior is largely independent of the zooids they belong to. The parts of the colony showing behavioral activity are the float, stem, and all the secondary zooids named above with the exception of the sexual medusoids and the bracts. Bracts undergo autotomy but are otherwise not active.

Food capture appears to be essentially a locally organized process, as in hydroids. Tentacles making contact with food paralyze it with their nematocysts and haul it up to the stem, where it is ingested by gastrozooids. Following food capture by the tentacles gastrozooids in the vicinity and for some distance along the stem begin to writhe and elongate (Mackie and Boag, 1963). This activity increases the likelihood of contact being made with the food object. Mackie (1964) suggested that the spread of the response was due to activation of nervous pathways in the stem. An alternative explanation in terms of the spread of a chemical activating substance from the site of food capture is possible, as it is known that crustacean tissue fluids and glutathione can evoke writhing behavior. As in *Physalia*, several gastrozooids may collaborate in ingesting the prey, but this behavior does not appear to be integrated. Electrical pulse patterns have been recorded (Mackie, unpublished) from gastrozooids during collaborative ingestion of food, and these patterns show no correlation with one another.

After the food has undergone preliminary digestion in the gastrozooids it is passed into the stem and flushed to and fro by rhythmic peristaltic movements performed by the gastrozooids and palpons. Gastrozooids which have *not* fed as well as those which have take part in these pumping movements. They show independent pumping rhythms, as do the palpons. The latter act as accessory digestive organs, carrying on intracellular digestion, releasing the end products into the coelenteron for dispersion through the colony, and eliminating wastes.

Sometimes a gastrozooid may fall into a reciprocating pumping pattern with a group of adjacent palpons, filling them when it empties and emptying them when it fills. It would appear likely that pressure changes transmitted via the coelenteric fluid are responsible for this type of coordination. Such collaborations are temporary. Nothing comparable to the triggering system in *Tubularia* has come to light in *Nanomia*.

Swimming ability is well developed in *Nanomia*. Each nectophore has its own pacemaker system which determines its swimming frequency. The direction in which the water jet is emitted from the nectophore is controlled by a pair of muscle bundles (Claus's fibers). When the fibers are relaxed, the water jet is emitted downward and the colony swims upward. When they contract, they deflect the water jet upward and reverse swimming results (Mackie, 1964).

The nectophores are quiescent except when "aroused" by excitation arriving from the colony. With weak tactile stimulation of the hinder regions locomotion begins gradually in the forward direction. One or a few nectophores start to pulsate and then others join in. Groups on the two sides tend to alternate, so that the colony moves in a zigzag

pathway. Before locomotion begins, the stem and tentacles usually contract slightly, indicating the buildup of a state of excitation in the stem.

When the hinder regions of the stem are stimulated more strongly, forward swimming ensues suddenly in the form of one or a few synchronous pulsations of all the nectophores in the column, driving the colony straight ahead for a considerable distance; at the same time the stem and appendages contract strongly. The ability to perform this coordinated forward swimming depends on the integrity of the nerve tracts connecting the nectophore margins with the stem. Following section of the nerves, the ability is lost (Mackie, 1964).

Reverse swimming also involves synchronous action of all the nectophores. It is elicited by stimulation of the float or anterior nectophores and, like forward swimming, is accompanied by strong stem contraction. Integrity of the connecting nerves in the nectophores is not essential for the response, and this, and other evidence, including electrical recordings, identifies the covering epithelium of the nectophores with the conduction pathway for the response. It appears that excitation in the epithelial system activates both the swimming muscle and Claus's fibers, whereas nervous excitation activates only the swimming muscle. Claus's fibers are homologous to the radial fibers which produce marginal curling in *Hippopodius* nectophores and crumpling in free medusae. *Nanomia* thus employs the protective closure mechanism inherited from a primitive ancestor but modifies it to achieve reverse locomotion, likewise protective in nature.

The stem contractions which accompany escape swimming in *Nanomia* have been explored from the neuromuscular viewpoint (Mackie, unpublished). Giant axons run the length of the stem, making synaptic connections with elements of the general nerve plexus. The giant axons do not penetrate the secondary zooids but are connected with them via the nerve plexus.

"Spasmic" stem contraction involves flurries of signals in the giant axons and, as these travel rapidly up the stem, they evoke contractions successively along the stem musculature. The spread of the contractile response is rapid, corresponding to the conduction velocity of the giant axons (up to 3 m/sec). Thus in a *Nanomia* 30 cm long, it takes only a few hundred milliseconds for the contraction wave to pass all the way along the stem, for the stem to contract, and for the nectophores to swim synchronously forward.

In addition to rapidly conducted, spasmic contractions, slowly conducted contractions of the stem and appendages can occur. Conduction velocities are here about 0.3 m/second. The general tonus of the stem is related to the level of activity in this slowly conducting "contraction pulse system." Changes in light intensity can affect contraction pulse frequency.

Stem-contraction pulses do not penetrate the secondary zooids. The zooids do, however, contract during spasmic stem contraction, and presumably do so in response to intensive nervous activity arriving via the nerve plexus. Transmission between the stem and appendages is not a simple, one-to-one process but involves conduction "blocks" which allow only relatively strong types of excitation to pass through.

Thus, from the point of view of coordination, gastrozooids and their tentacles and palpons lead a fairly autonomous existence but come under colonial control when excitation levels in the stem rise to a certain threshold. This is most clearly seen in the spasmic

contractions accompanying escape behavior. Nectophores, by contrast, are normally inactive but respond to excitation from the colony. They show autonomy only in the sense that once excited they beat at their own rhythms.

## CLASSIFICATION OF COORDINATED RESPONSES

### A. *Classification by mechanism*

#### 1. Mechanical

- a. Agitation: Movements of a zooid or water currents resulting from such movements agitate adjacent zooids and arouse activity in them. A possible example is the spread of swimming activity among the nectophores in *Hippopodius*.
- b. Pressure changes or fluid movements within the canal system trigger behavior within groups of connected zooids. Possible examples include the coordinated peristaltic movements of *Cordylophora* hydranths and the coordinated swellings and contractions sometimes seen in groups of palpons and gastrozooids in *Nanomia*.

#### 2. Chemical

- a. Diffusion through the external medium of triggering substances released by the organism itself: No examples are known. Inclusion of this category is prompted by the suggestion of Burnett et al. (1963) that mouth opening in *Hydra* may be caused by release of a chemical "retrohormone" from the polyp's own nematocysts when these discharge. The hypothesis remains unproved for *Hydra* and untested for colonies.
- b. Diffusion of triggering substances via the canal system: No examples are known but in *Hydra* the response known as "neck formation," which occurs following ingestion of food, involves activation of an internal tyrosine receptor (Blanquet and Lenhoff, 1968). Thus food breakdown components might serve as behavioral triggers in colonies.
- c. Spread of a triggering substance from cell to cell in the tissues connecting zooids: No examples are known, but quite large molecules can pass between cells in some tissues, and passage of such materials or "propagated" chemical changes involving such chemical activators might serve to coordinate activities of connected zooids over short distances.

#### 3. Electrical

- a. Impulses in the nervous system: Spasmodic stem contraction and accompanying contraction of zooids in *Nanomia* involves conduction in nerves. Coordinated forward swimming involves a specific nerve pathway. The distal opener system in *Tubularia* is thought to depend on nerves, and the incrementing system in *Hydractinia* may tentatively be considered in this category.
- b. Nonnervous impulses: The system coordinating polyp contractions in *Cordylophora* is probably epithelial, as nerves appear to be absent from the stem. The protective responses described in *Hippopodius* nectophores, and reverse swimming in *Nanomia* nectophores, are epithelially conducted as far as the nectophores are concerned, but it is not clear whether the spread of these

responses between the active zooids is epithelial or nervous. In forms such as *Hydractinia* and *Physalia*, where two sorts of conduction occur, nerves might be responsible for one sort of conduction (presumably incremental conduction) and epithelia for the other. By the same reasoning, the triggering system of *Tubularia* is likely to be epithelial.

#### B. Classification by function

1. Coordinated feeding behavior: With the possible exception of gastrozooid writhing activity in *Nanomia*, feeding behavior is not coordinated in hydrozoan colonies.
2. Coordinated digestive movements: Synchronized patterns of digestive movements are described in *Cordylophora*, *Nanomia*, and *Tubularia*.
3. Coordinated protective responses and escape behavior: Spreading zooid contractions or withdrawals are described in all hydroids except *Syncoryne*. In *Obelia* they are accompanied by luminescence. In *Hippopodius* stem withdrawal is accompanied by various changes in the nectophores, notably opacification, luminescence, and protective rolling up of the margin. In the diphyids and *Nanomia* escape swimming (bidirectional in *Nanomia*) accompanies the contraction of stem and attached zooids.
4. Nonescape locomotion: Fishing behavior in *Muggiaea* is a coordinated activity, as apparently is zigzag locomotion in *Nanomia*.

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