Osmoregulation in Juvenile and Adult Lampreys

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Nonparasitic lampreys are well adapted for a freshwater existence but are less tolerant of salt water than representatives of the parasitic species. Anadromous feeding juvenile sea lampreys, Petromyzon marinus, are able to control serum osmotic and ionic concentrations in all salinities between 0 and 34%. Juveniles of the anadromous European river lamprey, Lampera fluviatilis, are slightly less tolerant of salinity change. The transition of P. marinus to a landlocked existence has resulted in a reduction in the capacity for marine osmoregulation. Tolerance to salt water among landlocked P. marinus is related directly to size emphasizing the advantage afforded through a reduction of surface area relative to body volume. Changes in serum osmolality are primarily the result of corresponding shifts in sodium and chloride ions. Changes in chloride are not accompanied by an equivalent shift in sodium suggesting that the relationship between the two ions is not passive. Regulation of sodium by landlocked P. marinus is not precise as that exhibited by the anadromous form particularly in the higher salinities. Nontrophic upstream migrant lampreys display a reduction in their marine osmoregulatory mechanisms and a restoration of the freshwater osmoregulatory apparatus. Freshwater osmotic and ionic regulation deteriorates in spent adult lampreys.

Key words: blood, ionic regulation, osmotic regulation, parasitic and nonparasitic lampreys, salinity, life cycle


Les lamproies non parasites sont bien adaptées à une existence en eau douce mais sont moins tolérantes à l'eau salée que les représentants d'espèces parasites. Les jeunes lamproies marines, Petromyzon marinus, anadromes et se nourrissant peuvent régler les concentrations osmocratiques et ioniques de leur sérum à toute salinité entre 0 et 34%. Les jeunes de la lamproie fluviale européenne anadrome, Lampera fluviatilis, sont légèrement moins tolérants à un changement de salinité. Le passage de P. marinus à une existence confinée en eau douce entraîne une diminution de capacité osmoregulatrice en mer. Chez P. marinus confiné en eau douce, la tolérance à l'eau salée est directement liée à la taille, ce qui fait ressortir l'avantage d'une diminution de surface par rapport au volume du corps. Les changements d'osmolalité sérée résultent avant tout du glissement correspondant des ions sodium et chlorure. Les changements de chlorure ne sont pas accompagnés d'un glissement équivalent de sodium, suggérant que la relation entre les deux ions n'est pas passive. La régulation du sodium par P. marinus confiné en eau douce n'est pas aussi précise que celle de la forme anadrome, en particulier aux fortes salinités. Les lamproies se déplaçant vers l'amont montrent une diminution de leurs mécanismes d'osmorégulation en mer et une restauration de leur appareil osmorégulateur d'eau douce. La régulation osmotique et ionique d'eau douce se détériore chez les lamproies adultes qui ont frayé.

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Most vertebrates are tolerant of small changes in internal ionic composition and concentration. However, the variation compatible with life is extremely limited. Among marine teleosts and cyclostomes (Petromyzontia) body water is lost from the hypoosmotic blood

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ing and Morris 1976). Divalent ions remain in the gut and are removed in the feces (Hoar 1966). Freshwater homeostasis depends on the elimination of water from the hyperosmotic blood coupled with the transport of ions from the ambient environment or, in the case of teleosts, from skeletal stores. The osmotic influx of water in freshwater fishes is controlled by a copious dilute urine (Parry 1966; Morris 1972). Salt loss is replaced from ingested food (Hoar 1966) and active recruitment by the ion-transporting or “chloride” cells (Peek and Youson 1979a).

Juvenile lampreys are found in both fresh and saline waters. Those species which do not feed during the juvenile interval of their life cycle are found only in freshwater. Of the parasitic species some spend the juvenile trophic portion of their life cycle in saline water before returning as adults to freshwater rivers in which they reproduce and thereafter die. Other parasitic species remain in freshwater throughout their entire life cycle. This report summarizes present information on the capacity of juvenile and adult lampreys for ionic and osmotic regulation and the mechanisms by which control is achieved.

**Regulatory Mechanisms**

Water balance and ionic-composition and concentration are regulated in lampreys by the gills, kidney, gut, and integument. In a saline environment juvenile lampreys maintain water and ion balance by drinking seawater. Monovalent ions are absorbed by specialized cells located in the anterior portion of the digestive tract, with any excess being excreted via the gills. Most divalent ions remain in the gut and are excreted along with the nondigestible components of the ingested food. Excess divalent ions which enter the body fluids are excreted by the kidneys in concentrated urine. In juvenile lampreys the foregut is a new structure which develops during transformation by formation of a lumen in a solid epithelial chord (Hardisty et al. 1970). The timing of the opening of the foregut appears not to be in synchrony within and among species, a factor which would be expected to contribute to variability in osmoregulatory efficiency. Thus, while the foregut of most specimens of the anadromous Lampetra fluviatilis opens by late October, it may remain closed in some animals until May (Weissenberg 1927). Presumably the foregut opens earlier in Petromyzon marinus than in river lampreys (Hardisty and Potter 1971). In freshwater, ion balance is maintained by the active uptake of salts at the gills, gut, and kidney together with the production of dilute urine.

The gills of many teleosts and lampreys are characterized by specialized ion transport cells widely known as “chloride” cells. In the marine or estuarine environment, chloride cells are believed to be involved in ion excretion whereas in freshwater they are thought to be responsible for ion absorption. Chloride cells are involved also in the elimination of nitrogenous wastes in the form of ammonia (Read 1968; De Renzis and Maetz 1973; Evans 1975) which may account at least in part for their active appearance in lampreys adapted to freshwater (Peek and Youson 1979a). Several types of chloride cells are present within the gill epithelium of most fishes (Doyle and Gorecki 1961; Threadgold and Houston 1964) and the anadromous P. marinus (Peek and Youson 1979a), likely reflecting stages of cell differentiation (Conte and Lin 1967) or cells at various levels of activity (Shirai and Utida 1970). The appearance of cells is influenced also by the ambient salinity (Philpott and Copeland 1963; Shirai and Utida 1970).

Ultrastructural studies on the interlamellar regions of juvenile and adult lamprey gills (Nakao 1974, 1977; Pickering and Morris 1976; Youson and Freeman 1976; Peek and Youson 1979a) suggest the presence of chloride cells with similar features to those displayed by marine teleosts (Philpott and Copeland 1963; Shirai and Utida 1970; Newstead 1971; Kikuchi (1977). Chloride cells from lampreys have abundant mitochondria and a highly developed reticulum of smooth cytoplasmic tubules continuous with the lateral and basal plasma membranes. The continuity of the smooth endoplasmic reticulum with the plasma membrane in young juvenile landlocked P. marinus (Youson and Freeman 1976) has been observed also in the chloride cells of L. japonica (Nakao 1974; Nakao and Uchinomiya 1974) and early upstream migrants of L. fluviatilis (Morris and Pickering 1976).

Among larval lampreys, chloride cells are few in number and resemble those identified in freshwater teleosts in that their smooth endoplasmic reticulum is confined to the apical cytoplasm in the form of vesicles. Chloride cells in larval lampreys are rich in mitochondria (Morris and Pickering 1975; Youson and Freeman 1976) and are believed to assist in ion uptake. The rapid increases in osmolality which have been observed for landlocked sea lamprey during metamorphosis (Mathers and Beamish 1974) appear to coincide with the early formation of the juvenile type of chloride cell (Peek and Youson 1979b). During the upstream spawning migration the juvenile type of chloride cells degenerate and are replaced by the larval type (Morris and Pickering 1976).

The biochemical mechanism by which lampreys transport ions across the gill epithelium has only recently been studied (Beamish et al. 1978). At the site of the chloride cells a sodium–potassium dependent ATPase enzyme (Na–K)–ATPase has been identified in both teleosts (Epstein et al. 1967; Kamiya and Utida 1968; Pfeiler and Kirschner 1972; Zaugg and McLain 1976) and anadromous sea lampreys (Beamish et al. 1978). This enzyme is believed to constitute the pump responsible for the outward transport of sodium and inward movement of potassium across the gill epithelium (Adams et al. 1975). Gill (Na–K)–ATPase activity is absent in ammocoetes of the anadromous sea lamprey but present in young feeding juveniles of...
this species (Beamish et al. 1978). Peek and Youson (1979a) suggest that the site of (Na-K)-ATPase may be the membrane of the cytoplasmic tubules in the chloride cells.

Gill (Na-K)-ATPase activity declines with the age of the anadromous sea lamprey, being highest in young feeding animals in salt water and effectively absent from spawning migrants in freshwater. The functioning of (Na-K)-ATPase in small juvenile sea lampreys presumably enhances the efficiency with which they are able to make the transition from fresh to salt water. Once lampreys begin feeding, the composition of body fluids ingested from the host fish may facilitate osmoregulation and at the same time stimulate the animal's capacity for osmoregulation making the role of the enzyme less important. Further, as lampreys increase in size the corresponding reduction of the surface area in relation to volume lowers the osmotic stress exerted by the external medium.

Lamprey kidneys are largely responsible for excreting osmotic water and the absorption of solutes which in freshwater assists in the preservation of the ionic composition of body fluids (Morris 1960). The paired kidneys are usually unequal in size, with one longer and of greater cross-sectional area (Youson et al. 1974). The structure of the larval pronephros and opisthonephros has been described in detail (Wheeler 1899; Hatta 1900; Inukai 1929; Youson and McMillan 1970a, b, 1971a, b). The larval kidney degenerates anteriorly throughout life and disappears entirely during metamorphosis at which time the opisthonephros develops (Schneider 1879; Youson 1970; Ooi and Youson 1979). The opisthonephric kidney degenerates gradually until the end of the spawning migration when a massive deterioration occurs (Morris 1972). Details of the structure of the opisthonephros are given in Muller (1875), Meyer (1876), Wheeler (1899), Krause (1921), Vinnichenko (1966), Youson and McMillan 1970a, b, 1971a, b), and others.

Measurements of urine production and quality have been made for lampreys in freshwater (Wikgren 1953; Sawyer 1955; Morris 1956; Hardisty 1956; Bentley 1962; Bentley and Follett 1963; Bull and Morris 1967; Pickering and Morris 1970; Malvin et al. 1970). Most measurements are, however, subject to question due to handling diuresis (Morris 1972) or the effects of anesthesia (Moriarty et al. 1978). The most reliable measurements indicate that lampreys have a high urine production relative to that of freshwater teleosts. Some ions are excreted in association with the high production of urine. Wikgren (1963) estimated electrolyte excretion in the urine to represent 2.5-30% of the total ionic loss. Other estimates have been made and are discussed in detail in Morris (1972). Calculations by Morris (1972) for lampreys in freshwater suggest that sodium, potassium, and chloride are largely reabsorbed by the kidney although absorption efficiency for potassium is not high. Further, the kidney reabsorbs approximately one half of the water produced as a result of glomerular filtration (Morris 1972). Efficiency of ion absorption and water reabsorption varies directly with temperature (Wikgren 1953). Morris (1972) suggests that this is consistent with the hypothesis that water absorption is a passive process resulting from the osmotic flow of water from the urine to the blood. Thus, a reduction in ion absorption at low temperature could cause a decline in water reabsorption.

Permeability of the integument to water has been investigated for L. planeri and L. fluviatilis in freshwater by ligating the urinogenital papilla and measuring weight change (Hardisty 1956). Urine production determined in this manner coincided precisely with direct measurements made by Wikgren (1953). Hardisty (1956) suggests that the branchial epithelium plays the major role in water transport. On the basis of equal body weights the permeability of the integument to water was estimated to be about twice as great in L. planeri as in L. fluviatilis.

In salt water, juvenile lampreys are believed to produce very limited quantities of urine (Morris 1972). It is important to point out that kidney function in salt water is poorly understood for lampreys. On the basis of glomerular filtration rates obtained by Bentley and Follett (1963) together with consideration for tubular absorption of water, Pickering and Morris (1970) calculated that kidney tubules preferentially secrete divalent ions.

Regulation of salt and water balance in the higher vertebrates is under hormonal control. Water excretion among the higher vertebrates may be regulated by one or more hypophysial peptides such as arginine vasotocin (Robertson 1974). Among the primitive cyclostomes the physiological importance of hypophysial peptides is still uncertain (Hardisty 1972; Robertson 1974). Injection of arginine vasotocin into L. fluviatilis did not cause a change in body weight nor urine volume. It did, however, cause an elevation in urine sodium and potassium with an increased total renal loss of sodium (Bentley and Follett 1963). Presumptive adrenocortical cells exist in association with the cardinal veins of lampreys and may be the source of corticosteroids influencing salt and water balance (Chester Jones 1963). An attempt to identify and quantify cortisol and corticosterone in the plasma of the landlocked sea lamprey has shown only doubtful traces of these compounds (Weisbart and Idler 1970). Injections of aldosterone caused a slight decline in urine output but significant changes in total urinary loss of sodium or potassium were not demonstrable (Bentley and Follett 1963). In saline water aldosterone reduced the total loss of sodium which caused Bentley and Follett (1963) to suggest that the hormone inhibits the extrarenal loss of sodium at the gills. Certainly, at present it is not possible to generalize on the hormones present in the pituitary-hypothalamus complex or those of the adrenocortical tissue, or on their function in osmotic and ionic regulation (Robertson 1974; Larsen 1980; Gorbman 1980).
Regulation and Salinity Tolerance
During Metamorphosis

Subsequent to the freshwater sedentary larval stage, lampreys undergo a nontrophic period of metamorphosis during which a number of morphological and physiological changes occur (Manion and Stauffer 1970; Hardisty and Potter 1971; Potter et al. 1978). Among the parasitic lampreys, these changes include the machinery by which internal ionic and osmotic concentration can be regulated over a greater range of ambient salinities than can be tolerated by the larvae. Ammocoetes are well adapted for life in freshwater; however, in saline water they exhibit a rather ineffective control of their internal osmotic and ionic concentration (Hardisty 1956; Morris 1972; Mathers and Beamish 1974; Beamish et al. 1978). Accordingly larval lampreys have a relatively low tolerance for saline water. Mortalities of larval anadromous sea lamprey were recorded in a salinity as low as 10% with the 24-h LC50 being 14.8% (Beamish et al. 1978). Larvae of the nonparasitic species appear equally sensitive to salinity. Thus, Hardisty (1956) found mortalities among larval *L. planeri* in solutions of NaCl equivalent to about 280 mosmol·kg⁻¹ or 11%.

Osmotic regulation during metamorphosis has been measured only for the landlocked sea lamprey (Mathers and Beamish 1974). During the early stages of metamorphosis serum osmolality of the landlocked sea lamprey in freshwater increases rapidly reaching a plateau by the early macrophthalmia stage (Fig. 1, Mathers and Beamish 1974). Serum osmolality of larval sea lampreys in freshwater is ≈260 mosmol·kg⁻¹. By the early macrophthalmia stage osmolality increases to 304 mosmol·kg⁻¹ and remains at a similar level to the completion of metamorphosis. Not until the macrophthalmia stage is reached are lampreys able to osmoregulate in a saline solution equivalent to 10%. After 1 d exposure to a salinity of 10%, osmolality of ammocoetes and metamorphosing stages III and IV (Manion and Stauffer 1970) are ≈344, 333, and 335 mosmol·kg⁻¹, respectively. Osmolality of early macrophthalmia in 10% is about 300 mosmol·kg⁻¹, similar to that in freshwater.

Salinity Tolerance in Juveniles and Adults

On completion of metamorphosis, parasitic juvenile lampreys migrate downstream to either a lake or ocean where they begin the second trophic interval of their life cycle. Completion of the downstream migration may be delayed by as much as 6 mo during which time lampreys remain within the river without feeding (Applegate 1950; Potter and Beamish 1977). Of those species which spend their juvenile interval in freshwater only the landlocked *P. marinus* has been examined with respect to salinity tolerance and osmotic performance (Mathers and Beamish 1974). Among the marine lampreys, osmotic relationships have been determined for *P. marinus, L. fluviatilis,* and *Lampetra tridentata* (Fontaine 1930; Galloway 1933; Hardisty 1956, 1958; Pickering and Morris 1970; Potter and Huggins 1973; Beamish et al. 1978; J. Richards, Dep. Fish. Oceans, Nanaimo, B.C., personal communication).

Adjustment to seawater soon after metamorphosis has been demonstrated for *P. marinus* (Beamish et al. 1978), *L. fluviatilis* (Hardisty 1956; Potter and Huggins 1973), and *L. tridentata* (J. Richards personal communication). Direct transfer of young anadromous juvenile *P. marinus* and *L. tridentata* to full seawater did not result in any mortalities within a 2-wk experimental period. Indeed, the transfer of *L. tridentata* to full seawater appears to encourage the initiation of feeding. Young juvenile *L. fluviatilis* are slightly better able to withstand direct transfer from fresh to full seawater than metamorphosing individuals of the same species (Potter and Huggins 1973). However, for both stages some mortalities were recorded over the 3-wk experimental period. Mortality of downstream migrant individuals captured in March was 25% when exposed to full seawater compared with 20% among animals taken in May/early June. About 30% of the metamorphosing animals when transferred directly to full seawater died within the experimental 3-wk period. Survival of juveniles was almost complete if the transfer to full seawater was made by exposing animals to increments of one third seawater each for 4 d.

Tolerance to salt water among the landlocked *P. marinus* is related to size of the feeding animals (Mathers and Beamish 1974). Over one half of the landlocked feeding juveniles of 127–188 mm died within 10 d following direct transfer to 26%. Only when landlocked juveniles reached almost 280 mm did they survive direct transfer to full seawater for periods of ~2 wk.

Coincident with the completion of the juvenile interval and the migration into freshwater rivers prior to reproduction is a marked reduction in the marine osmoregulatory mechanism. Galloway (1933) and (1956) found that adult migrant anadromous *P. marinus* and *L. fluviatilis* immersed in one half seawater died within 24 h. Beamish et al. (1978) determined the salinity at which 50% of the anadromous early upstream migrant *P. marinus* died within 48 h to be ~15.2% which is in general accord with that found by Morris (1956).

Nonparasitic lampreys appear to be less tolerant of salinity than representatives of the parasitic species. Hardisty (1956) found some mortalities among juvenile *L. planeri* exposed to a solution of 10% NaCl. Mortality was complete at 22 and 34% NaCl within 6 and 3 h, respectively. More recently J. Richards (personal communication) found that gradual exposure of juvenile *L. richardsoni* to saline water equivalent to 15% resulted in total mortality within 4 or 5 d.

Osmotic and Ionic Regulation

The regulatory mechanisms in marine feeding lam-
preys are well developed but unable to provide for complete blood homoiosmoticity between fresh and full seawater. Juveniles of the landlocked forms and the nonparasitic species are unable to maintain as tight a control over their blood concentration in saline water as that exhibited by the anadromous species. Feeding individuals of all species that are tolerant of the saline environment maintain their blood hyperosmotic to freshwater and hypoosmotic to seawater.

In freshwater, feeding landlocked sea lampreys exhibit osmotic independence (Urist and Van der Putte 1967; Mathers and Beamish 1974). There is, however, a significant increase in osmotic concentration between the larval and juvenile stage which signals a change in

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**Fig. 1.** Osmolality, chloride, and sodium concentration of the life stages of the landlocked and anadromous *Petromyzon marinus* (Mathers and Beamish 1974; Beamish et al. 1978) and *Lampetra fluviatilis* (Dekhuyzen 1904; Galloway 1933; Hardisty 1956; Pickering and Morris 1970) in freshwater. Values for *P. marinus* (10 ± 1°C) are based on blood serum, those for *L. fluviatilis* on plasma. Mean length (mm) is given within or beside the bar and the sample size is provided on top of each bar.
the regulatory mechanisms during metamorphosis (Mathers and Beamish 1974). Serum osmolality declines precipitously during the period of reproduction to a level comparable to that for ammocoetes (Fig. 1). This decrease undoubtedly reflects an increase in skin permeability (Hardisty 1956; Morris 1958), and a degeneration of the kidney (Youson 1970), and the gut (Pickering and Morris 1970; Pickering and Dockray 1972).

The anadromous sea lamprey displays much greater variability in osmotic concentration in freshwater throughout the juvenile interval of its life cycle than the landlocked form (Fig. 1). Despite this variability osmotic concentration remains consistently below that for the landlocked form. The decline in osmolality with size of feeding anadromous individuals is likely a reflection of the adjustment of the regulatory mechanisms for a marine existence during this period of the life cycle.

Upstream migrant adults exhibit an osmolality in freshwater which is above that of feeding juveniles. This rise apparently signals the restoration of the marine state and the development of full marine osmoregulatory mechanisms for a marine existence during this period of the life cycle.

Changes in osmotic concentration in freshwater are mainly attributable to fluctuations in chloride and sodium concentrations (Fig. 1). Pickering and Morris (1970) suggest the low chloride values for early migrant  *L. fluviatilis* (Fig. 1). Unfortunately measurements have not been made on spent individuals. However, *L. fluviatilis* demonstrates greater osmotic independence than the anadromous sea lamprey during this phase of the life cycle.

Changes in osmotic concentration in freshwater are mainly attributable to fluctuations in chloride and sodium concentrations (Fig. 1). Pickering and Morris (1970) suggest the low chloride values for early migrant  *L. fluviatilis*, and  *L. tridentata* (Urist 1963) indicates that the freshwater regulatory mechanism is incompletely established when individuals first enter freshwater. However, in the anadromous sea lampreys both sodium and chloride were higher in early migrants than in feeding animals and decreased with the approach of sexual maturity.

Relatively few measurements have been made of other blood ions (Table 1). Consistent and low levels of serum calcium and phosphate are prevalent in the blood of the landlocked sea lamprey (Urist and Van der Putte 1967). Urist (1963) has shown that the lamprey is a typical freshwater vertebrate in its serum calcium and phosphate levels. About 28 and 11% of calcium and phosphate is present as a complex with protein. Early migrant female lampreys display higher calcium levels than males which Pickering and Dockray (1972) suggest is related to the process of producing calcium-rich vitellin by the maturing female. Serum potassium in a normally functioning animal is regulated by sodium and chloride and the gut (Youson 1970), and the gut (Pickering and Morris 1970; Pickering and Dockray 1972).

FIG. 2. Osmolality of migrant *Petromyzon marinus* in relation to length. Measurements were made in freshwater at 10 ± 1°C (Mathers and Beamish 1974; Beamish et al. 1978).
<table>
<thead>
<tr>
<th>Species</th>
<th>Stage</th>
<th>Salinity %</th>
<th>Serum/ plasma Osmolarity mOsm-kg(^{-1})</th>
<th>Na(^+) mmol-L(^{-1})</th>
<th>K(^-) mmol-L(^{-1})</th>
<th>Ca(^{++}) mmol-L(^{-1})</th>
<th>Mg(^{++}) mmol-L(^{-1})</th>
<th>Cl(^-) mmol-L(^{-1})</th>
<th>S04(^--) mmol-L(^{-1})</th>
<th>HCO(_3) mmol-L(^{-1})</th>
<th>P(^--) mmol-L(^{-1})</th>
<th>Protein mg.mL(^{-1})</th>
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<td>4.00</td>
<td>2.40</td>
<td>1.80</td>
<td>122</td>
<td>0.10</td>
<td>5.00</td>
<td>1.30</td>
<td>32.0</td>
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<td>186 ± 7</td>
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<td>0</td>
<td>Serum</td>
<td>139</td>
<td>6.20</td>
<td>2.37</td>
<td>1.90</td>
<td>113</td>
<td>0.87</td>
<td>5.18</td>
<td>1.40</td>
<td>39.0</td>
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</tr>
<tr>
<td></td>
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<td>0</td>
<td>Serum</td>
<td>136</td>
<td>5.10</td>
<td>2.47</td>
<td>1.75</td>
<td>112</td>
<td>0.74</td>
<td>5.21</td>
<td>1.31</td>
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<tr>
<td><em>P. marinus</em> (anadromous)</td>
<td>Juvenile Feeding</td>
<td>0</td>
<td>Serum</td>
<td>238 ± 7</td>
<td>117 ± 4</td>
<td>7.45 ± 0.82(^b)</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td>Beamish et al. (1978)</td>
</tr>
<tr>
<td></td>
<td>Stage I</td>
<td>8</td>
<td>Serum</td>
<td>236 ± 9</td>
<td>114 ± 5</td>
<td>6.08 ± 0.44(^b)</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Stage II</td>
<td>16</td>
<td>Serum</td>
<td>234 ± 5</td>
<td>106 ± 5</td>
<td>4.42 ± 0.37(^b)</td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Stage III</td>
<td>26</td>
<td>Serum</td>
<td>256 ± 4</td>
<td>115 ± 7</td>
<td>4.37 ± 0.33(^b)</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Stage IV</td>
<td>34</td>
<td>Serum</td>
<td>263 ± 3</td>
<td>135 ± 3</td>
<td>5.39 ± 0.42(^b)</td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Feeding (small)</td>
<td>0</td>
<td>Serum</td>
<td>203 ± 16</td>
<td>93 ± 7</td>
<td>3.49 ± 1.33(^b)</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td>Beamish et al. (1978)</td>
</tr>
<tr>
<td></td>
<td>Spawning</td>
<td>8</td>
<td>Serum</td>
<td>214 ± 26</td>
<td>95 ± 12</td>
<td>6.39 ± 2.00(^b)</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Feeding (large)</td>
<td>26</td>
<td>Serum</td>
<td>250</td>
<td>126 ± 3</td>
<td>5.63 ± 2.77(^b)</td>
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<td>Robertson, in Morris (1972)</td>
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<tr>
<td></td>
<td>Feeding</td>
<td>35</td>
<td>Serum</td>
<td>155 ± 7</td>
<td>31.6</td>
<td>3.51 ± 0.50(^b)</td>
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<tr>
<td></td>
<td>Adult Early migrant</td>
<td>0</td>
<td>Serum</td>
<td>285 ± 9</td>
<td>155 ± 5</td>
<td>4.95 ± 1.11(^b)</td>
<td></td>
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<td></td>
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<td>Beamish et al. (1978)</td>
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<tr>
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<td>Adult Early migrant</td>
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<td>Plasma</td>
<td>294</td>
<td>112</td>
<td>2.3</td>
<td>1.8</td>
<td>1.5</td>
<td>100</td>
<td>2.5</td>
<td></td>
<td>Pickering and Morris (1970)</td>
<td></td>
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<tr>
<td></td>
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<td>0</td>
<td>Plasma</td>
<td>319</td>
<td></td>
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<td></td>
<td></td>
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<td>Fontaine (1930, 1932)</td>
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<tr>
<td></td>
<td>Early migrant</td>
<td>0</td>
<td>Serum</td>
<td>259 ± 8</td>
<td>136 ± 7</td>
<td>5.57 ± 1.82(^b)</td>
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<td>Beamish et al. (1978)</td>
</tr>
<tr>
<td></td>
<td>Nearly mature</td>
<td>8</td>
<td>Serum</td>
<td>250 ± 8</td>
<td>128 ± 5</td>
<td>4.01 ± 1.25(^b)</td>
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<td></td>
<td>Spent</td>
<td>0</td>
<td>Serum</td>
<td>190 ± 10</td>
<td>92 ± 7</td>
<td>11.03 ± 2.03(^b)</td>
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<td>Hardisty (1956)</td>
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<td><em>L. tridentata</em></td>
<td>Adult Early migrant</td>
<td>0</td>
<td>Serum</td>
<td>87</td>
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<td>80</td>
<td>0.50</td>
<td>3.12</td>
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<td><em>L. planeri</em></td>
<td>Adult</td>
<td>0</td>
<td>Serum</td>
<td>227</td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td>101</td>
<td>Hardisty (1956)</td>
</tr>
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<td><em>L. fluviatilis</em></td>
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<td>Plasma</td>
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<td>Dekhuyzen (1904)</td>
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<td>Early migrant</td>
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<td>Plasma</td>
<td>265</td>
<td>115</td>
<td>3.1</td>
<td>0.95</td>
<td>1.00</td>
<td>92</td>
<td></td>
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<td>Galloway (1833)</td>
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<td>0</td>
<td>Plasma</td>
<td>288</td>
<td>112</td>
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<td>Robertson (1954)</td>
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<td>0</td>
<td>Plasma</td>
<td>289</td>
<td>122</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Hardisty (1956)</td>
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*Confidence limits 95%.
*Beamish (unpublished data).
*High values due to some hemolysis of the sample.
tain higher serum osmolalities than the anadromous form when compared at identical salinities (Beamish et al. 1978). The landlocked form is unable to maintain as tight a control over serum osmolality in saline water as that displayed by the anadromous form (Mathers and Beamish 1974; Beamish et al. 1978, Fig. 3). Only the large feeding landlocked sea lampreys are able to osmoregulate for long periods in salinities above 16%. Within 10 d in 26% over 50% of the juvenile lampreys (127-188 mm) died. Osmolality of lampreys (194 mm) surviving for 10 d (397 mosmol·kg⁻¹) was considerably above that of individuals (203 mm) after 1 d in 26% (354 mosmol·kg⁻¹). Osmotic concentration of the larger sea lampreys did not change significantly during the 15-d exposure period. The landlocked form of sea lamprey (220 mm) in 34% was able to maintain serum osmolality (401 mosmol·kg⁻¹) constant for 4 d. By the 9th d in 34% all animals died. Similarly lampreys of 250 mm did not survive longer than 9 d in 34%. The largest category of lampreys tested, 289 mm, survived the 15 d in 34% without mortality. Further, osmotic concentration did not vary appreciably from 400 mosmol·kg⁻¹ throughout the exposure period. Concordant with the lower serum osmolalities recorded for the anadromous form of *P. marinus*, Burian (1910) found the osmotic concentration for one feeding animal captured in the Mediterranean Sea, 42%, to be 317 mosmol·kg⁻¹, well below that for the landlocked form in a salinity of 34% and above that recorded for anadromous feeding juveniles by Beamish et al. (1978). More recently, Robertson (in Morris 1972) reported an osmolality of ~360 mosmol·kg⁻¹ for a sea lamprey caught off the coast of Scotland in a salinity of 35%.

Serum osmolality in freshwater relative to ambient salinity for the landlocked and anadromous forms of *P. marinus* were compared by Beamish et al. (1978). The ratio for landlocked juveniles decreased from 1.00 to 0.76 between 0 and 26% whereas that for the anadromous individuals declined only to 0.93 over the same salinity range. It appears that with the transition to a landlocked existence lampreys have experienced a reduction in their capacity for marine osmoregulation. The large landlocked juveniles are able to osmoregulate even in full seawater emphasizing the advantage afforded through a reduction of surface area relative to body volume.

Changes in serum osmolality appear to be primarily
the result of corresponding shifts in sodium and chloride ions (Table 1, Fig. 4A) (Urist and van der Putte 1967; Mathers and Beamish 1974; Beamish et al. 1978). Organic molecules such as glucose, glycerol, and amino acids along with some inorganic ions account for the difference between osmolality and sodium plus chloride (Potts and Parry 1964). In both landlocked and anadromous feeding sea lampreys, changes in chloride ion are not accompanied by an equivalent shift in sodium, suggesting that the relationship between the two ions is not passive (Fig. 4B). For a given change in chloride, that by sodium was less; however, this was not as pronounced in the higher salinities (Fig. 4A). The close control held over sodium has been demonstrated also for several teleosts (Houston et al. 1968; Byrne et al. 1972; Lutz 1972). Lutz (1972) suggests that the physiological significance of sodium is in the uptake of metabolites by the cell as well as in the regulation of potassium. Landlocked *P. marinus* are not able to regulate sodium as precisely as anadromous sea lampreys, particularly in the higher salinities, which may contribute to the difficulties they experience in salt water.

Early migrants of the anadromous *L. fluviatilis* fail to regulate their internal osmotic concentration in salinities above ~18% (Hardisty 1956). Between freshwater and the isosmotic salinity the hyperosmotic blood serum increases from a value between ~250 and 300 (Dekhuyzen 1904; Galloway 1933; Hardisty 1956; Pickering and Morris 1970) to 450 mosmol·kg⁻¹ (Hardisty 1956), well above the range of concentrations found for the feeding stages of both the anadromous and landlocked forms of *P. marinus* (Mathers and Beamish 1974; Beamish et al. 1978).

Osmoregulatory performance among the nonparasitic lampreys has been examined in relation to ambient salinity only for *L. planeri* (Hardisty 1956). Animals maintain a hyperosmotic blood serum to a salinity of about 12% at which regulation of the internal concentration ceases and some mortalities occur.

Nearly mature migrant anadromous sea lampreys are able to regulate their osmotic concentration in dilute saline solutions to about 8% (Beamish et al. 1978). Exposure of nearly mature sea lampreys to 8% for 4 d did not alter significantly the osmolality found after 1 d in this salinity. In 16% serum osmolality rose precipitously to 358 mosmol·kg⁻¹, a significant increase over that found at the lower salinities. The increase in osmolality continued to 24% at which it was 460 mosmol·kg⁻¹. Loss of the swallowing mechanism and a reduced capacity to absorb ions and water across the gut wall were suggested by Pickering and Morris (1970) as factors contributing to the breakdown of the marine osmoregulatory ability in upstream migrating sea lampreys and *L. fluviatilis*. Freshwater osmoregulation deteriorated in spent adults. Osmolality and the concentration of sodium and chloride dropped below those of any other stage in freshwater indicating that the tissues responsible for maintaining hyperosmoticity had ceased to function efficiently, perhaps coupled with a leakage of ions or water across the integument. An increase in integument permeability to water was reported by Morris (1958) and Pickering and Morris (1970) in *L. fluviatilis* and *P. marinus* on the spawning migration. Hardisty (1956) found increased body water in *L. planeri* and *L. fluviatilis* as each approached sexual maturity. Regulation is restricted further by a massive degeneration of the kidneys which

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**FIG. 4(A).** Serum sodium and chloride concentrations of the anadromous sea lamprey. Vertical bars around the mean denote 95% confidence limits. (B) Relationship of serum sodium to chloride concentrations. Redrawn from Beamish et al. (1978).
occurs at the time of spawning (Youson 1970).

The habitat of the earliest agnathans is uncertain. Robertson (1954, 1957) has argued in favor of a marine environment on the basis of paleontological and physiological evidence, the former being supported more recently by the findings of Denison (1956), White (1958), and Tarlo (1962). In contrast, Marshall and Smith (1930) proposed a freshwater origin and based their views on the presence of a glomerular kidney. Robertson (1957) and Morris (1965, 1972) have suggested the vertebrate glomerulus may have developed in seawater where it served primarily as an organ of ion balance. In support of this, Youson et al. (1974) were unable to detect significant differences in the cross-sectional area of the renal corpuscles of freshwater and marine sea lampreys. Certainly a glomerular kidney would have facilitated the entry of cyclostomes into freshwater. Volume regulation and conservation of ions by the production of a hypoosmotic urine together with the function of ion regulation would permit animals to maintain a hyperosmotic blood in an ion-deficient environment (Robertson 1957, 1974; Munz and McFarland 1964). On balance, Morris (1972) concluded the earliest agnathans were marine animals equipped with a primitive osmoregulatory mechanism similar to that of the present-day myxines. He suggests that cyclostomes more recently entered freshwater and adapted their metabolic processes to function in a concentration of blood ions below that which is prevalent in marine forms, thereby reducing the osmotic stress between the internal and external environment. The subsequent reentry into the marine habitat may have been facilitated by the development of a swallowing extrarenal excretory mechanism.

The present-day landlocked forms of parasitic lampreys as well as the nonparasitic species are believed to have evolved from marine parasitic species (Hubbs 1925, Hubbs and Potter 1971). Hardisty (1956) suggested that this evolution involved selection for individuals of smaller size and reduced osmoregulatory performance which is entirely consistent with recent observations on salinity tolerance, and osmotic and ionic regulation.

Acknowledgments

Technical assistance was provided by Mrs S. Sadler and Mrs E. Thomas.


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