LOCOMOTOR ADAPTATIONS OF SOME GELATINOUS ZOOPLANKTON

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Summary

Swimming behaviour and locomotor adaptations are described in chaetognaths, larvacean tunicates, some cnidaria, and thaliacean tunicates. The first two groups swim by oscillating a flattened tail, the others by jet propulsion. In chaetognaths, the locomotor muscle fibres are extensively coupled and relatively sparsely innervated, they exhibit compound spike-like potentials. The motoneurons controlling the rhythmic activity of the locomotor muscle lie in a ventral ganglion whose organization is briefly described. Rhythmic swimming bursts in larvaceans are similarly driven by a caudal ganglion near the base of the tail, but each caudal muscle cell is separately innervated by two sets of motor nerves, as well as being coupled to its neighbours. The external epithelium is excitable, and linked to the caudal ganglion by the axons of central cells. Mechanical stimulation of the epithelium evokes receptor potentials followed by action potentials and by bursts of rapid swimming. The trachyline medusa *Aglantha* and the small siphonophore *Chelophyes* also show rapid escape responses; in *Aglantha* these are driven by a specialized giant axon system lacking in other hydromedusae, and in *Chelophyes*.

Slow swimming in *Aglantha* apparently involves a second nerve supply to the same muscle sheets used in rapid swimming, whereas in *Chelophyes* slow swimming results from the activity of the smaller posterior nectophore.

Slow swimming in siphonophores is more economical than the rapid responses. In the hydrozoan medusa *Polyorchis* (as in *Chelophyes*) action potentials in the locomotor muscle sheet change in shape during swimming bursts, and their duration is related to the size of the medusa; they are not simply triggers of muscular contraction.

The two groups of thaliacean tunicates are specialized differently. *Doliolum* is adapted for single rapid jet pulses (during which it achieves instantaneous velocities of 50 body lengths s-l), whilst salps are adapted

for slow continuous swimming. The cost of locomotion is greater in *Doliolum*.

Few gelatinous zooplankton show special adaptations both for rapid escape movements, and for slow sustained swimming, those that do deserve further study.

Introduction

Many animal groups have gelatinous representatives in the zooplankton, as larvae, or as larvae and adults, and these range in size from protozoa and small larval forms to quite large animals, for example the big heteropod molluscs like *Carinaria* and *Pterotrachea* and large scyphomedusae. The great majority however, are only a few mm or cm long and operate at Reynolds numbers well below 5×10^{-3}. Even so,

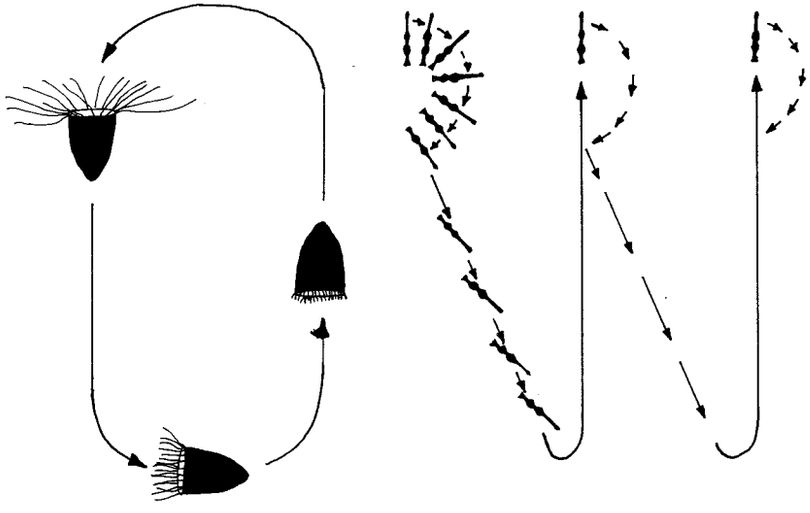


Fig. 1. Swimming patterns of alternate upwards swimming and passive sinking in the trachyline medusa *Aglantha* (after Mackie, 1980), and on the right, in *Sagitta hispida* (after Feigenbaum & Reeve, 1977).

some of these smaller animals achieve instantaneous velocities of 30 cm s^{-1} or so, which may correspond to 50 body lengths s^{-1}. Rapid swimming of this order is obviously only of brief duration, during attack or escape responses; most gelatinous zooplankton spend the greater part of their lives passively floating (excluding SO_4^{2-} to attain neutral or near neutral buoyancy, Denton & Shaw, 1962; Bidigare & Biggs, 1980), or slowly swimming intermittently or continuously as part of their feeding pattern. Thus, as Mills (1981) elegantly demonstrated, some hydrozoan medusae are neutrally buoyant and hang in the water with extended tentacles, waiting for their prey to blunder into them, whilst other negatively buoyant species search for their food by a regular cycle of swimming upwards and sinking down as swimming ceases. The trachyline medusa *Aglantha* shows this latter pattern (Fig. 1A) swimming upwards in the water column with its tentacles retracted and then sinking down inverted fishing with extended tentacles (Mackie, 1980). Similarly, chaetognaths show patterns of passive sinking alternating with bursts of activity driving them upwards (Fig. 1B); Feigenbaum & Reeve (1977) have shown how *S. hispida* thereby extends the area of water searched for prey. The energetic advantage of this kind of behaviour has been considered by Haury & Weihs (1976).

Such patterns of activity (and inactivity) are shown by animals that are on the whole, whatever group they belong to, characterized by simplicity of design, and economy in the number of elements they use in locomotion. Perhaps the most striking demonstration of economy of construction is shown by fritillariid larvaceans, where there may be only four chromosomes (Colombera & Lazzaretto-Colombera, 1977), and cell numbers are greatly reduced, but most gelatinous zooplankton animals have a rather simple locomotor apparatus and simple control system, with relatively small numbers of neurons, often using epithelia not only as permeability barriers or to secrete test and mesogloeal material, but also as conduction pathways. It is remarkable that even though the locomotor systems are 'simplified' they may double in different groups not only for cruising locomotion, but also for rapid escape responses.

The locomotion of rather few planktonic animals has been studied in any detail, and this short review will deal only with some cnidaria, with chaetognaths, and with pelagic tunicates. Many interesting forms are unfortunately omitted, such as the planktonic molluscs and veliger larvae, or the planktonic polychaetes like *Tomopteris* and the larger *Alciopa* (which would make interesting comparisons with the nereids examined by Clarke & Tritton, 1970).

The examples chosen generate forward thrust by two quite different methods: by oscillating a flattened body and tail (like fishes) and by

expelling propulsive jets (like squid). Since both methods are employed by quite unrelated groups of animals, independent solutions to similar problems are available for comparison.

Oscillatory propulsion of chaetognaths

Thrust generation by oscillating a flattened tail is used by chaetognaths and larvacean tunicates. In both groups, swimming is intermittent, and there is a characteristic pattern of regular short swimming bursts. During these bursts, *Sagitta setosa*, the only species as yet studied in any detail (Bone & Pulsford, 1984), oscillates the tail at 40–50 Hz, it is an active predator and if disturbed, makes very rapid darting escape movements. Since it is denser than seawater, *Sagitta* sinks slowly between the regular swimming bursts for 15–20 s and then a swimming burst drives it upwards to maintain its position in the water column. The regular swimming bursts persist if the animal is seized by the tail with a suction electrode (Fig. 2), and persist after decapitation, so that they are not controlled by the ganglia of the brain, but rather, by the large ventral ganglion lying about one third of the way down the body.

Rhythmic activity can be recorded from the isolated ganglion (Fig. 2) and ceases if the ganglion is removed; the motoneurons responsible for innervation of the locomotor musculature lie within the ganglion.

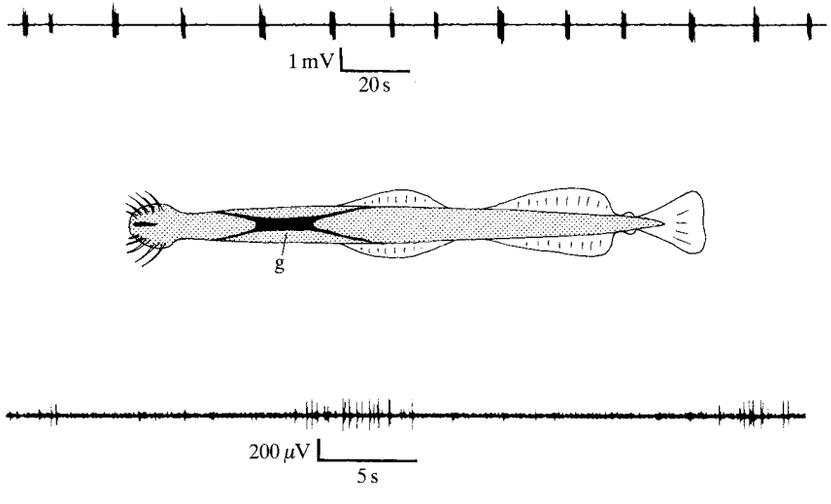


Fig. 2 *Sagitta setosa* showing position of ventral ganglion (g). Upper record: suction electrode on tail of decapitated specimen showing rhythmic swimming bursts; lower record: rhythmic activity recorded by suction electrode on isolated ventral ganglion. (From Bone & Pulsford, 1984).

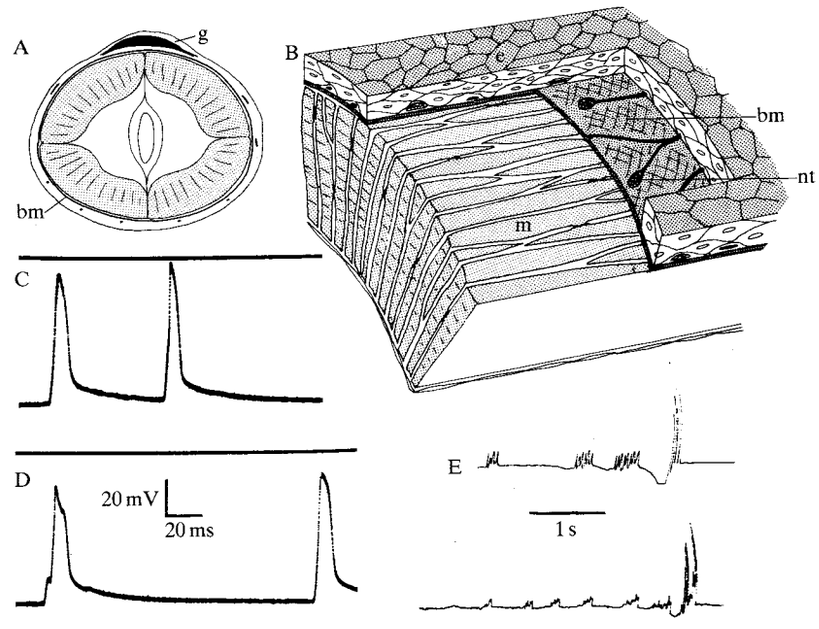


Fig. 3. Locomotor system of *Sagitta*. (A) Transverse section of body at level of ventral ganglion showing quadrants of locomotor muscle and position of ventral ganglion (g) external to basement membrane (bm); (B) simplified stereogram of muscle innervation. The muscle cells (m) are extensively coupled and covered with a basement membrane (bm) containing collagen fibres. Nerves and nerve terminals (nt) lie external to the basement membrane, the terminals do not contact the muscle cells. A multi-layered external epithelium (e) is not excitable. (C,D) Spike-like potentials recorded from locomotor muscle cells during spontaneous activity. Note compound nature of first potential in D, and difference in form of successive potentials. (E) Large and small spontaneous tail movements recorded by suction electrode placed on tail (C-E from Bone & Pulsford, 1984).

Curiously enough, the rather similar swimming bursts of larvaceans are also driven by a ganglion near the base of the tail, and are not interrupted if the brain is removed. However, the similarity between the two ends there for each group has a very different pattern of organization of the locomotor system.

In chaetognaths, the flattened tail lies in the horizontal plane, and the body flexes dorsoventrally during swimming. The locomotor muscles are arranged in four quadrants, two dorsal and two ventral, so that directional swimming such as the attack response to vibrating probes (Horridge & Boulton, 1967; Feigenbaum & Reeve, 1977) must depend upon unequal activation of these muscle quadrants. Each is composed of small spindle-shaped cross-striated muscle fibres which are extensively coupled to each other with numerous gap junctions. No nerve terminals are seen on the

muscle fibres; a curious situation which led Grassi (1883) to doubt whether *Sagitta* had any motor nerves! The paradox was recently resolved by Duvert & Barets (1983) who showed that vesicle-filled nerve terminals lay *outside* the tough basement membrane containing helical collagen fibres which surrounds the musculature. Apart from the brain ganglia and 16 axons in the two nerve bundles of the gut, the entire nervous system of *Sagitta* is external to this thick basement membrane. It seems likely that the basement membrane functions during swimming in the same way as the helical connective tissue fibres in the skin of sharks (Wainwright, Vosburgh & Hebrank, 1978; Wainwright, 1983), but this speculation has not been tested. Prof. E. R. Trueman (personal communication) has made preliminary measurements on the internal pressure in large specimens of *Sagitta* which indicate that during bending of the body, internal pressure peaks of around 1 KPa are observed, and work in this direction would be worth pursuing. The relative numbers of nerve terminals and muscle fibres in each quadrant are not known, but the rarity of terminals in sections of the body makes it clear that not all fibres are innervated, probably relatively few, and the majority are excited via the gap junctions connecting them to innervated fibres.

Fig. 3 illustrates the arrangement. Intracellular records from the locomotor muscle fibres obtained from animals cut open and pinned out on Sylgard show that during the locomotor bursts (which continue under these conditions) the electrical activity of the fibres consists of rapid spike-like events which are evidently compound (Fig. 3C,D) and do not overshoot. *Sagitta* is able to grade the activity of the locomotor muscles to make small and large movements (Fig. 3E) and it seems that gradation is brought about by recruiting different numbers of innervated fibres which excite varying numbers of fibres coupled to them by decremental

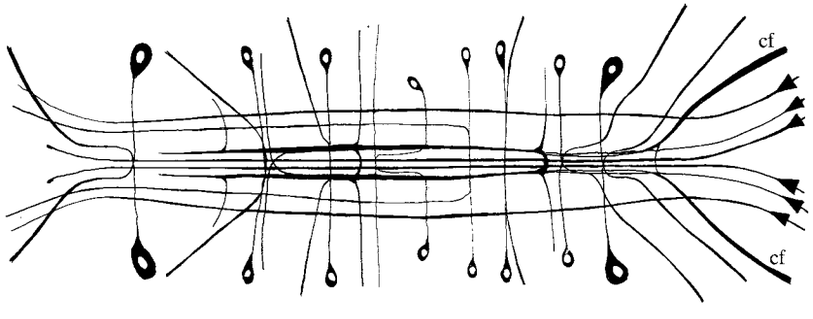


Fig. 4. Arrangement of larger fibres in ventral ganglion, anterior to right. The three pairs of fibres arrowed enter from the anterior ganglia. The largest fibres (cf) supply ciliary fence organs at the base of the head. (modified from Bone & Pulsford, 1984).

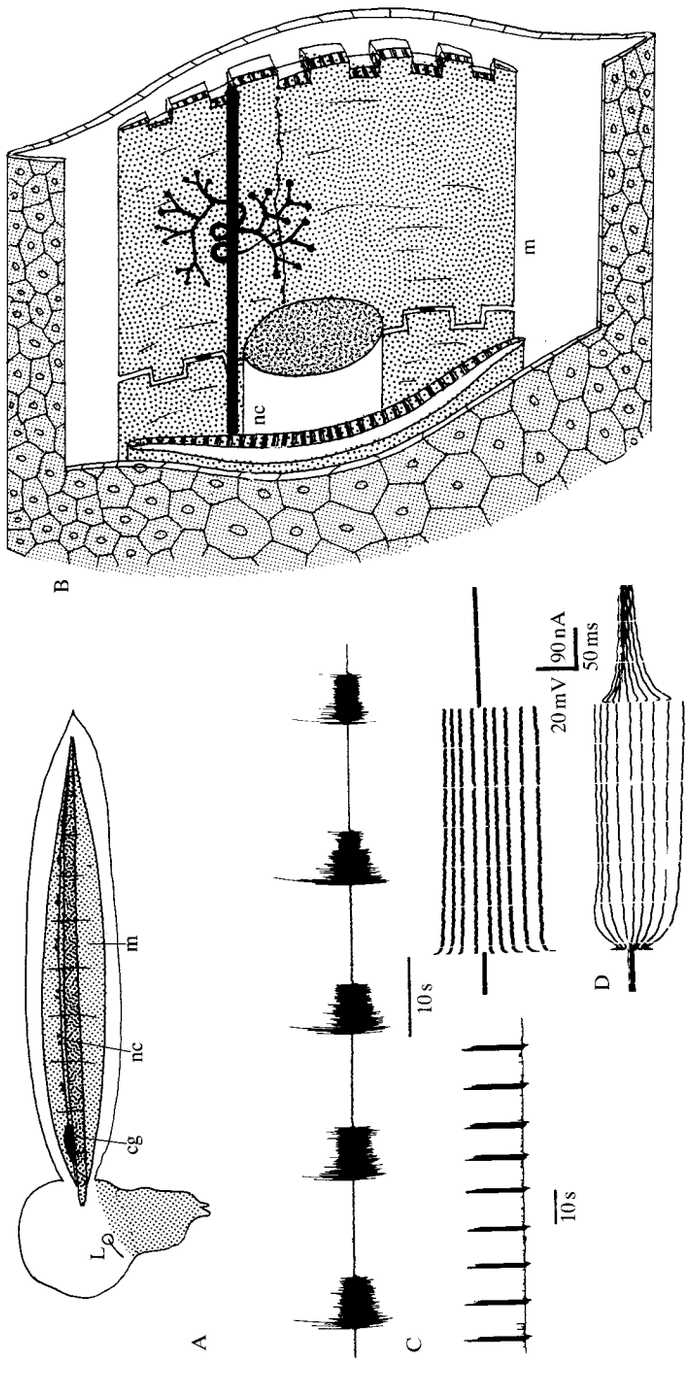
conduction, an economical solution to the problem of grading muscular activity that is not known so far in other planktonic animals. Two types of muscle fibres have been described in *Sagitta* (see Duvert & Salat, 1979) but the less common type is coupled by gap junctions to the more abundant, and its role is not known.

The ventral ganglion, which controls the locomotor muscles, is built upon a rather regular scalariform plan (Fig. 4) which shows a number of large fibres up to 6 μm in diameter that are constant in number and position between individuals, and very similar between species (Bone & Pulsford, 1984). Some of these are known to connect with the anterior brain ganglia, and others pass to the ciliary fence vibration receptors arrayed around the body, but details of the 'wiring diagram' of the ventral ganglion remain to be investigated. Since isolated ventral ganglia show the same rhythmic activity as seen in the muscle responses of intact animals it seems clear that this activity is not initiated or regulated by proprioceptive input, and no proprioceptors have been observed histologically. Acetylcholine and L-glutamate have no effect on this rhythmic activity, but it seems from some recent preliminary experiments that acetylcholine may be the neuromuscular transmitter.

I am not aware of any kinematographic analyses of *Sagitta* swimming, although these would make a rewarding comparison with other animals swimming in the oscillatory mode, and behavioural observations are limited to the escape responses evoked by touch and attack responses evoked by near field vibrations. Other sense organs are known in *Sagitta*, apart from the eyes, and these are chiefly found on the head, where there are what appear on histological grounds to be chemoreceptors at the margins of the mouth, and mechanoreceptors on the ventral surface of the head. The role that these may play in locomotor behaviour is unknown.

Oscillatory propulsion of larvaceans

The organization and behaviour of the other group swimming by oscillatory propulsion, the larvaceans, is better known, although here again, kinematographic analyses are lacking. Larvaceans oscillate a flattened tail, as do chaetognaths, but in this case, instead of a fluid-filled body cavity providing a hydrostatic skeleton, the tail is chordate like, with a central notochord flanked by ten pairs of rectangular thin muscle cells, and with a dorsal nerve cord containing motoneuron somata (Fig. 5). Oikopleurid larvaceans have quite a wide repertoire of tail movements (Bone & Mackie, 1975) which they use to enter their houses and to pump them up, and to pump water through the house filtering system (Flood,



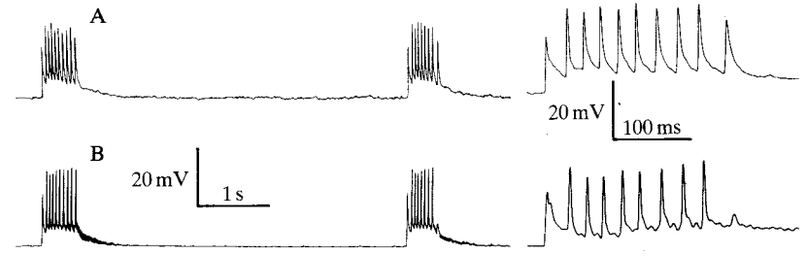


Fig. 6. Electrical activity of caudal muscle cells in *O. dioica*. Simultaneous intracellular records from two caudal muscle cells along trunk. Note similarity of records, but difference in amplitude of last potential of burst in lower trace. (From Bone, 1985).

1978) as well as for swimming. Normally, they sit quietly in the house, oscillating the tail at around 2 Hz (in *O. dioica*) to draw water through the house filters. If disturbed, they leave the house rapidly, and swim around in intermittent bursts, during which tail oscillation in *O. dioica* is around 20 Hz (Fig. 5C), and the animal swims at some 3 cm s^{-1}, equivalent to 15.6 $l.s^{-1}$. These swimming bursts are driven by a caudal ganglion at the base of the tail, which contains some 40–50 cell bodies (Martini, 1909). As in chaetognaths, the muscle cells are electrically coupled (Fig. 5D), although gap junctions have not yet been demonstrated histologically. The caudal muscle cells are cross striated, and receive two separate types of motor innervation (Flood, 1973, 1975; Bone & Mackie, 1975). One of these consists of large corymbiform motor terminals, below which acetylcholinesterase is found (Flood, 1973), the other simple elongate endings which do not show acetylcholinesterase staining. The motoneuron somata providing these terminals lie along the dorsal nerve cord.

This combination of electrical coupling between muscle cells with a dual motor innervation provides a situation that is not easy to analyse in functional terms, but obviously will permit several ways in which a single muscle cell may be activated. During the regular swimming bursts, electrical activity from the caudal muscle cells (Bone, 1985) consists of a

Fig. 5. Locomotor system of *Oikopleura*. (A) *Oikopleura dioica* (tail rotated for clarity) showing notochord (nc), muscle cells (m) and dorsal nerve cord containing caudal ganglion (cg) near tail base. Apart from the house-secreting epithelium (dotted) on the anterior part of the trunk, the entire outer epithelium is excitable. A pair of mechanoreceptors (L) lie on either side of the trunk near the junction of the two types of epithelia. (B) Stereogram of portion of tail showing interdigitated muscle cells (m), notochord (nc) and dorsal nerve cord containing cell bodies which supply corymbiform and elongate motor end plates to the muscle cells. (C) Rhythmic swimming bursts. Regular bursts of swimming in *O. labradoriensis* (upper) and *O. dioica* (lower) recorded with suction electrodes on tail tip. (D) Current pulses injected into one muscle cell (upper) are seen in a second muscle cell further along tail (lower). (Upper record in C from Bone & Mackie, 1975).

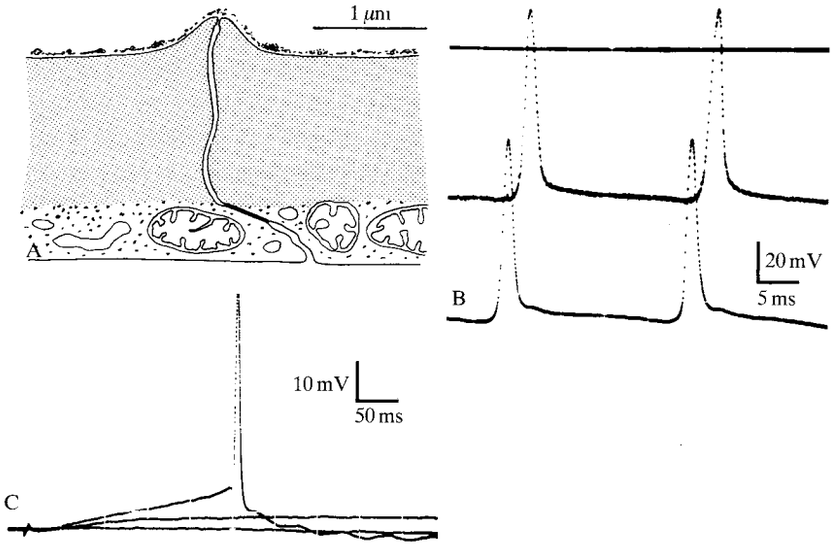


Fig. 7. Properties of external epithelium in *Oikopleura*. (A) Scheme of structure of epithelium in *O. dioica*. Note outer fine-fibril layer (dotted) covering inner mitochondrial zone. The two cells are coupled by gap junctions in the inner zone, and a tight junction is found at the external surface. (B) Propagated action potentials recorded from epithelial cells along tail of *O. longicauda*. (C) Epithelial action potential preceded by receptor potential recorded from epithelial cell where the outer membrane was mechanically stimulated by the recording electrode tip. (B and C from Bone, 1985).

series of rapid potentials around 50 mV, which therefore do not overshoot the 70 mV resting potential (Fig. 6A). Simultaneous records from different muscle cells show very similar activity in each, but often, the posterior cell along the tail shows an 'extra' potential at the end of the burst, which is only seen at much lower amplitude in the anterior cell (Fig. 6B). Perhaps the larger potentials in each cell represent the activity of nerve terminals, and the smaller potential in the anterior cell at the end of the burst corresponds to a potential arising from nerve activity in the posterior cell which is decrementally transmitted along the muscle cell chain via gap junctions. A striking feature of the potentials recorded from the muscle cells is that mechanical stimulation of the outer epithelium of the animal evokes potentials that are significantly larger and may overshoot resting potential (Fig. 6C). During the swimming bursts evoked by mechanical stimulation, in addition to increase in amplitude of the muscle potentials, they also increase in frequency. In the large species, *O. labradoriensis*, for example, the frequency increases from 5 Hz during a normal swimming burst, to 20 Hz in a burst evoked by mechanical stimulation.

The external epithelium in *Oikopleura* is mechanosensitive, and when stimulated mechanically, propagates overshooting action potentials which arise from depolarizing generator potentials provided these reach the threshold value of some 7 mV from resting potentials around 80 mV (Fig. 7B,C). This excitable epithelium covers the whole of the body, apart fom the anterior trunk region which secretes the filtering house, and is linked to the caudal ganglion via two axons arising from cell bodies in the caudal ganglion. These pass to two bristle-bearing mechanoreceptors on either side of the posterior part of the trunk, which were first described

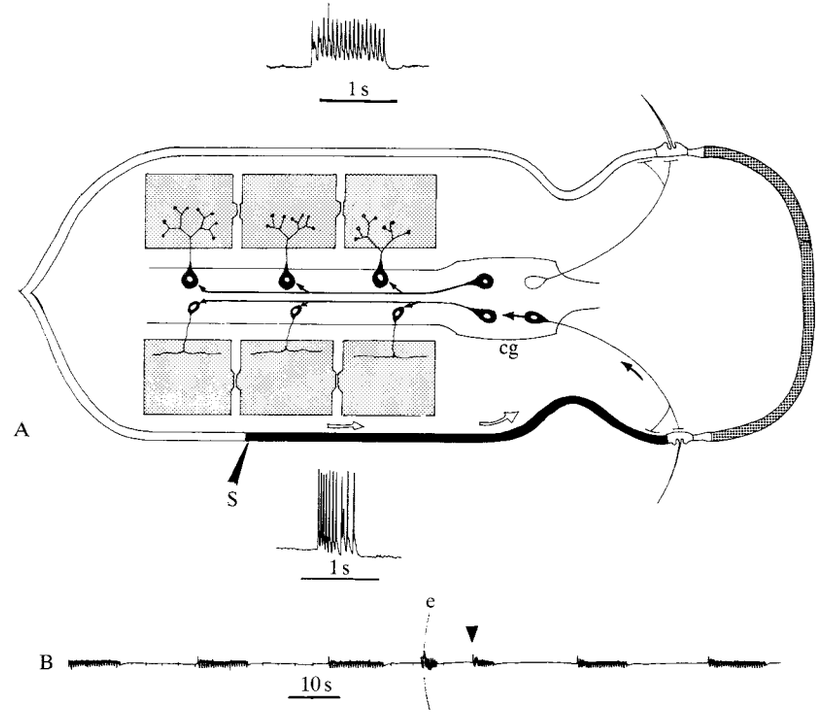


Fig. 8. Epithelial action potentials and locomotion in *Oikopleura*. (A) Schematic diagram illustrating operation of the system. Upper half of diagram, normal rhythmic swimming (intracellular record from caudal muscle cell at top). Lower half of diagram, epithelial action potentials travel along tail from stimulus site (S) and pass to the caudal ganglion (cg) via the axon linking the trunk mechanoreceptor to the ganglion. They then evoke rapid swimming bursts during which amplitude of potentials in caudal muscle cells (below) is larger than during the normal swimming bursts. (B) Suction electrode records caudal muscle activity of normal swimming bursts in *O. labradoriensis* followed by an out of sequence burst evoked by mechanical stimulation which begins with a larger epithelial action potential (e). This is followed by a second out of sequence burst (arrowed) evoked by direct stimulation of the mechanoreceptor bristle. (Intracellular records from Bone, 1985, suction electrode record from Bone & Ryan, 1979).

by Langerhans (1877). Here, the axon branches to form gap junctions with the base of the receptor cell, and with an adjacent epithelial cell, so that input to the caudal ganglion, and thence to the caudal muscle cells is identical whether the receptor itself is stimulated, or any point on the skin is stimulated (Fig. 8). In other words, the outer epithelium extends the field of the receptor cells, and the response evoked is a non-specific escape burst of high-speed swimming.

Apart from the two vibration receptors, *Oikopleura* has a statocyst, and chemoreceptors near the mouth, but nothing is known of the role of either; the statocyst does not seem to be involved in any kind of righting reflex since larvaceans do not appear to adopt any preferred attitude in the water.

Oikopleura operate at Reynolds numbers up to about 150, a region intermediate between that of very small oscillatory swimmers such as sperm, and larger animals like small fish, so that hydrodynamic analysis of their swimming should prove rewarding. It seems likely from preliminary kinematic records, which show large lateral movements of the trunk as the tail oscillates, that efficiency is low, and that swimming is energetically expensive. Since *Oikopleura* normally does not swim but slowly pumps water through its house, high-cost escape swimming can be accepted.

Rapid jet propulsion in hydrozoan medusae and siphonophores

In contrast to the oscillatory swimmers, jet-propelled animals in the plankton have received more attetion, both from the hydrodynamic aspect, and from the design and control of the muscles involved. For medusoid forms, Gladfelter (1973) has provided an interesting comparative analysis of shape and mesogleal properties in a variety of medusae and a diphyid siphonophore, whilst Daniel (1983) has modelled the mechanics and energetics of medusan jet propulsion, and Bone & Trueman (1982) have examined swimming in two siphonophore species from a combination of chamber pressure and kinematic records.

The properties of the neuromuscular systems in such forms have been studied by several workers, chiefly in hydrozoa (see Spencer & Schwab, 1982), which are well adapted for electrical recording, but there is also recent work on scyphozoa and cubozoa (see Passano, 1982). For the pelagic tunicates which swim by jet propulsion, the salps and doliolids, preliminary accounts have been given by Bone & Trueman (1983, 1984).

In both cnidaria and tunicata, some species are adapted for slow continuous cruising, where economy of operation must be paramount; whilst others show adaptations for short-term rapid-escape responses where

maximum speed is more important than economy. We shall examine the independent solutions achieved by the two groups to these two very different requirements, and how each have sometimes reconciled the two.

A fundamental difference between the two phyla is that the jet chamber of the medusoid forms has but a single posterior jet aperture, so that refilling has to be via the same aperture as the propulsive jet, and negative thrust must therefore be generated during refilling. In the tunicates, the jet chamber is provided with an anterior aperture as well as a posterior one, and refilling when the animal is swimming forwards is mainly via the anterior aperture, largely avoiding this negative thrust component of the cycle, as well as allowing the possibility of swimming in either direction by appropriate closure of the valves at each aperture.

Although most medusoid forms swim relatively slowly, rapid short bursts of escape swimming are found in diphyid siphonphores and in some Trachymedusae like *Pantachogon* and *Aglantha*. *Aglantha* is capable of instantaneous velocities of 50 cm s^{-1}, *Chelophyes* up to 30 cm s^{-1} (Fig. 9). A single contraction of *Aglantha* can drive it 8 cm, and Donaldson,

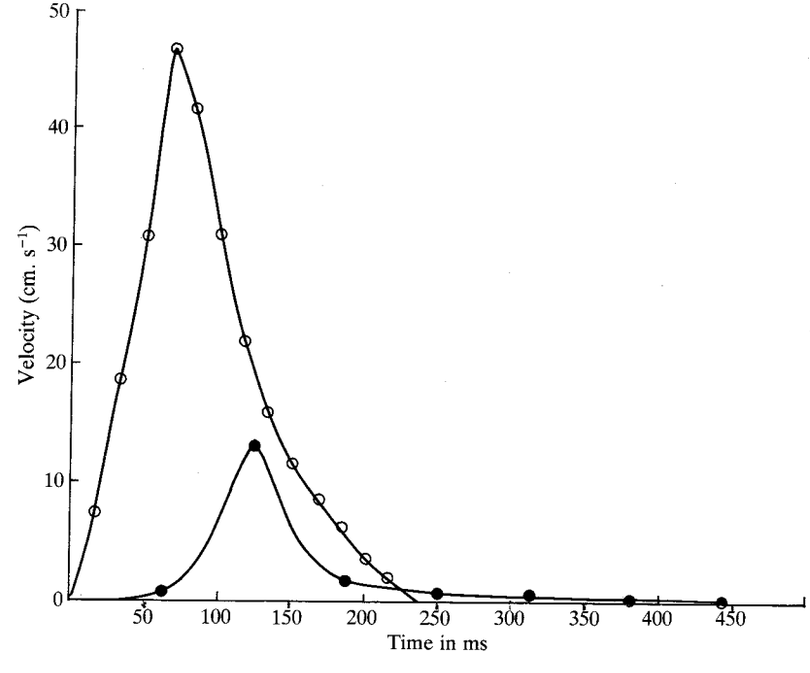


Fig. 9. Instantaneous velocity curves for single jet pulses of *Aglantha* (open circles), and *Chelophyes* (solid circles). *Aglantha* plotted from data in Donaldson et al. (1980).

Mackie & Roberts (1980) have shown that such single jet pulses suffice to break the medusa free from the embrace of the larger *Aequorea* and are indeed effective escape responses. Maximum accelerations during the movements of *Aglantha* are up to $7{\cdot}8\ m\ s^{-2}$; in *Chelophyes* up to $5{\cdot}3\ m\ s^{-2}$.

Aglantha makes up to three jet pulses in succession, of which the first is the most effective, since subsequent pulses begin before the bell has completely refilled and so drive the animal only 40–60 % of the distance it is driven by the first pulse.

The thrust produced during the jet pulse (mu_e) is the product of the mass of water ejected (m) and the velocity of ejection (u_e): evidently if the jet chamber is completely refilled, negative thrust during inhalation will be the product of the same mass and the velocity of inhalation (u_i). Unless u_i is less than u_e, the animal will simply oscillate backwards and forwards and there will be no net forward motion. During several jet pulses, *Aglantha* does reduce m, since the jet chamber is not completely refilled, but u_i is also reduced by increasing the duration of the refilling phase (three to four times the length of the expulsion phase), and by increasing the size of the aperture. During the jet pulse, the velar aperture is reduced by contraction of the velar muscles, which relax during inhalation.

In *Chelophyes*, the escape response is a burst of jet pulses (up to ten or more at frequencies up to 8 Hz) and here, the ratio of the refilling phase of the cycle to the expulsion phase is only 1:1·4, since refilling has to be rapid to permit such a rapid series of jet pulses. Positive thrust exceeds negative thrust in this case almost entirely because the jet aperture is reduced by about 50% during the expulsion phase, during which maximum jet velocity is up to $121\ cm\ s^{-1}$.

In both *Aglantha* and *Chelophyes*, the muscle contracting the jet chamber is a thin sheet of coupled cross-striated myoepithelial cells which propagate action potentials at around $30\ cm\ s^{-1}$. In *Aglantha* these myoepithelial cells do not have internal sarcoplasmic reticular tubules, nor invaginations of the cell membrane equivalent to a T-system, and thus it seems probable that the action potential is a mixed Na^+/Ca^{2+} event or carried by Ca^{2+} alone. In *Chelophyes* however, although an SR is absent, an analogue of the T-system is provided by regular invaginations of the basal membrane (Mackie & Carré, 1983; Chain, Bone & Anderson, 1981). Here, the action potential appears to be carried only by sodium ions, and the T-system analogue has been suggested to be responsible for calcium release during contraction (Bone, 1981). Not unexpectedly, in view of these different arrangements, the action potentials of *Aglantha* are relatively longer lasting events, compared to those of *Chelophyes* (Figs. 10 & 11).

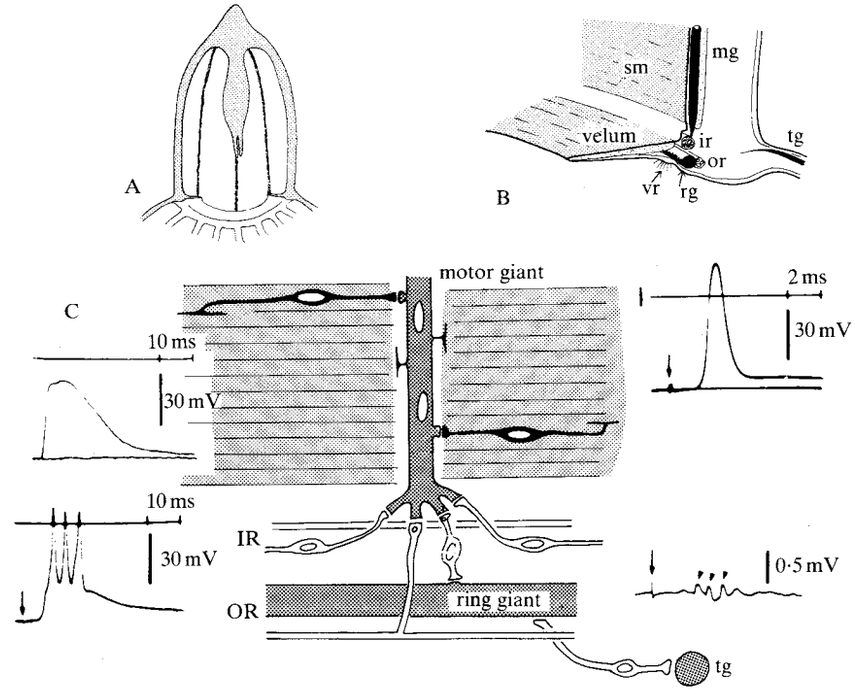


Fig. 10. The organization of the giant axon escape system of *Aglantha*. (A) Section of medusa showing subumbrellar muscle sheet divided by radial canals and radial nerves. (B) Stereogram of bell margin, showing third order motor giant (mg) running up subumbrellar muscle (sm) from inner nerve ring (ir) A ring giant axon (rg) lies in the outer nerve ring (or) and is coupled to tentacle giant axons (tg). Vibration receptors (vr) lie around the base of the velum. (C) schematic diagram of connexions involved in rapid escape response. mg: motor giant, synapsing directly with subumbrellar muscle (sm) and indirectly with the muscle via lateral neurons (ln) coupled to it. The motor giant is coupled to many small neurons in the inner ring (ir), and via chemical synapses to the ring giant (rg) in the outer nerve ring (or). The ring giant is coupled to the tentacle giant (tg). On left: action potential from subumbrellar muscle in high Mg^{2+} seawater (upper) and three spikes in ring giant (lower). On right: action potential from motor giant (upper) and suction electrode record of three spikes in tentacle giant (lower) recorded simultaneously to those in ring giant shown on left. A and B and electrical records in C from Donaldson *et al.* (1980) and Roberts and Mackie (1980); remainder of C based on Weber *et al.*, 1982).

In *Chelophyes* however, remarkably enough, the action potentials change form during the burst, from that shown above, to a much longer potential resembling that of *Aglantha* (and other medusae such as *Polyorchis*, Spencer & Satterlie, 1981). The functional explanation for this change in form is not clear, but as the action potentials lengthen (and increase in amplitude with magnificent overshoots up to 70 mV!) the tension exerted increases and pressures in the jet chamber during successive pulses rise (Fig. 11), so that the first few jet pulses of a burst are

less powerful than the succeeding pulses. Perhaps this allows the animal to withdraw its long fishing stem before maximum escape velocity is reached. In *Aglantha*, the fishing tentacles are much shorter, and there is no danger that they might be damaged by the first powerful contraction of the bell.

The nervous mechanisms controlling these two rapid swimming forms have been examined by Mackie and his colleagues (Roberts & Mackie, 1980; Mackie & Carré, 1983), and are interesting variations on the same basic plan. In *Aglantha*, (Fig. 10) eight large diameter (40 μm) third-order motor giant axons (accompanied by 15–20 smaller (0·3 – 1 μm) axons) run up the subumbrellar sheets from the inner nerve ring at the base of the velum, and make motor synapses with the muscle. Tracer injections of these multinucleate giants show that they give off short lateral branches to the muscle, and are coupled to small motor neurons running laterally across the subumbrellar muscle and innervating it. Since Lucifer yellow injections into the giant axon spread into the lateral motoneurons, but HRP does not, it seems likely that the lateral motoneurons are coupled to the motor giants by gap junctions (Weber, Singla & Kerfoot, 1982). Lucifer yellow injected into the motor giants similarly spreads into the small neurons of the inner nerve ring at the base of the velum indicating gap junction connexions. Axons from the outer nerve ring form chemical synpases with the motor giants; this outer nerve ring contains a single first-order ring giant (up to 24 μm in diameter). There are also smaller (up to 7·8 μm) 'giant' axons along each tentacle coupled to the ring giant (or perhaps branches of it). Fig. 10 shows the arrangement. Roberts & Mackie (1980) found that stimulation which evokes a short burst of spikes in the ring giant is followed by a single spike in each of the motor giants, and by a short identical burst in the tentacle axons (Fig. 10). Stimuli evoking ring giant activity, and escape swimming are water vibrations or mechanical stimuli to the tentacles, velum and bell margin. Numerous ciliated receptors around the bell margin probably mediate these responses.

In slow swimming medusae, the response to strong stimulation is involution of the bell (the crumpling response) which involves an epithelial pathway, but the crumpling response is absent in *Aglantha* and epithelial conduction systems play no part in the escape response.

In *Chelophyes*, although the basic plan of the system is similar, epithelial conduction systems here play an important role. The myoepithelial sheet is innervated only around the bell margin, there are no nerves upon the subumbrellar myoepithelial sheet itself. The inner nerve ring, which innervates the subumbrellar sheet at the bell margin,

consists of a chain of a few bipolar neurons whose axons are only some 2–3 μm in diameter; there are no giant fibres. Some sensory cells with long processes occur in the inner ring, these are presumably mechanoreceptors; the margin of the bell is very sensitive to light touch. The outer nerve ring also contains mechanoreceptors, and numerous epithelial cells of a special type which are richly innervated. Again, giant fibres are absent.

The ectodermal epithelium of the nectophore is excitable, and propa-

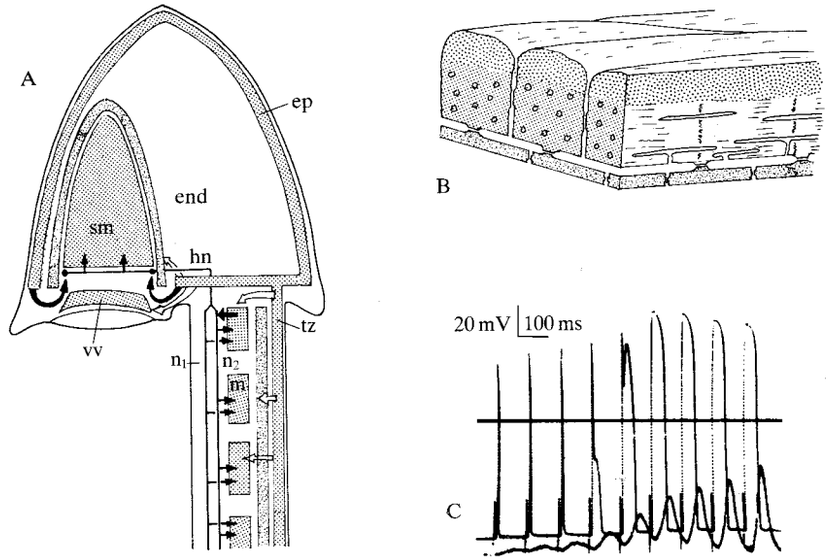


Fig. 11. The locomotor system in *Chelophyes*. (A) Organization of anterior nectophore and stem. Epithelial action potentials (open arrows) in the exumbrellar epithelium (ep) pass to the nectophore endoderm (end) which is coupled to the ectoderm at the bell margin, and to the radial muscles of the velum (rv). The nerve ring at the base of the nectophore is connected with the ectodermal epithelium by epithelio-neural synapses (solid arrows) as the two nerves (n1 and n2) of the stem. The latter connect with the nerve ring by a hydroecial nerve (hn). The subumbrellar swimming muscle (sm) is innervated by the nerve ring only at the nectophore base. In the stem, epithelial action potentials pass to the endoderm coupled to the ectoderm, and in a transitional zone near the base (tz) drive n1 and n2 which innervate the ectodermal stem muscles (m). Activity in these nerves if sufficiently large, evokes action potentials in the stem ectoderm at the transitional zone and thence drives swimming. (B) diagram showing arrangement of swimming subumbrellar muscle. The muscle cells have an outer mitochondrial zone (coarse stipple) and an inner myofilament zone containing regularly arranged tubular invaginations of the basal membrane. The cells are coupled to each other and to the underlying endoderm. c: burst of stimulated action potentials from subumbrellar muscle showing increase in tension (bottom trace) during successive potentials associated with increasing duration of action potential as a plateau phase develops. (A) redrawn from Mackie & Carré, 1982; (B) redrawn from Chain *et al.*, 1981; (C) from Bone, 1981).

gates impulses at 50 cm s^{-1}, when stimulated mechanically anywhere on its surface, these action potentials pass around the nectophore to reach the outer nerve ring, and evoke nervous activity which passes to the inner ring and activates the subumbrellar muscle sheet.

Rapid escape swimming bursts are also triggered by touching the velum and nectophore margin; presumably here the inner nerve ring may be directly stimulated via its sensory cells, as well as indirectly via the sensory cells of the outer nerve ring.

Fig. 11 summarizes the rapid escape system of the anterior nectophore, in comparison with that of *Aglantha* (Fig. 10). The situation in the siphonophore is however, more complex than has so far been described, because there is in addition a smaller posterior nectophore, and a long muscular trailing stem. Both epithelial and nervous pathways link the excitable epithelia of the anterior nectophore with two large axons (10 μm) running down the stem, which innervate the smooth myocytes in the stem; there is also a superficial plexus of small neurons. The nerve

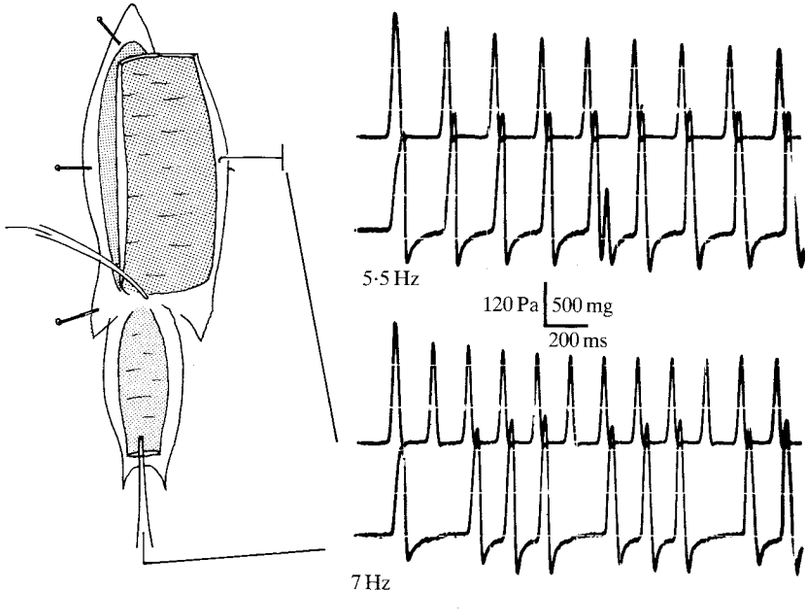


Fig. 12. Co-ordination between the anterior and posterior nectophores in *Chelophyes*. The anterior bell is pinned out and attached to a strain gauge, a suction electrode stimulates the nerve ring at its base. Pressure pulses from the intact posterior nectophore are recorded by a catheter placed in the velar aperture. At a stimulation frequency of 5·5 Hz (upper records) pressure pulses from the posterior nectophore (lower trace) follow contractions of the subumbrellar muscle of the anterior nectophore. At 7 Hz, the posterior nectophore is unable to follow 1 for 1 for more than a few contractions.

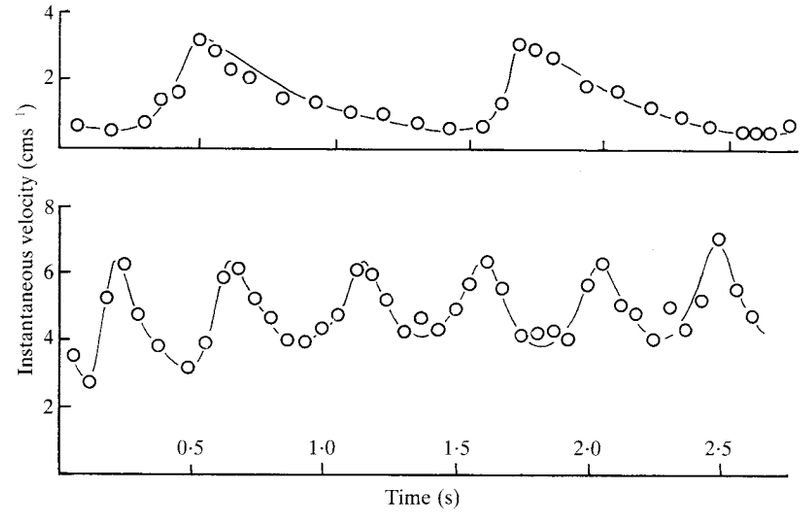


Fig. 13. Slow swimming in *Chelophyes* with the smaller posterior nectophore alone active, and in *Abylopsis* (lower) using the larger posterior nectophore. (From Bone & Trueman, 1982).

rings of the posterior nectophore are not directly connected to the nerve fibres within the stem, but the small nerve plexus synapses with the ectodermal epithelium at the apical peduncle of the posterior nectophore, and it is probable that these neuroepithelial synapses drive epithelial action potentials (such synapses are also known in salps) and the posterior nectophore, like the anterior, is stimulated via conducting epithelia.

During escape responses, when both anterior and posterior nectophores contract, maximum instantaneous swimming velocity is 25% higher than when the anterior nectophore alone contracts. In pinned-out preparations, contraction of the two is closely coupled at frequencies below 4·5 Hz when the preparation is stimulated on the velum of the anterior nectophore, but the posterior nectophore fails to follow at higher frequencies (Fig. 12). The close coupling at lower frequencies suggests a physiological mechanism, but as Mackie & Carré point out, it is possible that the posterior nectophore is simply stimulated mechanically by the contraction of the anterior.

Chelophyes and *Aglantha* are evidently designs specialized for rapid short-term escape swimming, and are both elongate (*Chelophyes* has a fineness ratio of 3–4, *Aglantha* somewhat less). Both however are also able to swim slowly. *Chelophyes* does so by using the smaller posterior nectophore alone, contracting at a frequency below 1 Hz. During such slow swimming, maximum instantaneous velocities are 3·5 cm s^{-1}

(Fig. 13A). Here, the same muscle sheet is used as in escape swimming, but at this low contraction frequency, the action potentials do not develop the maximum plateaus seen at higher frequency, and hence contract less forcefully, producing less powerful jets. *Aglantha* also uses the same muscle sheet for slow swimming as for rapid swimming, but in contrast to *Chelophyes*, electrical events in the muscle sheet during slow swimming are not the same as they are in escape swimming. During slow swimming, extracellular records show that propagated spikes (as are found during escape swimming) do not occur; it seems that the subumbrellar muscle sheet receives a dual innervation, and that the slow nerve system is incapable of generating propagated muscle spikes.

This is an interesting situation, paralleling the gradation mechanism in crustacean muscle, and it certainly appears that the rapid escape control system of *Aglantha* with its giant motoneurons is a specialization added on top of the usual single medusan slow system, as Mackie (1980) suggests. However, in *Polyorchis* a slow swimming hydrozoan medusa, the subumbrellar muscle sheet propagates muscle action potentials, although there is only a single motor innervation.

It would be interesting to examine slow muscle responses in *Aglantha* with intracellular electrodes, as Mackie (1968) has done for the dual innervated muscle of the stem of *Nanomia*.

Table 1.

Organism	Jet cycles	Mean forward velocity ($cm\,s^{-1}$)	Work ($J.kg^{-1}$) (underlined values for organisms designed for maximum escape velocity)
Siphonophora			
Chelophyes	30	16·0	28·2
Abylopsis	60	3·0	2·86
Tunicata			
Doliolum			
small	50	0·5	6·16
large	25	8·0	5·58
Salpa fusiformis			
* small blastozooid	52	3·8	2·5
† medium blastozooid	70	1·6	1·07
* large oozooid	30	6·6	0·55
blastozooid chain (16 zooids, 12 active)	400	6·2	1·15

* Animals operating at maximum performance.
† Estimated cruising operation.
Modified from Bone & Trueman (1984).

Slow swimming by jet propulsion in hydrozoan medusae and siphonophores

Most medusoid forms swim much more slowly than do *Aglantha* and *Chelophyes* during their escape responses. The slow swimming siphonophore *Abylopsis* for example swims at $3\,cm\,s^{-1}$ during which it achieves maximum instantaneous velocities of $8\,cm\,s^{-1}$ (Fig. 13B). Similar values were found by Gladfelter (1973) for a range of hydrozoan medusae, mean velocities being from $1·2 - 7·5\,cm\,s^{-1}$; maximum instan-

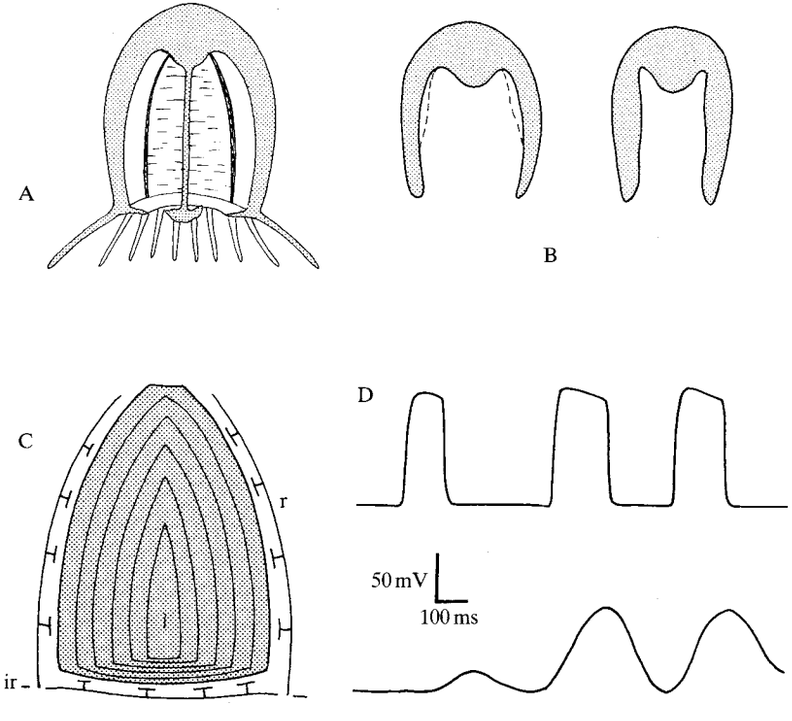


Fig. 14. The locomotor system in *Polyorchis*. (A) The sub-umbrellar sheet is divided into quadrants by radial canals and radial nerves (r). (B) Sections of *Polyorchis* during contraction cycle. On left, fully expanded (stippled) dotted lines showing beginning of contraction at apex of jet chamber. On right, fully contracted at end of jet pulse. (C) Invasion of one quadrant of subumbrellar muscle sheet by action potentials in sheet propagating at different velocities in radial and circumferential directions from neuromuscular junctions with inner ring nerve (ir) and radial nerves (r). Successive positions of wavefront outlined at 10 ms intervals. (D) Change in shape of action potentials and increase in tension with successive potentials (cf. Fig. 11,C). (A and B redrawn from Gladfelter, 1972; C, redrawn from Spencer, 1982; D, from Spencer & Satterlie, 1981).

taneous velocities being up to 11·8 cm s^{-1}. We should expect that this sustained slow swimming behaviour should be less costly than the escape responses of the rapid forms, and analysis of the pressure pulses of *Abylopsis* (Bone & Trueman, 1982) compared with those of *Chelophyes* (in the way outlined later (section 6)) indicates that *Abylopsis* performs about half the work during each jet cycle than does *Chelophyes*, although it expels about five times as much water (Table 1).

Similar figures are not available for hydrozoan medusae, although the valuable theoretical analysis of the mechanics and energetics of medusan jet propulsion by Daniel (1983) provides the basis for future comparisons.

Although some slow-swimming hydrozoan medusae (e.g. *Stomatoca*, Mackie & Singla, 1975; Mackie, 1975) show less complex swimming behaviour than others, such as *Polyorchis* (Gladfelter, 1972), the organization of their swimming muscles and neural control systems is probably similar in all. The subumbrellar muscle sheet is divided into segments by the radial canals, and innervated both by axons running up in radial nerves, and from the inner nerve ring around the bell margin (Singla, 1978; Spencer, 1979) (Fig. 14). In *Polyorchis*, Gladfelter's (1972) kinematic analysis of swimming showed that the bell contracted in such a way as to expel water progressively from the apex to the orifice, and Spencer (1982) pointed out that this could be simply achieved as a result of the difference in conduction velocity across the subumbrellar muscle segments in different directions. He found (Spencer, 1979) that conduction was approximately three times as fast in the circular direction (along the muscle cell axes) as in the radial direction, so that contraction in each segment of the subumbrellar muscle efficiently pushed water out of the velar aperture (Fig. 14). In *Abylopsis*, conduction velocity across the unsegmented subumbrellar myoepithelium is probably uniform in all directions, as it is in *Chelophyes*, and since the sheet is innervated only around the velar margin (see Fig. 11), the jet chamber does not contract 'peristaltically'.

Perhaps the most interesting locomotor adaptation of *Polyorchis* is that the action potential does not simply trigger contraction of the swimming muscle, but, as Spencer & Satterlie (1981) point out, it also carries information about the required duration of contraction! These authors found that the plateaued square-wave-form action potentials changed in length (by prolongation of the plateau) not only during successive action potentials of a swimming burst (Fig. 14), but also according to the size of the medusa, so that small medusae had short action potentials and larger medusae, larger potentials (Fig. 15). Change in action potential duration (and concomitant increase in tension in the subumbrellar muscle) during

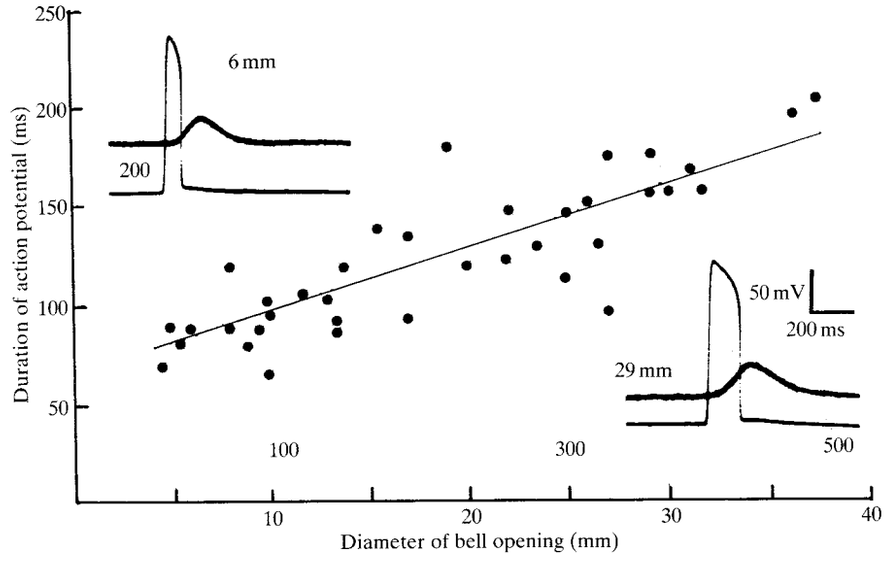


Fig. 15. Change in action potential duration with size in *Polyorchis*. Inset: stimulated action potentials and contractions in a medusa of bell opening 6 mm (left) and 29 mm (right). Scale bars: 50 mV, 200 ms. (From Spencer & Satterlie, 1981).

swimming bursts) is shown in a similar but much more striking manner in the siphonophore *Chelophyes*, but changes related to change in scale are unique. It seems reasonable to suppose as Spencer and Satterlie suggest, that larger jellyfish need longer contraction durations to eject water than do smaller, and that this is achieved by increasing action potential duration. Both Na^+ and Ca^{2++} are involved in the action potential, so that if the contractile process depends in part upon extracellular Ca^{2+} and Ca^{2+} enters during the plateau phase, then increasing action potential duration will increase contraction duration. Further investigations of this interesting situation are obviously desirable, and it seems probable that it may prove to be general in medusoid forms.

It is rather disappointing that neither slow-swimming medusae nor salps seem to increase their swimming efficiency by pulsing appropriately to induce vortex ring interaction in their wakes, in the way suggested by Weihs (1977). At least this seems true for hydromedusae (Daniel, 1983) and salps; perhaps scyphomedusae or cubomedusae are more ingenious.

Rapid jet propulsion in *Doliolum*

The two groups of pelagic tunicates that swim by jet propulsion are

quite differently adapted, for whilst salps swim slowly and continuously filtering food particles from the inhaled water, doliolids filter feed with an elaborate ciliated gill apparatus and give one or two rapid contractions at long irregular intervals or when they are stimulated. The apparently spontaneous contractions at irregular intervals shoot the animal upwards in the water column (they sink very slowly in an oblique attitude), a single contraction in an animal 1·5 mm long can drive it forwards 45 mm or more (Fedele, 1923). Similar contractions evoked by water vibrations or mechanical stimuli are evidently escape responses; depending upon the stimulus site the animal moves rapidly forwards or backwards.

In contrast, salps when stimulated mechanically merely accelerate or reverse the normal swimming rhythm; these reactions are much less effective escape responses.

Although doliolids are small animals, it has proven possible to obtain kinematic records of their swimming responses, as well as records of chamber pressures and intracellular records from the muscle bands. The animals are barrel shaped (Fig. 16) encircled by eight or nine thin muscle hoops; as in medusoid forms, restoration of body shape after contraction is brought about by elastic energy stored in the thin tunic. Both anterior

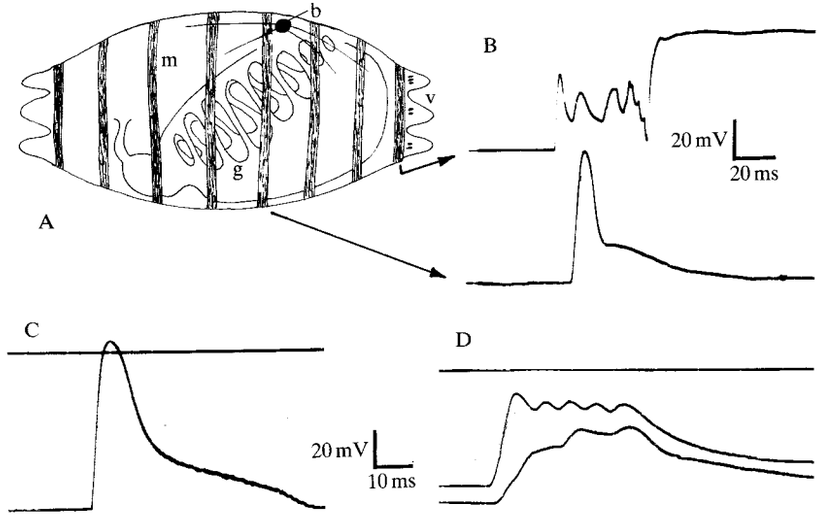


Fig. 16. The locomotor system in *Doliolum*. (A) diagram of animal showing muscle bands encircling animal (m), dorsal brain (b), anterior (right) and posterior flap valves (v), and gill apparatus (g). (B) Simultaneous records from anterior lip muscle band (upper) and locomotor muscle band (lower) showing sustained activity in lip band and single spike-like potential in locomotor band. (C and D) Electrical events in locomotor muscle bands associated with single contraction (C) and sustained contraction (D). In D simultaneous records from two regions of muscle band. (Modified from Bone & Trueman, 1984).

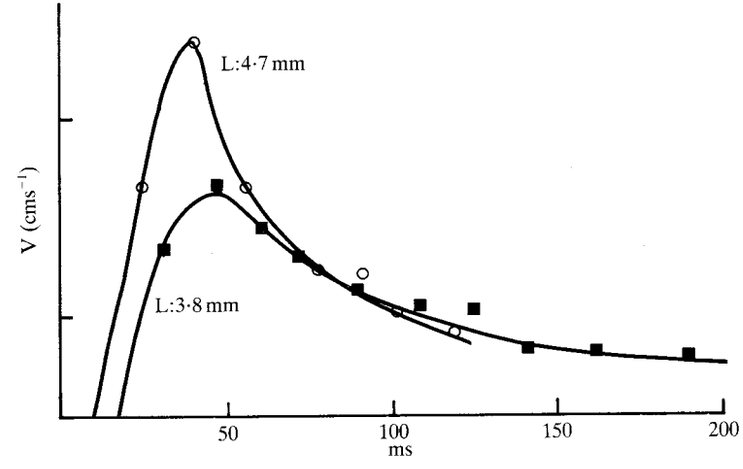


Fig. 17. Instantaneous velocity curves for single jet pulses in *Doliolum* of different sizes. (From Bone & Trueman, 1984).

and posterior apertures are provided with flap valves (Fig. 16) and forward or reverse locomotion is brought about by a sustained contraction of the anterior or posterior band, accompanied by a rapid contraction of the other muscle bands (around 8·5 L/s^{-1} at 17 °C). Single contractions produce instantaneous velocities up to 30 $cm\,s^{-1}$. (Fig. 17) with maximum accelerations up to 550 $cm\,s^{-2}$. The jet pulses are rapid (50 ms or so), chamber pressures are related to the size of the animal and can exceed 500 Pa, producing efflux velocities up to 80 $cm\,s^{-1}$ negative pressure during inhalation after the single jet pulse are only −20 Pa or less, reflecting the fact that water is inhaled both through the anterior as well as the posterior aperture, as well as a reduced exhalant aperture size during the jet pulse.

Preliminary investigation of the muscle bands encircling the jet chamber has shown that they are multiply innervated, and that contraction involves decremental spike-like potentials of characteristic form (Fig. 16). Since the obliquely striated muscle fibres in the bands are very small (3 μm wide by 40 μm deep), and apparently have no internal tubular systems, it is probable that the potentials seen in Fig. 16 are mixed Na^{+}–Ca^{2+} events, but their ionic basis remains to be studied.

The continued contraction of the anterior or posterior muscle bands during the jet pulse involves a train of similar events (Fig. 16), such tetani are also sometimes seen in the locomotor muscle bands if the animal remains contracted for a short time as Fedele (1923) occasionally observed.

It might be expected in view of the synchrony required for the contrac-

tion of the locomotor muscle bands during the jet pulse that their motoneurons might be electrically coupled, but no gap junctions have been observed in the brain.

Doliolid jet propulsion is obviously adapted for rapid escape movements (as in *Aglantha* a stimulus usually evokes only a single jet pulse), and it would be expected therefore that the system is specialized for maximum power output rather than economy. That this is so can be inferred from estimates of the work done during the jet pulse, obtained in the following way from records of the pressure pulses. Since volume changes follow pressure changes, provided the aperture remains constant during the pulse, the work done is given by the product of the pressure pulse and its integral (the volume change). A similar estimate of the work done during refilling can be obtained from records of the negative pressure pulse during inhalation, and if it is assumed that the resilience of the test material (whose expansion in all cases is solely responsible for the refilling of the jet chamber) remains at 100%, then the total work done during the jet cycle by the locomotor muscles overcoming test elasticity and expelling the jet is simply the sum of the work calculated from the two phases of the jet cycle (Fig. 18).

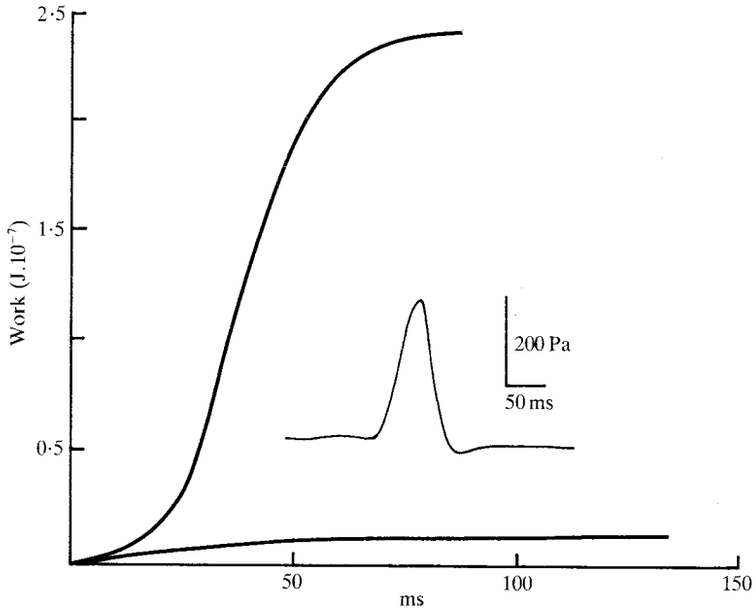


Fig. 18. Work performed by 2·1 mm *Doliolum* to expel jet (upper trace) and to overcome test elasticity (lower) during jet pulse, obtained as outlined in text. Inset: pressure pulse analysed. (From Bone & Trueman, 1984).

In order to compare the cost of locomotion in different animals which use jet propulsion for slow cruising and for short rapid bursts of escape swimming (Table 1) we may imagine that the latter could be stimulated to cover 1m at the same rate as during their much shorter escape swimming bursts. Table 1 shows that both *Chelophyes* and *Doliolum*, which are designed for rapid escape responses operate very much less economically than the cruising salps and *Abylopsis*.

Cruising jet propulsion in salps

Only one species, *Salpa fusiformis*, has been studied in detail by the same methods used for *Doliolum* (Bone & Trueman, 1983), but so far as known, all species have the same continuous rhythmical slow swimming pattern. In *S. fusiformis*, this slow forwards swimming results from rhythmic jet pulses at frequencies between 0·5 and 2 Hz, which give oscillatory instantaneous velocities up to 12·5 cm s^{-1}, and mean forward velocities of 1·3 – 6·6 cm s^{-1} (Fig. 19).

Slow continuous swimming of this sort is obviously very different to the

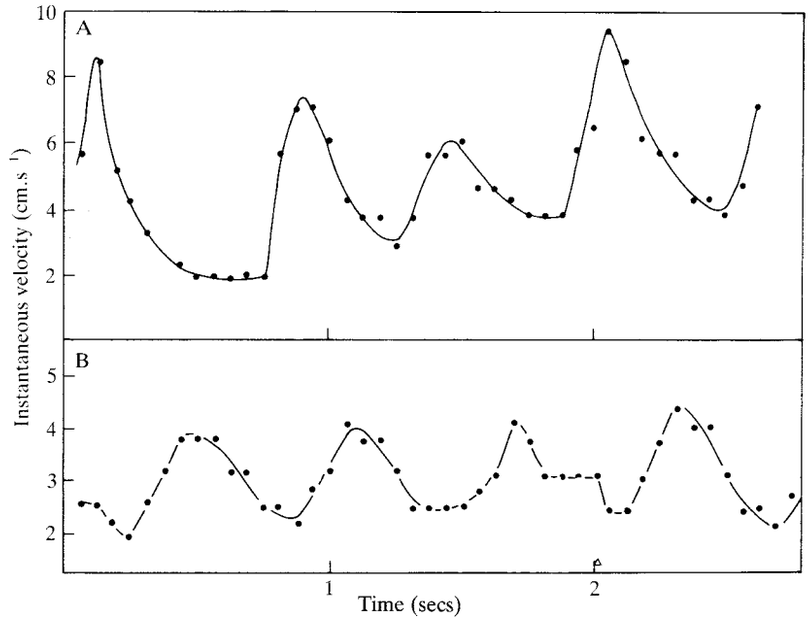


Fig. 19. Instantaneous velocity curves for slow sustained swimming by *S. fusiformis*. Oozooid (A) and blastozooid (B). (From Bone & Trueman, 1983).

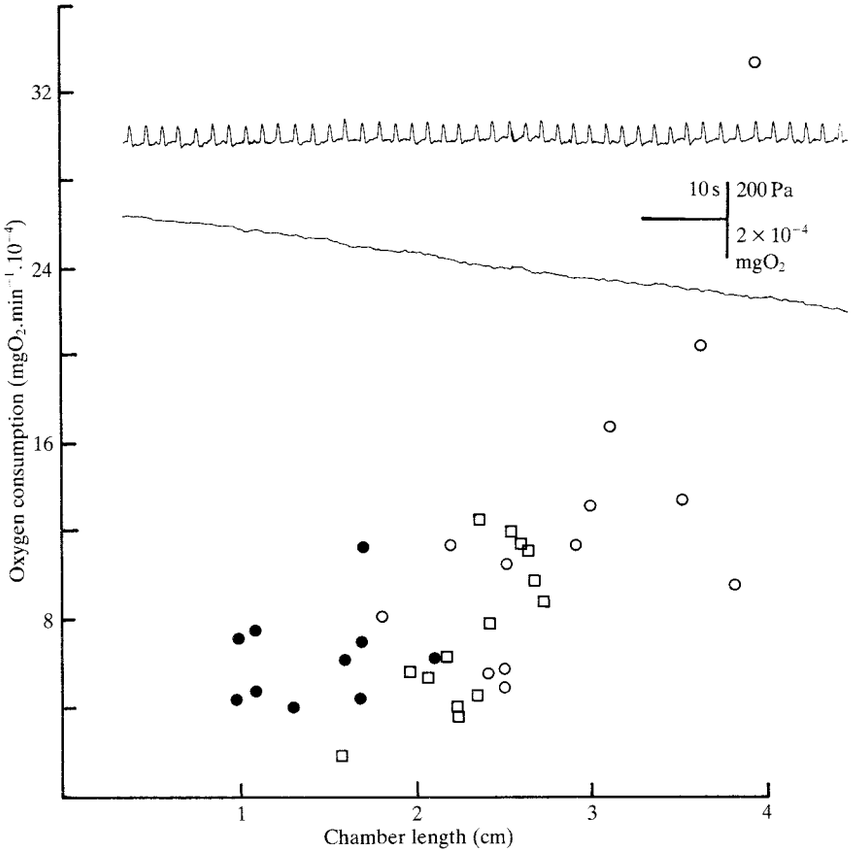


Fig. 20. Oxygen consumption of individuals of *S. fusiformis* swimming in a respirometer chamber. Oozooids: open symbols; blastozooids; solid circles. (From Trueman *et al.*, 1984).

rapid escape responses of doliolids, and the salp locomotor system is designed on a different basis. The thrust produced is the product of the mass ejected per second and its exhalant velocity (mu), but since the power needed to accelerate the fluid ejected is the rate at which kinetic energy is given to it ($0{\cdot}5\,mu^2/s$), it is more economical to eject a large mass of fluid at low velocity via a large aperture. Moreover, the efficiency of momentum transfer between the exhaled jet and the ambient water rises as the jet velocity approaches the forward velocity of the animal. Maximum economy therefore requires that the salp should emit large-diameter low-velocity jets during the jet pulse, and this is (not unexpectedly) what they do. Chamber pressures are relatively low (maximum values being only 45–100 Pa), the jet pulse is long (250–300 ms), and

calculated mean jet velocities are between 18·5 and 33·5 $cm\,s^{-1}$. These values were obtained from salps tethered in small dishes, where they were probably stimulated to pulse in a way corresponding to rapid continuous cruising, rather than the slower more economical normal cruising whilst they are filter feeding. Unfortunately, the animals are so delicate that it is not possible to measure chamber pressures in free-swimming animals using indwelling pressure catheters. Nevertheless, even the values obtained under experimental conditions indicate that salps operate economically; a similar analysis of the pressure pulse records to that in *Doliolum* showed that the work performed during each jet cycle ranged from 4·5 *F* $10{\cdot}65 \times 10^{-5}$ J, and to cover a metre, salps perform 0·55 – 2·5 J/kg body weight (Table 1), about half the doliolid value.

Results from oxygen consumption studies (Trueman, Bone & Brac-

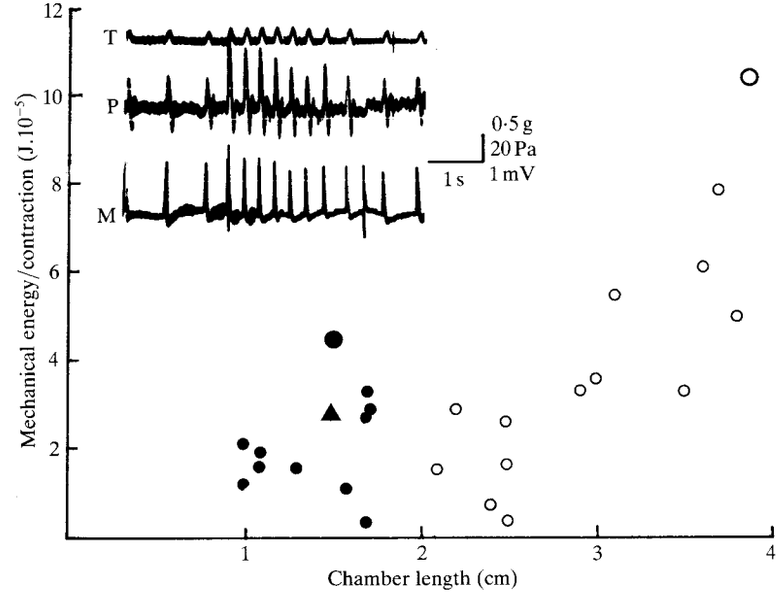


Fig. 21. Work performed during single jet cycles of oozooids (open circles) and blastozooids (solid circles) of *S. fusiformis* based on oxygen consumption data. The larger circles show work performed during single cycles at maximum performance (calculated from analysis of the pressure pulses). The triangle shows work performed similarly calculated for cruising performance.

Inset: acceleration escape response of tethered oozooid of *S. fusiformis* showing abrupt change in frequency and amplitude of pressure pulses (P) and tension (T). Compound muscle potentials (m) recorded from a muscle band of the rear lips show less obvious amplitude changes, and this suction electrode also records an epithelial action potential at the beginning of stimulation (arrow) as well as at the end of the burst of accelerated swimming. (Modified from Trueman *et al.*, 1984).

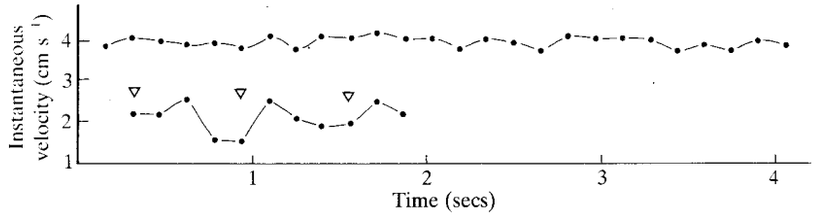


Fig. 22. Instantaneous velocity curves for the same 13-member chain of blastozooids when all zooids were active (upper), and when only a single zooid was active, showing flattening of curve due to lack of co-ordination between contractions of different zooids. (From Bone & Trueman, 1983).

conot, 1984) of salps swimming quietly in a respirometer chamber (Fig. 20) accord with the view that the salps tethered in small Petri dishes were operating above their normal slow rate, for the work they performed in the respirometer chamber (calculated assuming 20% efficiency of conversion of chemical to mechanical energy in the muscles) was half or less than that calculated from analysis of the pressure pulses in rapid cruising (Fig. 21).

As in doliolids, salp muscles contract synchronously, and are multiply innervated by nerves radiating from the brain, they do not propagate action potentials. Bursts of potentials in motoneuron axons evoke summating compound muscle potentials, whose size depends upon stimulation frequency and upon the distance of the recording electrode from an innervated site; salps grade their swimming not only by changing jet pulse frequency, but also by varying the contraction of the locomotor muscle fibres which are relatively slow, contracting at $1{\cdot}5\ l\ s^{-1}$, less than 1/5th the speed of doliolid fibres. Escape reactions involve the same system, but salps are unable to swim very rapidly, and can only increase chamber pressures and cycle frequency by relatively small amounts, perhaps doubling their normal slow cruising velocity for a few seconds before returning to the normal rate (Fig. 21, inset).

Like medusae, solitary salps show oscillations of forward velocity as a result of the intermittent jet propulsion system. Acceleration and decelerations of this kind are less efficient than operation at constant forward velocity as they result in drag increases. The blastozooid generation in *S. fusiformis* normally consists of a long chain of linked individuals aligned with their long axes along the chain. Since, when cruising along undisturbed, the jet pulses of the individual zooids along the chain are not co-ordinated, although they cycle at approximately the same rate, the forward velocity of the chain shows only minor oscillations (Fig. 22). Partly for this reason perhaps, the blastozooids are linked in chains,

where they swim more efficiently than if separated. It is interesting that Gladfelter (1973) found that in the siphonophore *Diphyes* contraction of the two linked nectophores was staggered, so smoothing the forward velocity curve, no doubt for the same reason. Curiously, no evidence for this was found for the related *Chelophyes*, where both nectophores seem normally to contract together (see Fig. 12).

Conclusions

Although the animals discussed are on the whole rather delicate and quite small, and above all are only available for study at certain favoured marine laboratories where plankton can be collected in good condition close to the shore, the past decade has produced a lot of information about their locomotor systems. The discovery and exploitation of suitable nerve muscle preparations in medusoid forms and the beginnings of intracellular recording from chaetognaths and tunicates have advanced our knowledge of the control systems in locomotion, whilst kinematic studies and theoretical analyses have in the same period allowed some estimates of locomotor efficiency and economics, at least for jet-propelled forms. It is unfortunate that no kinematic analyses for oscillatory swimmers have been made, so that comparisons between the two methods of generating thrust (see Alexander, 1978) are not yet possible.

Perhaps the least surprising feature to emerge from this survey is that different medusoid forms, whatever their taxonomic position, are specialized either for rapid swimming, or for slow cruising; in a few forms only are the locomotor systems capable of both kinds of activity. In most hydromedusae for instance, the response to a strong stimulus is 'crumpling', mediated by the excitable epithelium covering the bell, which causes the medusa to curl inwards, only in *Aglantha* is this response absent, and strong stimuli evoke rapid escape swimming, although the same muscle sheet is normally employed as it is in other hydromedusae for slow swimming. To evoke slow and fast responses from the same muscle sheet *Aglantha* apparently has evolved a dual motor innervation, and this situation seems to have arisen also in larvaceans for the same purpose. But in most forms, there is only a single type of response from the muscle, and a single motor innervation; gradation being brought about centrally by changing the discharge frequency of motoneurons (salps) or the number of motoneurons involved (chaetognaths, doliolids). In some medusoid forms, appropriate changes in muscle contraction as the animal increases in size (*Polyorchis*) or during a swimming burst (*Chelophyes*) result from changes in action

potential form, a peripheral mechanism not yet known in other animals. Finally, only a few locomotor adaptations in a few animals have been touched upon here; there is no question but that other groups of gelatinous animals in the plankton offer fascinating material for neurophysiologists interested in locomotor behaviour; although in medusae progress has been made in the analysis of the central pattern generators driving locomotor activity, it is perhaps here that we can expect most progress in other forms.

To zoologists familiar with rhythmic activity in other animals, it may seem strange that the role of proprioceptive input has not been mentioned, but no evidence exists for proprioceptors in any of the forms discussed; perhaps some neurons themselves may be stretch sensitive in some forms.

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