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Migration and spawning energetics of the anadromous sea lamprey, *Petromyzon marinus*

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Synopsis

Energy expended in migration and reproduction was determined from measurements of caloric concentration and body and gonodal weight for nontrophic sea lampreys collected from different sites along the St. John River, New Brunswick. The estimated cost of locomotion in swimming the 140 km which separates the estuary from the spawning redds was 300 and 260 kcal for males and females respectively. Acutal distance which lampreys swam as well as mean swimming speed were estimated from a linear regression equation relating energy expenditure for locomotion and body weight. Energy expenditure for breeding was considerably greater than that catabolized throughout the upstream migration.

Introduction

The adult period of the anadromous sea lamprey (*Petromyzon marinus*) is spent largely at sea where the species feeds on the tissue and body fluids of predominately teleost fishes (Bigelow & Schroeder 1948, 1953). The duration of this period in the life cycle is not precisely known but based on growth rates observed in field studies, Beamish & Potter (1975) estimated it to last for three or four years. Young adult sea lampreys leave the freshwater streams for the marine environment weighing as little as three grams (Potter & Beamish 1977). In the subsequent trophic interval lampreys increase their body weight to approximately 900 g at the commencement of the nontrophic upstream spawning migration. Energy requirements for the spawning migration and maturation of the gonads are derived exclusively from the catabolism of products stored during the marine feeding phase. In this context, Nikol'skii (1961, 1963) suggested that the amount of lipid, the principle energy source, deposited by lampreys prior to the migration is related to the distance that a particular species must travel to the spawning grounds. The amount of lipid accumulated by lampreys appears also to vary with the duration of the subsequent migration (Lanzing 1959, Moore & Potter 1976, Beamish et al. 1979).

The opportunity to collect upstream migrating sea lampreys from different sites along the St. John River, New Brunswick, facilitated the determination of the energy requirements for swimming and breeding. This information in concert with earlier metabolic studies (Beamish 1973) permitted an estimate of the speed at which sea lampreys migrate upstream and the distance actually covered.

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Materials and methods

The St. John River (longitude 67°14′ W; latitude 45° 58′ N) runs approximately 756 km from its source in northern Maine to its estuary, which discharges into the Bay of Fundy beside the city of St. John (Fig. 1.). The lower portion of the St. John River is characterized by the presence of numerous lake-like extensions into which run rivers and streams, the lakes themselves flowing into the main channel of the river. Approximately 140 km upstream from the river's mouth is located the Mactaquac Dam and hydroelectric installation which was completed in the mid 1960's. While the dam is a barrier to the upstream migration of fish, a fishway operated by staff from

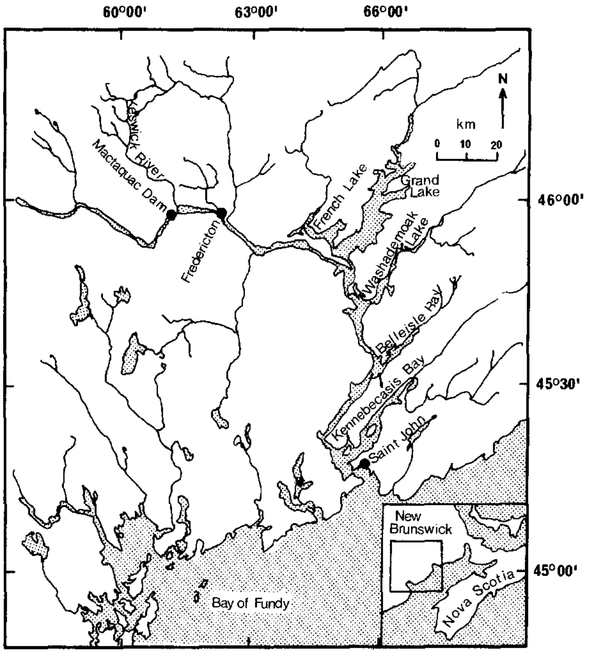

Fig. 1. Map of the St. John River showing the Mactaquac Dam, Keswick River, and Washedomoak Lake, from which animals were collected.

the Fisheries and Marine Service, Environment Canada, permits the transportation of animals to above the dam.

The earliest upstream migrants, captured during their spawning run were taken in trap nets set in Washademoak Lake (Fig. 1) during mid May. All were immature and from the bluish coloration which several of them exhibited, would appear to have only recently left the ocean (Beamish & Potter 1975). Upstream migrant sea lampreys first reached the Mactaquac Dam in mid-June and were abundant there until late June. It was assumed that lampreys entering Washademoak Lake in mid May were part of the same population that later moved approximately 60 km upstream to the Mactaquac Dam as well as into the various tributaries of the St. John River. Spent lampreys were captured by dip net between June 30 and July 1 in 1975 and between June 27 and 30 in 1976 at a site approximately 1 km upstream from the mouth of the Keswick River (Fig. 1).

Immediately after their capture lampreys were shipped via aircraft to the University of Guelph where they were sampled. After anaesthetization in carbon dioxide, the animals were sexed, weighed and measured to the nearest 0.1 g and mm respectively. The gonads were removed and weighed to the nearest 0.1 g.

In preparation for energy determination, animals were freeze-dried and thereafter homogenized. Caloric content of dried samples was measured with an adiabatic macro bomb calorimeter. All values represent the mean of at least two samples.

Results and discussion

Wet body weight of sea lampreys decreased throughout the spawning, migration being highest among the early migrants captured in Washademoak Lake and lowest following the release of gonadal products. In an earlier study by Beamish et al. (1979) in which large numbers of lampreys were collected, the mean weight of early upstream male lampreys was 876.1 g decreasing to 868.4 and 776.7 g in nearly mature and spent individuals. Similarly, early migrant females weighed 896.1 g with weight declining to 885.2 and 645.1 g when animals were nearly mature and following spawning.

Energy concentration followed a similar pattern to that for body weight. Thus, energy concentration of early migrant males was 6.607 ± 0.100 kcal g^{-1} dry weight (± 95% confidence limits, $n = 20$) declining to 6.296 ± 0.172 ($n = 9$) and 5.607 ± 0.157 kcal g^{-1} ($n = 10$) in nearly mature and spent animals. Significant differences in the caloric concentration were demonstrable among the three stages at $p < 0.05$. The pattern of change of energy concentration among females was similar to that for males but differences were less marked. Energy concentration of early migrant females was 6.482 ± 0.335 kcal g^{-1} ($n = 8$) declining to 6.296 ± 0.172 ($n = 9$) and 5.731 ± 0.557 kcal g^{-1} ($n = 8$) in nearly mature and spent animals respectively. Significant differences at $p < 0.05$ were demonstrable between the early or nearly mature migrants and spent females. Variation in energy concentration among the early and nearly mature migrant females sampled was such that significant differences were not demonstrable at $p < 0.05$. However, the mean caloric concentrations for early and nearly mature females (which followed a similar pattern to that for male lampreys where statistical significance was demonstrable), were presumed to be biologically significant and were applied in subsequent calculations.

Water content of whole animals, reported in Beamish et al. 1979, was lowest in the early migrant stages with relative values for males and females of

75.8 and 71.6%. Between Washademoak Lake and the Mactaquac Dam, the water content increased to 76.5 and 72.9% in males and females respectively with values after spawning of 82.6 and 82.3%. Conversely, dry weight of males decreased from 212.1 g for early migrants to 204.1 and 135.1 g in nearly mature and spent individuals respectively. Dry weight of early upstream migrant females was 254.5 g declining to 239.9 and 114.2 g in nearly mature and spent animals respectively. On the basis of the caloric concentration and dry weight, total energy content of male lampreys decreased from 1401 to 1209 to 758 kcal between the early migrant, nearly mature and spent stages. The total caloric content of early migrant females was 1650 kcal and that for nearly mature and spent individuals, 1510 and 655 kcal. Thus, the energy expenditure in swimming between Washademoak Lake and the Mactaquac Dam was 193 and 140 kcal for males and females.

The energy cost for locomotion by fish has been expressed independently of swimming speed as the caloric expenditure to transport one unit of body mass one kilometer (Schmidt-Nielsen 1972). This analysis was based primarily on information collected by Brett (1964) on the metabolic cost of swimming for sockeye salmon, *Oncorhynchus nerka*, but included also information on some other fish species. The results indicated a logarithmic linear decrease in energy expenditure to transport one gram of body mass one kilometer with increase in weight over a range of three orders of magnitude. Presentation of the energy cost of locomotion for a wide variety of other fish species in the manner suggested by Schmidt-Nielsen (1972) has indicated a remarkable similarity to that found for sockeye salmon of the same body weight (Beamish 1978). On the basis of this relationship, the total cost for locomotion by an adult sea lamprey of 877 g, the approximate mean weight of migrating adults, is estimated at 0.41 cal g^{-1} km^{-1}.

During the interval between the arrival of sea lampreys in Washedomoak Lake and the Mactaquac Dam, the gonads developed to a condition approaching sexual maturity. In an earlier study on the river lamprey, *Lampetra fluviatilis*, Claridge & Potter (1975) found that standard or basal metabolism increased with maturation of the gonads, a response described also for salmonids by Beamish (1964). Standard metabolism of river lamprey early in their spawning migration, which is of longer duration than that of the sea lamprey, was approximately 40 mg kg^{-1} h^{-1} and not significantly different between sexes. Thereafter there was a progressive increase in standard metabolism until the terminal stages of the migration when values for females showed a decline. In the final month of the migration, the mean metabolic rate for males was approximately 80 mg kg^{-1} h^{-1}, appreciably higher than the 60 mg kg^{-1} h^{-1} for females.

The relationship between the energy cost of swimming and body weight described by Schmidt-Nielsen (1972) did not consider the higher standard metabolic rates which accompany gonadal maturation in at least lampreys and salmonids, but more probably all fishes. Standard metabolism of the landlocked adult sea lamprey in the feeding phase of their life cycle was measured by Beamish (1973) in relation to body weight and temperature. Calculation of the standard oxygen consumption for anadromous sea lampreys of 877 g were based on respiration values for the landlocked form at 10 and 15° C respectively, the approximate temperature range of the St. John River between mid-May and late June, and a logarithmic regression coefficient of 0.8 (Winberg 1956, Beamish & Dickie 1967). Adjustment for the increase in standard metabolism attributable to gonadal maturation, based on the relationship found for river lampreys by Claridge & Potter (1975), indicated an additional energy expenditure of 124 and 62 kcal by male and female sea lampreys over the 35-day migration from Washedomoak Lake to the Mactaquac Dam.

Ultrasonic tagging experiments with teleosts have shown that migrating fish seldom follow a strictly linear course although directionality in their pattern of movement is generally apparent (Poddubny 1967, Hasler et al. 1969, McCleave & Horrall 1970, Yuen 1970, Dodson et al. 1972). Assuming lampreys followed a direct linear course in their upstream movement the total expenditure of energy between Washademoak Lake and Mactaquac Dam, a distance of 60 km, was 3.67 and 2.66 cal g^{-1} km^{-1} for males and females respectively. Correction for the estimated increase in standard metabolism provided the remarkably similar values of 1.31 and 1.48 cal g^{-1} km^{-1} for male and female lampreys respectively, which nevertheless are appreciably above the 0.41 cal g^{-1} km^{-1} predicted from Schmidt-Nielsen's regression. This discrepancy could reflect a difference in the distance lampreys actually swam from the direct linear route of 60 km. On this basis it can be calculated that male and female lampreys actually swam 192 and 217 km respectively. The migration between Washedomoak Lake and the Mactaquac Dam required approximately 35 days. Thus, the average net swimming speed calculated for males and females was 6.35 and

7.18 cm s^{-1} (0.09 and 0.10 body lengths s^{-1}) respectively. Swimming speeds reported for migrating fishes generally lie within the range of 0.1 to 0.9 body lengths s^{-1} (Johnson 1960, Thorson 1971, Madison et al. 1972, Malinin 1973, Tesch 1974).

Observed rates of upstream migration by the landlocked sea lamprey are consistent with the estimated swimming speed for the anadromous form. In the slow flowing regions of Cayuga Inlet, Wigley (1959) reported an average rate of upstream migration of just under 5 cm s^{-1}, a value similar to the observations of Skidmore (1959) in the Pancake River, a tributary of Lake Superior. In a laboratory study, Beamish (1974) found that adult landlocked sea lampreys could not swim for more than 30 min at 30 cm s^{-1}, the lowest velocity applied. A number of factors may contribute to the relatively poor swimming performance exhibited by lampreys including the tidal system of respiration and the absence of a hydrostatic organ and paired fins. Because of poorly developed ventral and caudal fins, posterior turbulence is probably higher than that in most anguilliform fishes. Furthermore, the reduced caudal fin does not appear well adapted for providing a propulsive thrust.

The distance between Washedomoak Lake and the Mactaquac Dam or the spawning redds in the Keswick River (Fig. 1) is approximately equal. Thus, the difference in caloric content between nearly mature migrants caught at the Mactaquac Dam and spent adults captured in the Keswick River reflects the energy expenditure of spawning and the loss of gonadal products. The total loss of energy attributed to spawning was 451 and 856 kcal by males and females respectively. Wet and dry weights of the testes and ovaries in nearly mature migrants were 11.58 and 148.63 g and 1.84 and 70.47 g respectively (Beamish et al. 1979). Caloric content of testes was 5.553 ± 0.247 kcal g^{-1} (n = 10) yielding a total gonadal energy content of 10.2 kcal. Ovarian energy concentration was 6.173 ± 1.33 kcal g^{-1} (n = 10). Total mean energy of the nearly mature ovary was 435 kcal.

Thus among males, 98% of the energy lost during spawning, 441 kcal, is attributable to the metabolic expenditure of nest construction and the vigorous locomotory activity associated with breeding. Apart from the loss of ovarian products, female sea lampreys expended 421 kcal in spawning. The slightly greater expenditure of energy for breeding exhibited by males is consistent with the general observation that they play a more active role in spawning than females (Hardisty & Potter 1971).

Energy expended for breeding was considerably greater than that catabolized during the upstream migration from Washedomoak Lake to the spawning site. The energy expenditure for the entire migration between the estuary and the Keswick River, a distance of about 140 km, is likely not more than 300 and 260 kcal for males and females respectively. This assumed no increase in standard metabolism during the early phase of the migration due to gonadal maturation and that the distance lampreys actually swam between the estuary and Washedomoak Lake was in direct proportion to that estimated further upstream. In fact, the actual expenditure was probably less than the estimated values due to the lower temperature of the river during early April when migrating lampreys most likely enter the estuary of the St. John. Thus, the energy expenditure by both male and female lampreys for the migration represented only about 68 and 62% of that catabolized during breeding. On completion of spawning, the energy content of males and females was remarkably similar and about one half of that in the early upstream migrants. While depletion of energy in spent sea lampreys was severe, relative values of proximate body constituents reported in an earlier study (Beamish et al. 1979) were in all cases greater than those found for the small adults which had just begun to feed after many months of food deprivation. It would seem therefore, that the natural death which follows spawning may not be mainly attributable to the depletion of stored energy.

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References cited

Beamish, F. W. H. 1964. Seasonal changes in the standard rate of oxygen consumption of fishes. Can. J. Zool. 42: 189–194.

Beamish, F. W. H. 1973. Oxygen consumption of adult *Petromyzon marinus* in relation to body weight and temperature. J. Fish. Res. Board Can. 30: 1367–1370.

Beamish, F. W. H. 1974. Swimming performance of adult sea lamprey, *Petromyzon marinus*, in relation to weight and temperature. Trans. Am. Fish. Soc. 103: 355–358.

Beamish, F. W. H. 1978. Swimming capacity. In: W. S. Hoar D. J. Randall (ed.), Academic Press inc., New York and London.

Beamish, F. W. H. & L. M. Dickie. 1967. Metabolism and biological production in fish. pp. 215–242. In: S. D. Gerking (ed.), The Biological Basis of Freshwater Fish Production. Blackwell, Oxford and Edinburgh.

Beamish, F. W. H. & I. C. Potter. 1975. The biology of the anadromous sea lamprey (*Petromyzon marinus*) in New Brunswick. J. Zool. Lond. 177: 57–72.

Beamish, F. W. H., I. C. Potter & E. J. Thomas. 1979. Proximate composition of the adult anadromous sea lamprey, *Petromyzon marinus* L., in relation to feeding, migration and reproduction. J. Anim. Ecol. 00: 00–00.

Bigelow, H. B. & W. C. Schroeder. 1948. Fishes of the western North Atlantic. 2. Cyclostomes. Mem. Sears Fdn. Mar. Res. No. 1, pt. 1: 29–58.

Bigelow, H. B. & W. C. Schroeder. 1953. Fishes of the Gulf of Mainee. U.S. Fish. Bull. 53: 1–577.

Brett, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Board Can. 21: 1183–1226.

Claridge, P. N. & I. C. Potter. 1975. Oxygen consumption, ventilatory frequency and heart rate of lampreys (*Lampetra fluviatilis*) during their spawning run. J. Exp. Biol. 63: 192–206.

Dodson, J. J., W. C. Leggett & R. A. Jones. 1972. The behaviour of adult American shad (*Alosa sapidissima*) during migration from salt to fresh water as observed by ultrasonic tracking techniques. J. Fish. Res. Board Can. 29: 1445–1449.

Hasler, A. D., E. S. Gardella, R. M. Horrall & H. F. Henderson. 1969. Open water orientation of white bass, *Roccus chrysops*, as determined by ultrasonic tracking methods. J. Fish. Res. Board Can. 26: 2173–2192.

Hardisty, M. W. & I. C. Potter. 1971. The general biology of adult lampreys. pp. 27–206. In: M. W. Hardisty & I. C. Potter (ed.), The Biology of Lampreys. Academic Press Inc., New York.

Johnson, J. 1960. Sonic tracking of adult salmon at Bonneville Dam, 1957. U.S. Fish. Bull. 176: 471–485.

Lanzing, W. J. R. 1959. Studies on the river lamprey, *Lampetra fluviatilis*, during its anadromous migration. Uitgeversmaatschappij, Neerlandia-Utrecht: 11–82.

Madison, D. M., R. M. Horrall, A. B. Stasko & A. D. Hasler. 1972. Migrating movements of adult sockeye salmon (*Oncorhynchus nerka*) in coastal British Columbia as revealed by ultrasonic tracking. J. Fish. Res. Board Can. 29: 1025–1033.

Malinin, L. K. 1973. Speed of fish migration. Rybnoye Choz. (In Russian). Transl. Ser. Vol. 3146 (8): 16–17. Fisheries and Marine Service, Canada. 1974.

McCleave, J. D. & R. M. Horrall. 1970. Ultrasonic tracking of homing cutthroat trout (*Salmo clarki*) in Yellowstone Lake. J. Fish. Res. Board Can. 27: 715–730.

Moore, J. W. & I. C. Potter. 1976. Aspects of feeding and lipid deposition and utilization in the lampreys, *Lampetra fluviatilis* (L.) and *Lampetra planeri* (Bloch). J. Anim. Ecol. 45: 699–712.

Nikol'skii, G. W. 1961. Special Ichthyology. Second ed. Gosudarstvennoye izdatel'stvo, Moscow. Translated from Russian by the Israel Program for Scientific Translations. Jerusalem. Originally published 1954.

Nikol'skii, G. W. 1963. The Ecology of Fishes. Translated from Russian by L. Birkett. Academic Press, London. 352 pp.

Poddubny, A. G. 1967. Sonic tags and floats as a means of studying fish response to natural environmental changes and to fishing gear. FAO Conference on Fish Behaviour in Relation to Fishing Techniques and Tactics. Bergen, Norway, Exper. Pap. 46: 1–8.

Potter, I.C. & F. W. H. Beamish. 1977. The freshwater biology of adult anadromous sea lampreys, *Petromyzon marinus*. J. Zool. Lond. 181: 113–130.

Schmidt-Nielsen, K. 1972. Locomotion: Energy cost of swimming, flying and running. Science 177: 222–228.

Skidmore, J. F. 1959. Biology of spawning-run sea lamprey (*Petromyzon Marinus*) in the Pancake River, Ontario. M.Sc. Thesis, University of Western Ontario. 87 pp.

Tesch, F. W. 1974. Speed and direction of silver and yellow eels, *Anguilla anguilla*, released and tracked in the open North Sea. Ber. dt. Wiss. Komm. Meeresforsch. 23: 181–197.

Thorson, T. B. 1971. Movement of bull sharks, *Carcharhinus leucas* between Caribbean Sea and Lake Nicaragua demonstrated by tagging. Copeia 2: 336–338.

Wigley, R. L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. U.S. Fish. Bull. 59: 559–617.

Winberg, G. G. 1956. Rate of metabolism and food requirements of fishes. Belorussian State University, Minsk. Fish. Res. Board Can. Transl. Ser. 194.

Yuen, H. S. H. 1970. Behaviour of skipjack tuna, *Katsuwonus pelamis*, as determined by tracking with ultrasonic devices. J. Fish. Res. Board Can. 27: 2071–2079.