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JET PROPULSION OF THE CALYCOPHORAN SIPHONOPHORES *CHELOPHYES* AND *ABYLOPSIS*

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(Figs. 1–6)

Jet propulsion in the small siphonophores *Chelophyes* and *Abylopsis* was investigated by measuring chamber pressures and thrust exerted in tethered nectophores, and by cinephotography of free swimming colonies. Although of similar design, the two siphonophores swim at different speeds, and with very different chamber pressures in the locomotor nectophores. Estimates of drag incurred during swimming, and of the cost of the process in the two forms are discussed.

INTRODUCTION

Several important groups of animals use jet propulsion for locomotion (see review by Trueman, 1980), and some progress has been made in analysing the process by a combination of kinematic records, and records of chamber pressures. The difficulty in obtaining kinematic data for larger animals (such as squid) or chamber pressures for smaller forms (such as small medusae) has prevented a complete analysis in any. The development of smaller and more sensitive pressure transducers has now made it feasible to obtain reliable records from small animals for which kinematic data can also easily be obtained. This paper reports the results of such a study on two species of small (1–2 cm) siphonophore colonies which swim by jet propulsion, using locomotor nectophores with a single inhalent and exhalent aperture.

MATERIAL AND METHODS

We examined the diphyid *Chelophyes appendiculata* (Eschscholtz), and the abylid *Abylopsis tetragona* (Otto) which were collected in plankton nets from 0–30 m depth in the Rade de Villefranche during March and April 1979 and 1980. Some colonies were collected individually by dipnetting from the sea surface. The colonies could be maintained in good condition for several days in large bowls of sea water in a cold room. Kinematic records were made with a Bolex 16 mm camera, using incident lighting; detailed measurement of changes in chamber apertures during jet cycles were made on nectophores lightly stained with methylene blue and restrained in a vertical position base upwards in small tubes. In some experiments, dried milk suspensions in sea water were introduced into the nectophore chamber to visualize flows during the jet cycle. The films were analysed with a Photo-optical data analyser model 224A.

Simultaneous chamber pressure and force measurements were made on nectophores in Petri dishes tethered by 25 μm stainless-steel wire to a strain gauge (Devices type ST 01 or Dynamometer UF1), accurate to $\pm 2{\cdot}3$ mg at 100 mg. A Millar instruments microtip pressure transducer fitted with a short polyethylene catheter tip was introduced into the chamber via the jet aperture.

Outputs from the calibrated pressure and tension transducers were led to a Tektronix 5103 storage oscilloscope and thence to a Gould Brush 220 pen recorder. The thickness of the locomotor muscle sheet was measured on electron micrographs of material fixed in 5 % glutaraldehyde in sea water buffered with 0·5 M sodium cacodylate and processed in the usual way.

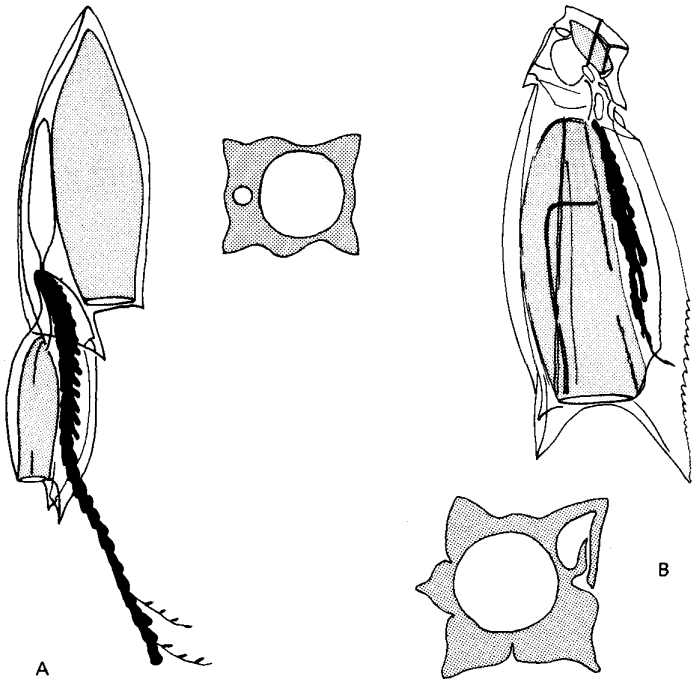

Fig. 1. *Chelophyes* (left) and *Abylopsis* showing two nectophores in each, with the myoepithelial subumbrella sheet lining the chamber stippled. Cross-sections of the mid-region of the larger nectophores of each show the arrangement of the mesogloeal flanges. Drawn from photographs kindly loaned by Dr Claud Carré.

OBSERVATIONS

General features of the colonies

Both species are predators, catching small organisms with a long fishing stem that depends from two linked nectophores which are unequal in size. In *Chelophyes* (Fig. 1 A) the anterior nectophore is larger than the posterior, but of similar streamlined shape: both are important in locomotion of the adult colony. In *Abylopsis*, on the other hand (Fig. 1 B), the anterior nectophore is cubic, and very much smaller than the posterior. It seems improbable that it can play any significant role in the locomotion of the adult colony.

The locomotor nectophores are lined with a thin subumbrellar myoepithelium in which individual cells are aligned circumferentially, transverse to the long axis of the nectophore. The cells are cross-striated, and propagate muscle action potentials (Chain, Bone & Anderson, 1981).

Contraction of the myoepithelium lining the chamber of the nectophore results in the

expulsion of a jet of water through the velar aperture during the first phase of the jet cycle. During the second phase of the cycle, water is drawn in through the same aperture to refill the chamber. There are no extensor muscles and refilling is brought about by the elasticity of the mesogloeal wall of the chamber. Narcotized animals are still elastic. In section, the chamber is circular, as is the exhalent aperture at its base, but the mesogloeal wall bears conspicuous flanges (Fig. 1). In different species, the form of the flanges is varied, and their shapes are used as taxonomic characters (Totton, 1954). Partly in consequence of this arrangement of flanges, the elasticity of the mesogloea surrounding the chamber rapidly restores resting volume after contractions of the subumbrellar sheet.

When first collected from the plankton, both species are usually very slightly denser than sea water, and sink slowly to the bottom of their containers. In large aquaria, they swim intermittently, apparently spontaneously, and also swim in response to vibration or to light touch. The two species show very characteristic and different swimming patterns.

Locomotor behaviour

The minute anterior nectophore of *Abylopsis* contracts when the large posterior nectophore is active, but it can hardly play any role in the swimming of the adult colony. The anterior nectophore develops first, and presumably is used during locomotion of the young colonies before the posterior nectophore develops.

The adult colonies which we observed rarely showed 'spontaneous' activity, but if stimulated, swam by a series of contractions of the posterior nectophore around 2·5 Hz, reaching instantaneous velocities up to 8 cm/s (Fig. 2A). Similar contraction bursts were observed in tethered colonies (Fig. 3A), and in addition, occasional pairs of apparently 'spontaneous' contractions were also occasionally observed (Fig. 3B).

It seems possible that the former long series of contractions represent an escape response to stimulation, or a means of translating the colony to a more favourable patch of water for fishing, whereas the latter pairs of contractions may represent a reflex for maintaining the position of the colony in the water column, driving it briefly upwards in the intervals of sinking slowly.

The locomotion of *Chelophyes* is more complicated, and was briefly described by Totton (1954, p. 129). When it is fishing, the colony hangs vertically in the water with the anterior nectophore upwards and the stem extended. It sinks slowly, but maintains its horizontal position in the water column by an occasional series of contractions of the posterior nectophore at frequencies around 0·5 Hz, which drive it slowly upwards at speeds up to 1 cm/s. Such reflex maintenance of horizontal position is typical of many planktonic animals that are denser than sea water, such, for example, as chaetognaths or doliolids.

When the colony is disturbed, however, it shoots away with astonishing rapidity, attaining instantaneous velocities up to 30 cm/s during short bursts of contractions of both anterior and posterior nectophores at frequencies up to 8 Hz. During such escape movements, the stem is retracted to minimize drag and increase escape speed, and the colony is driven 20 cm or so from its original position. Figs. 2B and C show instantaneous velocities of the colonies during these two different swimming modes. In large aquaria,

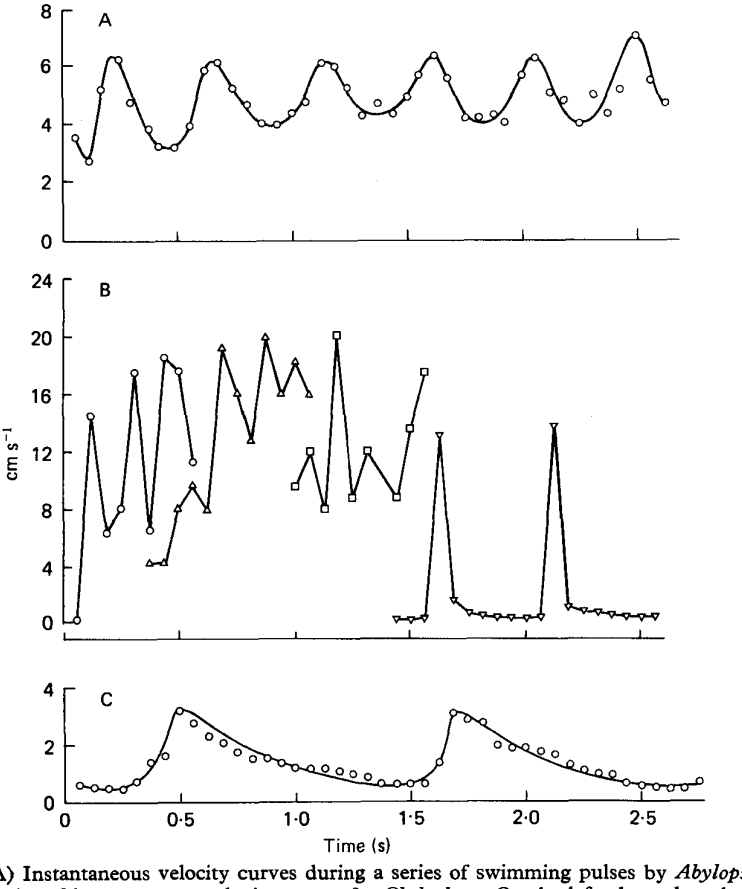

Fig. 2. (A) Instantaneous velocity curves during a series of swimming pulses by *Abylopsis*. (B) Similar series of instantaneous velocity curves for *Chelophyes*. On the left, three short bursts of jet pulses by both nectophores; on the right, two single pulses showing deceleration after each pulse. (C) Instantaneous velocity curves from a series of locomotor pulses by the small posterior nectophore alone in *Chelophyes*.

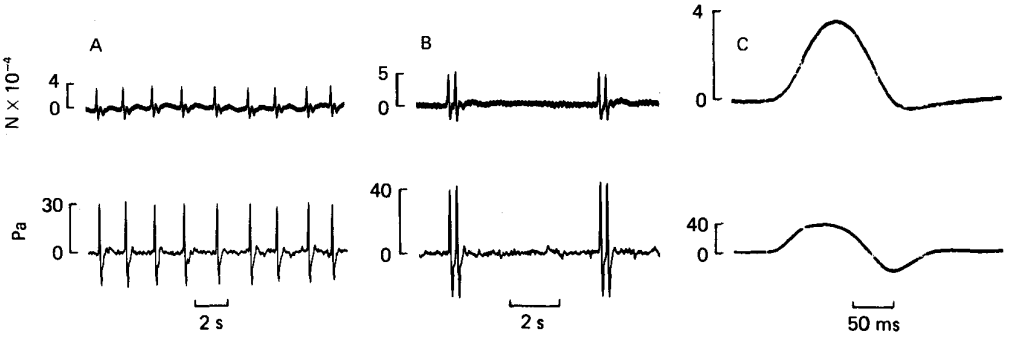

Fig. 3. (A) Simultaneous tension (upper) and chamber pressure records during a series of pulses by a tethered colony of *Abylopsis* (scale bars: 4×10^{-4} N; 30 Pa; 2 s). (B) Similar records from colony showing pairs of jet pulses (scale bars: 5×10^{-4} N; 40 Pa; 2 s). (C) Single jet cycle (scale bars: 4×10^{-4} N; 40 Pa; 50 ms).

colonies show more or less regular 'spontaneous' short bursts of activity (as do anterior nectophores isolated in small dishes) and it is possible that normal fishing involves this kind of rapid activity, which serves to allow the fishing filaments to sample a larger area of water in the same sort of way as does the 'veronica' behaviour pattern of the diphyid *Muggiaea* described by Mackie & Boag (1963). In *Chelophyes* it seems that such movements only involve the anterior nectophore (Mackie & Boag), unlike the escape reaction in which both nectophores are active.

It is obviously difficult to know whether patterns of behaviour observed in artificial conditions approximate to those exhibited under natural conditions, but in any event, it is clear that the two functional nectophores of *Chelophyes* permit a wider range of swimming speeds than are shown by *Abylopsis*, and this difference in design has important bearings on the efficiency of locomotion.

Table 1. *Summary of measurements made*

	Chelophyes			
	Anterior nectophore	Posterior nectophore	Both nectophores	*Abylopsis*
Overall length (cm)	1·2	0·88	1·89	2·2
Chamber length (cm)	1	0·6	—	1·7
Body volume, including chamber (cm^3)	0·1	0·05	0·15	1·1
Volume water expelled in jet (cm^3)	0·035	0·006	0·041	0·17
Jet orifice (velar opening) inhalent/ during jetting (cm^2)	0·02/0·014	0·0095/0·0064	—	0·07/0·07
Cycle frequency (Hz)	4–8	4–5	4–8	0·6–2·5
Maximum chamber pressure (Pa)	750	360	—	42
Mean maximum chamber pressure during burst of jet cycles (Pa)	400	250	—	25–30
Maximum inhalent pressure (below ambient) (Pa)	35–80	15	—	18
Duration of jet pulse (s)	0·035–0·08	0·1	—	0·11
Duration refilling chamber (s)	0·05–0·1	0·18	—	0·25
Maximum tethered thrust ($N \times 10^{-3}$)	1–2	0·3	—	0·4–0·55
Maximum instantaneous swimming velocity ($cm\ s^{-1}$)	24	3·2†	30*	8
Mean swimming velocity during burst ($cm\ s^{-1}$)	16	1·5†	20*	3
Mean jet velocity during jetting ($cm\ s^{-1}$)	30	9·5	—	22
Maximum jet velocity at maximum pressure ($cm\ s^{-1}$)	121	83·7	—	28·6
Maximum acceleration ($cm\ s^{-2}$)	358	58†	530*	23
Deceleration from maximum velocity ($cm\ s^{-2}$)	−335	−14†	−530*	−10

* Both anterior and posterior nectophore contracting simultaneously.
† Linked anterior and posterior nectophores, posterior nectophore alone contracting.

Chamber pressures and measured thrust

Abylopsis

The jet cycle in *Abylopsis* occupies some 300–360 ms, peak pressure of 40 Pa being reached after 50 m (Fig. 3). Static thrust was around 5×10^{-4} N (Table 1). During the jet cycle, the velar aperture only changes insignificantly and the ratio of the duration of the exhalent to inhalent phase of the jet cycle is around 1:2·3. These values are for the

large posterior nectophore; we did not attempt to record pressure or static thrust from the minute anterior nectophore.

Chelophyes

The jet pulses of the anterior nectophore of *Chelophyes* are much more rapid events than those of *Abylopsis*, lasting some 35–80 ms, and rising to peak pressure over 800 Pa in less than 30 ms (Fig. 4). The whole cycle lasts some 80–180 ms, the ratio between the

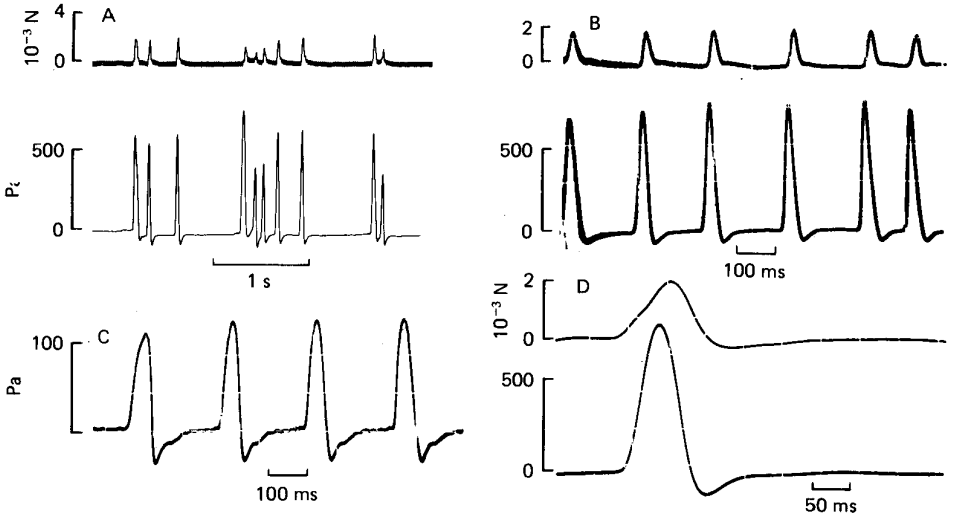

Fig. 4. (A) Simultaneous tension (upper) and pressure records from tethered anterior nectophore of *Chelophyes* (scale bars: 4×10^{-3} N; 500 Pa; 1 s). (B) Similar record taken during a 'spontaneous' burst (scale bars: 2×10^{-3} N; 500 Pa; 100 ms). (C) Pressure pulses from posterior nectophore (scale bars: 100 Pa; 100 ms). (D) Single jet cycle of anterior nectophore (scale bars: 2×10^{-3} N; 500 Pa; 50 ms).

duration of expulsion and inhalation phases being 1:1·3. Unlike *Abylopsis*, the velar aperture varies in size during the jet cycle, being at its smallest during the expulsion phase (Table 1). Maximum thrusts of $1–2 \times 10^{-3}$ N were recorded from tethered nectophores, but plots of chamber pressure *vs* static thrust showed a large scatter, and it seems probable that values for static thrust included a dynamic component (see Discussion) and are therefore biased high. The posterior nectophore produces similar jet pulses to the anterior, but maximum pressures and measured thrust are lower (250 Pa and 3×10^{-4} N). The whole cycle occupies some 150–180 ms, and peak pressure is reached after 50 ms.

During rapid escape responses, both nectophores contract at frequencies up to 8 Hz, and this rapid succession of jet cycles in a swimming burst not only requires that the cycles should be rapid events, but also leads to the notable difference between *Chelophyes* and *Abylopsis* in the control of the velar aperture (see Discussion).

From these measured values for chamber pressure, and the duration of the phases of the jet cycle, together with measurements of jet aperture, maximum instantaneous

velocities, accelerations and deceleration during swimming from kinematic records (Table 1) we can proceed to calculate the expected performances of the two designs. Mean jet velocity was calculated by dividing the volume expelled in unit time (estimated from dimensional changes of the nectophore) by the area of the jet aperture, while maximum jet velocity was calculated from the relation between jet velocity and pressure (jet velocity, $q = \sqrt{(2P)/\rho}$, where P is the chamber pressure and ρ the density of sea water; Johnson, Soden & Trueman, 1972). In the case of *Abylopsis*, jet velocities could also be directly measured by examination of kinematic records of colonies where milk suspensions had been injected into the posterior nectophore. Successive frames from a film of this kind of experiment are shown in Fig. 5. As the fluid passes out of the jet orifice so surrounding fluid interacts with the borders of the jet to form a vortex ring that proceeds backwards at a velocity lower than that of the main jet stream. Presumably these rings are turbulent (see Sallet & Widmayer, 1974) and hence their translational velocity is considerably lower than that of the fluid emerging from the orifice. It might perhaps be expected that the jet would break up close to the orifice, but it actually persists with a pattern of vortex rings passing away from the base of the nectophore.

DISCUSSION

The nectophores of both species are well streamlined, in shape similar to artillery shells or rockets, of fineness ratio 3–4. *Chelophyes* swims at two different velocities (according to which nectophores are active), whilst *Abylopsis* swims only at an intermediate velocity between these, much more slowly than the rapid swimming of *Chelophyes*. The two species thus offer an interesting contrast between essentially similar jet propulsion designs operating in different ways at Reynolds numbers between 500 and 5000. For example, in one design the jet aperture changes markedly during the cycle, whereas in the other it does not, and the two operate at very different chamber pressures and jet cycle times.

During a single jet cycle we can assume that the same volume of water is inhaled as is exhaled, ready for the next cycle to begin. In *Abylopsis*, where the jet aperture remains almost constant throughout the cycle, if the two phases of the cycle were equal in duration, the colony would simply oscillate backwards and forwards, but net forward thrust is obtained by increasing the duration of the inhalent phase, and hence negative pressure and inhalent jet velocity is lower than the positive pressures and jet velocities during the propulsive phase. Refilling the chamber through the jet aperture in this way inevitably produces negative thrust (or refill drag) in addition to normal profile drag. In the nectophores of *Chelophyes*, where cycle frequency is high, there is insufficient time simply to lengthen the inhalent phase as compared to the exhalent, and although in the anterior nectophore the refilling phase is slightly longer than the exhalent, it is necessary to reduce inhalent chamber pressures and jet velocities by increasing the size of the aperture from its size during the expulsion phase. In *Chelophyes*, therefore, the velar muscle ring surrounding the aperture contracts as the subumbrella contracts, reducing the jet aperture by some 50% during expulsion, relaxing and enlarging the aperture during inhalation.

To determine how these differences in the jet cycles are reflected in the performance

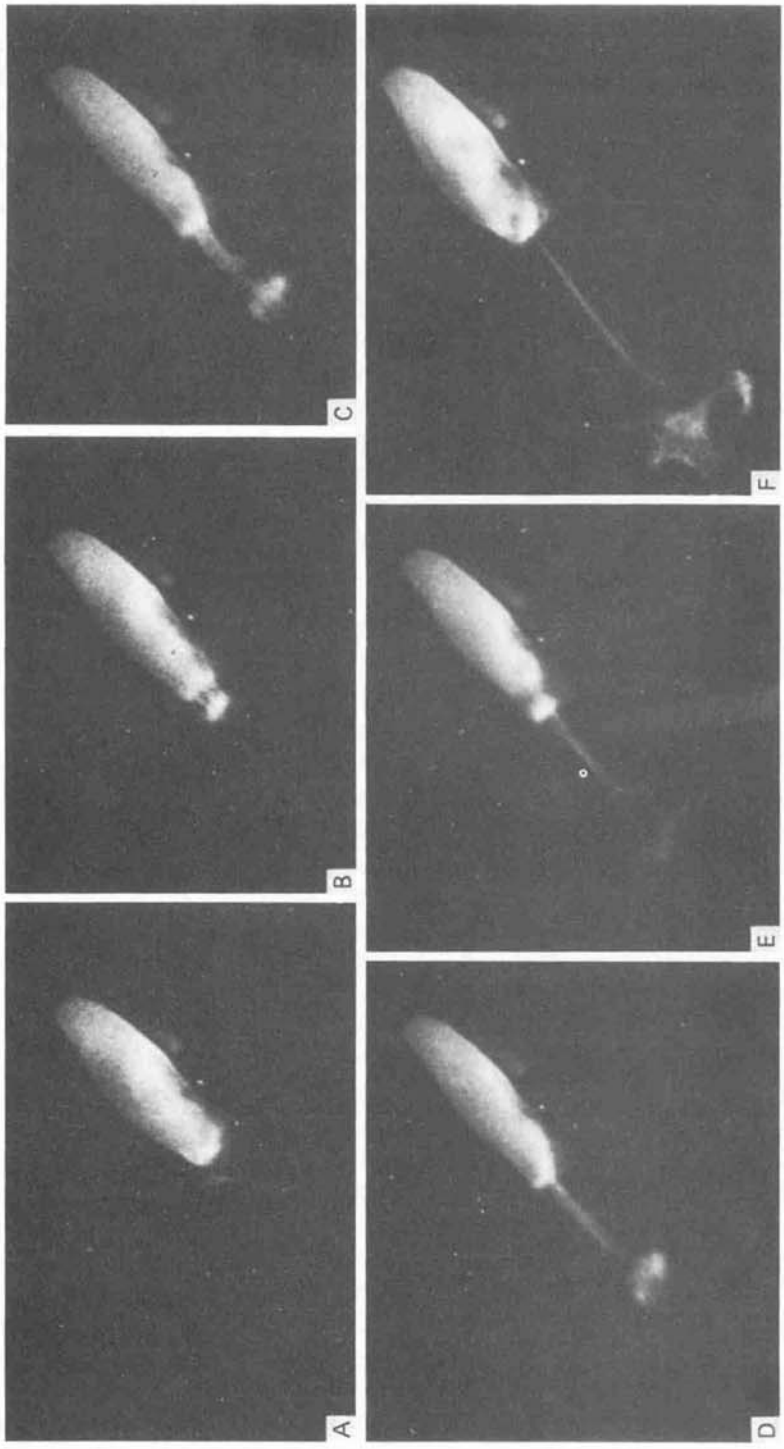

Fig. 5. Successive frames from sequence of *Abylopsis* jet cycle after injection with milk suspension. The pictures are 62·5 ms apart. Note expanded chamber (opaque) in (A) and (F); contracted in (C); refilling begins in (D). The milk trace from the aperture in A is from the tip of the cannula used to introduce milk into the chamber. Only the chamber is visible in these photographs (cf. Fig. 1).

of the two designs, we first compare the thrust generated by each and discuss methods of estimating the drag incurred, and then consider the work done in each cycle.

Thrust and drag

We have measured the thrust generated during single jet cycles of tethered animals, where chamber pressure was simultaneously monitored (Figs. 4, 5), so that under conditions where the jet pulse operates on stationary water behind the aperture, measured thrust can be compared with that calculated from $T = 2aPC_{dn}$ (where a is the jet aperture area, P the chamber pressure and C_{dn} the drag coefficient of the jet nozzle; Johnson *et al.* 1972). In the limiting case where viscosity is neglected and no frictional losses take place at the jet nozzle, $C_{dn} = 1$. Thrusts calculated on this basis are expected to be significantly greater than those actually measured, for at the low Reynolds numbers involved viscous effects will predominate, and frictional losses will certainly be incurred at the jet nozzle, so that C_{dn} will be less than unity. However, values of C_{dn} to yield identity of calculated and measured thrust were usually *greater* than unity for the anterior nectophore of *Chelophyes*! This anomaly probably arises because the powerful rapid oscillatory activity of this nectophore results in the addition of a dynamic component to the static thrust measured. The nectophores were attached to a strain gauge by a short, thin, inextensible (but flexible) stainless-steel wire, and during the jet cycle this connexion probably slackened and tautened slightly. In this way, measured thrusts for the *Chelophyes* anterior nectophore were over-estimated. Measurements on the larger *Abylopsis* operating at a much lower frequency and the much smaller posterior nectophore of *Chelophyes* did not suffer so seriously from this problem, and C_{dn} values for these are less than unity.

The values for C_{dn} obtained for the posterior nectophore of *Chelophyes* and for *Abylopsis* are higher than that estimated for squid ($C_{dn} = 0{\cdot}6$) by Johnson *et al.* (1972), but maximum jet velocities for siphonophore nectophores are considerably less than for squid, and losses are expected therefore to be less. As a first approximation, we have estimated C_{dn} to be around 0·7 for the anterior nectophore of *Chelophyes*, 0·8 for the posterior nectophore, and 0·85 for *Abylopsis*.

During the jet cycle the effective thrust generated will vary for two reasons (apart from change in chamber pressure). First, the values for C_{dn} inferred above are based on the *mean* jet velocity throughout the period that chamber pressure is above ambient, and in reality, C_{dn} is likely to vary throughout the cycle, depending upon jet velocity. Secondly, during unrestrained swimming, the ratio between jet velocity and forward velocity will change, and thus effective thrust inferred from chamber pressure will vary.

However, at the peak of the instantaneous velocity curves for free-swimming colonies (Figs. 2, 3), thrust may be estimated from $T = C_{dn}\, paQ^2$ (where C_{dn} is the drag coefficient for the jet orifice, p the density of sea water, a the area of the jet orifice and Q the jet velocity – forward velocity).

Using the values of C_{dn} assumed above, calculated thrust at maximum velocity is $0{\cdot}238 \times 10^{-3}$ N for *Abylopsis* colonies, and $0{\cdot}641 \times 10^{-3}$ N for *Chelophyes* colonies. It is important to notice that lower values for C_{dn} (i.e. higher frictional losses at the jet aperture) will reduce these thrust estimates, and as we have seen, the values taken for C_{dn} can only be considered reasonable approximations.

Several possible approaches to estimates of the drag incurred by the colonies during swimming (and hence to the problem of the work performed) are possible. It is a simple matter to determine the drag incurred under steady-state conditions by making kinematic measurements upon weighted nectophores falling freely in large cylinders of sea water. Both the anterior nectophore of *Chelophyes* and the *Abylopsis* colony yielded values for drag coefficients under these conditions around 0·4, i.e. values similar to those obtained by streamlined shapes (water beetles) at low Reynolds numbers by Nachtigall (1976). However, the volume drag coefficient during the rapidly accelerating and decelarating motions of the jet cycles is likely to be significantly higher than this, since steady-state boundary layers will not be formed, and shear stresses will be higher than under steady-state conditions.

At the peak of the instantaneous velocity curves the colony is neither accelerating nor decelerating, and at this single point, therefore, thrust will be equal to drag. If steady-state boundary-layer conditions were applicable at this point, volume drag coefficients could be calculated from:

$$C_{dv} = \frac{\text{thrust } (= \text{drag})}{0{\cdot}5 \times \rho \times V^2 \times \text{volume of colony}^{\frac{2}{3}}},$$

where V is the forward velocity. This method yielded volume drag coefficients significantly higher than that obtained by filming nectophores dropping in water to terminal velocity (anterior nectophore of *Chelophyes*, $C_{dv} = 0{\cdot}85$; *Abylopsis* colony = 0·68) but it is inappropriate for rapid oscillatory motion.

A third approach to the problem of drag is to obtain drag coefficients from the decelerations observed during the inhalation phase of the jet cycles. This gave, for the *Chelophyes* colony, volume drag coefficients between 0·57 and 0·89 (mean 0·68); and for the *Abylopsis* colony values between 0·6 and 1·1 (mean 0·83). These values are obviously only approximate, but again, they suggest that C_{dv} will be above that inferred from steady-state measurements. Deceleration involves refilling the chamber, hence these drag estimates include refill drag in addition to profile or volume drag. Drag estimates obtained in the ways mentioned above may be used to determine power outputs and the work performed during swimming, but as indicated, each approach suffers from objections. In the next section, a different approach will be considered that enables direct estimates of the work performed to be made, including the work required to overcome the elastic force of the mesogloea responsible for refilling the chamber.

Work done during locomotion

The pressure pulses resulting from contractions of the subumbrella muscle can be followed accurately (Figs. 4, 5) in tethered nectophores. The pressure transducer tip occupied 9·0% of the aperture area in the anterior nectophore of *Chelophyes*; 1·8% of the area in the larger *Abylopsis*. Measurements of pressure pulses in single individuals using tips of different sizes showed that no significant change in pressure resulted from increase in tip area to occupy 6·0% of the aperture in *Abylopsis*, whilst in *Chelophyes* the pressures recorded were probably biased high by 2–5% (neglected in our calculations). These results are in accord with work on the effects of restrictions in pipes on pressures

before and after the restriction (de Bernardinis, Graham & Parker, 1981) that suggest that the effect of aperture restriction in our experiments was unlikely to be large.

Since jet efflux velocity during the exhalent pulse depends upon the difference between chamber pressure and ambient pressure, volume changes will follow pressure changes, and can be obtained by integration of the pressure pulse, provided initial and final chamber volumes are known. The work done during the pulse is pressure (FL^{-2}) × volume (L^3) and can therefore simply be obtained by multiplying the digitized pressure pulse by its integral, assuming that the volume changes during the exhalent pulses observed from kinematic records of free-swimming nectophores are the same as those during the pressure pulses monitored on tethered nectophores, and that the jet orifice does not change during the exhalent pulse. This approach, suggested to us by Dr J. V. Howarth, can also be applied to the inhalent pulses, so the total work performed by the subumbrella muscle sheet in overcoming mesogloeal elasticity and in expelling water from the chamber can be estimated.

Table 2. *Summary of swimming performance*

Details of estimates in text.

	Chelophyes			
	Anterior nectophore	Posterior nectophore	Both nectophores	*Abylopsis*
Reynolds number at maximum velocity	2900	550	5100	1800
Estimated jet thrust at maximum instantaneous velocity, C_{dn} as text ($N \times 10^{-3}$)	0·538	0·102	0·641	0·238
Volume drag coefficient (C_{dv}) during steady motion	0·41	—	—	0·40
C_{dv} at maximum instantaneous velocity estimated from maximum thrust above	0·51	0·83	0·56	0·50
Estimated maximum negative thrust during inhalation ($N \times 10^{-3}$)	0·168	0·017	—	0·15
Maximum muscle tensions (N/cm^2) (not including mesogloeal elasticity)	17·94	3·9	—	0·84
Muscle tension to overcome mesogloeal elasticity (N/cm^2)	1·96	0·165	—	0·36
Maximum muscle stress during contraction (N/cm^2)	19·7	4·07	—	1·2
To swim 1 m				
Time (s)	6·25	66	5	33
Approx. no. of jet cycles	30	260	25	60
Volume water jetted (cm^3)	1·05	1·56	1·025	10
Work performed over 1 m (J/kg) (body wt. includes water in chamber)	29	—	—	3

This method gave the total work per cycle for *Abylopsis* to be $5{\cdot}4 \times 10^{-5}$ J and for the anterior nectophore of *Chelophyes* $9{\cdot}7 \times 10^{-5}$ J. At maximum swimming speed, *Abylopsis* operates at 2 cycles s^{-1}, *Chelophyes* at 8 cycles s^{-1}, so that these values for the work performed correspond to power outputs of 1·08 and $7{\cdot}75 \times 10^{-4}$ W respectively. One way of comparing the different performance of the two, and comparing them with other animals, is to consider unit locomotory cost, in terms of the work required to travel 1 m per kg of body mass. This is evidently an entirely artificial comparison, for neither

siphonophore travels for 1 m with a sustained burst of contractions. A single contraction of both nectophores of *Chelophyes* drives the colony forwards some 2·5 cm, and a typical short swimming burst would drive the colony forwards at most some 25 cm. However, the comparison (Table 2) clearly shows that the unit cost for *Chelophyes* is about 10 times greater than that for *Abylopsis*, despite the fact that to cover the same distance, *Abylopsis* ejects nearly 10 times the volume of fluid (during more than twice the number of jet cycles) than does *Chelophyes*.

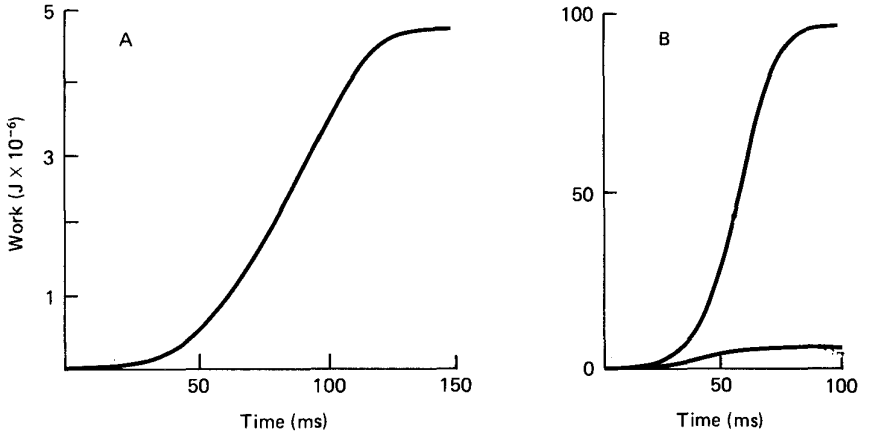

Fig. 6. (A) *Abylopsis*: cumulative work performed during pulse (joules $\times 10^{-6}$) work/g/pulse: $2{\cdot}12 \times 10^{-3}$ J. (B) *Chelophyes*: cumulative work performed during pulse by anterior (upper curve) and posterior nectophores (joules $\times 10^{-6}$). Work/g/pulse: $32{\cdot}6 \times 10^{-2}$ J.

The greater economy of *Abylopsis* certainly reflects the fact that it is a more economical process to achieve the forward thrust required by ejecting a large volume of water at low velocity from a large aperture than by ejecting a smaller volume at higher velocity from a small aperture. It also has to be borne in mind that the short swimming bursts of *Chelophyes* can be considered as escape reactions, where maximum speed rather than economy of operation is paramount, and thus lower efficiency can be accepted.

To achieve their performance the two siphonophores employ thin sheets of subumbrella muscle. How do the forces generated by these sheets compare with those known from more 'conventional' muscles? We can estimate the maximal stresses produced by the myoepithelial sheets as they perform work during the jet cycle from $T = Pr$ (P is the chamber pressure; r the chamber radius), using the dimensions of the sheet obtained by direct measurement (Table 1). The force/unit area is very different in the two species.

In *Abylopsis*, maximal stress is only 0·84 N/cm^2, whilst in *Chelophyes* it is 17·94 N/cm^2 in the anterior nectophore at chamber pressures of 820 Pa, around 7 N/cm^2 at 320 Pa. These values do not take account of the forces required from the muscle to overcome the elastic force resulting from deformation of the mesogloeal chamber wall, responsible for refilling the chamber when the muscle relaxes. Our attempts to measure this force directly, by deforming the chamber artificially, were unsuccessful, since we could only deform it in a single plane, quite differently from the natural symmetrical changes in shape of the nectophore as the muscle sheet contracts. However, if we assume insignificant

hysteresis in the mesogloeal wall, the elastic force can be estimated from the negative chamber pressures during refilling, and this force can then be added to the maximal muscle stresses calculated above.

As seen in Table 2, the mesogloeal elastic stress is a significant fraction of the total in the slower contracting *Abylopsis*; in the more rapidly-contracting *Chelophyes* it is a smaller proportion of the total. But in *Chelophyes* (where rapid refilling is needed to enable high cycle frequency) the elastic stress of the mesogloeal wall would be expected to be higher than in the slower *Abylopsis*, and this is the case. Addition of this component to the maximal muscle force gives values for maximal muscle stress for *Chelophyes* around 20 N/cm^2; for *Abylopsis* around 1·2 N/cm^2.

The muscles are not contracting isometrically, but the maximum value for *Chelophyes* is comparable to those of twitch fibres in other forms operating under isometric conditions (20–50 N/cm^2). Assuming that the density of the myoepithelial sheet is 1060 (Méndez & Keys, 1960), the anterior nectophore of *Chelophyes* contains $3{\cdot}67 \times 10^{-4}$ g of muscle, the posterior nectophore $1{\cdot}1 \times 10^{-4}$ g, whilst the posterior nectophore of *Abylopsis* contains $2{\cdot}26 \times 10^{-3}$ g. From this the posterior nectophore of *Abylopsis* develops $2{\cdot}4 \times 10^{-3}$ J/g muscle per cycle and the anterior nectophore of *Chelophyes* about 100 times as much, $26{\cdot}4 \times 10^{-2}$ J/g/cycle (Table 2).

No information is available for the force/velocity relations in these siphonophore muscle sheets, but estimates of contraction speed from measurements of chamber radius when relaxed and fully contracted show that in the anterior nectophore of *Chelophyes* the muscle contracts at some 2·2 cm s^{-1} so that the unloaded speed is presumably higher than this, and the maximum power developed likely to be greater than that from, say, frog twitch muscle fibres.

Comparison with other forms

Chelophyes and *Abylopsis* represent two extremes of calycophoran organization; the one well streamlined with a much larger anterior nectophore, the other well streamlined, with the power for swimming provided solely by the large posterior nectophore. Other species are differently organized, for example the poorly streamlined *Abyla* has a smaller anterior nectophore, but unlike *Abylopsis* this is some two-thirds the size of the posterior. Almost nothing is known of the habits of other diphyids but what is known about *Chelophyes* and *Abylopsis* suggests that all are either designed for maximum escape velocity, or for slower and more continuous swimming, and that the former have larger anterior nectophores, the latter larger posterior nectophores. Thus the well-streamlined *Lensia* resembles *Chelophyes*, whilst the less-well-streamlined *Sulceolaria* and *Abyla* resemble *Abylopsis*, and have larger posterior nectophores.

When the stem is extended, thrust from either anterior or posterior nectophore will result in forward motion more or less in a straight line, but retraction of the stem (to reduce drag) must be common to all forms except perhaps during the few nectophore contractions required to maintain horizontal position. The function of the escape responses of the rapidly swimming forms is to drive the colony as far as possible from the site where it was stimulated, and with the stabilizing stem retracted it is likely to be simpler to swim rapidly in a direct line if thrust is provided by the anterior nectophore,

rather than by a posterior nectophore. We do not know why it is that rapid escape responses are apparently characteristic only of some diphyids but the possession of two functional thrust-producing nectophores obviously confers more flexibility on the way in which the colony swims than is found in *Abylopsis* for example.

Several more 'advanced' groups than diphyids use jet propulsion; and have more complex systems of doing so. Thus, salps inhale water into the jet chamber anteriorly, and expel it through a different aperture posteriorly, whilst squid inhale through a large mantle aperture, and exhale through a much smaller siphonal aperture. The most similar forms to diphyids are hydrozoan medusae, most of which swim relatively slowly, but the trachyline *Aglantha* (Donaldson, Mackie & Roberts, 1980) has a striking rapid escape response, when it achieves peak velocities of 0·3–0·4 m s^{-1}. *Aglantha* is an elongate streamlined medusa and its performance is of the same order as *Chelophyes*, but it is about twice as long. Unfortunately, no data are available on the pressures w.thin the chamber of *Aglantha* during the jet cycle, and no estimates can be made of the thrust generated and the work performed. Gladfelter (1972) has provided a detailed kinematic analysis of *Polyorchis*, which swims at peak velocities of 0·03 m s^{-1} and has estimated efficiency ranging from 0·34 to 0·64 in jet cycles by different individuals.

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