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Jet propulsion in salps (Tunicata: Thaliacea)

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(With 14 figures in the text)

This paper describes the locomotion of salps by jet propulsion, from a combination of measurements of chamber pressures, static thrust, and electromyographic activity, with kinematic records of free-swimming and tethered salps. From such measurements, estimates are made of the thrust exerted, the drag incurred, and the work performed by single salps, and by chains of linked individuals. It is concluded that salp jet propulsion is a more economical process than is jet propulsion in other animals.

Contents

Introduction

The pelagic salps and the smaller doliolids are unique amongst animals using jet propulsion for locomotion, since they swim forwards by inhaling water into the jet chamber mainly through an anterior aperture, expelling it via a second posterior aperture. Other jet-propelled animals, such as medusae or siphonophores (Gladfelter, 1972; Bone & Trueman, 1982) refill the jet chamber by the same posterior aperture through which the propulsive jet emerges. One consequence of the unique salp design is that by appropriate changes in the time of closure of the anterior and posterior apertures, they are able to swim backwards as well as forwards. In addition, the apertures of salps are relatively large, and since the locomotor

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muscle bands, which decrease the volume of the jet chamber, contract slowly, chamber pressures and exhalant jet velocities are presumably low.

These considerations suggest that jet propulsion in salps is likely to be a more economical process than in other animals, and this is indeed the case, as is shown in this paper.

Salps show a wide repertoire of locomotor behaviour, for as well as slow forward swimming, they can accelerate, reverse, or stop swimming altogether when appropriately stimulated (Mackie & Bone, 1977; Anderson & Bone, 1980). Not only this, but in addition, their life cycle shows a striking alternation of generations between the solitary asexual oozooid stage, and the sexual blastozooid stage where many individuals may be linked to form a long chain, or may become detached to swim individually. Salp locomotion thus offers interesting problems, which heretofore have received little attention. The locomotor behaviour of both solitary and linked salps has been examined by a combination of kinematic recording with records of chamber pressure, static thrust, and muscle activity.

Material and methods

Most of our observations were made upon oozooids and blastozooids of *Salpa fusiformis* (Cuvier) collected from the surface waters of the Rade de Villefranche either in plankton nets or dipnets, during March and April between 1979 and 1982. Some observations were made for comparison upon the larger *Pegea confederata* (Forskål), and upon the very large *Salpa maxima* Forskål.

Chamber pressures were measured with a Millar Instruments microtip pressure transducer fitted with a short polyethylene catheter tip; static thrust with a strain gauge (Dynamometer UF 1 or Devices type ST 01) attached to the rear of the test with a hook made from a long stainless steel pin; and muscle electrical activity by fine polyethylene suction electrodes placed on the test surface above the muscle bands. The delay between muscle electrical activity and contraction was examined in salps opened and pinned to Sylgard in such a way as to permit simultaneous recording of muscle tension and electrical activity.

Transducer and electrode outputs led to a Tektronix 5103 storage oscilloscope and thence to a Gould Brush 220 pen recorder. Kinematic records of free-swimming salps in large crystallizing dishes were taken with a Bolex or Beaulieu 16 mm camera, usually at 16 frames s. Dried milk suspensions were sometimes injected into the jet chamber of placed in the inhalant stream to visualize flows and apertures and changes in chamber dimensions during the jet cycle; such experiments were mainly carried out on salps tethered to lead anchors in small dishes, where simultaneous records of chamber pressures and changes in jet chamber dimensions could be obtained. Dead drag measurements were made upon anaesthetized individuals and blastozooid chains weighted with small lead weights and photographed when they reached terminal velocity sinking in large aquaria. The films were analysed with a Photoptical data analyser model 224A.

The chief difficulty with these methods of investigation was that it unfortunately proved impossible to record chamber pressures from free-swimming salps; salps are delicate animals and could not swim normally when attached to the relatively inflexible pressure probe. We have therefore been obliged to assume that the maximum swimming performances observed kinematically resulted from the maximum chamber pressures recorded from the same or similar individuals when tethered, and have not been able to make quantitative observations on cruising locomotion.

Observations

The organization of the locomotor system in ***Salpa fusiformis***

The oozooid and blastozooid stages are rather different in form, and have different locomotor capabilities, but both are essentially similar. The cylindrical jet chamber is partially

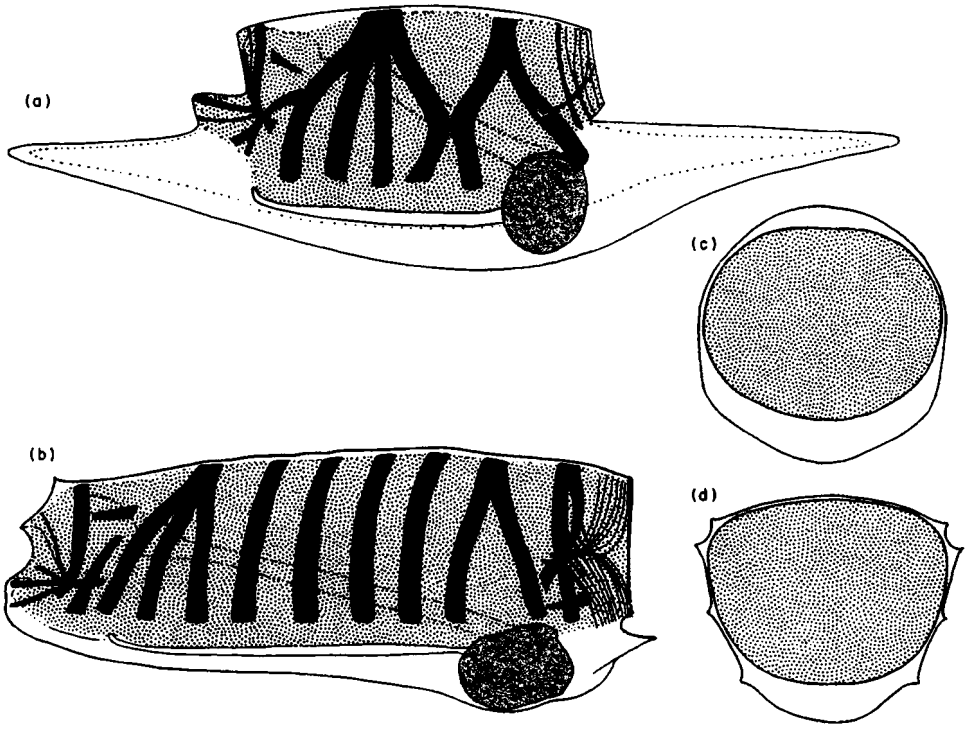

FIG. 1.(a) Side view of blastozooid; (b) side view of oozooid; (c) mid-section of blastozooid; (d) mid-section of oozooid. Side views (anterior to left) and mid-sections of blastozooid (upper) and oozooid of *S. fusiformis*. Muscle bands: black, visceral mass: fine stipple; jet chamber: coarse stipple. Note greater complexity of muscle bands controlling rear lips in oozooid stage.

encircled by a series of wide flattened muscle bands (Fig. 1(a) and (b)) whose contraction diminishes the volume of the chamber. The muscle bands lie between outer and inner epithelial layers, and are thus just internal to the test, whose elasticity returns the chamber to its initial volume when the muscle bands relax. The test itself varies in thickness (Fig. 1(a) and (b)) and is hence stifffer in some regions (e.g. ventrally); as a consequence contraction of the locomotor muscle bands deforms the jet chamber unequally and when contracted it is flattened rather than circular in section. At the posterior end of the chamber, a wide exhalant aperture is surrounded by a series of thin muscle rings, and there are also small lateral muscle slips whose contraction presumably serves to incline the jet efflux. There are 13 muscle rings around the exhalant aperture of the oozooid, only five around that of the blastozooid (Fig. 1(a) and (b)); in both, the test is very thin in this region so that contraction of the muscle rings can seal the aperture during reverse locomotion.

The anterior aperture is rather different from the posterior for its oval opening is provided with flexible valves of test material, and there is a special and rather complex series of muscles associated with the valves. The test valves are arranged to permit water to flow into the chamber as its volume increases, and to close when chamber pressure rises, so that a jet is emitted from the posterior aperture. The muscles of the anterior valves however, are

capable of holding the valves open, so that when appropriately stimulated, the anterior aperture may remain open, and the posterior aperture be closed: the locomotor jet issues from the anterior aperture and the salp swims backwards.

The wide locomotor muscle bands, and the specialized muscles of the anterior and posterior apertures are innervated by axons passing from the brain in mixed nerves; they bear multiple nerve endings and do not propagate muscle action potentials (Mackie & Bone, 1977; Anderson, Bone, Mackie & Singla, 1979). The muscle fibres of the bands lack a transverse tubular system (Bone & Ryan, 1973) their structure, innervation and electrical activity suggest that they contract relatively slowly. Our measurements of the change in chamber dimensions during the active phase of the jet cycle show indeed that they are relatively slow muscle fibres (normalized velocity of contraction 1·5 L/s at 17°C).

In both oozoid and blastozooid stages, the outer epithelium overlying the brain and muscle bands, just internal to the test, is capable of propagating action potentials (outer skin pulses or OSPs) when mechanically stimulated. These OSPs interact with the nervous system probably via the axons of peripheral sensory cells to evoke changes in locomotor behaviour such as reversal or accelerated swimming. They play a particularly important role in the co-ordination of the individual blastozooids linked in the chain (Mackie & Bone, 1977; Anderson & Bone, 1980).

With this brief outline of the locomotor system in mind, we consider first the swimming of oozoids and isolated blastozooids, and then consider the swimming of chains of linked blastozooids.

Locomotion of oozooids and single blastozooids

General observations

If undisturbed in large aquaria, both oozooids and single blastozooids swim forwards in a rhythmical and regular manner. They are very close to neutral buoyancy (by virtue of the exclusion of sulphate ions from the test, Denton & Shaw, 1961), and normally swim forwards in a horizontal plane. Oozooids in particular are able to alter their swimming attitude with ease, sometimes looping the loop as they swim along; presumably such manoeuvrability is the result of small changes in the symmetry of the exhalant posterior aperture. *Salpa fusiformis* undergoes extensive vertical migrations (Franqueville, 1971), and there seems little doubt that the locomotion of all salps is directional.

In aquaria, jet pulses are produced at frequencies up to 2·0 Hz (Table I), driving the salps forwards at mean velocities between 1·3 and 6·6 cm/s. Figure 2 shows instantaneous velocity profiles resulting from such swimming. This rhythmic behaviour is little altered if the animals are tethered in small petri dishes so that the pressure transducer tip may be placed in the jet chamber, and suction electrodes attached to the surface of the test to record muscle activity; under these conditions rhythmic activity persists for long periods (Fig. 3) as indeed it also does if the salp is cut open and pinned to Sylgard, provided that the brain and nerves remain intact.

Although this pattern of rhythmic locomotor activity is seen in all individuals of *S. fusiformis* collected from the plankton, whether kept in large aquaria or confined under various experimental conditions, it seems probable that it is not the most commonly occurring pattern of behaviour of free-living salps in the sea. Such regular forward swimming is too rapid and oscillatory a process to permit the salps to filter feed using the mucus strand

filter depending from the peripharyngeal bands and when feeding with the filter deployed, *S. fusiformis* must swim more slowly, with more gentle and probably less frequent jet pulses. Whilst other salp species have been observed to feed under laboratory conditions (for example, we have often observed *Thalia democratica* feeding), it is extremely rare to observe *S. fusiformis* doing so (Braconnot, pers. comm.) and we have never observed feeding in this species.

TABLE I
Summary of measurements made on oozooids and single blastozooids

	Blastozooids		Oozooids	
Chamber length (cm)	1·0–1·7	2·25–2·75	2·0–2·5	3·5–4·2
Body volume including full chamber (cm^3)	0·91–1·6	3·4	1·2–1·75	4·2–6·7
Volume ejected (cm^3)	0·4–0·6	1·1	0·6	2·3
Area front aperture (cm^2)	0·09	0·22	0·17	0·38
Area rear aperture (cm^2)	0·07	0·15	0·13	0·275
Cycle frequency in forward swimming (Hz)	0·5–2·0	0·5–1·5	1·2–1·6	1·2–2·0
Cycle frequency in reverse swimming (Hz)	1·6		1·1	
Maximum chamber pressure (Pa)	128	80	45	50–60
Chamber pressure during pulse series (Pa)	60–100	40–60	40	30–50
Maximum negative inhalent pressure (Pa)	12	7	12	14
Jet pulse duration during forward swimming (ms)	250	250	200–300	180–300
Jet pulse duration during reverse swimming (ms)		400		400
Refill duration during forward swimming (ms)	400	400	400	400
Max. instantaneous forward velocity (cm/s)	5–7	5·5–7·0	6·5	9·5–12·5
Mean forward velocity during series of pulses (cm/s)	1·6–3·8	1·5–4·8	1·3–3·8	2·5–6·6
Max. instantaneous reverse velocity (cm/s)	4·4		6·4	8·0
Mean exhalant jet velocity from vol expelled/rear aperture area × time (cm/s)	22·8	29	18·5	33·5
Max. exhalent jet velocity (from $\sqrt{\frac{2 \times \text{Chamber pressure}}{\text{Sea Water density (1027)}}}$)	44	39	30	34
Mean inhalent jet velocity (as above, brackets: observed) (cm/s)	11	12·5	8·8(8·0)	15·0(15·0)
Max. acceleration (cm/s^2) in forward swimming	43	41	35	91
Max. deceleration during forward swimming (cm/s^2)	8	9	24	30

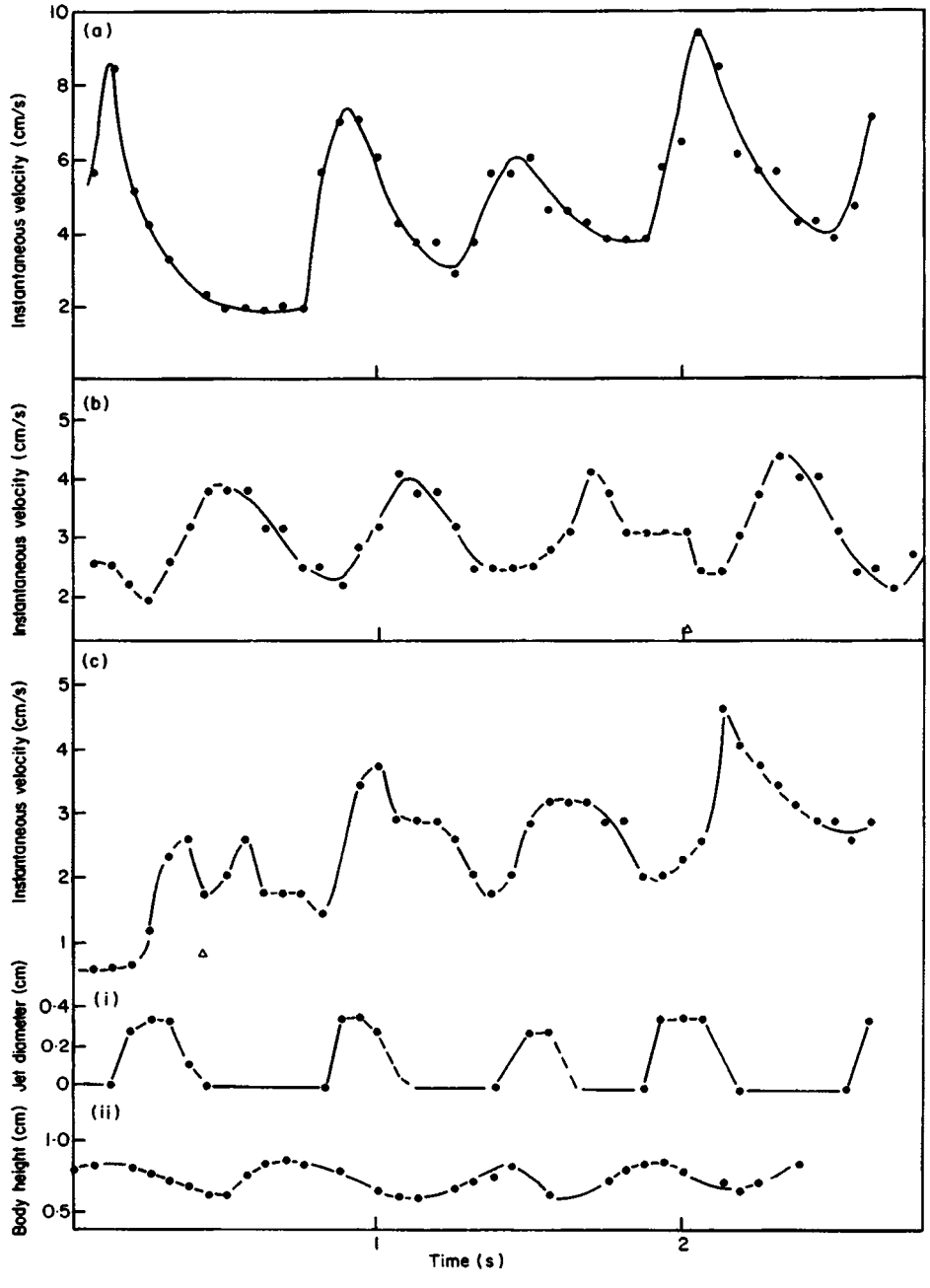

FIG. 2. (a) Instantaneous velocity curve for an oozooid, chamber length 3 cm. (b) Instantaneous velocity curves for a blastozooid, chamber length 1·7 cm during continuous swimming, (c) Instantaneous velocity curves for the same accelerating from coasting forwards at low velocity. The lower record shows also simultaneous measurements of (i) jet diameter (diameter of rear lips) and (ii) body height (jet chamber height). The triangles indicate points where the blastozooid touched the bottom of the container.

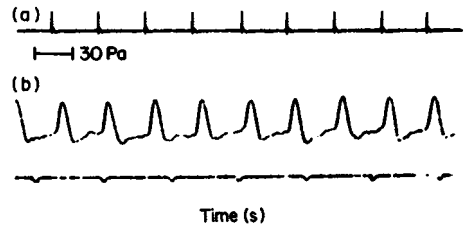

FIG. 3. Regular cycles of (a) the electrical activity of the front lip muscles and (b) the chamber pressure in a tethered blastozooid, chamber length 1·8 cm.

It seems probable therefore that all our observations on forward swimming of *S. fusiformis* relate to active non-feeding locomotion; a slower pattern of forward locomotion involved in feeding presumably occupies the greater part of the time of free-living salps in the sea.

The regular forward swimming seen in Fig. 2 is modified in a characteristic way by mechanical stimuli to the margins of the apertures. When touched anteriorly, the regular rhythm may be inhibited for a few cycles before resuming, or if stimulated more strongly, the front lips remain open during contraction of the locomotor muscle bands, the rear aperture closes, and the salp swims backwards for a few cycles. Similarly, touching the margins of the posterior aperture evokes accelerated forward swimming, for five or six jet cycles. During such reversal and acceleration responses, chamber pressures are increased, and may rise to double those seen during normal forward locomotion (Fig. 4). Despite the increased chamber pressure during reversals, maximum instantaneous velocities in reverse swimming are lower than those during forward swimming (Table I). For example, maximum instantaneous velocity in reverse for a large oozooid was 8 cms, and maximum reverse acceleration was 80 cm/s^2, as compared with 12·5 cm/s and 91 cm/s^2 in forward swimming. Two factors probably account for the lower values during reverse swimming. First, the exhalant (anterior) aperture in reverse swimming is smaller than the normal posterior aperture (since the valves partially occlude the anterior aperture), and secondly, the form of the test means that oozooids in particular are less well streamlined when reversing than when swimming forwards. It is also the case that the first reverse pulses (where chamber pressures are highest) decelerate the salp before it begins to swim backwards.

These acceleration and reversal responses are "escape" responses, serving to remove the salp from obstructions in the water, and from possible predators, in fresh animals they usually involve the OSP system (Fig. 4(c)), but in animals that have been maintained in the laboratory for some time, although OSPs are still elicited by mechanical stimuli, they may not affect the locomotor behaviour (Bone, 1982). Acceleration and reversal responses are still observed, and then result from direct stimulation of the sensory cells around the margins of the apertures, as they do when the animals are stimulated by chemicals (such as MS 222).

In addition to such rapid responses, salps are also capable of gradual changes in forward swimming speed, as a result of small changes in the contractile activity of the locomotor muscle bands, which may persist over longer periods, so that swimming can be controlled in a graded way. Changes of this kind may be evoked by changes in light intensity (Mackie & Bone, 1977). It is hardly surprising that with the capability of varying chamber pressures and cycle frequency in this way, as well as the possibility of reverse swimming, that salps are able not only to swim in a directed manner, but that they can also operate over a fairly wide speed range.

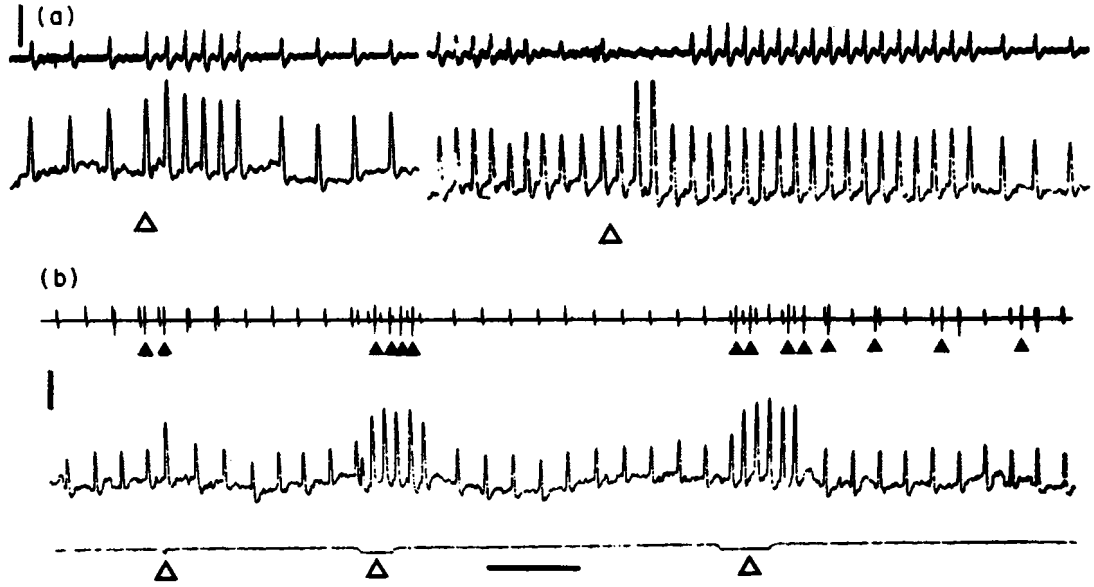

FIG. 4. (a) Simultaneous tension (upper) and chamber pressure records from a large tethered blastozooid (chamber length 2·7 cm) stimulated by touching anterior or posterior lips. On left: increased chamber pressure and cycle frequency as salp attempts to accelerate forwards when touched posteriorly (at open triangle). After a few rapid cycles, the initial slower rhythm recurs. On right: when touched anteriorly, (open triangle) during a period of rapid cycles, frequency does not change, but the salp reverses, and tension disappears. The two reverse pulses at increased chamber pressure are followed by a series of rapid pulses as the salp attempts to accelerate forwards, before the usual slow unstimulated activity recurs. (b) Simultaneous records of electrical activity of anterior lip muscles (upper) and chamber pressure in a small blastozooid (chamber length 1·5 cm). Mechanical stimulation of the anterior lips for longer or shorter times (shown by open triangles indicating event marker line below pressure record) evokes increased chamber pressures in reverse pulses, and diminished electrical activity from anterior lip muscles. The larger electrical events on the muscle activity record are OSPs, indicated by small solid triangles. Time scale bar: 5s; pressure: 20 Pa; tension: 0·5g.

The events of the jet cycle

Figure 5 summarizes the events of the jet cycle in a blastozooid (that of the oozooid is essentially similar). In forward locomotion the cycle begins with the contraction of the muscle bands controlling the anterior aperture, followed after some 30 ms by the contraction of the body locomotor muscle bands. All of these contract more or less simultaneously (Mackie & Bone, 1977). Since the motor axons supplying the muscle bands are small (less than 1 μm in diameter) delays in activation of the locomotor muscle bands far from the brain (consequent on conduction velocity delays in the motor axons) are evidently compensated by their motoneurons firing in advance of those supplying the muscle bands close to the brain.

Contraction of the muscle bands associated with the anterior aperture begins closure, and the test valves of the aperture ensure that it remains shut passively once chamber pressure rises as the locomotor muscle bands contract. There is a small leak through the anterior aperture (seen when the chamber is injected with milk suspensions) as chamber pressure begins to rise, but this soon stops when chamber pressure rises sufficiently to close the valves firmly.

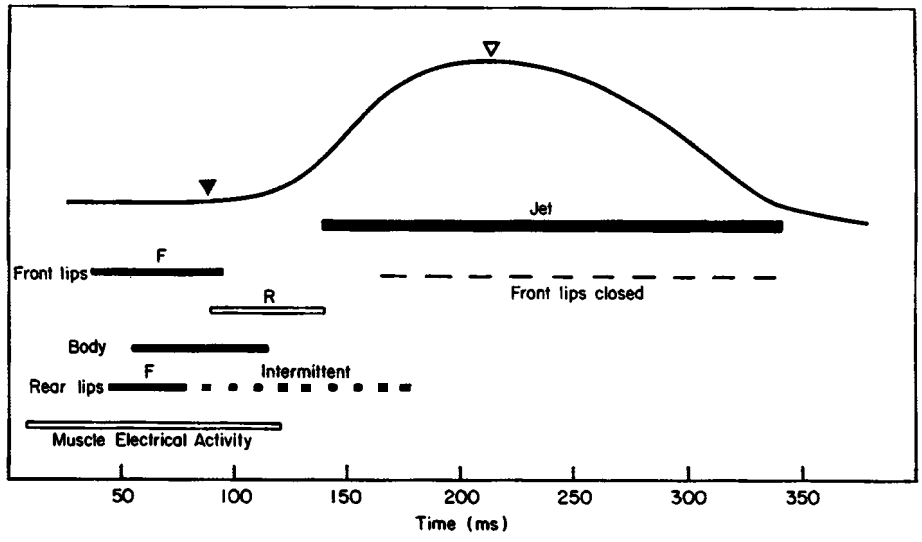

FIG. 5. Diagram illustrating events of the propulsive part of the jet cycle in a blastozooid (chamber length 1·5 cm). During forward swimming, the cycle begins with the electrical activity of the front lip muscles, followed by those of the rear lips and the locomotor muscle bands of the body. The delay between the muscle electrical activity and the beginning of contraction is indicated for the locomotor muscle bands by the black triangle which shows the beginning of contraction. Chamber pressure then rises, and the jet pulse begins (thick line). The front lips close firmly, and remain closed during the pressure pulse (dotted line). Maximal tension is developed by the locomotor muscle bands at the peak of the pressure pulse (open triangle). The open bars at left indicate the electrical activity of the muscles of front and rear lips during *reverse* swimming. Diagram combined from kinematic observations on free-swimming blastozooids, electromyograms and chamber pressure records from tethered blastozooids, and tension records from opened blastozooids pinned to Sylgard.

It might perhaps be expected that the thin muscle rings encircling the unvalved posterior aperture would remain inactive until the locomotor muscle bands had fully contracted, acting simply to close the posterior aperture at the end of the propulsive phase of the cycle, so that inhalation took place only via the anterior aperture. However, this is not the case, for the muscle rings around the posterior aperture first become active 30 ms after the locomotor muscle bands, (i.e. during the propulsive phase), and this activity lasts for some 60 ms. The muscle rings then relax, and show a second period of activity some 50 ms later. The whole jet cycle occupies some 250 ms in blastozooids (Table I); between 180 and 300 ms in oozooids. The dual contraction of the muscle rings around the posterior aperture probably reflects their dual role in swimming: the first period of contraction aligning the jet for directional control, whilst the second period closes the aperture.

During reverse swimming evoked by mechanical stimulation the activity of the locomotor muscle bands is prolonged (Mackie & Bone, 1977) and the exhalant phase of the cycle lasts some 400 ms in both blastozooids and oozooids. The first event of the cycle is activation of the muscle rings around the posterior aperture, followed by contraction of the locomotor muscle bands, and finally, by the activation of the muscles associated with the anterior aperture. As in forward swimming, the muscle rings of the rear aperture show two phases of activity, some 60 ms apart. We have only recorded muscle activity from the larger band associated with the anterior aperture (which is at once the most accessible, and the least

altered mechanically by attachment of the suction electrode) we assume that during the propulsive phase in reverse swimming, other muscles of the anterior group actively hold the test valves open until contraction of the locomotor muscle bands ceases. It is not evident why the muscle rings associated with the rear aperture should show two phases of activity in reverse swimming as they do in forward swimming, for it would seem natural to suppose that effective reverse swimming requires that the rear aperture remains closed during the entire pressure pulse.

During the expulsion phase of the cycle, about a third of the volume of the expanded jet chamber is expelled. In forward swimming, this is expelled entirely via the posterior aperture (apart from the small anterior leak at the beginning of the cycle before the test valves close completely). Refilling involves entry of water via both apertures, as shown schematically in Fig. 6. Only around a fifth of the inhaled water enters via the rear aperture, and this probably results from the fact that the margins of the rear aperture are surrounded by a very thin layer of test material, so that when the muscles have relaxed, and the jet chamber expands, the rear aperture is soon effectively sealed by the lip margins being sucked against each other and distorted, thus preventing entry of water. Evidently, the test valves at the anterior aperture permit water to flow in during the refilling phase, for not only do they operate in the appropriate sense, but they also serve to maintain the shape of the aperture and prevent it sealing in the same manner as the rear aperture. The values for the relative volumes inhaled by each aperture given in Fig. 6 were obtained by measurements upon tethered salps which thus had no forward velocity component. In free-swimming salps, inhalation via the anterior aperture will be assisted by dynamic (or ram) pressure, and this will presumably slightly increase the relative amount inhaled anteriorly. Apart from this anterior dynamic contribution, refilling of the jet chamber is brought about entirely by the elasticity of the test. We attempted to measure the energy stored in the test by deforming the test of anaesthetized salps in seawater with a small metal plate attached to the tip of a strain gauge racked up and down with a micropositioner. Allowance was made for the effects of the upthrust of seawater. Hysteresis curves so obtained indicated that the resilience of the test was around 60%. However, loading and unloading of the test in this way was performed at a much lower rate (over 1 min) than occurs in an active animal, and furthermore, the varying thickness of the test around the jet chamber (Fig. 1) in both oozooids and blastozooids, made it impossible to deform the test artificially in a way approximating to the change in shape resulting from contraction of the locomotor muscle bands. It seems most probable that real values for test resilience are considerably higher than 60%.

During forward locomotion, swimming speed is varied by changes in cycle frequency (between 0·5 and 2·0 Hz under our experimental conditions), and by variation in the

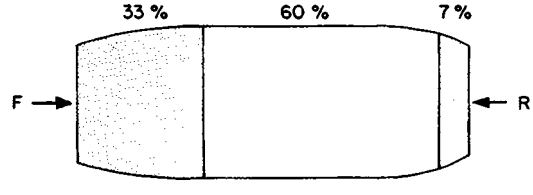

FIG. 6. Diagram showing refilling of jet chamber via front aperture with a small contribution via rear aperture. Some 40% of the total volume is ejected at each pulse.

contraction of the locomotor muscle bands, so that although maximum forward velocities are found in the largest individuals, and are lowest in the smallest, plots of forward velocity against chamber length (Fig. 7) show a large scatter.

A similar scatter is found in the chamber pressures recorded from salps of different sizes (Fig. 8), but it is clear that oozooids normally operate at lower chamber pressures than blastozooids (see Table I). Chamber pressures in the larger *Pegea* and *S. maxima* (both swim very slowly) are relatively low (Fig. 8): both have large exhalant apertures.

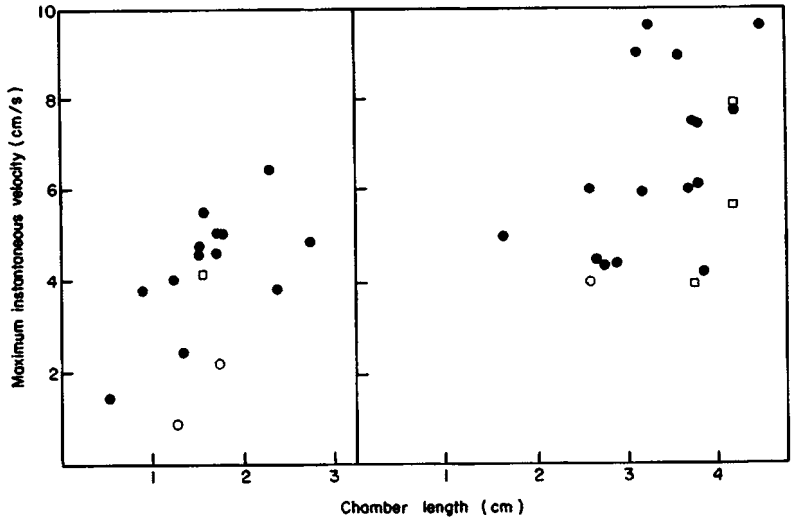

FIG. 7. The relation between maximum instantaneous velocity and chamber length in blastozooids (left) and oozooids. Open circles: minimum velocities; squares: velocities in reverse swimming.

Thrust and drag

In oozooids and isolated single blastozooids, the pulsatile jet system of thrust generation produces cyclical oscillations in forward velocity (Fig. 2) which inevitably complicate any analysis of the system, since both thrust and drag vary as the salp swims forwards. In this section, we consider various ways in which thrust and drag may be estimated in order to gain some idea of the energetic cost of swimming in salps.

Thrust

Our direct measurements of static thrust obtained from animals pulsing whilst attached to a strain gauge ranged from 0·6 to $2{\cdot}0\times10^{-3}$ N (Table II). Because salps are able to vary widely the contraction of their locomotor muscle bands (and hence the resulting chamber pressures, Fig. 8), the static thrusts recorded from salps of different sizes vary widely. Although oozooids have lower chamber pressures than blastozooids, maximum static thrusts obtained from oozooids are greater than those from blastozooids, indicating that greater amounts of water are expelled during the cycle. There are some difficulties in measuring static thrusts, owing to the geometrical restrictions imposed by the need to keep the strain

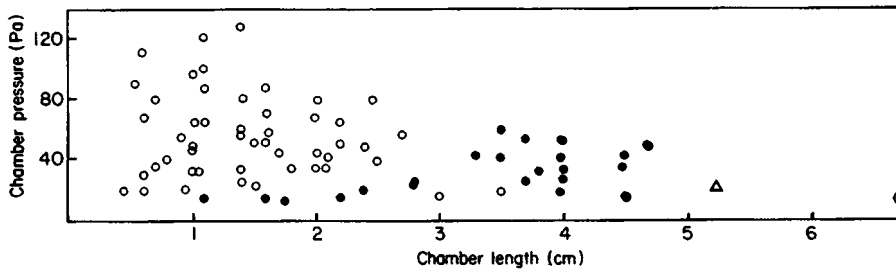

FIG. 8. The relation between chamber length and chamber pressure. Open circles: *S. fusiformis* blastozooids, filled: *S. fusiformis* oozooids; triangle: *Pegea* blastozooid large circle: *S. maxima* oozooid.

gauge above the water level, and we regard the values given in Table II to be under-estimated, since the anterior ventral region of the salps may have been in contact with the dish, particularly in the case of the blastozooids with their long anterior horns. Another consideration suggests that the measured maximum static thrusts (Table II) are probably biased low.

When chamber pressures are measured simultaneously with static thrusts, the measured thrust can be compared with that expected from $T=2aPC_{dn}$ (where *a:* exhalant aperture area; *P:* chamber pressure; and C_{dn}: a drag coefficient for the jet nozzle; Johnson, Soden & Trueman, 1972). C_{dn} will be unity only if viscous effects are neglected (i.e. if there are no frictional losses at the jet aperture), but at the low Reynolds numbers involved in jets issuing at 15–40 cm/s viscous effects will certainly be important, and C_{dn} will be below unity. For examples, in squid (Johnson *et al.* 1972) and in siphonophores (Bone & Trueman, 1982), C_{dn} values of 0·6–0·7 have been estimated. Identity of calculated and measured values for static thrust of oozooids is given by C_{dn} values ranging from 0·5–0·72; corresponding values for blastozooids being 0·5–0·54 for maximum thrusts. For less than maximum performance by blastozooids, C_{dn} values as low as 0·3 are obtained.

It is clear that frictional losses of this magnitude would be unacceptable, and this again suggests that static thrusts were underestimated. Taking C_{dn} to be 0·7 for both oozoids and blastozooids, static thrust estimates for the former range up to $2{\cdot}3\times10^{-3}$N, and for the latter up to $1{\cdot}7\times10^{-3}$N (Table II).

These estimates are in reasonable accord with thrust estimates obtained in a different way, from free-swimming salps, by measuring maximum accelerations from instantaneous velocity curves (such as those of Fig. 2) where *T: ma (m:* mass of salp, and *a:* acceleration). Two corrections are required to the "resting" mass of the salp: an addition of 10% for the added mass of water carried along with the salp as it swims forwards, and a reduction to take account of the water exhaled, since maximum acceleration is seen during the mid-period of the jet pulse, when 50% of the chamber volume has already been ejected. With these corrections to the "resting" mass, maximum thrusts derived in this way range from $0{\cdot}65-5{\cdot}34\times10^{-3}$N (Table II). The thrust generated is required to overcome the drag incurred as the salp swims forwards, but unfortunately, drag values for swimming salps are not easy to estimate, as indicated in the next section.

Drag

Calculation of the drag incurred during swimming (hence of the thrust required) is complicated for several reasons. For example, refilling of the jet chamber after the propulsive phase

TABLE II
Summary of swimming performance of oozooids and single blastozooids

	Blastozooids		Oozooids	
Chamber length (cm)	1·0–1·7	2·25–2·75	2·0–2·5	3·5–4·2
Reynolds number range	200–1000	400–1750	250–1750	625–5000
Measured static thrust ($N \times 10^{-3}$)	0·6	0·75	0·75	1·0–2·0
Maximum thrust estimated from *T*: $2aPC_{dn}$. $C_{dn}=0{\cdot}7$ ($N \times 10^{-3}$)	1·25	1·7	0·82	2·3
Maximum thrust estimated from *T*: ma; 10% added mass 50% chamber volume ejected ($N \times 10^{-3}$)	0·65	1·34	0·56	5·34
Volume drag coefficient (C_{dV}) measured from drops	0·36	0·5	0·33	0·3
†Work/cycle (from P × V) to expel jet ($J \times 10^{-5}$)	3·8			8·0
†Work/cycle to refill jet chamber ($J \times 10^{-5}$)	0·68			2·64
†Total work/cycle ($J \times 10^{-5}$)	4·5			10·65
†Work/g muscle/pulse ($J \times 10^{-2}$)	5·66			3·7
†Power output at 2 Hz ($W \times 10^{-5}$)	8·98			21·3

†These estimates are made from *maximum* pressure pulses and hence represent *maximum* performance; total work per cycle, and power outputs during cruising will be substantially less than this.

of the jet cycle increases drag, despite the fact that the greater part of the water inhaled enters via the anterior aperture during forward swimming. Deceleration after the propulsive phase is thus more rapid than might be expected, until the chamber is refilled (Fig. 2). Different drag coefficients are therefore appropriate during different phases of the cycle.

Volume drag coefficients (C_{dV}) obtained by dropping weighted anaesthetized salps in columns of water, range from 0·3 to 0·5. The higher values were given by blastozooids, which are difficult to drop in a vertical path owing to the asymmetry of the body; the lowest value for all of the blastozooids tested was 0·36.

C_{dV} values of 0·3–0·35 are to be expected from shapes such as salps at low Reynolds numbers. Drag coefficients of this order are only applicable to salps during the last phase of the cycle, when they have completed refilling the jet chamber, and are coasting just before the next jet pulse begins. It is not clear whether the oscillatory nature of the instantaneous velocities achieved during swimming are such that boundary layer thickness is less than under steady state conditions (hence that C_{dV} is greater than under steady state conditions) but it seems probable that during the acceleration phase of the cycle, this consideration applies and C_{dV} will be greater than 0·35. At the peaks of the instantaneous velocity curves, when the salp is neither accelerating or decelerating, C_{dV} may be estimated from:

$$C_{dV}: \frac{\text{Thrust} = \text{Drag}}{1027 \times 0{\cdot}5 \times U^2 \times \text{Volume}}$$

(where U forward velocity and 1027: seawater density) if it is assumed that steady state conditions apply at this point, and thrust is estimated from chamber pressure, taking C_{dn} as 0·7). Making these assumptions, and further correcting the volumes of the salp (Table I) for added mass (+10%) and for reduction in volume for the water already exhaled (30% of chamber volume, Table I), C_{dV} at the peak of the instantaneous velocity curves for large oozooids is between 0·3 and 0·57, depending upon the chamber pressure taken to estimate thrust. Unfortunately, as noted in the Methods section, the delicacy of the animals precluded positioning an indwelling pressure catheter into a free-swimming salp, so that simultaneous pressure and instantaneous velocity records were not obtained. There is, therefore, some uncertainty about the phase relations between the velocity curves and the pressure curves. Observations of lip closure on free-swimming animals, and on tethered animals where chamber pressures were measured indicate that at maximum instantaneous velocity chamber pressure is 30% of its maximum, and hence C_{dV} for large oozooids is at this point 0·34. After the end of the jet pulse (30 ms after maximum instantaneous velocity), refilling of the jet chamber begins, and the salp decelerates rapidly. Drag can now be estimated from the product of mass and deceleration, and applying corrections to the mass to account for carried water, and for the appropriate chamber volume, C_{dV} for a large oozooid derived from the drag estimated is now 0·55 at 9 cm/s. Not until the jet chamber is completely refilled, and the salp coasts just before the next jet pulse do C_{dV} values fall again to around 0·30.

The striking increase in drag coefficient as the salp refills the jet chamber (nearly doubling the drag resulting from skin friction and profile drag) is almost entirely the consequence of the momentum change of the water inhaled into the jet chamber. From being inhaled anteriorly at some 15 cm/s (Table I), it is then carried in the opposite direction in the jet chamber, at the forward speed of the salp. Only a very small fraction of the increased drag during refilling can result from the volume increase of the body, and hence change in profile drag.

Our estimates of the drag coefficient during different stages of the cycle are obviously only approximate, but they suffice to show that refilling of the jet chamber produces a significant increase in the drag expected.

Power and work during a single jet cycle

Acceleration power during the cycle is given by the product of instantaneous velocity and thrust (Lang, 1966). Taking maximum values for thrust estimated from $T=Ma$ and maximum accelerations (Table I), maximum acceleration power for large blastozooids is some $0{\cdot}8\times10^{-4}$W, and for large oozooids $6{\cdot}7\times10^{-4}$W. This estimate is the rate at which useful work is performed, and is thus less than the rate at which the muscles are doing work. The latter quantity can be estimated from records of pressure pulses, as was done for siphonophores by Bone & Trueman (1982). If the pressure pulse during the cycle can be accurately monitored, then it can be used to calculate volume changes (since the jet efflux velocity depends upon the differences between ambient and chamber pressures, volume changes follow chamber pressure changes, provided that the exhalant aperture area remains unchanged during the pulse). Thus if the initial and final volumes of the jet chamber are known, volume changes during the cycle can simply be obtained by integration of the digitized pressure pulse. Work done during the pulse is then the product of the pressure pulse and its integral. This approach can also be applied to the inhalant negative pressure pulse, so that the total work

done by the locomotor muscle bands in overcoming the elasticity of the test and in producing the propulsive jet may be estimated.

During maximal contractions (i.e. at maximum recorded chamber pressures), the total work per cycle for a small blastozooid estimated in this way was $4{\cdot}5\times10^{-5}$J (Fig. 9) corresponding to a power output at a cycle frequency of 2 Hz of $9{\cdot}0\times10^{-5}$W. The equivalent values for a large oozooid are $10{\cdot}65\times10^{-5}$J and $21{\cdot}0\times10^{-5}$W. As we have seen, salps are able to vary the contraction of the locomotor muscle bands to produce a wide range of chamber pressures, and during cruise swimming at lower chamber pressures, power outputs will be considerably less than this. At the maximum performances above, 15% of the total work per cycle is required to overcome the elasticity of the test in the blastozooid; in the oozooid (with its thicker test), around 25% of the total work per cycle is required.

The power for locomotion is provided by the locomotor muscle bands, which make up some 0·4–0·6% of the total mass of the salp. Table III shows the dimensions of the muscle bands in different sizes of blastozooids and oozooids of *S. fusiformis*, together with values for three other species for comparison. Muscle weight was calculated assuming muscle density to be 1060 (Mendez & Keyes, 1960). The work performed for each pulse by oozooids and blastozooids for each g of muscle was similar; for the blastozooid examined $5{\cdot}66\times10^{-2}$J/g/pulse, for the oozooid $3{\cdot}7\times10^{-2}$J/g/pulse. Muscle stresses, calculated from

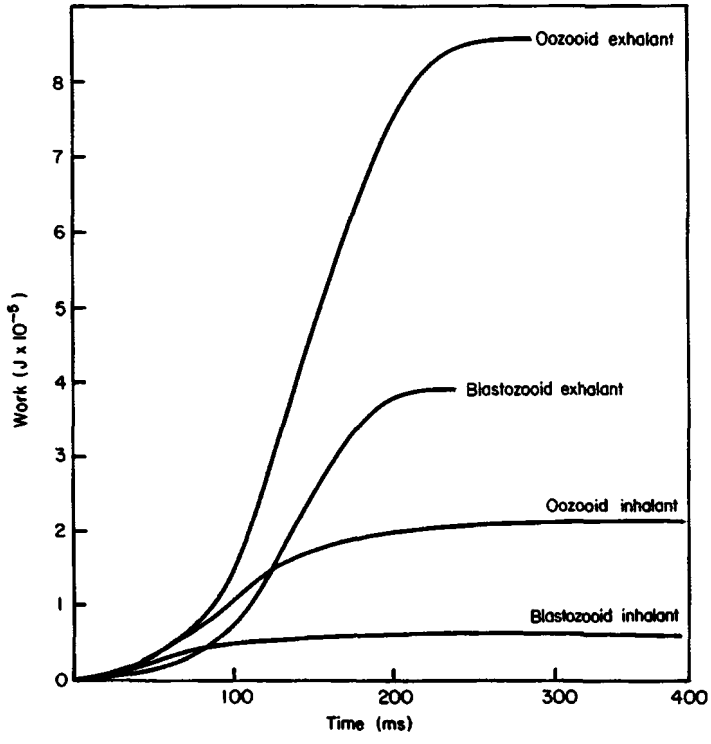

FIG. 9. Cumulative work curves for exhalent and inhalent jet cycles of an oozoid and blastozooid obtained from chamber pressure pulses as described in text.

the product of chamber pressure and radius and corrected for the stresses involved in overcoming test elasticity, were between 3·87 N/cm² and 7·89 N/cm² for oozooids operating at chamber pressures between 40 and 55 Pa, whilst for a small blastozooid operating at 100 Pa, muscle stress was some 10·26 N/cm². These values for non-isometric slow muscle contractions are naturally considerably smaller than those for the rapid non-isometric contractions of the sub-umbrellar muscle sheet of the siphonophore *Chelophyes* (20 N/cm², Bone & Trueman, 1982), and for isometric contractions of such twitch muscles as frog sartorius (20–50 N/cm²).

TABLE III
Locomotor muscles in different salps

Species	Chamber length (cm)	Total muscle area (cm²)	Cross-sectional area (cm² × 10⁻³)	Weight (g × 10⁻³) (assuming: 1060)
S. fusiformis				
Blastozooids	1·0	0·25	0·35	0·33
	2·1	0·95	0·40	1·26
Oozooids	1·8	0·45	0·35	0·48
	2·2	0·80	0·64	1·02
	2·5	1·0	0·82	1·33
	3·6	2·15	1·13	2·85
Pegea confederata				
Blastozooid	3·6	0·52	0·34	0·82
Salpa maxima				
Oozooid	15	11·59	1·71	6·14
Blastozooid	19	22·88	1·8	12·12
Iasis zonaria				
Blastozooid	2·1	2·11	1·63	4·47

Note relatively small amounts of locomotor muscle in *Pegea* and *S. maxima*, and the large amount in the active *Iasis*.

The locomotion of blastozooid chains

General observations

Salp blastozooids differentiate from the oozoid stolon as it elongates, and eventually a linked chain of blastozooids breaks free from the stolon to grow independently. The zooids in the chain are linked by special attachment plaques (Bone, Anderson & Pulsford, 1980); according to the species they may lie side by side transversely to the axis of the chain *(Pegea)*, or they may be staggered with their long axes parallel to that of the chain *(Salpa fusiformis, S. maxima* and *lasis)*. In *S. fusiformis* enantiomorphic zooids fit snugly together to make an essentially tubular well-streamlined chain (Fig. 10). They lie in such a way that the jet pulses issuing from the posterior aperture of each as the chain swims forwards are directed outwards at an angle of some 15°–19° to the long axis of the chain; in this way posterior zooids do not inhale water that has passed through anterior zooids.

In large aquaria, chains of *S. fusiformis* swim forwards unless stimulated, but their forward speed is very variable. For example, the mean forward speed of a chain of 14 zooids ranged

FIG. 10. 5-Member chain of small blastozooids (chamber length 1·7 cm), drawn from photograph of living chain.

from 0·5 cm/s to 6 cm/s (Fig. 11). This wide speed range is due in part to different numbers of zooids in the chain being active on different occasions, for not all zooids are always active. In Fig. 11, the highest velocities were observed when most zooids were active. But it is also partly due to large variations in activity of those zooids that are active. Thus in Fig. 11, the same chain achieved velocities around 4 cm/s when 13 zooids were active, and when only three zooids were active. Despite this wide scope for activity of individual zooids, there is, as we should expect, a general relation between the mean velocity at which the chain travels, and the number of jet cycles per second produced by the zooids of the chain, as seen in Fig. 12.

During normal forward swimming, active zooids usually pulse at approximately the same frequency, but their activity is not necessarily in phase (Fig. 13) and some zooids are usually inactive: the activity of the zooids in the chain is not co-ordinated. The result of this random pattern of activity is that the instantaneous velocity curves for chains of blastozooids are much less oscillatory than for single salps (Fig. 2), and maximum and minimum instantaneous velocities only differ by 2 cm/s or less (Table IV and Fig. 13). In line with this, as expected, static thrust records from chains show minor peaks resulting from the activity of zooids anterior to that from which chamber pressures were recorded.

The unco-ordinated activity of zooids in the chain changes strikingly when the chain is stimulated. Mechanical stimulation of the anterior or posterior end of the chain (i.e. of the anterior end of the foremost zooid, or of the hinder end of the most posterior) evokes co-ordinated reversals or accelerated swimming of *all* the zooids of the chain, including those

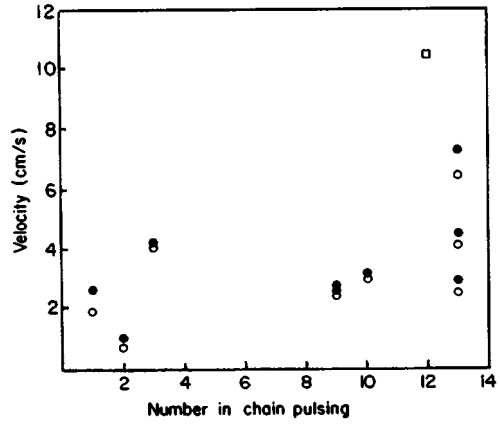

FIG. 11. Swimming velocities of 14-member chain of small blastozooids (chamber length 0·75 cm) with different numbers of zooids active. Filled circles: maximum instantaneous velocities; open circles: mean forward velocity; square: maximum instantaneous velocity during reverse swimming.

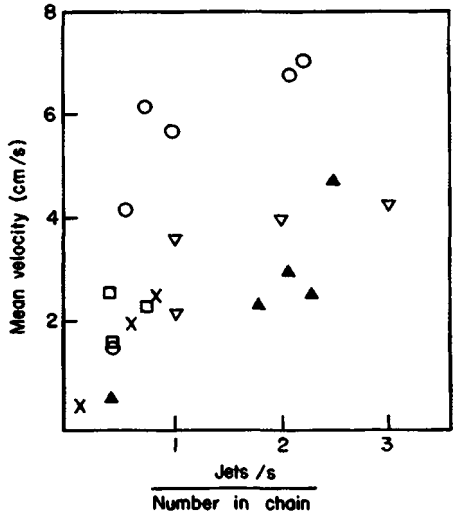

FIG. 12. Mean swimming velocities of chains of small blastozooids when different numbers of zooids are active. Circles: 16- and 17-member chain; solid triangles: 14-member chain; squares: 13-member chain; crosses: 9-member chain; open triangles: 2-member chain.

that were previously inactive. An example of such a reversal response in a 15-member chain is seen in Fig. 14. Touch with a forceps on the anterior lips of the anterior zooid of the chain produced simultaneous reverse pulses (at the upward pointing arrow) involving the previously inactive zooids 12–15, and 6, followed by co-ordinated rapid reverse swimming of the anterior zooids, which prior to stimulation were pulsing out of phase. These co-ordinated responses are brought about by the OSP system (as are reversals and accelerations in single salps); OSPs travel along the chain from the zooid stimulated at up to 12·5 cm/s (Mackie & Bone, 1977). They do so by a complex alternating arrangement of epithelioneural and neuro-epithelial synapses involving the connexion plaques between zooids in the chain, and central epithelio-motor neurons (Bone, Pulsford & Anderson, 1980; Anderson & Bone, 1980).

Since the activity of the zooids when stimulated is now co-ordinated, and more or less in phase, instantaneous velocities are now higher than in unstimulated chains and there are greater oscillations in instantaneous velocity. The highest instantaneous velocities observed were found during reverse swimming of the chain, as is appropriate for what may be regarded as an escape response.

Thrust and drag of blastozooid chains

During normal unstimulated cruising, the velocity of a chain with several members active is more or less uniform, so that unlike the situation for single salps, steady state conditions apply, and drag and thrust may be calculated from: $T=D=0{\cdot}5\times 1027\times U^2\times \text{Voli}\times C_{dV}$ provided that C_{dV} can be estimated.

Volume drag coefficients derived from films of weighted chains descending in columns of water ranged from 0·3 to 0·33 (Table IV); under steady state conditions this value of C_{dV}

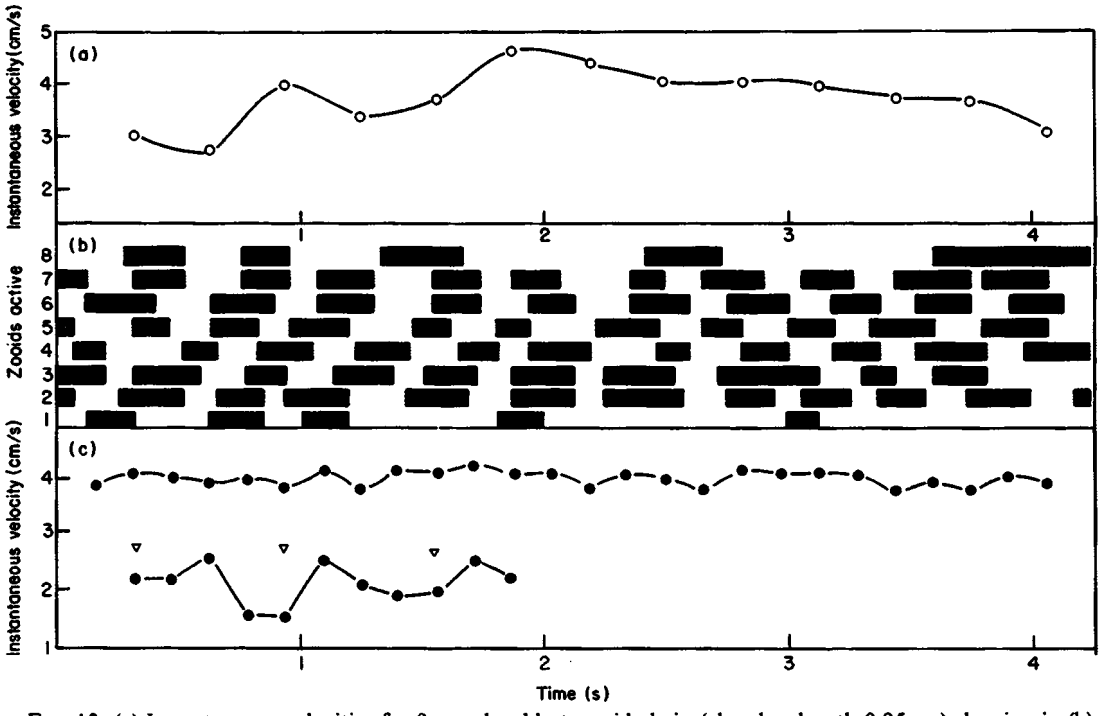

FIG. 13. (a) Instantaneous velocities for 8-member blastozooid chain (chamber length 0·95 cm) showing in (b) the activity of the individual zooids of the chain. The solid bars indicate the exhalant phase of the jet cycle for each zooid; note lack of coordination between adjacent zooids. (c) Instantaneous velocity curves for the same 13-member blastozooid chain (chamber length 0·75 cm) when all zooids were active, and when a single zooid alone drove the chain along. Note near-flat curve resulting from random activity of all zooids, whereas marked oscillations occur when the single zooid contracts (triangles show beginning of its jet pulses).

accounts for the skin friction and profile drag of the chain. Table IV shows values for the thrust generated by chains assuming that C_{dV} is 0·33. However, the drag coefficient estimated from dropping weighted chains does not take account of the increased drag resulting from the momentum change of the water entering the jet chambers during refilling, and it is evident that the increase in C_{dV} required to account for this will depend upon the number of active zooids in the chain, and their rate of pulsation. For example, if a single zooid alone is active in the chain, refilling this single zooid will only require a small increase in C_{dV} from that estimated by dropping the chain, whereas if all zooids are active at the same rate, what may be termed refill drag will be greater, and C_{dV} larger.

It is difficult to estimate C_{dV} for chains, because we were not able to obtain chamber pressure measurements from swimming chains, and thus do not know whether even the fastest swimming velocities observed represented the maximum activity of the zooids as measured on isolated tethered individuals.

However, several considerations suggest that chains are capable of higher velocities than were observed. If all the active zooids in the chain were operating at the maximum performance of individual zooids, then thrust calculated from the steady state equation should be similar to that calculated from the momentum of the exhaled jets $(T=D=nmu)$, taking

TABLE IV
Blastozooid chains. Examples of measurements made and performance

Chamber length (cm)	0·75					0·95*						1·3		
No. of zooids in chain	14	14	14	14	14	17	17	17	6	2	1	16	16	16
No. of zooids active	13	12	9	3	1	14	11	8	6	2	1	16	12	9
Chain volume (cm^3)	4·82	—	—	—	—	6·46	—	—	5·8	1·9	0·9	9·1	—	—
Cycle frequency (Hz)	35	32	26	6	3	38	36	8	21	6	2	38	25	18
Mean forward velocity (cm/s)	4·7	2·3	2·4	0·27	2·0	7·1	6·6	1·6	7·5	4·3	1·7	5·7	6·2	4·2
Max. instantaneous velocity (cm/s)	5·1	2·6	2·4	0·3	2·6	7·2	6·70	2·0	8·8	6·9	3·5	8·9	7·8	5·0
Reynolds number	400–7000					1300–8000						2300–14,000		
C_{dV} from drops	0·02					0·3–0·33						0·32		
Thrust ($N \times 10^{-3}$) (estimated from $T=\frac{1}{2}\times 1027 \times \text{Vol}\ \frac{2}{3}\times C_{dV}$; assuming that $C_{dV}=0·33$)	0·11				0·0035	0·29	0·246	0·01	0·31			0·04		0·009
Thrust from $D=T=nmU$ assuming max. output as in single blastozooids (Table 1) ($N \times 10^{-3}$)	2·46				0·92	3·56	3·37	0·75	1·97					

*The chain of 0·95 cm chamber length blastozooids was successively shortened.

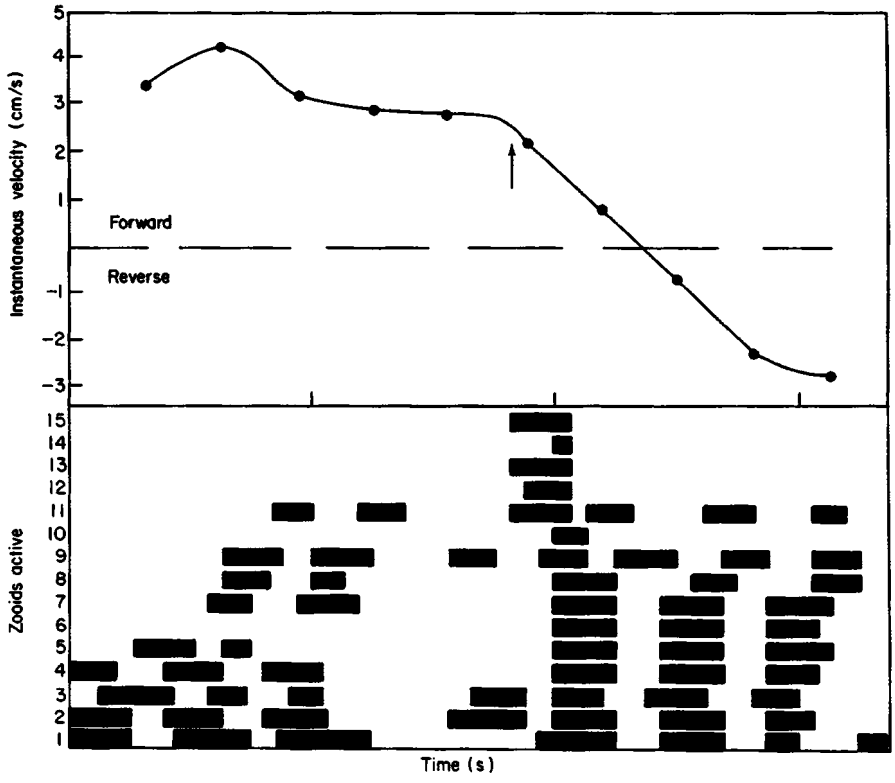

FIG. 14. Similar diagram to Fig. 13 showing coordination of activity of zooids (bars) when the chain is gently mechanically stimulated anteriorly to produce a reverse pulse (upward arrow), followed by a series of coordinated reverse pulses. Note that reverse involves activity of all zooids, including those previously inactive at the rear of the chain.

maximum values for m and u from the performance of single individuals (Table I). Thrust calculated in this way greatly exceeds that estimated from the steady state equation. During the fastest runs recorded, cycle frequency of the active zooids was 2·7–3·3 Hz (Table IV), exceeding the highest frequency recorded from single blastozooids (Table I), and this indicates that the jet cycles were "shallower" than those of single blastozooids, so that less water was exhaled at each pulse. Moreover, it is clear from Table IV that similar velocities were obtained from the same chain when different numbers of zooids were active. For example, in the chain of 14 individuals, similar forward velocities were obtained when 12 zooids were pulsing at 2·7 Hz as when a single zooid was pulsing at 3 Hz. The activity of the 12 zooids together only exerted as much thrust as that of the single zooid alone which must have been ejecting a similar volume of water. In this case, if all 14 zooids were operating at the same rate as the single zooid alone, the chain would have exceeded 6·5 cm/s if C_{dV} is assumed to be 0·45, and 7·6 cm/s if C_{dV} is taken to be 0·33. Similarly, for the 17 member chain, if all members operated at the same rate as the 11 members driving it forwards at 6·6 cm/s then the chain would have travelled at 6·93–8·1 cm/s depending on the value for C_{dV} taken. In neither case, is it evident that the single zooid, or 11 zooids were operating at their maximum performance, so that actual maximum swimming velocities for the chains when all members

are active may be higher than these estimates. The uncertainty about the performance of the active zooids in the chain makes it impossible to estimate C_{dV} from the momentum of the exhaled jets. It was pointed out at the beginning of this section that if all active zooids operated at the same rate, then C_{dV}would be higher the greater the number of zooids active in the chain, perhaps rising to 0·4–0·45, as compared with around 0·3–0·33 when few zooids are active. However, if the same velocity is achieved by a single zooid as by many active zooids operating at a lower rate, then C_{dV} will remain low even though many zooids are active, since the total momentum change involved in refilling the jet chambers will be the same as it is for the single zooid operating at a higher rate. Thus cruise locomotion by many active zooids will be as economical a process as cruise driven by a single zooid operating at a higher rate.

Maximum activity by all members of the chain only results from stimulation, eliciting an escape or avoidance response (the maximum velocity observed for any chain was 9 cm/s in reverse) lasting for a few jet cycles only; under these conditions a higher C_{dV} is not so disadvantageous as it would be during cruising. We assume that the normal feeding behaviour of the chains involves the activity of a few zooids only, the remainder feeding by filtering water driven at low velocity through their jet chambers by dynamic pressure.

Discussion

This preliminary study of the locomotion of *S. fusiformis* has shown that all stages in the life-cycle have a wide variety of locomotor behaviour observable under experimental conditions, although we have not observed feeding behaviour either in oozooids or blastozooids. The species is an active one, and undertakes extensive vertical migrations. In the Mediterranean, diel vertical migrations of 500–800 m have been reported (Franqueville, 1971), and Harbison & Campenot (1979) have shown that jet cycle frequency is little altered by the changes in temperature such migrations involve. Different salp species differ much in their locomotor behaviour, as they do in size and morphology, for example *Pegea* is much less active and swims very slowly, with low chamber pressures; but the mode of jet propulsion in each is essentially the same, as apparently is the way in which locomotor behaviour is controlled, for in all species thus far investigated, an OSP system and neuro-epithelial synapses are found.

The chief difference between different species however, is that in some, chains of blastozooids are formed which swim actively, with all zooids aligned along the long axis of an essentially tubular chain, whereas in others, they are aligned across the long axis, either in a long chain (like *Pegea*) or in *Cyclosalpa* in small groups forming "wheels" of blastozooids. In these cases, swimming is very much slower than it is in the tubular chains. Our observations suggest that there are significant advantages in the association of blastozooids into tubular chains, for the lack of co-ordination during normal forward swimming means that some zooids alone may provide the propulsive force needed, whilst the remainder feed passively by filtering the water entering their chambers by dynamic pressure. Whilst this is also true for chains such as those of *Pegea*, in the tubular chain directed forward locomotion and escape responses are possible, as well as "cruise" feeding, and the smooth instantaneous velocity curves for the chain means that steady state conditions apply, and there will be less drag incurred than during the locomotion of isolated individuals; furthermore, the snug fit of the zooids in the chain means that the surface area of the chain is less than that of the

zooids within it if they were separated, again reducing drag. Feeding and swimming in the chain thus is a more economical process than if the blastozooids separated from the stolon and operated individually. Since chains with the zooids arranged across the long axis present a much greater volume drag than tubular chains, stimulation can only result in slow avoidance responses, and it is perhaps for this reason that tubular chains are found in most species.

In comparison with other jet propelled animals, salps produce propulsive jets which emerge relatively slowly from large exhalent apertures. Since the thrust generated is the product of the mass ejected per second and the velocity of the issuing jet, *mu*, the same thrust may be generated by ejecting a large mass at low velocity through a large aperture, as by ejecting a smaller mass at higher velocity through a small aperture. However, since the power required to accelerate the fluid 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 at low velocity, as salps do. Further the efficiency of transfer of momentum to the water increases as the efflux jet velocity approaches the forward velocity of the animal, so that a large slow jet is more efficient than a narrow fast jet. It is for this reason that modern jet airliners have larger diameter engines and slower jet effluxes than earlier designs. For continuous jets, a measure of the efficiency of transfer of

TABLE V

Relative mechanical efficiency of various jet-propelled designs operating at maximum performance†

S. fusiformis	Chamber pressure (Pa)	Mean jet velocity, $\bar{u}$ (cms^{-1})	Mean Forward velocity, $\bar{U}$ (cms^{-1})	$E\ \frac{2\bar{U}}{(2\bar{U}+\bar{u})}$ ‡
Small blastozooid	100	22·8	3·8	0·25
Large blastozooid	80	29	4·8	0·25
Small oozooid	45	18·5	3·8	0·29
Large oozooid	60	27·9	6·6	0·32
Blastozooid chain				
1 active of 14		22·8	+2·0	0·15
Same chain all active		22·8	+6·5(est.)	0·36
Siphonophores				
Chelophyes, *anterior	400	71	16	0·31
Abylopsis, *nectophore	30	22	3	0·21
Squid				
*Alloteuthis***	20,000	625	80	0·20

*From Bone & Trueman, 1982.

**Trueman, unpublished data.

†This assumes that active zooids in chain were operating at maximum performance, if they were not, then E would be greater.

A single active zooid in a chain operating at maximum performance is relatively inefficient since the forward speed of the chain is low in relation to jet velocity; efficiency increases as other members become active.

‡Note that U and u are *mean* forward and exhalent jet velocities, and that $E\frac{2U}{(2U+u)}$ applies to a steady state situation where U and u are constant (see text).

TABLE VI
Comparison of the mechanical work performed to cover a distance of 1 m when operating at 2 Hz and maximum performance

S. fusiformis	Jet cycles	Mean forward velocity (cm)	Work (J/kg)
Small blastozooid	52	3·8	2·5
Large oozooid	30	6·6	0·55
Blastozooid chain			
16 Zooids, 12 active	400	6·2	1·15*
16 Zooids, 9 active	428	4·2	1·29*
Siphonophores			
†*Chelophyes*	30	16	28·3
†*Abylopsis*	60	3	2·86

*Total mass includes inactive zooids. For all, mass includes contained water
†From Bone & Trueman, 1982.
Note that *Chelophyes* operates at 5 Hz.

momentum is given by $E: 2U/(2U+u)$ (where U: forward velocity, and u: jet efflux velocity). Although salp jet propulsion is oscillatory (as is that of almost all other animals, with the exception of *Pyrosoma* where the jet is produced by ciliary action), the same considerations obtain and application of this formula may give an idea of the *relative* efficiency of different designs (although steady state conditions obviously do not apply) (Table V). It is important to note that the values given for salps are *maximum* performance values, and that when cruising at lower chamber pressures and lower velocities, they still show jet cycles of the same length so that the volume ejected is less, and efflux velocity is lower than at maximum performance. Thus when cruising, relative values for efficiency will be higher than those shown in the Table. At maximum performance, the relative efficiency of salps on this basis exceeds that of other animals investigated, with the exception of the anterior nectophore of *Chelophyes* which is particularly well-streamlined and has a very high swimming velocity. During cruise locomotion, salps may be expected to operate more economically than do other designs.

Another way of looking at the economy of operation of salps is to compare the work they require to perform to travel 1 m, in comparison with that required by other designs (Table VI) we can only compare the different designs at *maximum* performance, for we have been unable to estimate the work required during cruise locomotion, and the comparison is in any case somewhat artificial, for neither salps nor the siphonophores swim at maximum performance for other than much shorter distances, but nevertheless, the comparison does emphasis the greater economy of the salp design.

One obvious reason for this is that unlike other animals, salps inhale the greater part of the water ejected as the propulsive jet via an anterior aperture, rather than via the same posterior aperture through which the propulsive jet issues. Assuming for simplicity that the salp travels forwards at constant velocity, consideration of momentum conservation indicates that inhalation anteriorly will lead to half the retarding force during refilling (refill drag) experienced if the salp operated like a siphonophore, and inhaled posteriorly; so that refilling the

jet chamber via the anterior aperture is significantly more economical than refilling from both ends, or refilling via the posterior aperture alone.

Finally, Weihs (1977) has made the interesting suggestion that animals using jet propulsion do so by emitting pulsatile jets, because these offer significant gains in thrust as compared with continuous jets. Whilst we may doubt his premise that continuous jet propulsion by muscular action is feasible for animals, his analysis shows that the thrust to be gained from pulsatile jets increases significantly when the ratio of the radius of the jet nozzle to jet frequency is three or less. For *S. fusiformis* operating at maximum performance, this ratio ranges from 3·2 for large blastozooids to 5·33 for small blastozooids (Table I) but will decrease as the salp swims more slowly. It seems reasonable to assume that the jet aperture and jet frequency of salps are arranged so that the salp gains the maximum advantage from the pulsatile jet system when it is cruising, as Weihs' analysis suggests.

Summary

Salps swim by jet propulsion, mainly inhaling water into the jet chamber via an anterior aperture, and exhaling the propulsive jet through a posterior aperture. They are capable of wide variations in the contraction of the locomotor muscle bands which produce the propulsive jet, so that there is a wide range of chamber pressures and of forward velocities. In addition, they can swim backwards by exhaling through the anterior aperture. The timing of the events of the jet cycle are described in *Salpa fusiformis*, and kinematic and pressure records are used to estimate the thrust generated, drag incurred, and work performed during forward swimming. Similar observations on chains of linked blastozooids indicate advantages for operating as chains rather than as isolated individuals.

It is concluded that in comparison with other jet-propelled designs, salps are more economical in operation.

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