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OXYGEN CONSUMPTION IN SWIMMING SALPS (TUNICATA: THALIACEA)

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The pelagic salps swim in a regular rhythmic manner, by contracting their muscle bands and so emitting propulsive jets of water from the tubular body. Since they will continue to swim when confined in small chambers in which their oxygen consumption can be measured whilst their activity is monitored, it is possible to make direct estimates of the energetic cost of locomotion, and to compare these with estimates derived from the hydrodynamics of the process (Bone & Trueman, 1983). We show here that salp locomotion is an economical process, and that respirometric and hydrodynamic estimates of the energy expended are in good agreement.

Two kinds of observations were made, using *Salpa fusiformis* (Cuvier) collected from the Rade de Villefranche in coarse plankton nets during May and June 1983.

In the first, single freshly caught oozooids and blastozooids were placed in a small (approx. 30 ml) chamber filled with sea water filtered through a 0·25 μm filter and shaken with air to saturate with oxygen before the animals were placed in the chamber. The chamber was placed in a bath at constant temperature (14·5 °C) and oxygen levels in the chamber were monitored with a Strathkelvin Instruments 781 b oxygen meter and Radiometer Instruments oxygen electrode. The salps were usually quiescent for a few minutes before beginning to pulse at a steady rate, monitored throughout the experiment. The activity of the salp sufficed to stir the water within the chamber. After each run, the chamber was opened, and a small amount of MS 222 added. This stopped locomotor activity, but not the action of the cilia of endostyle and gill bar, nor that of the heart. Since the salps were inactive, the water within the chamber was stirred by shaking the chamber at intervals; readings were taken at set intervals after each stirring. The same procedure was adopted for blank runs on filtered sea water. In some of these experiments, a Millar instruments microtip pressure transducer fitted with a small polyethylene catheter tip recorded pressure changes in the body chamber of the salp, and so monitored swimming activity, but for most runs, the rate of swimming was simply noted with a stopwatch. Outputs from the pressure transducer and oxygen meter led to a Gould Brush 220 pen recorder *via* a Tektronix 5103 oscilloscope.

Key words: Salps, respirometry, swimming.

In the second series of experiments, salps were placed in filtered sea water (at 10 °C) in dark vessels (approx 125 ml) and the oxygen consumed determined by Winkler titration after 3 h. To ensure that the salps were swimming during the experiments, the vessels were placed on a shaker agitating the vessel at 0·5 Hz.

Fig. 1 shows the total oxygen consumption of a size range of blastozooids and oozooids determined using the oxygen electrode, together with data from Winkler titrations for a series of oozooids. During these experiments, the salps swam at a regular rate as seen in the inset of Fig. 1, and oxygen consumption was correspondingly uniform. Fig. 2 shows the oxygen consumption resulting from locomotor activity, after subtraction of the basal (anaesthetized) rate from total oxygen consumption. In Fig. 1 the numbers of contractions min^{-1} are shown next to each measurement.

Although contraction frequency remained the same during an experiment, salps are able to grade their locomotion over a wide speed range not only by altering contraction

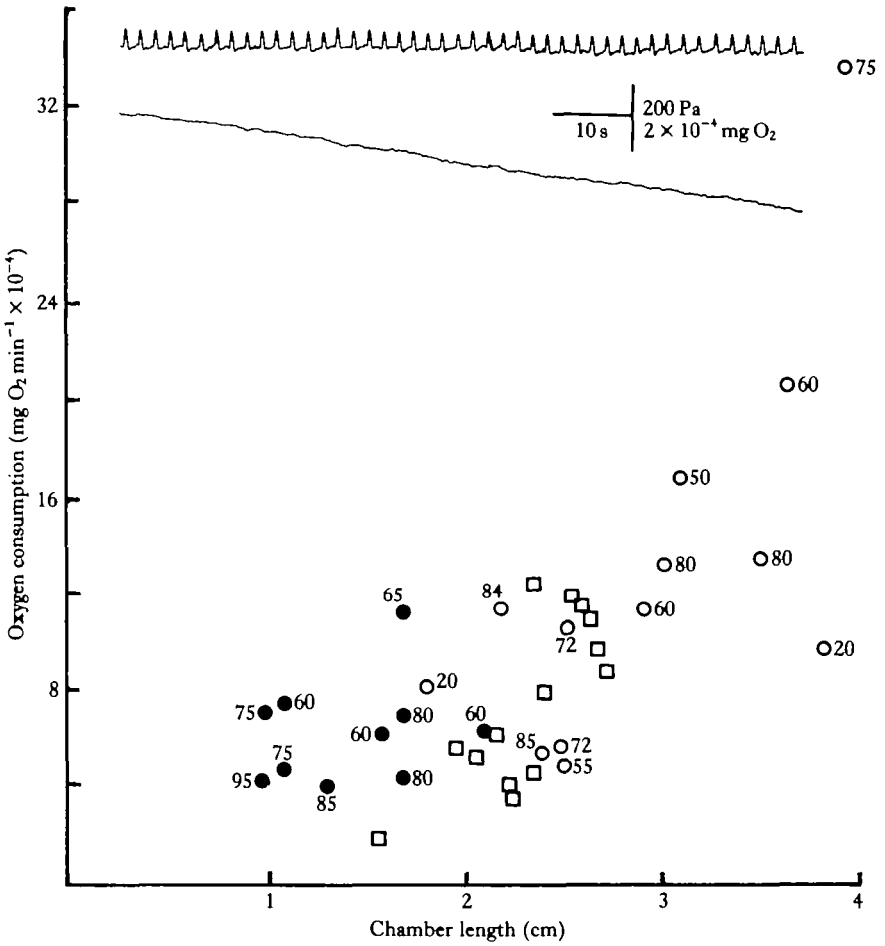

Fig. 1. Total oxygen consumption of a size range of blastozooids (filled circles) and oozooids (open circles and squares). Numbers next to points are contractions (jet pulses) min^{-1}. Circles determined with oxygen electrode: squares by Winkler titration. Inset: record of pressure pulses (upper) and oxygen consumption of blastozooid 1·7 cm chamber length showing regular swimming in respirometer chamber.

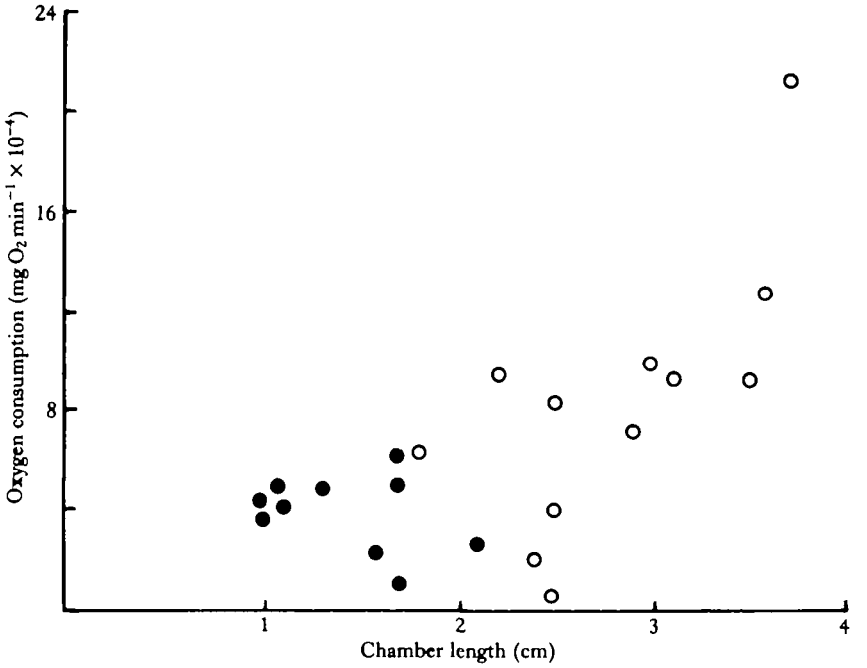

Fig. 2. Oxygen consumption of locomotor muscles in blastozooids (filled circles) and oozooids (open circles). Basal respiratory rate subtracted from total consumption.

frequency, but also by changing the extent of contraction of the locomotor muscle bands at each contraction. Thus, even though two individuals (or the same individual on different occasions) may show the same number of contractions min^{-1}, in one case the contractions may be shallow, with low chamber pressures and hence low velocity jet pulses, whilst in the other, the muscles may be more active, and chamber pressures and jet pulses correspondingly greater. Some of the scatter seen in Figs 1 and 2 may be ascribed to differences in basal rate (and our method of estimating basal rate by addition of MS 222 is not free from objection); however, the greater part of the variability between different animals almost certainly results from the wide variability in swimming performance reflecting the delicate control of the locomotor system in salps. It is not surprising therefore that salps of similar size show considerable variation in the oxygen consumed by the locomotor muscles, and that oxygen consumption is not necessarily directly related to contraction frequency (Fig. 1).

From the measurements shown in Fig. 2, the mechanical energy expended during each contraction may be estimated (Fig. 3), assuming that the efficiency of conversion of chemical to mechanical energy in the aerobic locomotor muscles is 20 %.

The open and closed large circles in Fig. 3 represent the calculated mechanical energy per contraction for an oozooid and blastozooid, obtained by analysis of the pressure pulses recorded during *maximum* performance (Bone & Trueman, 1983).

The animals swimming in the respirometer chambers were certainly not swimming at maximum performance (for example, the solid large circle represents calculated mechanical energy expended by a blastozooid operating at 128 Pa chamber pressure, whereas measured chamber pressure for a similarly-sized blastozooid swimming in the

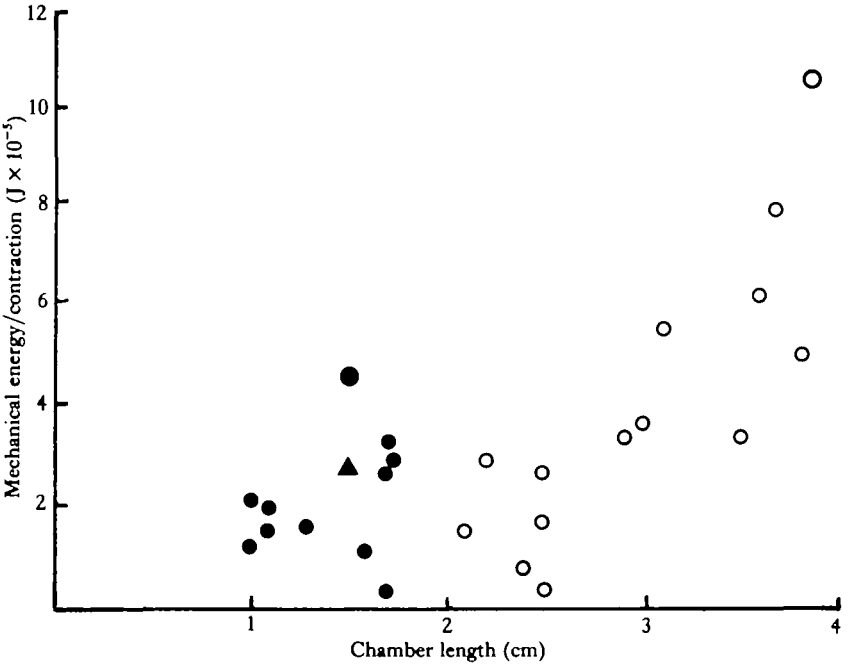

Fig. 3. Work performed during each contraction (assuming 20 % efficiency of conversion of chemical to mechanical energy) in blastozooids (filled circles) and oozooids (open circles). Large circles: work performed during maximum performance calculated from analyses of pressure pulses. Triangle: work performed similarly calculated for cruising performance (see text).

respirometer was only 85 Pa). The solid triangle in Fig. 3 gives the mechanical energy expended as calculated from this lower pressure pulse, assuming that a similar volume of water was ejected in a similar time as during the higher pressure pulse.

It seems safe to conclude that, when cruising, salp expend about half the energy required during maximum performance. We have shown previously (Bone & Trueman, 1983) on hydrodynamic grounds, that there are significant energy savings to be gained by the linkage of blastozooids into long chains, but even for isolated individuals, cruise locomotion involves little energy expenditure. Dry weights of watery gelatinous animals like salps are difficult to determine (although Mayzaud & Dallot, 1973 give a value for oxygen consumption of *S. fusiformis* of 7·7 μl O_2 mg^{-1} dry wt day^{-1}, it is impossible to compare their results with ours). We have therefore taken wet weights by assuming that salp tissues are of the same density as sea water and have included the sea water in the jet chamber. On this basis, during cruise locomotion a medium-sized blastozooid (chamber length, 1·7 cm; weight with a full jet chamber, 1·6 g) operating at 70 contractions min^{-1} and swimming forwards at 1·6 cm s^{-1} would perform 1·07 J kg^{-1} of work to cover 1 m. Mean forward swimming speeds of oozooids and blastozooids are discussed in Bone & Trueman (1983); they range up to 6·6 cm s^{-1} in large oozooids.

During cruise locomotion of the calycophoran siphonophore *Abylopsis* (Bone & Trueman, 1982) similar in size to the salp, some 3 J kg^{-1} of work are needed to cover 1 m. This less economical performance is partly, at least, the consequence of the fact that *Abylopsis*, in common with most other jet-propelled animals, inhales water into

the jet chamber by the same posterior aperture through which the jet pulse is expelled, whereas in salps, the jet chamber is mainly filled *via* the anterior aperture.

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