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BREEDING HABITS OF THE LAND-LOCKED
SEA LAMPREY

(*PETROMYZON MARINUS* var. *DORSATUS* WILDER)

BY

A. F. COVENTRY

OF THE DEPARTMENT OF BIOLOGY
UNIVERSITY OF TORONTO

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Nearly all that has been recorded concerning the life-history of the land-locked sea lamprey (*Petromyzon marinus dorsatus* Wilder) refers to the earlier description of Jordan and Fordice (1885) and the very inclusive study by Gage (1893) and his associates of the variety as it occurs in Cayuga and similar lakes of northern New York. For many years it has been known locally that a lamprey occurs in Lake Ontario at least some miles east and west of Toronto, where it is sometimes greatly in evidence, attaching itself temporarily to boats in motion or more especially to food-fishes and thus brought up by fishermen operating gill nets for whitefish and lake trout in the open waters. This lamprey has been confused to some extent with the silver lamprey (*Ichthyomyzon bdellium* Jordan). Its identity with *P. marinus dorsatus s. unicolor* was suggested by Bensley (1915), as a result of studies of the animal and of the surface wounds on fishes in relation to reports of fishermen as to occasional lamprey marks on whitefish in Georgian Bay; and confirmed by Huntsman (1917) as a result of a systematic review of the known records of lampreys from Ontario waters. So far as the writer is aware no young have been recorded hitherto from the Toronto area, though there is a single metamorphosed specimen of 13.5 cm. taken in a swamp near Whitby in the university collection.

While it is evident from what is known of the glacial history of the Great Lakes Basin that a community of conditions is to be expected as between the New York lakes and Lake Ontario, and also between both and the Gulf of St. Lawrence, the relative isolation of the habitat previously described lends interest to its more open occurrences in

Lake Ontario and also to the comparison of its breeding habits and development with that of the Cayuga lamprey. At the same time it will be recognized that the term "land-locked" as applied to the animal is largely a matter of descriptive convenience. The case is analogous in some respects to that of the land-locked sea salmon in its original occurrence in Lake Ontario. Of these and other species of fishes related as respectively fresh water and marine we know neither the nature of the original medium nor the environmental factors associated with their varietal and specific differences.

On Friday, May 27, 1921, Mr. J. R. Dymond of the Department of Biology reported that large numbers of land-locked sea lampreys were in the Humber river, just west of the city of Toronto. The vast majority of those he saw, and they numbered hundreds, were in a small rocky pool immediately below the Lambton weir; many were swimming about, others hung on to the rocks from which they could be picked by hand. They appeared to be blocked in their ascent of the stream by the weir, which is about three feet high. Mr. Dymond did not see any nests on this date. It was then decided to attempt to follow the progress of the breeding season, and with this object in view frequent visits were made to the river during June.

The stretch of the river in which nests were found is about three-quarters of a mile long and terminated upstream by the weir already mentioned; no nests or adults were seen above this in spite of careful search. Downstream, nests were not discovered below the rapids at the Old Mill Bridge, below which point the river becomes deep with a muddy bottom for the rest of its course to Lake Ontario, a distance of about two miles. Between the weir and the bridge the river averages about thirty yards in width and two feet in depth at this season of the year, with occasional holes as much as six feet deep. The river bed is composed of clean gravel or shingle interrupted here and there by large flat slabs of solid rock, and the stream is broken up by frequent rapids, none steep enough to make real 'white water', although the larger are difficult enough to wade against. The general

direction of the stream is from north to south and the valley is so wide that in spite of the high banks (80-100 feet) the sun reached the water by 8 o'clock in the morning (standard time).

As was subsequently found during repeated wanderings along this stretch of the river, nests were excavated only in the more rapid regions and indeed only in the shallower parts of these. The majority were in not more than a foot of water and none were seen at a greater depth than two feet. Large stretches of gravel of apparently exactly the same physical qualities as in the rapids, but covered instead by comparatively slowly moving water, were completely neglected, while a few yards up or down stream nests were abundant.

The nests are shallow depressions in the bed of the stream usually oval in outline, with the long axis in the direction of flow. They vary considerably in size, from about 12 inches by 18 inches to 24 inches by 30 inches. They are constructed usually by a pair of lampreys, but single animals have been seen working, and in one case at least two pairs occupied one large nest, all four individuals moving stones.

The stones moved are in general not larger than an inch in diameter, and most of them are smaller than this; occasionally, and with great effort, stones as big as two inches across are dragged from the excavation. In no case were two animals seen combining to move one stone, although in a number of cases this would have enabled them to make a much more convenient nest; if a stone too large to be moved by individual effort lies within the ambit of the nest, it remains. The material is deposited on the downstream side of the nest so as to form a kind of parapet of which the curve conforms to that of the oval hollow. An animal, having attached itself to a stone, allows itself to drift tail first with the current, until its mouth is over the downstream edge of the nest, it then brings itself to a halt with a sharp movement of its tail and at once drops the stone in position. While choosing stones the animal's movements are rather indeterminate; it will often lift and drop immediately a number of

pebbles before carrying one clear, and often it will remain stationary in the nest for minutes on end, either adhering to a large stone or lying at rest in the still pocket of water caused by the parapet. At the upstream edge of the nest there is nearly always a stone of markedly large size. No factor determining the site of the nest could be discovered other than the general ones of gravel of the right degree of coarseness and a sufficiently rapid current; given these, nests seemed to be impartially distributed in mid-stream or near the banks, at the upper edge of a rapid or down its full extent; in places they were so numerous as to suggest aeroplane photographs of heavily shelled fields.

The actual process of laying was watched a number of times. The two animals concerned cease carrying stones and take up a position with their heads at the upper edge of the nest; this is achieved in one of two ways; either both attach themselves to the large stone already mentioned, or the female alone takes this position, the male clinging to the top of her head; at once after this the posterior halves of their bodies twist together for about a complete turn and simultaneously make very rapid flapping movements, so fast, indeed, as to be almost vibrations. During this process, which lasts only a few seconds, eggs may be seen pouring from the female as a number of small white specks, which become mixed with the very small stones and sand stirred up by the agitation of the parents' bodies. As soon as this movement ceases eggs and sand together settle down at the bottom of the nest. The male and female then separate and resume their stone-hauling, often moving stones from points a foot outside the nests and placing them on the parapet, but after a few minutes the laying process is repeated; how often this interruption and resumption of laying may occur was not determined, but certainly as many as four.

In the large nest already mentioned as being the work of four animals one and the same male was seen to pair with each of two females, eggs from different mothers being mixed in the nest.

The eggs when they are first laid stick so firmly to stones

that any attempt to detach them usually destroys them; after about fifteen minutes, however, they do not adhere at all so closely and may be washed off with a gentle stream of water from a pipette; in the course of a day or two they lie loose among the pebbles.

During the period over which nesting was watched the temperature of the water varied from 18° C. on June 4th, to 23° C. on June 21st and 27th, the temperature being taken between 8 and 9 o'clock a.m., standard time.

The nesting season lasted approximately a month. As already noted abundant adults were seen on May 27th, but no nests. On June 1st nests were found in a rapid stretch about six hundred yards below the weir; the animals had apparently relinquished the attempt to go higher upstream, since on this date none were seen in the pool, nor were any seen subsequently this far up. The nest of June 1st had probably been provided with eggs the previous day, as those from which samples were taken all showed segmentation stages. The last nestings observed were on June 21st and no adults were seen later than June 22nd.

As to whether the parents die after spawning I cannot make a definite statement. I have, however, a strong feeling that they do not, and this opinion is based on the very small number of dead lampreys as compared with the abundance of the living seen during the nesting season. During June not more than a dozen or a dozen and a half dead were seen either in the nesting reach itself or in the slower stretch of water between this and Lake Ontario, while in the course of a few hours 150 living individuals were taken from the pool below the weir at the beginning of the season. If, then, the parents die at the end of the breeding season, they appear to return first to the lake, for it is hardly imaginable that so many individuals dying in so short a space of time and in so limited an extent of water should leave so slight a trace of the event.

An attempt was made to determine the time that elapses before the young leave the nest, and although the data are not quite conclusive, a probable estimate can be made.

There are two sources of possible error, first the necessity of disturbing the pebbles at the bottom of the nest among which the larvae are developing. The young after hatching are found one to two inches below the surface and in the undisturbed nest have presumably reached a position in which they are not affected by the flow of the stream; to get samples the overlying stones have to be turned gently aside with the point of a pipette until the larvae appear, when they are at once sucked up. In this process a number are inevitably dislodged from their crannies among the pebbles and swept away by the current, and it is not improbable that during the readjustment which must follow any such violent invasion of the colony new circulations of water are established, carrying still more of the young prematurely from the nest, which will thus be empty before its normal time. This error involves probably not more than two or three days.

The other complication is the difficulty of deciding when a nest is quite empty. The larvae are often distributed in patches over different parts of the nest, and while the greater part of the nest may not reveal a single larva, finally a thickly populated area may be touched by the pipette. The danger lies in overlooking such spots, and this is the greater since thoroughly to search a nest is a tiring procedure, the most practicable way being to kneel by it and, using a water-glass for clearer observation, bend close over it while turning the stones. With practice, however, likely spots are soon recognized, and in this case again the total inaccuracy is probably not large, almost certainly within the limits of variation due to changes in temperature. The two errors, further, tend to balance one another.

A nest called No. 3 may be taken as typical. It was first observed on June 1st, and the eggs were within a few hours of laying; on June 22nd no more larvae could be found in it. It should be mentioned here that specimens collected from this nest at various times and allowed to develop in the laboratory had by this time become quite transparent owing to the gradual disappearance of the shining white

yolk, that they were taking solid food from the mud provided, that they could swim powerfully and fast, and that they always made vigorous efforts to get under small stones or into the mud in the vessel. They were thus properly equipped to start the new phase of their existence. It is certain that these laboratory-bred animals were normal since they were compared time and again with specimens brought freshly from the nest, and no difference could be found; they could be used, therefore, as a sort of indirect check on the likelihood of the nest's being fully vacated.

The young, therefore, left the nest after about three weeks: this result is confirmed by observations on other nests and may be accepted as the average length of time for such conditions as prevailed during the breeding season of 1921. That the young leave the nest voluntarily and by their own exertions can, I think, hardly be doubted, since during the breeding season no rain fell after June 4th, and the stream became steadily lower and consequently the current less likely to disturb the nests. The young hatch out of the egg in seven or eight days.

I have not yet been able to discover where the next stage of life is spent despite careful examination of many samples of mud collected below the spawning reach at all depths down to 4 feet.

It is worth remark that in all the nests examined a number of eggs failed to develop; the percentage was not accurately determined, but is estimated at 10 to 20 per cent. of the total. These eggs become a light brown colour and may be found in the nest throughout the whole period of 'incubation.' On examination they prove to be covered with a delicate felt-work of almost colourless fungal hyphae, and if any of these infected eggs are by accident introduced into a dish in which larvae are developing there is formed on the floor of the vessel a strong growth of fungus, in which the larvae, as they become active and attempt to burrow, entangle themselves and perish. The causes of this non-development were not discovered, but three possibilities seem available; (1) that some eggs are incapable of fertilization, (2) that the

rather haphazard method of fertilization fails to ensure that a sperm reaches every egg, (3) that the eggs begin to develop, but owing to some weakness are at an early stage invaded by the fungal parasite. Further research is required to clear up this point.

Finally it seems worth while to call attention to the combination of unattached eggs with the position of the nest in the fastest accessible water, a condition that would hardly be, *a priori*, expected. It is true that for the first few minutes of their free existence the eggs are attached, apparently just long enough for the stones to which they adhere to settle into a permanent arrangement under the current conditions obtaining in the nest; subsequently they lie scattered loosely among the pebbles. The parapet on the downstream side of the nest certainly creates an eddy of comparatively still water in the nest, but a very slight disarrangement destroys the effect of this, as many experiences while collecting have shown. The aetiology of so curious a laying habit presents some interesting problems.

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Fig. 1. The weir at Lambton.



Fig. 2. A typical rapid, the site of a number of nests.



Fig. 3. A characteristic reach of the R. Humber, showing a succession of rapids and the nature of the banks.