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OXYGEN CONSUMPTION DURING THE METAMORPHOSIS OF THE PARASITIC LAMPREY, *LAMPETRA FLUVIATILIS* (L.) AND ITS NON-PARASITIC DERIVATIVE, *LAMPETRA PLANERI* (BLOCH)

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SUMMARY

1. Standard oxygen consumption has been measured during the six stages of metamorphosis in both the anadromous parasitic lamprey, *Lampetra fluviatilis*, and in its non-parasitic derivative, *Lampetra planeri*.

2. At 10 °C, the standard rates in larval *L. planeri* and *L. fluviatilis* of metamorphosing size were 20·3 and 29·3 μl g^{-1} h^{-1} respectively.

3. After a slow rise in oxygen consumption during the initial stages of metamorphosis, the rates reached 50·5 and 60·4 μl g^{-1} h^{-1} at stage of 6 of *L. planeri* and *L. fluviatilis* respectively.

4. Following the completion of metamorphosis in *L. planeri* and the development of secondary sexual characters, the mean rate in males rose to 73·3 μl g^{-1} h^{-1}, compared with a decline in females to 44·1 μl g^{-1} h^{-1}.

5. Although no circadian rhythm was detectable in the oxygen consumption of larvae, an elevation in the metabolic rate was present during darkness in *L. fluviatilis* at the end of metamorphosis.

6. Standard oxygen consumption and ventilatory frequency were influenced greatly by temperature, e.g. values for stage 6 of *L. fluviatilis* rose from 24·3 μl g^{-1} h^{-1} and 33·0 beats min^{-1} at 5 °C to 103·8 μl g^{-1} h^{-1} and 98·2 beats min^{-1} at 15 °C.

7. The results are discussed in the context of the radical changes taking place during metamorphosis and in terms of the differences between larvae and adult and between the life cycles of parasitic and non-parasitic lampreys.

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INTRODUCTION

All species of lampreys undergo a protracted larval phase lasting several years, during which they remain burrowed in the silt deposits of streams and rivers (Hardisty & Potter, 1971*a*). After metamorphosis, the young adults of anadromous parasitic species migrate downstream to the sea where they feed parasitically on fishes (Hardisty & Potter, 1971*b*). Many other species, however, remain in fresh water for the whole of their life cycle and do not feed after they have entered metamorphosis (Hardisty & Potter, 1971*c*). In these non-parasitic (brook) lampreys, which are believed to have been envolved from parasitic species (Hubbs, 1925), spawning takes place some 6–10 months after the completion of the larval phase.

The oral hood of the ammocoete helps channel water into the branchial chamber. During metamorphosis it becomes converted into an oral disc that can be used for attachment (Hardisty & Potter, 1971*b*). The concomitant switch from a unidirectional to a tidal mechanism for ventilating the gills enables parasitic lampreys to remain sucked on to host fishes for long periods of time (Parker & Lennon, 1956; Randall, 1972). In the two species employed in the present study, the parasitic *Lampetra fluviatilis* and its non-parasitic derivative, *Lampetra planeri*, the morphological changes that occur in the branchial chamber are similar (Lewis & Potter, 1976).

Apart from a study of oxygen consumption in metamorphosing *Ichthyomyzon fossor* by Leach (1946), previous studies on metabolic rates in lampreys have been restricted to either the larval (Hill & Potter, 1970; Potter & Rogers, 1972) or adult phases (Beamish, 1973; Johansen, Lenfant & Hanson, 1973; Claridge & Potter, 1975). Furthermore, there is evidence that in Leach's experiments the absence of a substrate may have resulted, at least in larvae, in values which do not correspond to standard oxygen consumption (Potter & Rogers, 1972). Although data on oxygen consumption in lampreys strongly indicate the presence of a greater metabolic rate in adults than in larvae, it must be remembered that the measurements on adults are based on very much larger animals than those used for the larval experiments. This is of considerable significance in view of the marked differences in the regression coefficients for the logarithmic relationship between oxygen consumption and body weight during the two different stages of the life cycle.

In this study, attempts have been made to obtain standard rates of oxygen consumption during the metamorphosis of the river lamprey, *L. fluviatilis*, and the brook lamprey, *L. planeri*. Such values are of importance in discussions of the critical initial phase of transformation, when marked changes are occurring in many parts of the body, including the branchial chamber. They are also relevant to comparisons between the metamorphosis of parasitic lampreys, during which little gonadal development takes place, and that of non-parasitic species, where transformation is accompanied by rapid gonadal maturation (Hardisty, Potter & Sturge, 1970). Finally, the values at the end of metamorphosis can be compared with those obtained for larvae of comparable size to ascertain the degree to which the metabolic rates of larvae and adults vary.

MATERIALS AND METHODS

The staging of the metamorphosing animals was carried out using the descriptions given by Bird (1976). Six stages are therefore recognized for *L. fluviatilis*, the last corresponding to individuals about to migrate downstream to commence their trophic phase in the sea. Six stages are also present in *L. planeri*, but unlike *L. fluviatilis*, they are immediately followed by stages we have designated as 7 and 8, which in our scheme refer to sexually mature and spent animals respectively. Stage 7 corresponds to the much larger sexually mature adults of *L. fluviatilis* caught at the end of the upstream migration, the respiratory characteristics of which have already been studied (Claridge, Potter & Hughes, 1973; Claridge & Potter, 1975).

Ammocoetes and metamorphosing stages of both species were obtained using an electric fish shocker, while the spent and partially spent *L. planeri* were collected from on or near their redds. The brook lampreys came from Highland Water in the New Forest, Hampshire and the river lampreys from Bransford Bridge on the River Teme, a tributary of the River Severn in Gloucestershire. Although several different streams and rivers are known to contain allopatric populations of *L. planeri*, the Bransford Bridge site is one of only two that recent studies have demonstrated as consisting solely of metamorphosing *L. fluviatilis* (Hardisty & Huggins, 1970; Potter & Osborne, 1975). An absence of measurements for stages 4 and 5 of *L. fluviatilis* reflects our dependence on the Bransford Bridge site for the collection of these stages, and our inability in three successive years to obtain samples at the relevant time.

The ammocoetes of *L. fluviatilis* and *L. planeri* used for the experiments were selected such that their lengths corresponded approximately to the lengths of their respective early metamorphosing stages. Ammocoetes and metamorphosing animals were kept in aquaria containing well aerated aged tap water and a natural silt substrate into which they could readily burrow. The temperature of the water was generally maintained at 10 ± 1 °C, although a few animals were acclimated at either $5 \pm 0{\cdot}5$ °C or 15 ± 1 °C. The lighting was adjusted to provide a cycle of 11 h light–13 h darkness. Animals were acclimated at the experimental temperature for at least 7 days before experiments, except for the spent and partially spent animals which were collected from their spawning beds and used for experiments after only 24 h acclimation.

Oxygen consumption was measured with a respirometer that allowed measurement in borrowed animals and provided a surface on which they could readily attach at the completion of metamorphosis. The respirometer, whose mechanism has been described in detail by Hill & Potter (1970), consisted of twelve 225 ml circular animal chambers, each having a height of 10 cm and a diameter of 6 cm. A substrate of glass beads (0·5–1·0 mm diam) occupied the bottom of the chamber to a depth of 3 cm. Above the substrate there was sufficient water to permit the animal to swim without undue hindrance. A multichannel peristaltic pump maintained a continuous flow of aerated water through the animal chambers. A flow of 100–120 ml h^{-1} was used for those stages with low rates of oxygen consumption, and 160–180 ml h^{-1} was employed where the metabolic rate was appreciably greater. The oxygen content of the sampling bottles, located immediately after each animal chamber, was determined by a modified Winkler analysis (Pomeroy & Kirschman, 1945).

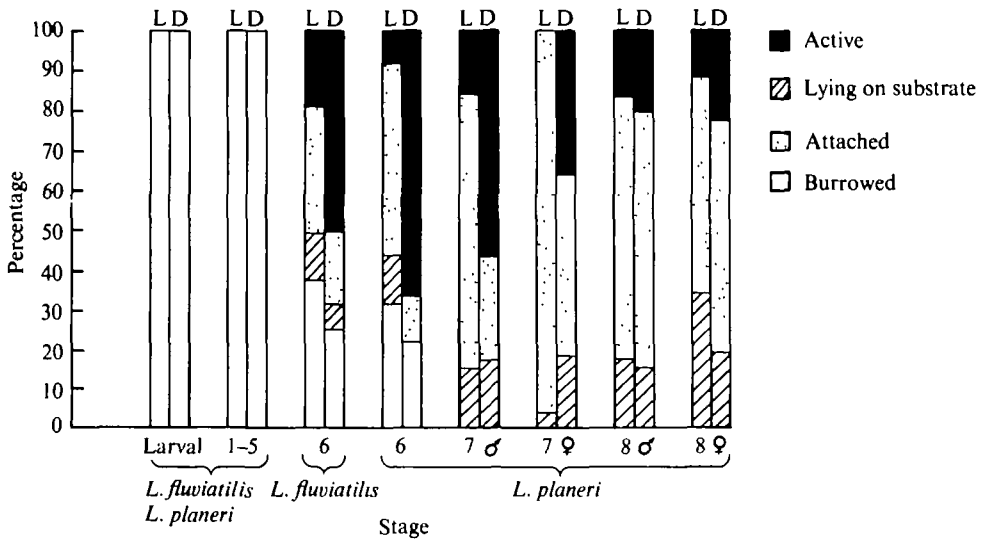

Fig. 1. The amount of time experimental animals remained burrowed, lying on the substrate, attached to the wall of the animal chamber or exhibiting some form of movement. L, Light phase; D, Dark phase.

Differences between each of these and identical controls involving no animals were then used, in conjunction with the known flow rates and the weight of the animal (measured to the nearest 10 mg wet w), to ascertain the rates of oxygen consumption which are expressed as $\mu l\ g^{-1} h^{-1}$. Oxygen determinations were made at 4 h intervals over a 28 h period, readings commencing 24 h after the animals had been placed in the chambers. Standard oxygen consumption of each animal refers to measurements made after it had been observed to be inactive for some time, either when burrowed, lying on the substrate or attached to the wall of the chamber. 111 *L. planeri* and 61 *L. fluviatilis* were used for the measurements, with at least three separate measurements being made on each animal. Although the data on standard oxygen consumption are based largely on measurements made during the light phase, a number of observations were made in the dark with the aid of a 40 watt red bulb. Ventilatory rates were measured by timing a number of branchial contractions in inactive animals and expressing these as beats min^{-1}.

The mean weights and lengths of larval *L. fluviatilis* ($\pm 95\%$ confidence limits), measured at the end of each experiment after anaesthetization in MS222 (Sandoz), were $1{\cdot}42 \pm 0{\cdot}22$ g and $100{\cdot}6 \pm 5{\cdot}25$ mm respectively. The corresponding figures for *L. planeri* were $2{\cdot}81 \pm 0{\cdot}39$ g and $123{\cdot}7 \pm 5{\cdot}45$ mm. The mean weights and lengths of post-larval *L. fluviatilis* ranged from $1{\cdot}59 \pm 0{\cdot}56$ g and $96{\cdot}4 \pm 4{\cdot}91$ mm near the beginning of metamorphosis to $1{\cdot}27 \pm 0{\cdot}13$ g and $96{\cdot}7 \pm 2{\cdot}99$ mm at stage 6. The mean weights and lengths of stages 1–8 in *L. planeri* ranged from $3{\cdot}49 \pm 0{\cdot}11$ g and $125{\cdot}3 \pm 5{\cdot}6$ mm to $2{\cdot}08 \pm 0{\cdot}77$ g and $116{\cdot}3 \pm 9{\cdot}11$ mm.

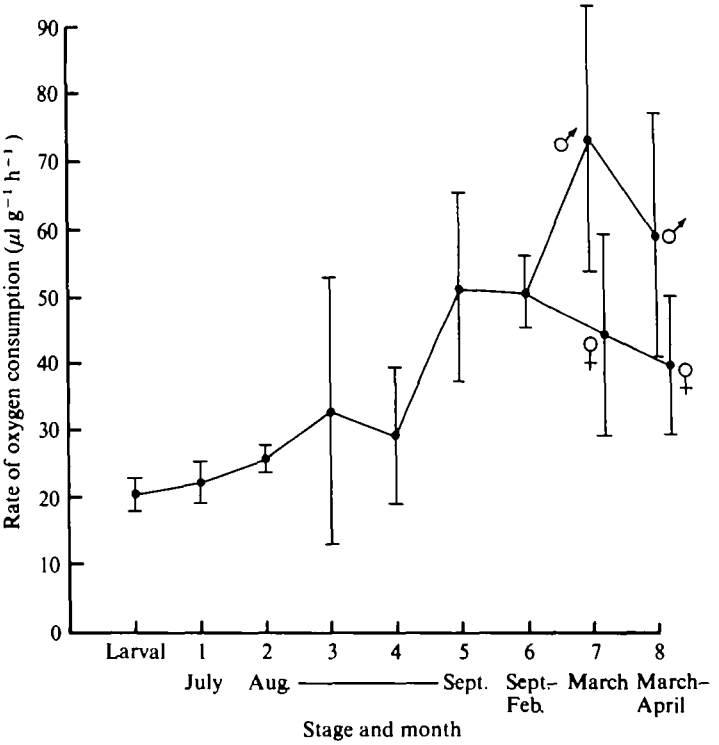

Fig. 2. The mean standard rate of oxygen consumption (± 95% confidence limits) for larval, metamorphosing (1–6), mature (7) and spent or partially spent (8) *L. planeri*, together with the approximate time they are found in the rivers.

RESULTS

Behaviour of animals

All ammocoetes and stages 1 and 2 of both species burrowed into the glass bead substrate of the respirometer within 30 s of being removed from the holding tanks (Fig. 1). Although stages 3–5 took rather longer to burrow they eventually remained burrowed throughout the whole of the experimental period. The retention of a burrowing habit by all the above stages parallels observations made in the field. In stage 6, however, animals started emerging at times from the substrate and in many cases they did not burrow at all after their introduction into the animal chamber. They spent most of their time when they were inactive either lying on the substrate surface or attached to the wall of the chamber. Activity was more pronounced in the dark phase, as with young adults of *L. fluviatilis* examined in March and April (Potter & Huggins, 1973). The burrowing habit was lost entirely at sexual maturity in *L. planeri*.

Although the sexually mature animals, and more particularly the males, were more active in the dark than in the light, this does not reflect the situation found in the field during the spawning period, when vigorous spawning behaviour takes place during the day (Lohnisky, 1966; Hardisty & Potter, 1971*b*; Dines, 1973). This behaviour is apparently triggered by the attainment of a threshold water temperature of about 11 °C. Since in the field this temperature is first attained during daylight hours, the spawning animals are more active in the light than in the dark.

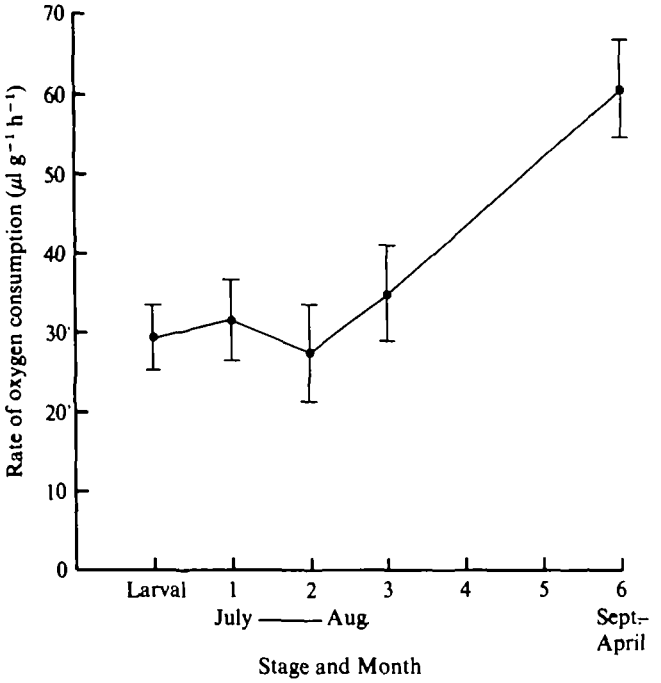

Fig. 3. The mean standard rate of oxygen consumption (± 95% confidence limits) of larval and metamorphosing *L. fluviatilis*, together with the approximate time they are found in the rivers.

Oxygen Consumption and Ventilatory Frequency

At 10 °C, the mean rates of standard oxygen consumption in larval *L. planeri* and *L. fluviatilis* of metamorphosing size were 20·3 and 29·3 μl g^{-1} h^{-1} respectively (Figs. 2, 3). The significant difference ($P < 0{\cdot}01$) between oxygen uptake in the species is almost certainly related to differences in the weights of the two groups of ammocoetes, which were (±95% confidence limits): 2·8 ± 0·4 g for *L. planeri* and 1·4 ± 0·2 g for *L. fluviatilis*. The size differences are not the result of a sampling error, but a genuine reflexion of the larger size of the non-parasitic lamprey at the commencement of metamorphosis (Hardisty & Potter, 1971*c*). The mean rates of oxygen consumption in the larvae of the two species lie either side of the mean rate recorded for larval *Ichthyomyzon hubbsi* at approximately the same temperature (Hill & Potter, 1970), providing further evidence that ammocoetes are characterized by a low metabolic rate for their size.

In *L. planeri* the standard rate of oxygen consumption showed little change during the initial period of metamorphosis before rising to reach mean levels of just above 50 μl g^{-1} h^{-1} at stages 5 and 6 (Fig. 2). A similar pattern is apparent for *L. fluviatilis* (Fig. 3) despite the lack of measurements for stages 4 and 5. Thus, at stage 6 the mean standard rate had increased to 60·4 μl g^{-1} h^{-1}, a value approximately twice that of the larva. In stage 6 of both species the rates of oxygen consumption of burrowed animals were the same as those of individuals which had been attached to the inside of the chamber for some time. A rise in oxygen consumption during the dark periods was present in stage 6 of *L. fluviatilis*, contrasting with the situation in larvae (Fig. 4), but paralleling that found in upstream migrants (Claridge & Potter, 1975). The

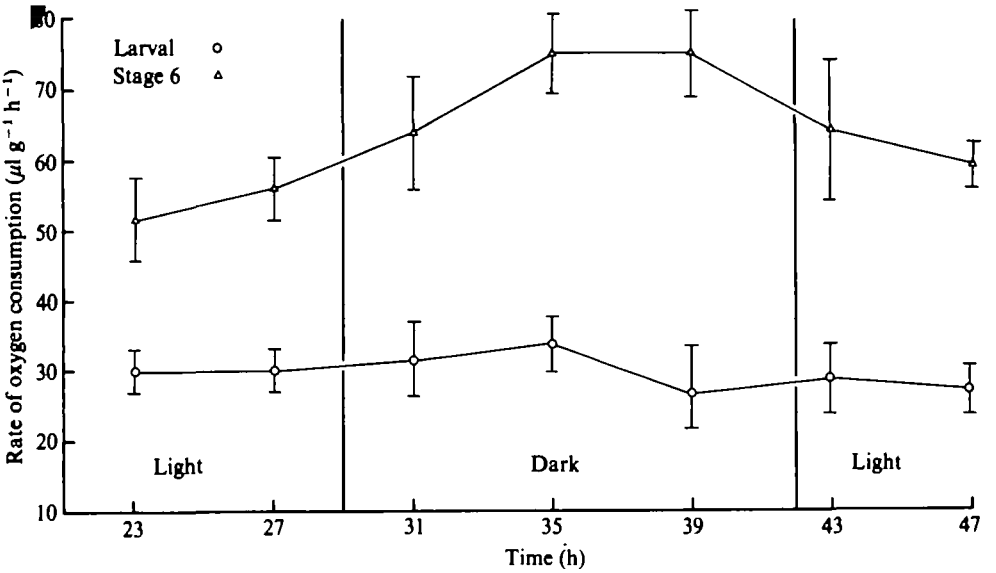

Fig. 4. The mean standard rates of oxygen consumption (± 95% confidence limits) during the light and dark periods in a single experiment using five larvae and five metamorphosing stage 6 representatives of *L. fluviatilis*.

assumption of a circadian rhythm of oxygen consumption during metamorphosis is almost certainly related to the development of the eyes that takes place during this period.

Sexually mature (stage 7) and spent and partially spent representatives (stage 8) of *L. planeri* exhibited a sexual dimorphism in their rates of oxygen consumption (Fig. 2). Changes in oxygen consumption in males between stages 6, 7 and 8 are accompanied by similar changes in ventilatory frequency (Fig. 5).

That oxygen consumption is influenced markedly by temperature is illustrated by the differences in the standard values obtained at 5, 10 and 15 °C (Fig. 6). For example, in stage 6 of *L. fluviatilis*, the rate at 5 °C was only 24·3 μl g^{-1} h^{-1} compared with 60·4 μl g^{-1} h^{-1} at 10 °C and 103·8 μl g^{-1} h^{-1} at 15 °C. For a given temperature range the Q_{10} was lower in stage 6 than in the larva (Table 1). Temperature also greatly affected the rate of branchial pumping (Fig. 7). For example, the ventilatory frequency in stage 6 of *L. planeri* rose from 45·8 at 5 °C to 66·2 at 10 °C to 107·6 at 15 °C.

DISCUSSION

Although Leach's (1946) data on *Ichthyomyzon fossor* suggest that oxygen consumption decreases during the early stages of metamorphosis, no such indications were found in this study of comparable stages in the life cycle of *L. fluviatilis* and *L. planeri*. It is possible that the decrease observed by Leach can be attributed to the differential effects of the absence of a substrate on the different stages. The lack of substrate has been shown to result in increased oxygen consumption in ammocoetes, due to the presence of a limited movement even after the animals have been in the chamber for some hours (Potter & Rogers, 1972). Since early metamorphosing

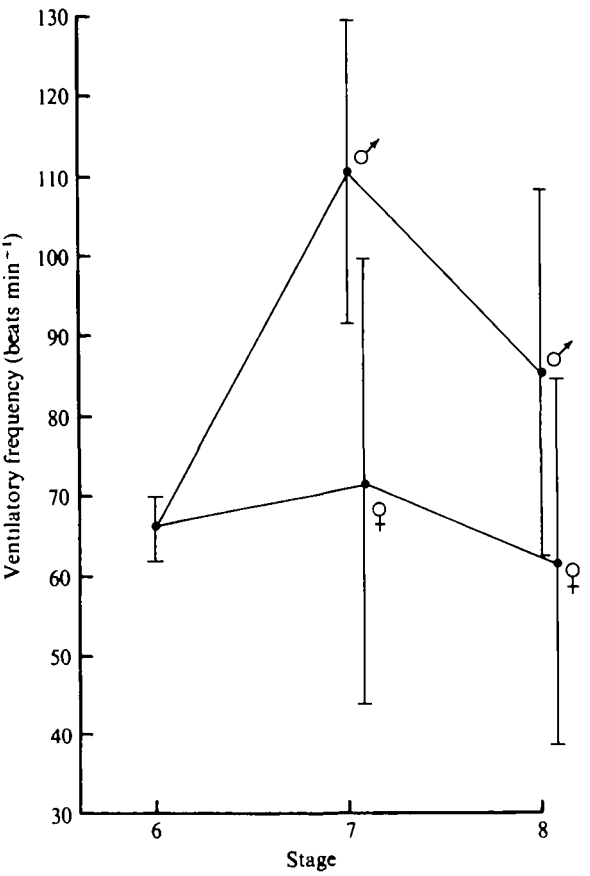

Fig. 5. The mean ventilatory frequency (± 95% confidence limits) for the last three stages in the life cycle of *L. planeri*.

individuals, which also burrow, tend to exhibit even less movement when deprived of a substrate, their apparently reduced rate of oxygen consumption compared with larvae may thus, in Leach's study, have been only a reflexion of a small decline in activity.

It has been suggested by Damas (1935) that the alterations in the pharyngeal apparatus during the early stages of metamorphosis result in the animal entering a situation which he likened to partial asphyxiation. However, since the many changes occurring at this time in a variety of different structures presumably require oxygen, it would seem unlikely that there would be a decline in the standard rate of oxygen uptake. At the same time, changes in the pharynx may be sufficiently drastic to lower the maximum rate attainable from that which can be achieved in the ammocoete during activity. Indeed, the great sensitivity of the early metamorphosing stages, exemplified by the care with which they have to be transported after capture in the field, may be due to their inability to extract sufficient oxygen under stress.

This study clearly shows that the rate of oxygen consumption increases markedly during the metamorphosis of both *L. fluviatilis* and *L. planeri*. Thus, at 10 °C, the rate in stage 6 of both species had risen to levels at least twice that of larvae of co

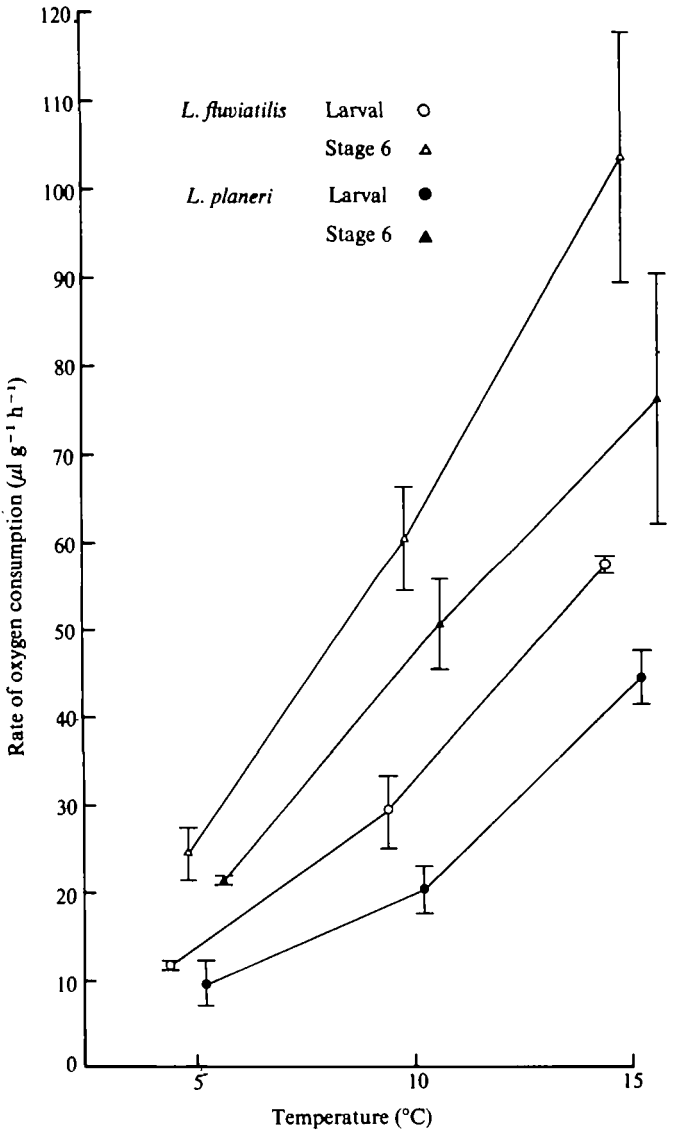

Fig. 6. The mean rate of standard oxygen consumption (± 95% confidence limits) for larval and representative metamorphosing stages of *L. planeri* and *L. fluviatilis* at 5, 10 and 15 °C.

parable size. It is of interest that the sexual dimorphism in oxygen consumption in the subsequent stage in the brook lamprey parallels almost exactly the situation found in the river lamprey at maturity (Claridge & Potter, 1975). The dimorphism may, however, be partly due to the fact that at maturity the body weight of females increases markedly due to the uptake of water into the body cavity (Larsen, 1973; Claridge & Potter, 1975). A higher rate of standard oxygen consumption in males is consistent, however, with their greater activity at spawning time both in the preparation of the redd and in breeding behaviour (Hardisty & Potter, 1971*b*).

Another parallel between brook and river lampreys is that the actual oxygen

Table 1. *The Q_{10} for standard oxygen consumption and ventilatory frequency for larvae and stage 6 of* L. fluviatilis *and* L. planeri

	Temperature Range (°C)	Oxygen consumption	Ventilatory frequency
L. fluviatilis			
Larvae	5·0–10·0	7·26	—
	10·0–15·0	3·85	—
	5·0–15·0	5·29	—
Stage 6	5·0–10·0	6·18	3·09
	10·0–15·0	2·95	2·83
	5·0–15·0	4·24	2·96
L. planeri			
Larvae	5·0–10·0	6·41	—
	10·0–15·0	4·76	—
	5·0–15·0	5·51	—
Stage 6	5·0–10·0	5·60	2·09
	10·0–15·0	2·28	2·64
	5·0–15·0	3·57	2·35

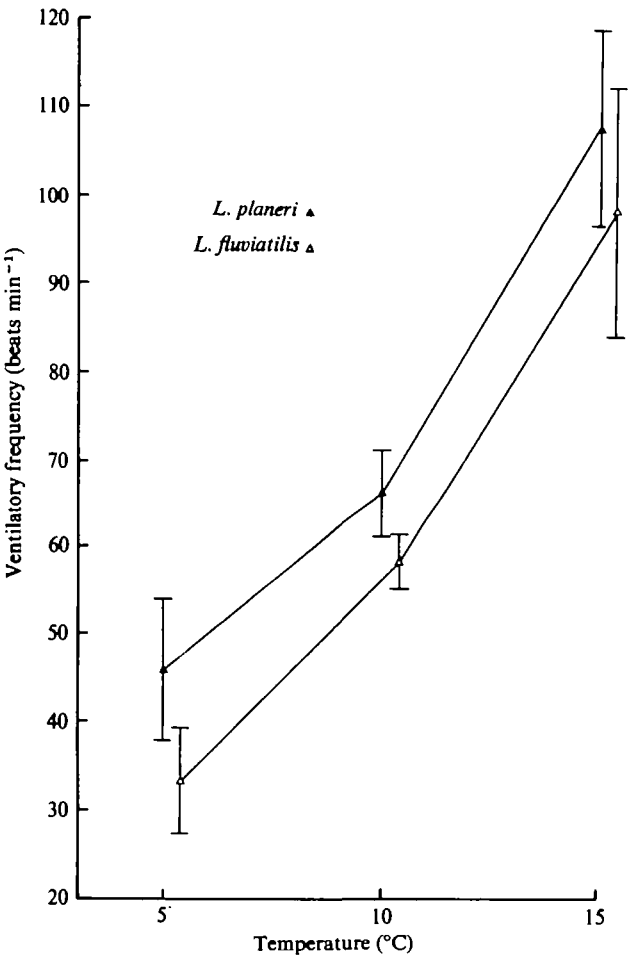

Fig. 7. The mean ventilatory frequency (± 95% confidence limits) for stage 6 of *L. fluviatilis* and *L. planeri* at 5, 10 and 15 °C.

nsumption values for the two species are similar at spawning. Thus, in *L. fluviatilis* at 9·5 °C, the mean rates recorded for males and females were 63 and 36 μl g^{-1} h^{-1} respectively (Claridge & Potter, 1975) compared with 73 and 44 μl g^{-1} h^{-1} obtained at 10 °C in this study of *L. planeri*. The fact that the difference between the two species is not greater is perhaps surprising in view of the vast disparity in the size of the mature stages of the river (mean 45 g) and brook (mean 2·8 g) lampreys. In most animals the metabolic rate decreases markedly with body size (see Prosser, 1973; Schmidt-Nielsen, 1975); a change reflected by a regression coefficient of less than unity in the logarithmic equation relating oxygen consumption and body weight. In contrast to a regression coefficient of 0·75 calculated for the values for a wide variety of different animals (Hemmingsen, 1960), the regression coefficients for adult lampreys are much nearer to unity. For example, regression coefficients of 0·912 and 0·925 have been recorded for *L. fluviatilis* (Claridge & Potter, 1975) and an even higher mean of 0·949 has been recorded for experiments carried out on the landlocked sea lamprey at different temperatures (Beamish, 1973). The above regression coefficients for adults are, however, much greater than the single coefficient that has been recorded for an ammocoete: namely the 0·718 given for *I. hubbsi* by Hill & Potter (1970).

The marked increase in metabolic rate during metamorphosis helps to confirm the view that adult lampreys have a higher rate of oxygen uptake than their larval stages. In some cases the increase can be related to the various changes occurring in the animal's physiology during transformation. It has been shown for example that the haemoglobins undergo a complete change during metamorphosis (Potter & Brown, 1975) and that this results in a pronounced shift in the oxygen affinity of the blood (Bird, Lutz & Potter, 1976). The various physiological changes are also almost certainly related to the far greater activity exhibited by the adult during its predatory, migratory and spawning phases, compared with the rather sedentary mode of life normally displayed by the larvae.

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