PHYSIOLOGICAL ASPECTS OF THE LIFE CYCLE OF THE RIVER LAMPREY, *LAMPETRA FLUVIATILIS* L.

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The lampreys, together with the hagfishes, are the only living members of the most primitive group of vertebrates, the Agnatha. As such they occupy a unique evolutionary position and are becoming the subject of intensive scientific investigation. Modern lampreys have several characteristics in common with the earliest fossil agnathans and it seems likely that these reflect a common ancestry in the Silurian period or even earlier. Such features include the absence of jaws, the possession of only two semicircular canals in the labyrinth and the lack of paired pelvic fins. Despite these and other primitive characters, it is a mistake to consider the lampreys simply as relics, because they also exhibit several highly specialized adaptations. The most remarkable specialization, and perhaps the main reason for the survival of the lampreys until the present day, is the development in the adult of a suction disc around the mouth (Plate 4b). The adult lamprey feeds by attaching itself to another fish by means of the sucker and ingesting the tissue and body fluids removed by the rasp-like tongue. A secretion from special buccal glands prevents coagulation of the blood of the prey and promotes tissue breakdown. This specialized feeding mechanism, which overcomes many of the problems associated with the lack of jaws, has also resulted in modifications of the branchial system. The adult lamprey spends long periods of time attached by its mouth to the host fish or to the substratum and as a consequence the ventilation of the gills is tidal instead of unidirectional. The respiratory current enters and leaves each gill pouch by a single opening, thus enabling the animal to remain attached by its mouth. Hence, modern lampreys present the biologist with a fascinating yet subtle combination of primitive, specialized and degenerate characters.

However, this is not the sole reason for the interest in this group of animals. Lampreys have also attracted attention as a direct result of their predation on teleost fish in the Great Lakes of North America; the severity of this predation was emphasized by the collapse of several commercial fisheries in this area. Thus, research into lamprey biology is of interest from both academic and economic viewpoints.

Three species of lamprey occur in the British Isles, two of which, the sea lamprey *Petromyzon marinus* L. and the river lamprey *Lampetra fluviatilis* L., are parasitic. The third species, the non-parasitic brook lamprey *Lampetra planeri* Bloch, is closely related to and probably evolved from a form similar to the river lamprey. This review is concerned with the life cycle of the river lamprey although some of the aspects under consideration will be applicable to other lamprey species.

In all species of lamprey the life cycle is divided into two quite distinct phases, larval and adult. The larval lamprey, or ammocoete, is a blind, filter-feeding animal which normally lies concealed in the silt deposits of streams and rivers. This microphagous habit probably imposes a restriction on the growth of the animal so that even after 4 years feeding in fresh water the ammocoete of the river lamprey weighs less than 2 g. The ammocoete is a stenohaline, freshwater animal which osmoregulates in a manner similar to that of the freshwater teleost. A large osmotic influx of water is balanced by copious urine production and diffusional and excretory losses of salts are replaced by an active uptake mechanism thought to be located in the interplatelet epithelium of the gills (Morris & Pickering 1975). Both the efflux and influx components of the ion-balance system in ammocoete river lampreys are extremely sensitive to stress stimuli (Pickering 1973).

After a period of 3–5 years in fresh water the ammocoete undergoes a metamorphosis into a sexually immature, non-feeding stage known as the macrophthalmia. In marked contrast to the ammocoete, the macrophthalmia is an active, large-eyed, silvery animal which, because of its tidal respiratory system, usually moves to the more stony areas of the stream to avoid silt damage to the gills. Furthermore, the macrophthalmia now has the ability to osmoregulate equally successfully in either fresh water or sea water (Pickering & Morris 1976). The mechanism of marine osmoregulation is similar to that of the marine teleost and it seems likely that parallel evolution in the lampreys and teleosts has resulted in almost identical physiological mechanisms (Pickering & Morris 1970). In sea water the lamprey is subjected to a continuous osmotic loss of water together with a diffusional influx of ions. Water balance is maintained by the ingestion of sea water with a concomitant uptake of monovalent ions and water by certain columnar cells of the anterior intestine (Pickering & Morris 1973). Excess monovalent ions in the blood stream are actively expelled across the gill epithelium and divalent ions are excreted via the kidney. The changes in gill function from ion-uptake in the ammocoete to ion-uptake or ion-secretion in the macrophthalmia are reflected in the ultrastructure of the interplatelet epithelium. Thus, only one type of mitochondria-rich, ion-transporting cell was found in the ammocoete gill (Morris & Pickering 1975) whereas in the macrophthalmia two cell types have been described (Pickering & Morris 1976).

Metamorphosis also involves reorganization of many of the other body tissues of the lamprey, the most remarkable of which is the transformation of the endostyle into the thyroid gland. In the ammocoete the endostyle is closely associated with the microphagous feeding mechanism, as it is the organ responsible for the production of a mucous secretion which traps food particles as they pass through the pharynx. However, the endostyle also has the capacity for synthesis of the thyroid hormones, a phenomenon which can be demonstrated by the administration of radioiodine to the animals (Pickering 1972). During metamorphosis, cellular elements of the endostyle are reorganized to form a typical, follicular, vertebrate thyroid gland. It is of interest that most of the research has so far failed to demonstrate the control of thyroidal activity by the pituitary gland of the lamprey (Pickering 1972, 1976a). This is in marked contrast to the well-developed pituitary/thyroid axis found in many representatives of the other vertebrate groups.

Metamorphosis of the river lamprey occurs during the summer months (July-September) but the downstream migration does not take place until the late winter. The macrophthalmia is well adapted to the changes in salinity encountered during this migration from its native freshwater stream to the feeding grounds in the coastal waters of the British Isles. Our information concerning the parasitic feeding habits of the adult river lamprey is extremely fragmentary and much more work in this area is required. It is believed that small clupeids and gadoids predominate as hosts for the feeding river lamprey (see Hardisty & Potter 1971) and on a more local basis one might speculate that the river lamprey may feed on the flounder, *Platichthys flesus*, in the intertidal areas of Morecambe Bay. Information from local fishermen tends to support this view but as no real data are available, this period in the life cycle of the river lamprey remains to be investigated.

After 18 months feeding as a parasite on other fish, the river lamprey (which may now weigh up to 100 g) returns to spawn in fresh water. The anadromous spawning migration, one of the more intensively studied aspects of the lamprey's life cycle, is characterized by a prolonged period of starvation, during which time the animal reorganizes its osmoregulatory system yet again and achieves its gonadal development at the expense of other body tissues. River lampreys normally enter fresh water from the estuaries during the late summer and autumn of the year prior to spawning. This migration takes place almost exclusively during the night and is favourably influenced by high water levels in the rivers and low light intensity. Since the river lamprey ceases to feed whilst out at sea, the total metabolic demands of the animal during the anadromous migration and subsequent freshwater stage prior to spawning (a total period of up to 9 months) have to be met from stores within the body tissues.

During the early stages of the anadromous migration the river lamprey exhibits a limited degree of euryhalinity. "Fresh-run" animals can osmoregulate successfully in dilute seawater solutions (Pickering & Morris 1970, 1973) but this ability is lost soon after the animals enter fresh water. Breakdown of the marine osmoregulatory mechanism involves changes in the ion-transporting properties of the gills, a reduction in the ability of the animal to swallow sea water and of the intestine to absorb monovalent ions and water from the ingested fluid, and an increase in the permeability of the integument. Massive reorganization of the gill tissue is indicated by the

apparent phagocytic properties of many of the gill cell-types at this time (Morris & Pickering 1976). The net result is a replacement of the large, mitochondria-rich, ion-excretory cells by smaller ion-uptake cells similar in structure to those of the ammocoete gill. The osmoregulatory ability of the intestine appears to be intimately associated with gonadal development. It is well-known that, when the river lamprey migrates into fresh water and becomes sexually mature, the intestine degenerates until it is no more than a thin strand of tissue in the coelom. Histologically, this degeneration appears as a reduction in epithelial cell height together with intense cytoplasmic vacuolation (Dockray & Pickering 1972). However, if the gonad of the river lamprey is removed at the start of the spawning migration, intestinal degeneration is inhibited (Pickering & Dockray 1972). Moreover, the ion-transporting properties of the intestine are maintained in gonadectomized animals made to osmoregulate in 50% sea water, but are lost in sham-operated animals (Fig. 1). Thus, the presence of the gonad has a marked influence on the marine osmoregulatory mechanism of the migrating river lamprey.

This effect of gonadectomy on intestinal degeneration may be abolished by administration of the sex steroids, oestradiol and testosterone (Pickering 1976b). Similar degenerative changes are known to occur in certain salmonid species and these may also be influenced by gonadectomy and sex steroid administration. However, in the case of salmonid fish, it is possible that these effects may be mediated by the interrenal system. It seems most unlikely that a similar mechanism exists in the lamprey because most attempts to measure corticosteroids in the blood serum have failed to detect significant levels of these hormones. Thus, it is possible that the secretion of androgens and oestrogens by the lamprey gonad has a direct effect on the degeneration of non-essential body tissues. A mechanism of this type could be advantageous for gonadal development in a starving animal. This working hypothesis is too simple, however, to explain all the available data. If gonadectomy is delayed until the intestine has degenerated, the operation results in a hypertrophy of the alimentary canal which is unaffected by the administration of oestradiol or testosterone (Pickering 1976b). Further work is needed to clarify this situation.

As in other vertebrates, oestradiol plays an important role in the maturation of the ovary. Implantation of this hormone in fresh-run female river lampreys results in an increase in the size of both the liver and the ovary. At the same time the levels of serum calcium, organically bound phosphorus and protein increase significantly (Pickering 1976c). These observations indicate that oestradiol acts by stimulating the liver to produce calcium-rich phosphoprotein yolk-precursors which are transported by the blood stream to the ovary for incorporation into the developing oocytes. In certain higher oviparous vertebrates (e.g. amphibians) the rate of uptake of yolk-precursors into the ovary is

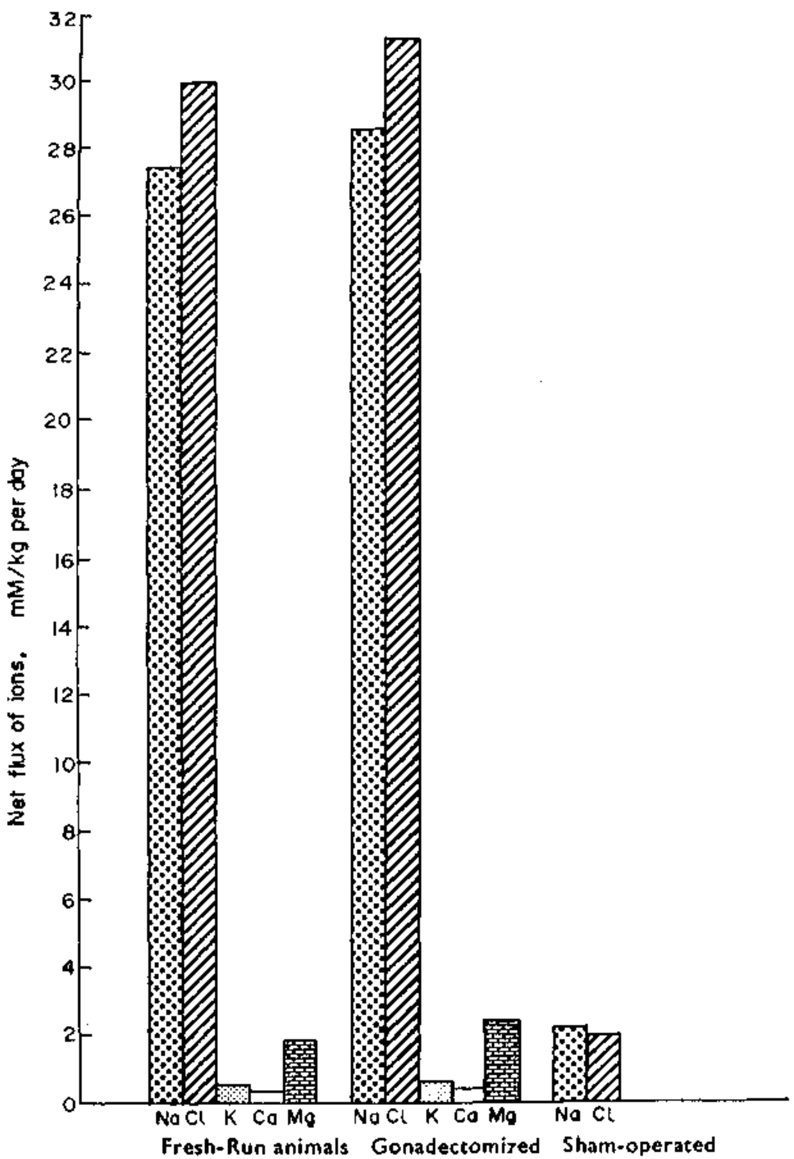

FIG. 1. The mean net mucosa → serosa ion fluxes across the intestine of fresh-run, gonadectomized and sham-operated river lampreys during 24 h immersion in 50% sea water.

dependent upon the pituitary hormone, gonadotrophin. Furthermore, chronic oestrogen administration appears to inhibit yolk uptake by means of a negative feedback on the release of pituitary gonadotrophin. The data obtained at the Windermere laboratory (Pickering 1976c) show no evidence of inhibition of yolk uptake as a result of oestradiol implantation in the lamprey. Indeed, they suggest that the incorporation of yolk-precursors by the ovary of oestradiol-treated animals is greater than normal. This now raises the possibility that either yolk uptake by the lamprey ovary is independent of the pituitary gland, or that there is no oestrogen-gonadotrophin feedback in the lamprey.

Sexual maturation of the river lamprey is normally completed during April-May. At this time many of the body tissues show signs of severe degeneration as the energy stores within the animal are exhausted. Major changes occur in the gill tissues but it is not clear whether these are related to degeneration, changes in ion-balance or to the secretion of a pheromone involved during the spawning behaviour. The interplatelet areas of the male lamprey gill contain abundant sudanophilic cells with ultrastructural similarities to certain ion-transporting cells (Pickering & Morris 1977). This cell type, however, is not found in the gill of the spawning female lamprey.

The river lamprey normally dies within a few days after spawning and none survives to spawn the following year. Thus, the complex life cycle of this unique animal culminates in a short, final spawning period of only 3-4 weeks. Spawning lampreys are obvious even to the most casual observer but during the rest of the life cycle the river lamprey is either concealed in the silt as an ammocoete, hidden in the gravel as a macrophthalmia, out in the coastal waters of the British Isles during the parasitic feeding stage or active only at night during the anadromous migration. Hence, the popular belief that lampreys are uncommon creatures is understandable but totally inaccurate for many areas of the country. The fossil record suggests that the lampreys have changed little during the past 280 million years yet there can be little doubt that they are still a highly successful group of animals.

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THE IMPACT OF COW GREEN RESERVOIR ON INVERTEBRATE POPULATIONS IN THE RIVER TEES

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Cow Green is a new reservoir situated in Pennine moorland (Fig. 1). It has an area of 312 ha, a capacity of $40{\cdot}9 \times 10^6$ m^3 and a maximum depth of 22.8 m. The reservoir began filling in June 1970 and was 2 m below top water level (489 m above sea level) in March 1971. The climate at this altitude is characterized by high annual mean wind speeds (24 km h^{-1}), high rainfall (1800 mm a^{-1}) and low annual mean temperatures (5 °C). Because of its exposed location, the reservoir water is well mixed and oxygenated. Water derived from the peaty catchment is coloured brown and about 90% of surface light intensity is extinguished in the first 2 m and no light penetrates further than about 5 m depth (Dr R. Fisher pers. comm.). More physical and chemical data are given by Crisp (1977).

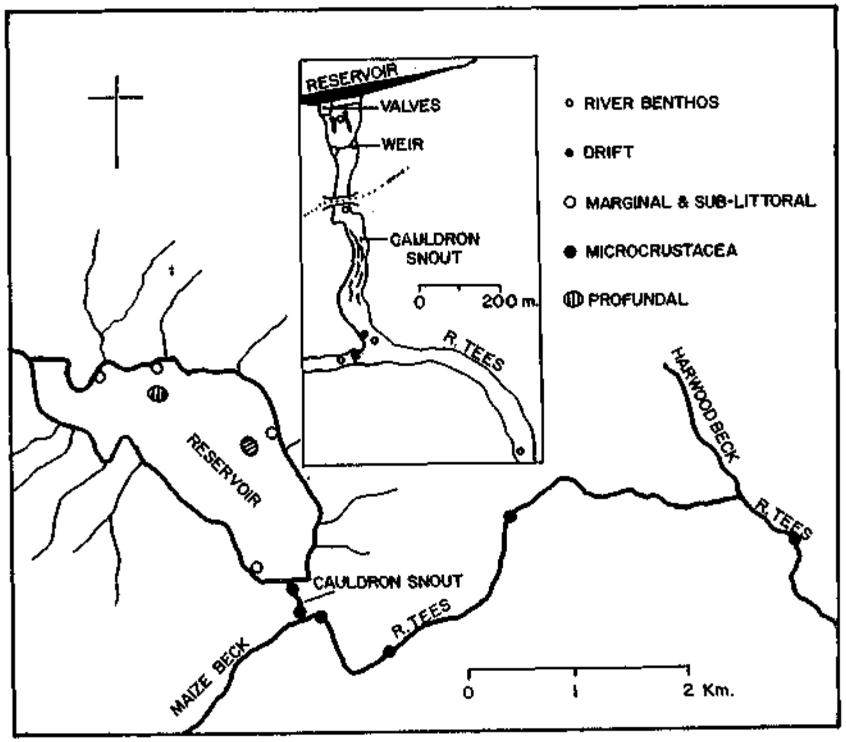

FIG. 1. Sketch map of the general study area and, inset, detail of the River Tees below the dam, showing position of the sample sites.