

DEFENSIVE STRATEGIES IN PLANKTONIC COELENTERATES

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Some planktonic coelenterates respond to potentially harmful stimulation by protective involution, others by escape behaviour. Examples of protective involution are seen in the 'crumpling' behaviour of various hydromedusae (*Sarsia*, *Euphysa*) and of siphonophores such as *Hippopodius*. Involution may be accompanied by striking visual displays e.g. light emission in *Euphysa*, light emission and blanching in *Hippopodius*. These displays probably serve to startle or blind interlopers. In *Hippopodius*, light emission in the dark would have the same effect as blanching in the light, an example of behavioural self-mimicry.

Animals employing escape locomotion include the ctenophore *Euplokamis*, the siphonophore *Nanomia* and the rhopalonematid medusa *Aglantha*. All of these forms have evolved giant axons that facilitate escape by reducing response time. The central nervous circuitry underlying locomotion in *Aglantha* is reviewed.

In a few cases (e.g. *Aglantha* and possibly *Nanomia*), the responses described can be seen as defensive against predators, but in the majority of cases, the responses probably serve primarily to reduce the risk of damage due to accidental contact with other organisms.

Anyone who can go down in a submersible in productive waters like those around Vancouver Island will be struck by the diversity and often the high density of the zooplankton and the evidence of frequent interactions and intense competition. This is true both in the photic zone and in depths where not enough light can penetrate to affect behavior (Mackie and Mills, 1983; Mackie, 1985). We see overwintering *Neocalanus plumchrus* at densities greater than $1000.m^{-3}$ being preyed upon by five or six species of siphonophores, hydromedusae and ctenophores, *Aglantha digitale* in densities up to $25.m^{-3}$ capturing euphausiid larvae and escaping rapidly from contact with adult euphausiids which are often even more abundant, *Clione limacina* locked in mating pairs or pursuing *Limacina helicina*, and hyperiid amphipods riding on and devouring *Aegina citrea*, their luckless jellyfish prey. One is often struck by the obvious need for animals to protect themselves from damage due to casual contact, particularly in high density regions. Even a glancing blow from the bristly leg of a rapidly swimming amphipod can be quite destructive to a fragile jellyfish. The epithelium may heal, tentacles torn off can be replaced, even neurons in the marginal nerve rings can regenerate, but minimization of damage is clearly at a premium in coelenterate evolution judging by the ubiquity of defensive responses. My thesis in this article is that many, probably most of the defensive responses shown by planktonic medusae and ctenophores are significant primarily in terms of reduction of the risks inherent in accidental contact with other planktonic animals rather than being directed against predators.

INVOLUTION

Many hydromedusae show what Romanes (1887) called "spasms" when stimulated on their outer surfaces. The response takes various forms but typically consists of contractions of subumbrellar radial muscles resulting in involution of the margin. In Leptomedusae, involution causes the contracted subumbrella to fall into irregular folds – Hyman's (1940) "crumpling" response. Mackie and Singla (1975) reviewed the literature on crumpling and analysed the response in *Stomatoca*. Involution is typically accompanied by contraction of the tentacles. In forms like *Sarsia* the long manubrium normally hangs down well below the level of the margin but it contracts into the subumbrellar cavity during involution. As the gonads lie on the wall of the manubrium, they are automatically brought into the shelter of the subumbrellar cavity. A marginal sphincter muscle may be present, acting like a purse-string to constrict the velar opening. In the crumpled state, the animal stops swimming. No one has seriously questioned that involution is a protective response. All the vital organs are protected – the gonads, tentacles and marginal nerve centres. The response is only seen following tactile stimulation, it is graded according to the strength and duration of stimulation and can be sustained for long periods. Interestingly, the ability to crumple has been lost in adult *Aglantha*, an agile, streamlined medusa with a well developed escape swimming response (see below, p. 8) but it is present in early post-metamorphic stages which are probably too small and immature to perform effective escape locomotion.

The sensory basis of the response was established by electrophysiology. The ectodermal epithelium covering the exumbrella is sensitive to tactile stimulation and impulses propagate through it to the marginal nerve centres and endodermal epithelium. There are no nerves in the exumbrella, and it is the epithelium itself that acts like a giant mechano-sensory transducer covering the whole outer surface. The electrical characteristics of the conducting epithelium were analysed in *Euphysa* by Josephson and Schwab (1979) and the secondary involvement of the nervous system in *Polyorchis* by King and Spencer (1981). Inhibition of swimming during crumpling is associated with hyperpolarization of the swimming motor neurons, presumably due to epithelial input (Spencer, 1981).

The swimming bells (nectophores) of siphonophores can be thought of as captive, non-feeding, asexual anthomedusae. Though lacking tentacles, they possess the usual medusoid locomotory system and show modified versions of the crumpling response. The exumbrellar epithelium is typically excitable and capable of conducting impulses which trigger radial muscle contractions in the subumbrella and velum.

INTIMIDATION

I refer here to certain visual displays that may serve to confuse, blind or alarm interlopers. These include bioluminescent responses falling within Morin's (1983) category of "contact flash predator deterrents", though I would argue that they are directed less against predators than against accidental intruders. Electrophysiology shows that these responses are evoked by the same sorts of stimuli that evoke crumpling and are conducted by the same excitable epithelia. As adjuncts or embellishments of crumpling, the responses are therefore best explained on the same basis, that is, as components of an overall defensive strategy serving to minimize damage due to contact with animals capable of seeing the displays.

a. Euphysa japonica

This tubulariid medusa has excitable epithelia and crumpling effectors similar to those of *Stomatoca* and *Sarsia* (Mackie and Passano, 1968; Josephson and Schwab, 1979) but unlike these it emits light when crumpling. Light emission is incremental, each epithelial action potential producing a discrete flash in synchrony with the step-wise, contractions of the subumbrellar radial muscles. Both contractions and flashes sum, so that light intensity increases progressively with involution. The flashes also show facilitation at pulse frequencies above 5 Hz. The light-emitting tissue proves to be the subumbrellar endodermal sheet, which is a cellular monolayer spanning the gaps between the four radial canals. Impulses propagate through the sheet at about 20 cm.s^{-1} presumably via gap junctions, as the gap-junction blocker octanol prevents spread of the response (Mackie, 1991).

The most striking feature of bioluminescence in *Euphysa* is the precision of the coupling between involution and flashing. Both are graded and incremental with similar thresholds and decay times. The response is quite unlike the flashing of *Halistaura* and other Leptomedusae, where the photophores are localized patches at the bases of the tentacles and where the response is local rather than propagated. *Euphysa's* emission spectrum has not been measured but the light appears bluer than in the leptomedusae where the photoprotein is associated with a green fluorescent protein (Morin and Hastings, 1971).

b. Hippopodius hippopus

Hippopodius and its spiny cousin *Vogtia* are chunky, sluggishly swimming, prayomorph siphonophores which vividly exemplify the strategy of static self-defence, contrasting markedly with the agile, streamlined diphyids. The colony consists of a cluster of tightly interlocking nectophores arranged like musk-oxen in a defensive configuration around a central space into which the vulnerable trailing appendages and gonophores can be completely withdrawn. The nectophores are covered with an excitable epithelium. Tactile stimulation evokes propagated epithelial action potentials which spread to the velum and subumbrellar endoderm. "Crumpling" takes the form of contraction of radial muscles in the margin of the nectosac, causing the margin and velum to fold inward and roll up tightly, effectively protecting the marginal nerve centres from the outside world (Mackie, 1965). The response spreads via the stem to all the nectophores, and the stem contracts simultaneously, withdrawing into the interior space. These muscular protective movements are accompanied by striking visual displays.

- (i) Light emission. Observed in the dark, propagating epithelial action potentials evoke summing flashes of light, much as in *Euphysa*, but in the ectoderm rather than the endoderm. The duration of bioluminescent episodes varies according to the number and time-relationships of evoked action potentials. Though seen only following stimulation, flash sequences can become self-sustaining and rhythmic for several seconds, recalling the "frenzy" display of *Renilla* (Nicol, 1955) and a similar display in the coronate medusa *Atolla* (P. J. Herring and E. A. Widder, personal communication). Intense blue light emissions are also reported for other prayomorph siphonophores. In *Vogtia*, Nicol (1958) calculated that the light could be seen 30 m away by an animal with the equivalent of human photosensitivity. When photographing *Praya*, Widder *et al.* (1989) had to reduce the lens aperture on

their camera by two f-stops in order not to overload their image-intensifier tube! Morin (1983) uses the phrase "flash-bulb effect" to describe such strong emissions and points out that they may literally blind interlopers.

- (ii) Blanching. Observed by day, *Hippopodius* responds to tactile stimulation by going white. Like marginal involution and light emission, the response is spread by epithelial action potentials initiated in the ectoderm at the site of stimulation and spreads throughout the colony. The whiteness is not produced in the epithelium itself but in the mesoglea underlying it (Mackie and Mackie, 1967) and is due to the formation of light-scattering granules in the otherwise transparent matrix. Granulation occurs within a few seconds, but resumption of transparency takes 15–30 minutes. Recordings made in the dark show the nearly simultaneous onset of blanching and luminescence, both following closely upon the arrival of the propagated potentials that cause involution (Bassot *et al.*, 1978).

Like the luminescent response seen in the dark, blanching by day makes the normally invisible siphonophore loom up suddenly out of nowhere as an imposingly large object and one likely to evoke avoidance reactions in visual plankters in the vicinity. The visual displays of *Hippopodius* and *Vogtia* possibly serve an additional function, the aposematic warning of distastefulness: they are accompanied by discharge of a secretion from a patch of gland cells in the subumbrella (Mackie, 1976).

ESCAPE

In marked contrast to the tortoise-like, static defence strategies of the forms discussed above, many planktonic coelenterates emulate the hare, and escape rapidly from threatening situations. Such species are invariably streamlined, powerful swimmers and their nervous systems may contain fast conduction pathways enabling them to react rapidly when stimulated. Escape locomotion invariably occurs in conjunction with contraction of the fishing tentacles and may be accompanied by bioluminescent displays, though the deterrent effect of these is less obvious than in the case of static self-defenders. Three cases will be discussed (there are many more!): a ctenophore, a siphonophore and a rhopalonematid medusa.

a. Euplokamis dunlapae

First described by Mills (1987), this cydippid ctenophore was long overlooked because it disintegrates completely in plankton hauls, lives below the zone of light penetration, does not perform vertical migrations and is only brought to the surface during unusual mixing conditions. In our dives with PISCES IV (Mackie and Mills, 1983; Mackie, 1985) Claudia Mills and I soon realized that it is probably the most abundant midwater ctenophore in the Strait of Georgia and adjacent fjords and that it can swim rapidly and in either direction. After ten years we had finally obtained enough animals to describe its locomotory adaptations (Mackie *et al.*, 1992). This mini-saga illustrates the difficulty of doing physiology on midwater gelatinous plankton.

Euplokamis normally swims at a cruising speed of about 2 cm. s⁻¹ with the mouth leading and with the tentacles trailing behind. If stimulated at the front, it immediately goes into reverse and swims backwards at about 4 cm. s⁻¹. If stimulated at the rear end, it leaps forwards at 5.5 cm. s⁻¹. These are clearly avoidance responses, and they are brought about by changes in either the direction or the frequency of beating of the comb plate

cilia, or both. Reaction time is about 130 ms. The animal is long, lean and agile. It contracts its tentacles when showing escape behavior, reducing drag, whilst letting them trail behind when cruising. Physiological recordings revealed a fast conduction pathway along each comb row, which was identified by optical and electron microscopy as a chain of giant axons. The axons are about $10\ \mu\text{m}$ in diameter, roughly ten times the size of non-giants in the same animal and in other ctenophores. The giant axons conduct at $0.5\ \text{m. s}^{-1}$, four or five times faster than non-giant neurons in the same animal.

These findings show that the same selective pressures which have led to the evolution of giant-axon mediated startle responses in muscular swimmers can apply equally to ciliary swimmers, though escape velocities are relatively low and response latencies long. Like many muscular escapers, *Euplokamis* luminesces when disturbed, releasing glowing particles from a region adjacent to the comb rows (Widder *et al.*, 1992).

b. Nanomia cara

Nanomia and several other agalmid siphonophores have developed the ability to swim forwards and backwards, doing so when stimulated at the rear and front ends, respectively. Reverse swimming involves the contraction of radial muscles in the velum during swimming. These muscles are placed asymmetrically so that when they contract they deform the opening from the bell, causing deflection of the water jet. An interesting feature of reverse swimming is that the radial muscles of the nectophores are evidently the homologues of the muscles that cause protective involution in other siphonophores, and that transmission of the reverse swimming response is mediated in part by the excitable epithelium covering the nectophores. In other words, the same components that serve for involution of the margin in typical siphonophores and hydromedusae have been adapted by *Nanomia* for reverse locomotion. We are dealing with defensive responses in both cases, but the strategy of the tortoise has been converted into that of the hare (Mackie, 1964).

Both forwards and reverse escape locomotory responses in *Nanomia* are mediated by giant axons conducting at velocities of up to $3.0\ \text{m. s}^{-1}$. These run along the dorsal side of the stem and are physiologically linked with the action systems of all the zooids in the colony. During escape swimming the nectophores contract in synchrony, producing powerful thrusts. In non-escape locomotion, they beat at their own intrinsic rhythms, producing a smoother, slower, gliding motion. Siphonophores are probably the best coordinated of all animal colonies (Mackie *et al.*, 1987). Functionally, they behave like single, well-integrated unitary organisms.

Nanomia has mobile chromatophores that expand and contract according to ambient light intensity (Mackie, 1962; Mackie *et al.*, 1987). Their distribution is patchy, suggestive of disruptive coloration, i.e. serving to conceal the animal by making it appear to consist of scattered pinpoints of colour, like a swarm of copepods. Such an adaptation may well assist prey capture but it could also make the siphonophore less obvious to predators. At night when disturbed, *Nanomia* swims away emitting flashes of light from numerous scattered photophores (Mackie, 1964; Freeman, 1987). Again, a form-disrupting role seems likely.

c. Aglantha digitale

Aglantha and its relatives in the Rhopalonematidae are the only hydrozoan medusae showing a specialized and distinctive form of escape swimming superimposed upon

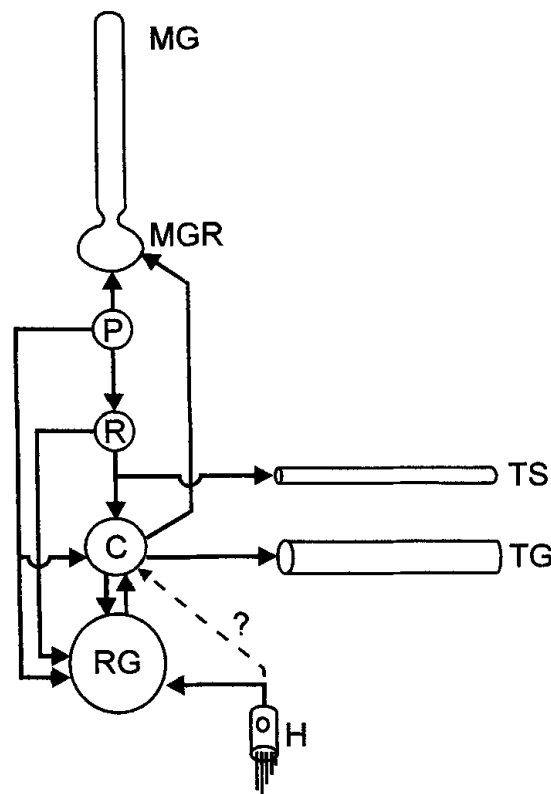


Figure 1 Circuit diagram for central nervous organization in *Aglantha digitale* as explained in the text (from Mackie and Meech, 1995b). C, carrier system; H, hair cell; MG, motor giant axon; MGR, motor giant axon rootlets; P, pacemaker system; R, relay system; RG, ring giant axon; TG, tentacle giant axon; TS, slow-conducting tentacle system.

the normal, "slow" swimming shown by all medusae. Slow swimming is exhibited spontaneously in a rhythmic pattern generated by pacemaker neurons in the margin. It occurs in cyclic episodes related to fishing behavior (Mackie, 1980). Escape swimming is seen only as a response to tactile stimulation. It is much more powerful than slow swimming: a single contraction can displace the animal by seven body lengths, compared with one body length in the slow swim (Donaldson *et al.*, 1980). Since the discovery of giant axons in *Aglantha* the animal's neurophysiology has been the subject of a series of studies and the main features of the circuitry underlying the two types of swimming (Figure 1) are now understood (Mackie and Meech 1995 a, b; Meech and Mackie, 1995).

Aglantha is acutely sensitive to touch and can sense water-borne vibrations. It is equipped with hair cell mechanoreceptors, arranged in clusters on the tentacle bases and velum. These feed into an enormous "ring giant" axon that runs around the margin. Giant axons in the tentacles also feed into the ring giant so that pinching or tugging tentacles evokes escape. Thus, both tactile and vibratory stimuli excite the ring giant, producing action potentials that propagate rapidly round the margin. Impulses are relayed to eight motor giant axons that run up the subumbrella and innervate the swimming muscles both directly and through smaller motor neurons running out on either side. Delays at the neuromuscular junctions are among the shortest known for any animal.

We originally thought that there must be a second set of nerves for the innervation of the muscles in slow swimming, as the motor giants were presumably tied up with escape behavior. It turned out however, that the motor giants are used for both types of swimming. In escape swimming they conduct sodium-based action potentials which propagate rapidly and spread to the lateral motor neurons, exciting the entire muscle field. In slow swimming, the motor giants conduct calcium-based action potentials which propagate slowly and excite the muscles only in a narrow band adjacent to each motor giant.

Another interesting point concerns the innervation of the tentacles. It is clearly essential for the tentacles to contract at the start of escape swimming for drag to be minimized and this is ensured by the one-to-one firing of the tentacle giants with the ring giant. Tentacle contractions also occur during slow swimming but the picture here is not quite so simple. The swimming pacemaker neurons not only excite the motor giants to produce slow swims, they simultaneously fire a system of "relay" interneurons that excite non-giant nerves in the tentacles, causing graded, tonic contractions. In addition, the relay system can fire the ring giant through a closely associated pathway, the "carrier" system. The ring giant in turn excites the tentacle giants, producing twitch contractions in the tentacles. In some way not yet understood, the pathway from the ring giant to the motor giants is blocked when this happens, so that there is no escape swim, but the tentacles contract sooner and more strongly than they could if the ring giant were not involved.

From this necessarily brief survey, four points may be singled out as specially significant.

- (i) *Aglantha's* vibration-sensitive mechanoreceptors bear a remarkable resemblance to those of vertebrates. Each cell has a single kinocilium surrounded by a group of stereocilia graded in length from long on one side to short on the other. The cells are organized into regular arrays where all the cells in a given row show the same polarity, but different rows have different polarities. Presumably this arrangement maximizes responsiveness to vibrations in different planes (Arkett *et al.*, 1988).
- (ii) Many animals can perform escape and non-escape locomotion but they do so by having separate fast and slow muscles supplied by separate fast and slow motoneurons. This is true of crustaceans, squids and vertebrates. Only in *Aglantha* do we find an animal with one set of muscles and one set of motor neurons that can swim in two ways. The novel feature that allows it to do this is a unique type of neuron (the motor giant) that can conduct two different sorts of action potential with different post-synaptic effects (Mackie and Meech, 1985).
- (iii) Some crustaceans show shared circuitry in which slow pathways are utilized during escape responses but *Aglantha* is apparently unique in being able to commandeer its ring giant axon (normally part of the escape circuitry) to augment tentacle contractions during its non-escape swimming (Mackie and Meech, 1995a).
- (iv) Giant axons are necessary for fast conduction in animals where the nerves are not myelinated. To achieve a giant axon the size of the ring giant, *Aglantha* has had to use a space that would accommodate about 200 normal axons. The metabolic cost of maintaining such a large unit must be considerable, to say nothing of the space requirement. What is achieved? A saving in reaction time of at most 1.5 milliseconds. Nothing more dramatically illustrates the intensity of the selective pressures bearing on these rhopalonematid medusae during their evolution than their "willingness" to invest so heavily in giant axons that reduce response time by such small amounts.

CONCLUSIONS

a. Self-mimicry in siphonophores

In *Hippopodius* the all-over blanching response seen in the light resembles the all-over luminescent response seen in the dark. I have argued that both serve to scare off interlopers. Similarly in *Nanomia* the patchy pattern of chromatophores seen by day is like a positive print of the patchy luminescent "negative" seen in the dark. In both cases, the siphonophore's outline is disrupted. *The animal in the dark mimics itself as seen in the light*. A comparable case is that of the squid *Heteroteuthis* which emits a "distracting" cloud of ink that is also luminescent. The luminescent secretion clings to the ink particles (Herring, 1977, and personal communication). J. G. Morin (personal communication) suggests that such self-mimicry is not uncommon. Among other examples he mentions various ophiuroids, enteropneusts and pennatulaceans whose bright colour patterns, thought to be warnings of distastefulness, are matched by luminescent patterns seen in the dark. The self-mimicry of siphonophores is not perfect. The patterns do not exactly correspond and they are produced by different effectors, but the overall resemblances are quite striking.

b. Anti predator defences

The adaptations reviewed here can all reasonably be regarded as defensive in function, but in each case we have to ask-defensive against what?

There is now a considerable body of evidence showing that pelagic coelenterates are preyed upon by fishes (Mackie *et al.*, 1987; Arai, 1988). It is hard to see how involution (crumpling) of a small hydromedusa could reduce the effectiveness of fish predation except in the case of a small fish whose mode of attack was to nibble at the exposed parts, as (on a larger scale) the ocean sunfish systematically demolishes its scyphozoan jellyfish prey, luridly described by MacGinitie and MacGinitie (1949) ("The sucking noise that *Mola* makes as it bites off pieces of the jellyfish can be heard at some distance"). The visual displays that accompany involution in *Euphysa* and *Hippopodius* would seem counterproductive as anti-fish strategies as they would draw attention to the prey object. The escape response of *Euplokamis* is probably too slow to be effective against a fish predator. The escape behavior of *Nanomia* might be somewhat more effective. As a colony with many duplicated parts and the ability to replace lost zooids by budding new ones a siphonophore can survive loss of a large portion of its siphosome. Following an attack, *Nanomia's* rapid escape response could enable it to avoid further damage. It would be less likely to survive severe damage to the nectosome, as the float cannot be regenerated and without it the siphonophore's posture and locomotory ability would be severely affected. It is interesting however, that detached nectophores do not simply float away, but swim jerkily around for several seconds. This might distract a visual predator, allowing the siphonophore to make good its escape. Loss of several nectophores can be tolerated, as the stem contracts and rotates, closing up the gaps (Mackie, 1964).

The only really good case of a response effective against fish predation would seem to be that of *Aglantha*. We know that *Aglantha* is subject to attack from mackerel (Runge *et al.*, 1987). The fish actually seem to prefer it to copepods! *Aglantha's* ability to detect water disturbances at a distance, its extremely short reaction time (about 15 ms), the

vigor of its escape response and the unpredictability of the direction of escape would all seem likely to reduce the incidence of capture by fishes. The tentacles have an autotomy joint at the base and are actively shed if tugged or pinched (Bickell-Page and Mackie, 1991), so the animal could not easily be caught by its tentacles, even if they were not already fully contracted.

Some of the same arguments made above with regard to predation by fishes probably apply to predation by invertebrates, though evidence is scant. To the extent that nematocysts have a defensive role (and this is unclear) they are likely to be more effective against invertebrates than fishes, as they are used effectively against many invertebrates as offensive weapons (Purcell and Mills, 1988). The chief invertebrate predators of pelagic coelenterates seem to be other pelagic coelenterates, along with nudibranch and heteropod molluscs and hyperiid amphipods. As with fish predation, only rapid escape responses such as those of *Nanomia* and *Aglantha* would seem likely to be effective against such predators.

c. Minimization of contact damage

Hydromedusae have no exoskeleton and are protected from the outside world by a single layer of epithelial cells only 5–10 μm thick. Damage to the epithelium may lead to bacterial infection and possibly to loss of buoyancy, as buoyancy ultimately depends on ionic pumping by the epithelia enclosing the mesoglea. A small copepod accidentally sucked into the subumbrellar cavity of a swimming *Sarsia* can cause terrible lacerations to the swimming muscles and nerves. A larger crustacean entangled in the tentacles can tear the tentacles off. Gelatinous animals in general must be more susceptible to accidental damage than planktonic crustaceans, worms, molluscs or chaetognaths. Most pelagic tunicates are protected by their tunics but appendicularians lack a tunic and face the same problem as jellyfish. In *Oikopleura*, the covering epithelium is heavily reinforced with fibrillar material, but it retains the ability to conduct electrical impulses. *Fritillaria* however has lost the epidermis, leaving only a fibrous layer, and without an epidermis it has no surface excitability (Bone *et al.*, 1977).

The involution response of hydromedusae is initiated by contact strong enough to be potentially damaging, so some damage may well occur before the response takes effect. This does not mean that the response is ineffective however. The intruder may remain in the area and make further contacts. By crumpling, the jellyfish reduces the impact of repeated, potentially damaging contacts. In *Euphysa* and *Hippopodius*, the visual displays of luminescence and blanching that accompany involution presumably tell the intruder that here is a large object best avoided. We may imagine the “object” looming up out of nowhere causing “either momentary distraction or immobilization (disturbance of neuromotor control) or temporary blinding (sensory blanking)” (Buck, 1978). The intruder may be innocent of all predatory intent, but its mere presence is a threat, because of the jellyfish’s susceptibility to damage. Even where, as in *Aglantha*, an escape response is effective against predators, it may also be effective in minimizing contact damage due to accidental encounters with other animals. We are only beginning to understand the intricacies of life in the midwater realm, aptly described by Young (1983) as “a peculiar battle in which stealth and luminescence are major weapons”.

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