FEEDING MECHANISM OF THE SEA LAMPREY AND ITS EFFECT ON HOST FISHES

BY ROBERT E. LENNON

FISHERY BULLETIN 98

UNITED STATES DEPARTMENT OF THE INTERIOR, Douglas McKay, *Secretary*

FISH AND WILDLIFE SERVICE, John L. Farley, *Director*

ABSTRACT

The feeding mechanism and predatory habits of the sea lamprey, *Petromyzon marinus*, have extensive and complex effects on host fishes which are not always lethal but are invariably serious. Comparative observations on the parasite-host relations were obtained from lampreys and their prey in Lake Huron and in aquariums at the Fish and Wildlife Service Laboratory at Hammond Bay, Mich.

The feeding mechanism consists of the buccal-gland system, the armed tongue, the tooth-studded oral disk, and the suctorial mouth. The secretion of the buccal glands, which bathes the wound of a victim fish, possesses a property for inducing lysis in the torn tissues, in addition to its anticoagulant and hemolytic powers.

The effects of lamprey attacks on fishes, both in aquariums and in the lake, were ascertained from examination of a total of 2,879 wounds on 20 species of fishes. No type of host tissue was wholly impervious to injury by the parasite. Hematological tests on eastern brook trout, brown trout, rainbow trout, and white suckers demonstrated that the volume and constituents of blood are drastically altered in mortal attacks by sea lampreys. The fungi *Saprolegnia parasitica* and *Leptomitus lacteus* occurred at times as contaminants of wounds on fishes that had survived lamprey attacks, and some mortalities were attributed to them.

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BY ROBERT E. LENNON, *Fishery Biologist*

Economic and biologic consequences of the invasion of the upper Great Lakes by the sea lamprey have been extensively reported (e. g. Applegate 1947). Basic features of the life history and possibilities for control of this predatory parasite have been described in detail by Gage (1929), Hubbs and Pope (1937), Shetter (1949), and others.

The sea lamprey is a primitive and anadromous fish of the north Atlantic Ocean and its tributary waters. It spends 4 or 5 years of larval life in the parent stream before it metamorphoses and descends to the sea as a parasitic feeder on fish. Its growth and development in the ocean are rapid, and the animal may attain a length of 30 inches before it ascends a stream to spawn and die. The species is also native to Lake Ontario, but Niagara Falls prohibited access to the upper lakes until the Welland Canal was completed in 1829. Nearly a century elapsed before sea lampreys were observed in Lake Erie, and their establishment there was not verified until 1932 (Creaser 1932). By 1937 the parasites had been reported from Lakes Huron and Michigan, and adult specimens were collected in Lake Superior in 1946 (Applegate 1950).

Recent statistics of the commercial fisheries on the Great Lakes indicate the efficiency and deadliness of sea-lamprey attacks on fishes (Hile, Eschmeyer, and Lunger, 1951). The production of lake trout (*Salvelinus namaycush*) from United States waters of Lake Huron and from Lake Michigan declined from 8,600,000 pounds to less than 26,000 pounds in a period of 10 years. The production of lake whitefish (*Coregonus clupeaformis*), burbot (*Lota lota maculosa*), suckers, and several other varieties had also been drastically reduced.

As late as 1950, little was known of the exact effects of lampreys on host fishes. It was necessary to collect a large quantity of data on the feeding mechanism employed by parasitic-phase sea lampreys, on the locations of their attachments on the bodies of host fishes, on the nature of the wounds and the effects on the tissue and blood of the victims, and on the properties of the lamprey's buccal-gland secretion. Additional material was needed on the incidence of secondary infections in wounds inflicted on fishes by sea lampreys. This work was part of the sea-lamprey investigations carried on to devise a practical lamprey-control program.

Several special adaptations are to be found in sea lampreys that make possible the parasitic feeding habit—an extremely rare behavior among vertebrates. Outstanding among these structural features are the buccal glands and their secretion, the rasping tongue, and the oral sucking disk. Singular morphological and physiological aspects of these organs and the results of their action on host fishes make up the major considerations of this study.

The Fish and Wildlife Service's laboratory at Hammond Bay on Lake Huron provided the aquarium facilities. Fishing operations in Lake Huron by the laboratory staff made it possible to collect data on attacks by the sea lamprey in nature during the period from July 1950 to September 1952. The studies reported here were begun as a project of the Trust Fund for Fishery Research of the Sport Fishing Institute (formerly the Associated Fishing Tackle Manufacturers). They were expanded and in large part completed while I was employed for the purpose by the Fish and Wildlife Service.

The assistance of the staffs of agencies involved in this investigation is deeply appreciated. Special thanks are due Karl F. Lagler, Chairman, Department of Fisheries, University of Michigan; James W. Moffett and Ralph Hile, Great Lakes Fishery Investigations; Vernon C. Applegate, Phillip S. Parker, and other members of the staff at the Hammond Bay Fishery Laboratory; and W. James Leach, Department of Anatomy, Ohio State University.

FOOD OF ADULT SEA LAMPREYS

The evidence is overwhelming that the principal food of adult sea lampreys is blood sucked from prey fishes. Body juices enter the parasitic diet to a lesser extent. A considerable amount of reduced flesh is also ingested by the parasites since their buccal-gland secretion possesses a property for liquefying certain fish tissues; the study of wounds made on a large number of fish by actively feeding lampreys supports this conclusion. Whether the products of cytolysis are utilized is unknown, but reason dictates that they probably are.

Many investigators have reported on the food of adult lampreys. Günther (1853) listed worms and insects as well as fish, and Abbott (1875) stated in reference to *P. americanus* Le Sueur that they wander over breeding grounds of other fishes and devour every egg they can find.

Gage (1893 and 1929) reported that in all lake lampreys (*P. marinus*) obtained out of breeding season, the digestive part of the alimentary canal contained blood or was empty. He found no partly digested worms, insects, small fish, or parts of fish flesh, although diligent search was made; consequently he believed that this species is wholly parasitic during its adult life and lives on blood sucked from other fishes. Dawson (1905) concluded that *P. marinus unicolor* may feed not only on blood but on more solid tissues as indicated in the extensive injuries produced on hosts.

Creaser (1933) listed blood and muscle fiber as the food of sea lampreys, whereas Hubbs and Pope (1937) and Storer (1943) described the food as blood. In a brief account of their life history, Vladykov (1949) wrote that parasitic lampreys feed on blood which is obtained by attaching themselves to fishes and rasping holes through their body covering. Applegate (1950) stated that the parasitic sea lamprey in the Great Lakes feeds on the blood and body juices of fishes.

The feeding mechanism of the sea lamprey is adapted for obtaining liquid food. Blood and body juices are sucked from host fishes and swallowed; fish flesh which is liquefied at the site of the injury is also ingested and may be utilized by the parasite.

FEEDING MECHANISM

The Sucking Disk

The sucking or oral disk of a lamprey serves as the entry to the mouth, or buccal funnel. It is on the anterior, ventral side of the head (fig. 1) and is armed with sharp, horny teeth which are of taxonomic significance in their number and arrangement. The size of the disk of the mature sea lamprey approximates the length of the branchial region (Vladykov 1949).

The mouth of a free-swimming sea lamprey is carried almost closed. The lateral margins of the disk are folded in a ventral and median direction, creating a slit-like opening from the posterior to anterior margins of the oral disk. Dawson (1905) stated in reference to inland species that when swimming the adult lamprey brings the sides of the buccal funnel together to form a vertical, wedge-shaped cut-water which is more streamlined than the open funnel. When a lamprey attaches itself to an object, however, the sucking disk is extended laterally as well as anteriorly and posteriorly (fig. 1). It is in this open position that the lamprey applies itself to host fishes, as well as to stones and, in the case of the male, to its mate during spawning (Reynolds 1931).

As a sea lamprey grows, the diameter of the sucking disk increases and hence the size of the wound inflicted on a host fish becomes greater. From the regression of diameter of sucking disk on length of lamprey it is possible (1) to estimate length of a lamprey responsible for a disk mark on a fish and (2) to verify earlier estimates by Applegate (1950) of the length of the parasitic-feeding period of the sea lamprey in the Great Lakes.

During 1951 and 1952, sucking-disk diameters were measured on 487 sea lampreys ranging from 4.8 to 22.1 inches long. Included in the total were small, newly transformed sea lampreys, 4.8 to 6.9 inches in length, obtained during their downstream migration in Carp Lake River. Some measurements of larger adults were obtained from specimens reared in aquariums at the Hammond Bay Fishery Laboratory. Most of the large lampreys were taken in weirs in Ocqueoc and Trout Rivers and Carp Creek during their spawning migrations. A few adults were captured in trap nets in Hammond Bay and Duncan Bay, Lake Huron. It was impossible to gather as many data as desired, and for one size group it was necessary to interpolate to reach an estimate of the mean diameter of the disk.

The mouths of the lampreys were pressed firmly against a piece of plate glass. The disk diameters were measured through the glass, from the anteriormost part of the marginal membrane to the posteriormost point of the margin, that is, across the center of the mouth from front to rear. This measurement was consistently the maximal diameter. The relations between total lengths of lampreys and diameters of their oral disks are shown in table 1 and figure 2. In the preparation

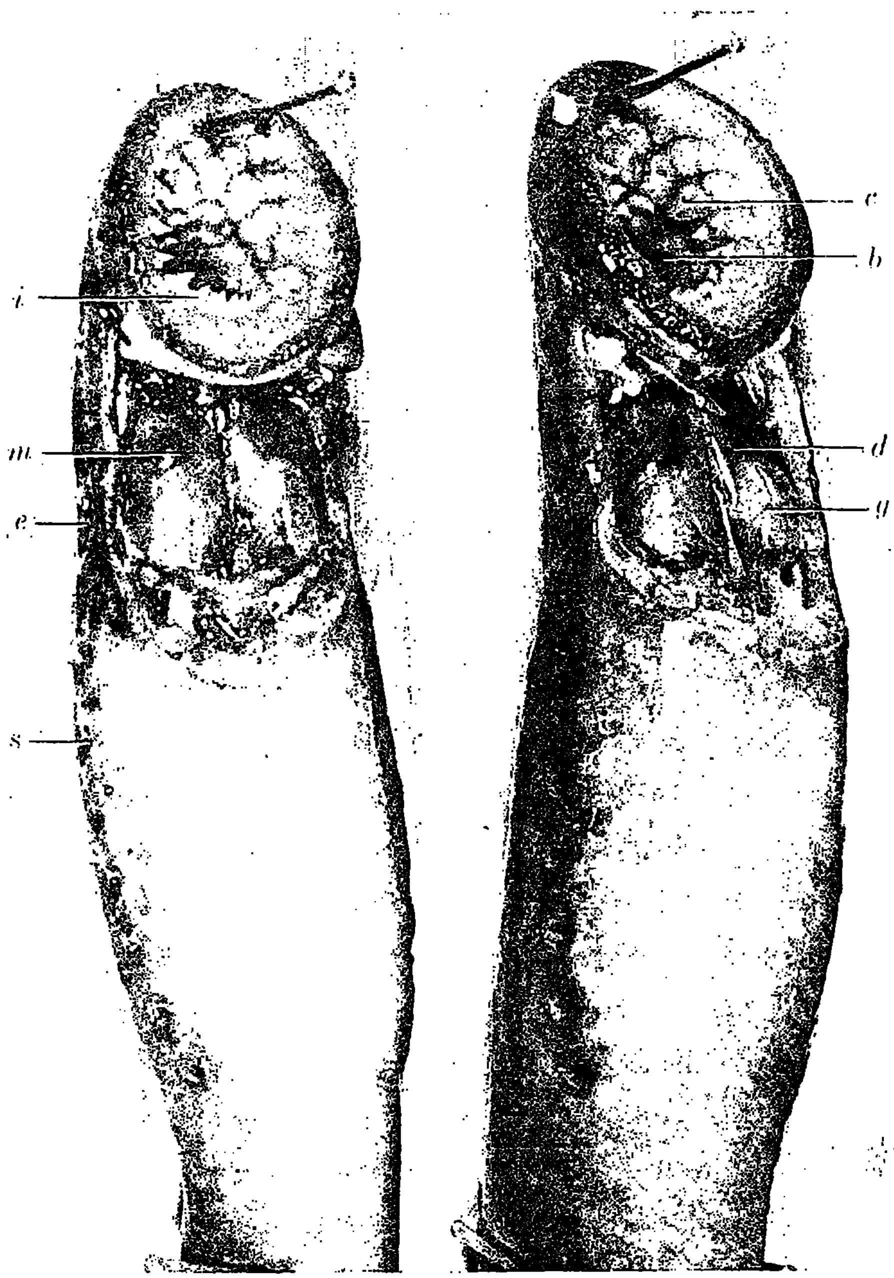

FIGURE 1.—Ventral view of sucking disks and buccal glands of two sexually mature sea lampreys. *i*=infraoral lamina; *c*=circumoral cusps; *b*=buccal funnel; *m*=musculus basilaris; *d*=duct of buccal gland; *g*=buccal gland; *e*=eye; *s*=gill sac.

of the table and the figure, the data for the sexes were combined. The males did tend to have slightly larger disks than females of corresponding length, but the difference was not great enough to warrant separate tabulations. There was a trend toward relatively smaller disks with an increase in length of lampreys as shown when the disk diameters are expressed as percentages of body length (table 1). All percentages greater than 9.0 included lampreys from 4.0 to 10.9 inches long; all percentages in range of 8.6 to 9.0 included lampreys from 9.0 to 14.9 inches long; and the percentages less than 8.5 included the larger lampreys 15.0 to 22.9 inches long.

TABLE 1.—*Relation of diameters of sucking disks to lengths of lampreys in 487 specimens from northern Lakes Huron and Michigan or their tributaries*

Length range (inches)	Number of lampreys	Mean length		Mean diameter of sucking disks	Ratio, disk diameter to body length
		Inches	Millimeters		
				Millimeters	*Percent*
4.0–4.9	6	4.9	124	11.5	9.3
5.0–5.9	78	5.5	140	12.9	9.2
6.0–6.9	49	6.2	157	14.4	9.2
7.0–7.9	0	[1] 7.2	[1] 182	[1] 17.5	[1] 9.6
8.0–8.9	3	8.2	208	20.7	10.0
9.0–9.9	2	9.4	237	21.5	9.0
10.0–10.9	4	10.3	260	24.0	9.2
11.0–11.9	12	11.5	293	26.3	9.0
12.0–12.9	27	12.5	318	28.3	8.9
13.0–13.9	37	13.4	340	30.5	9.0
14.0–14.9	49	14.5	367	31.6	8.6
15.0–15.9	69	15.5	393	33.1	8.4
16.0–16.9	50	16.4	416	34.6	8.3
17.0–17.9	36	17.5	444	36.6	8.2
18.0–18.9	25	18.4	467	37.9	8.1
19.0–19.9	24	19.3	480	38.8	8.1
20.0–20.9	12	20.3	514	40.2	7.8
21.0–21.9	3	21.4	543	43.3	8.0
22.0–22.9	1	22.1	561	45.0	8.0

[1] Values obtained by linear interpolation.

The Tongue

The development and form of the tongue are similar in adults of the various species of both parasitic and nonparasitic lampreys (Leach 1940, *I. fossor;* Vladykov 1949, *P. marinus, Entosphenus lamottenii,* and *Lampetra aepytera;* Johnels 1948, *P. marinus*). The tongue appears during metamorphosis and, in the parasitic forms at least, it develops into an effective organ accessory to feeding. Reynolds (1931, p. 15) described the tongue of *E. tridentatus* as a unique structure—

made up of a number of complex elements that by combining their functions, make that organ an efficient vacuum pump, or when occasion requires, direct its anterior cutting edge against the body wall of the lamprey's host.

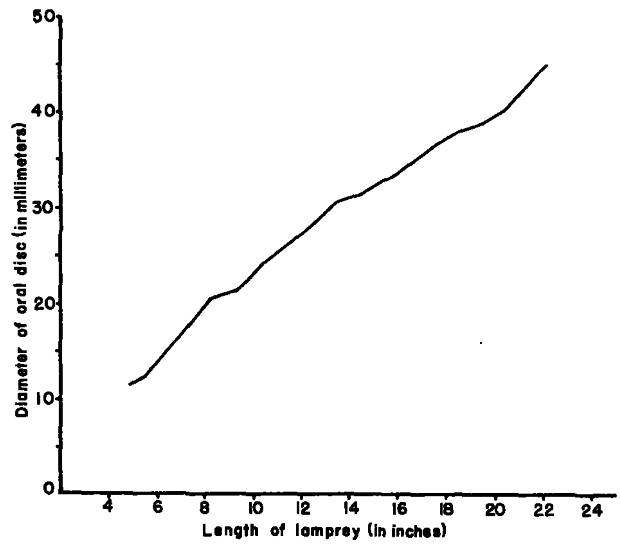

FIGURE 2.—Relation between total lengths of sea lampreys and diameters of their oral disks.

General structure

The tongue of the sea lamprey is a prominent organ in the buccal funnel. The anterior end of the tongue, the apicalis, is furnished with two sets of corneous laminae, each set bearing toothlike cusps. The laminae constitute the cutting armament. The anterior one is termed the transverse lamina, and the posterior two are termed the longitudinal laminae; all these laminae bear strongly denticulate ridges (Hubbs and Trautman 1937). The transverse lamina, which is bilobed and bent strongly inward along a median longitudinal line, forms the main cutting edge.

The lamprey tongue is supported by the long lingual or glossal cartilage which is median and lies between the large, paired basilaris muscles (fig. 1). According to Reynolds (1931), the lingual cartilage in *E. tridentatus* is practically fixed in position and takes up the thrust of the working member of the tongue, the apicalis. In this Pacific species, the lingual cartilage can be moved slightly forward by the paired muscles, the basilariglossus, which originate on the basilaris muscles and insert on the glossal cartilage. The chief function of the lingual cartilage is to furnish a firm base to support the tissue-cutting mechanism which is erected on an apical cartilage and is united to it by a tendon in a hingelike bond. The system allows the dorsal tip of the tongue to be rocked backward over a considerable arc into the funnel of the mouth. These observations on *E. tridentatus* by Reynolds appear to apply equally well to *P. marinus*.

A sea lamprey attaches itself to a fish by a strong suction pressure which serves also to bring the skin of the victim into contact with the lamprey's tongue-teeth. The rocking motion of the armed tongue causes a feeding hole to be rasped through the skin and tissues of the host.

Throughout the parasitic life of a sea lamprey, the teeth of the tongue and sucking disk are continually replaced by new ones. Hubbs and Trautman (1937) wrote that each new tooth is formed on the core of its predecessor and is the image of the former tooth which is sloughed off as a hollow corneous structure. The new teeth are invariably hard and sharp, but I concur with Vladykov (1949) who noted that the cusps of fully mature, parasitic lampreys are weaker than cusps of half-grown adults. It seems reasonable to hold that the feeding efficiency of older lampreys is impaired by truncated teeth, a failing that is not wholly remedied by regeneration.

Tongue-teeth in newly transformed sea lampreys

A study of the seasonal development of the tongue-teeth, or lingual laminae, was made on newly transformed sea lampreys. Small, parasitic individuals of this species usually emerge from their larval beds in cool seasons of the year and then migrate to their adult habitat. In Michigan, the migration is characterized by a low peak of activity in November and a greater one during late March and early April. All increases in emergence appear to be closely associated with rising water levels (Applegate 1950).

During the winter months, newly transformed sea lampreys held in aquariums did not feed. On November 22, 1950, 41 recently transformed lampreys, captured during the peak of the fall downstream migration in Carp Lake River, Emmett County, Mich., were stocked in the laboratory aquariums, and small eastern brook trout (*Salvelinus fontinalis*) and white suckers (*Catostomus commersoni*) were added as prey. Water temperatures in the aquariums ranged from 33° to 35° F. until spring. In April 1951, coincident with spring thaws and the peak downstream migration of the lamprey species, the captive individuals suddenly began to feed on the trout and the suckers. On May 3, 1951, 60 spring migrants were placed in the laboratory tanks, and they too began to prey immediately on the fishes provided for them. The temperature of the water in the tanks averaged 44° F. at this time.

Winter water temperatures alone would not seem to explain the tardiness of the fall migrants in starting to feed, since larger, older specimens continued to feed during the same time in adjacent aquariums. The condition of dentitional structures was studied for explanations. Downstream migrants captured in January 1952 possessed tooth characters typical of parasitic individuals except for the tongue-teeth. In the three specimens examined, the transverse and longitudinal lingual laminae were soft and pale yellow, evidencing that they were as yet incompletely cornified and probably incapable of efficient rasping action.

To verify further the influence of the development of the tongue-teeth of both fall and spring emigrants on feeding efficiency, certain collections preserved in 10-percent formalin were examined. Whereas it is known that this preservative tends to harden tissues stored in it, the corneous nature of fully formed teeth was easily distinguished from immature teeth of no feeding value. The observations were made macroscopically; the fingers, probes, and a sharp scalpel were used to test the hardness of the structures. Complete, functional laminae were orange brown, and their cusps were sharply pointed and hard. Incomplete teeth were pale yellow or white and had cusps comparatively blunt and soft. Other specimens possessed teeth of intermediate color and hardness; these were recorded as partially complete (table 2).

TABLE 2.—*Tooth development on tongues of newly transformed sea lampreys captured in Carp Lake River, Emmett County, Mich.*

Item	Fall migrants	Spring migrants
Number of lampreys	96	50.
Date captured	Nov. 15 and 17, 1949.	Apr. 4, 1951.
Length:		
Average ... inches	5.7	5.8.
Range ... do	4.9–6.5	4.8–6.9.
Weight:		
Average ... grams	4.0	5.1.
Range ... do	2.0–7.0	3.0–10.0.
Tongue-teeth:		
Complete ... percent	9.4	72.0.
Partially complete ... do	16.7	18.0.
Incomplete ... do	73.9	10.0.

Although the criteria for evaluating the development of the lingual laminae were not sharply quantitative, a great difference in laminal development was found between the fall and spring downstream-migrant sea lampreys. At least 74 percent of the fall migrants were judged to be incapable of feeding on fish owing to incomplete development of the transverse and longitudinal teeth on the tongue. Of the spring migrants only 10 percent showed incomplete tongue-teeth development.

Additional support for the view that most fall migrants are incapable of feeding before the next spring is found in my data concerning the incidence and progressive increase in size of sea-lamprey wounds on host fishes in Lake Huron. For example, on February 28, 1951, a lake-incurred lamprey wound, 18 millimeters in diameter and penetrating the body-cavity wall, was observed on a white sucker, 16.5 inches long, captured in our trap nets in Duncan Bay, Lake Huron. This was the earliest date on which evidence of attack by a newly transformed sea lamprey was ever found. The wound was judged to be that of *P. marinus* because of the scarcity of parasitic *I. castaneus* and *I. unicuspis* in the area.

Factors besides development of lingual laminae may be concerned in the delayed start in parasitic feeding by fall-migrant sea lampreys. This study of the tongue-teeth indicates only that metamorphosis is incomplete in the majority of individuals migrating to the lake in the fall and that the animals are incapable of feeding until spring.

The Buccal Glands

A most interesting feeding mechanism possessed by the sea lamprey is the buccal-gland system whose secretion exhibits anticoagulant, hemolytic, and cytolytic properties when applied to blood and tissue of prey fishes. The mechanism consists of the glands, the central lumina of which serve as reservoirs for the secretion, and the connecting ducts which lead to openings in the mouth cavity.

The buccal glands are a pair of conspicuous, roughly bean-shaped bodies partly imbedded in the ventral surface of the two basilaris muscles of the head (fig. 1). One gland is associated with each of these muscles, and the pair are so situated that a transverse section of the head at eye level passes through them. These secretory organs in the European lamprey, *Petromyzon fluviatilis*, are called salivary glands by foreign workers (Johnels 1948). I concur with Gage (1928) and others in designating them as buccal glands, for this term does not imply homology with the salivary glands of higher vertebrates—a relationship that has not yet been demonstrated.

Buccal glands first become evident, in lampreys in general, during transformation of free-living larvae into the parasitic phase, as shown by Kaensche (1890) for *P. fluviatilis* and Gage (1928) for *P. marinus*. They result from the invagination of solid cords of cells from the oral ectoderm before the tongue musculature begins to differentiate.

In serial sections of the nonparasitic *Ichthyomyzon fossor*,[1] and the parasitic *P. marinus* that I examined, the buccal glands are well formed at early metamorphosis. They contain but little secretion and are lined with simple, columnar, epithelial cells. These cells have their nuclei basally located and, apically, tiny globules of what appears to be secreted material.

Each buccal gland is drained by a duct which leaves its medial, convex side about the middle of its length and turns sharply in an anterodorsal direction in the basilar muscles. The pair of ducts follow the median piston cartilage which lies between the basilar muscles, until the mouth region is reached. There they turn laterally to their respective openings into the mouth cavity, one on each end of the infraoral lamina. In the newly metamorphosing specimen of *I. fossor* the ducts appeared solid at their anterior extremities, although hollow posteriorly; those in *P. marinus* were open.

In serial sections of several actively parasitic lampreys (*P. marinus* and *I. fossor*) that I studied, the development of the buccal system was complete (fig. 3). The reservoirs were turgid with secretion. In each gland, underlying the inner layer of simple columnar epithelium, was a stratum of dense, areolar-type connective tissue. Prominent constrictor muscles, striated and voluntary, partially enveloped the gland externally to this fibrous zone. These muscles doubtless serve to force the secretion into the mouth by way of the duct system. Sharp and irregular contractions of

[1] I am indebted to Dr. W. James Leach of Ohio State University for making available his preparations of this species.

the muscles of exposed glands were observed in adult specimens of *P. marinus* that were anesthetized with urethane. Outlying the muscle layer was a strong capsule of connective tissue which isolated the organ from the *musculus basilaris* which largely surrounded it.

At the point where the duct leaves a buccal gland a sharp transition occurs from glandular epithelium to duct epithelium. The latter is stratified and columnar, and the cells possess large basal nuclei. The lumen is not lobate like that of the gland. The duct is surrounded by a sheath of connective tissue which is prominently extended in the dorsal and ventral directions. Longitudinal muscle fibers course through the sheath to aid in the propulsion of the glandular secretion to the mouth.

The Buccal-Gland Secretion

Physical characteristics

The secretion pooled in the reservoir of a buccal gland was easily and quickly obtained. Portions of the ventral integument and superficial skeletal muscles were removed (fig. 1), leaving the pair of prominent buccal glands exposed. A small-gage hypodermic needle mounted on a syringe was then inserted into the glands in turn, and the contents were withdrawn. Each gland collapsed quickly as its contents were exhausted. Opening of organs collapsed by this routine demonstrated that practically all the fluid was removed. The yield per gland was measured to the nearest 0.01 milliliter on the graduated barrel of the syringe.

I called the secretion from buccal glands of the sea lamprey lamphredin. The color of fresh samples of this fluid ranged from light amber to straw. The material was slightly sticky and somewhat less labile than water. Macroscopically it appeared clear, but at a magnification of 430 diameters much suspended material could be seen which was finely divided and bore no resemblance to cells or crystals of any sort. In addition, numerous translucent, light-refracting globules that resembled fat or oil droplets were present. Their size varied from about 2 to 8 microns. The largest globules were also the largest of inclusions; collectively they were the only objects observed that had consistent form in the samples.

Upon desiccation, the globular constituents of fresh, or frozen and thawed, samples of lamphredin became more pronounced and darker in color when observed under magnification. Before dehydration became complete, numerous transparent, rodlike crystalliform objects formed throughout the sample. These structures were slender, their margins were well defined, and their ends tapered to sharp points. Many were variously branched (fig. 4). The formation of these rods progressed rapidly as the liquid dried. One or more of the globules were observed at each branching or along the shaft of each rod, but most of the globules remained free. Both kinds o.

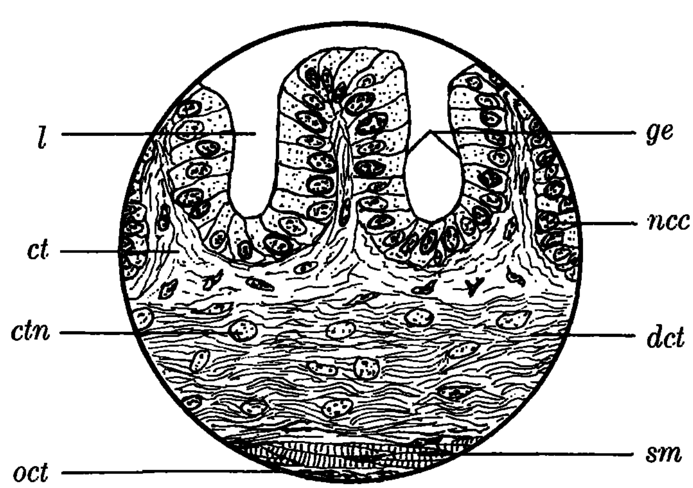

FIGURE 3.—Sketch of a portion of buccal-gland wall taken from a parasitic sea lamprey 7.5 inches long and 10 grams in weight: *l*=lumen of gland; *ge*=gland epithelium; *ct*=connective tissue; *ncc*=nucleus of columnar cell; *ctn*=connective tissue nucleus; *dct*=dense connective tissue; *oct*=outer layer of connective tissue; *sm*=striated muscle layer (x800).

structures appeared dark when desiccation was complete.

In all, I aspirated the buccal glands of 301 sexually mature, spawning-migrant sea lampreys for experiments. These specimens were captured in weirs operated by the Fish and Wildlife Service in Trout and Ocqueoc Rivers and Carp Creek, tributaries to Lake Huron in Presque Isle County, Mich., during the 1951 and 1952 spawning seasons. It is at this time only that sea lampreys of mature size and sufficient numbers can be collected to provide any sizable quantity of secretion, although many glands are past their prime. Applegate (1950) reported on the degeneration of the viscera and other tissues of the sea lamprey as it attains sexual maturity and ceases active feeding. The buccal systems of some of the 301 lampreys showed similar structural and functional deterioration. In general, the more obviously sexually mature lampreys had one or both buccal organs devoid of fluid content. In the 602 glands examined, 25.1 percent yielded little or no secretion; the remaining 74.9 percent were in good condition (table 3). In 10.8 percent of the lampreys both glands possessed nothing, and in 13.6 percent a single gland of the pair was void. Eight fall-caught feeding lampreys of comparable size had completely functional organs; the yield of secretion from their buccal glands was not appreciably greater than that obtained from sexually mature migrants with glands in good condition.

TABLE 3.—*Yields of secretion from buccal glands of 301 spawning-migrant sea lampreys captured in Trout and Ocqueoc Rivers and Carp Creek, Presque Isle County, Mich., April–June 1951 and 1952*

Length range (inches)	Number of lampreys	Number of glands that were—		Mean yield per pair of glands	
		Good	Degenerate	All glands	Good glands only
				Milliliters	*Milliliters*
10.0–10.9	1	2	0	0.10	0.10
11.0–11.9	7	10	4	.09	.12
12.0–12.9	26	33	19	.07	.10
13.0–13.9	47	78	16	.09	.10
14.0–14.9	51	92	10	.11	.12
15.0–15.9	52	73	31	.10	.13
16.0–16.9	40	59	21	.12	.15
17.0–17.9	27	39	15	.13	.17
18.0–18.9	24	36	12	.14	.18
19.0–19.9	21	25	17	.13	.22
20.0–20.9	4	4	4	.11	.23
21.0–21.9	1	0	2	.10	----------

Functional degeneration of the buccal glands was accompanied by definite morphological manifestations. Some of these organs were of nearly full length but were flaccid; others were greatly reduced in all dimensions. In either of these conditions, little or no secretion was present. The reservoirs of a small number of glands in obvious deterioration contained a black fluid which, under magnification, showed no discernible differences from the normal product, except in color. Under a microscope, the most atrophied glands showed a reduction in height of epithelial cells from columnar shape to cuboidal.

The average yield of lamphredin per sea lamprey was determined. The lengths of the 301

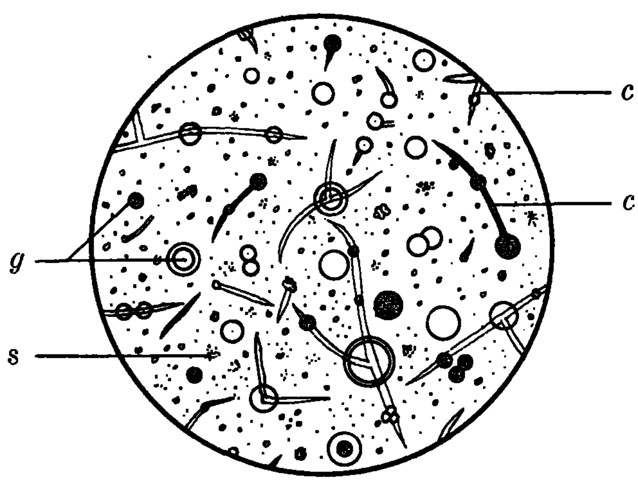

FIGURE 4.—Sketch of desiccated sample of lamphredin (buccal-gland secretion) from mature sea lampreys; *c*=crystalline rods; *g*=globules; *s*=secretion granules (x430).

lampreys from which lamphredin was aspirated (table 3) ranged from 10.6 to 21.4 inches. No sex difference could be detected, and the yields for the males (61 percent of the sample) and females (39 percent) have been combined. The data show that there is a regression of yield of secretion on the length of lampreys; the glands of large lampreys usually contain more secretion than the glands of smaller individuals. The average yield of buccal-gland secretion per lamprey (including those specimens with degenerate glands) was 0.106 milliliter. The mean yield of the 226 lampreys with glands in good condition was 0.142 milliliter. On this basis, 7 lampreys, 15.5 inches in length, would be required to obtain 1 milliliter of lamphredin.

Anticoagulant properties

Experiments by Gage and Gage (1927) indicated that buccal-gland secretion of certain lampreys inhibits clot formation in blood and has hemolytic properties. I tested the action of lamphredin on fresh blood specimens from the hearts of anesthetized sea lampreys, rainbow trout (*Salmo gairdneri*), eastern brook trout, longnose suckers (*Catostomus catostomus*), and white suckers. Most of the lamphredin was obtained from spawning-migrant sea lampreys in good condition. The secretion of six full-grown, sexually immature sea lampreys, taken from Lake Huron in the fall of 1950, was used as a control on the quality of material taken. The lamphredin drawn from the glands of the active feeders and tested on the blood taken from the hearts of wild brook trout and white suckers gave results identical with those obtained with the secretion from spawning migrants.

Lamphredin prevented coagulation of fish blood within specified time limits in all trials when the concentration of buccal-gland secretion equalled or exceeded 25 percent of the total volume of the mixture. Tests were declared positive and observations were terminated when no coagulation took place within 20 to 30 minutes, whereas untreated samples of blood used as controls usually coagulated within 3 minutes. With lesser proportions of secretion, the clotting of the blood was retarded, not prevented. The extent of delay in the coagulation was directly proportional to the quantity of lamphredin in the mixture.

Results were similar when the glandular secretion was diluted with Ringer's physiological saline solution for fish and mixtures made up containing 25 percent or more of lamphredin and 50 percent fish blood; that is, the blood did not clot. Again when the amount of secretion was less than 25 percent, the coagulation of the blood was only delayed.

Effect of storage on anticoagulant properties

Tests were made not only with fresh lamphredin but with lamphredin that had been stored under various conditions. Comparison of the results of experiments based on the secretion in fresh-frozen, dried, and refrigerated conditions showed that the anticoagulant and hemolytic properties of lamphredin are altered by storage. No biochemical analyses were made to determine the causes of the changes.

Freezing.—Several tests proved that frozen lamphredin could be kept for at least a month with no apparent loss of anticoagulant powers, but longer storage reduced the effectiveness. Three samples of lamphredin collected in July 1951 were placed in 1-milliliter amounts in centrifuge tubes, sealed, and frozen. One year later, July 1952, they were thawed and tested on the blood of white suckers and rainbow trout. The lamphredin prevented the coagulation of the fish blood only when mixed in equal proportions. Lamphredin used at less than equal proportions merely delayed the clotting. The strength of the anticoagulant had been reduced as compared with fresh material.

Alternate freezing and thawing seemed to hasten the deterioration of lamphredin. A sample of the material collected on August 4, 1950, was kept frozen in a sealed tube until September 5, 1950, when it was thawed completely. Fifteen minutes after the last ice had disappeared, it was refrozen in the same container and held until October 6, 1950, when it was melted again and tested with blood specimens from the heart of a white sucker. In each of two experiments the slide that contained undiluted blood clotted in 5 minutes; equal parts of lamphredin and sucker blood coagulated solidly in 10 minutes; fish blood and distilled water in a 1:1 ratio clotted in 15 minutes.

Refrigeration.—A milliliter of lamphredin aspirated from live lampreys in June 1951 was placed in a centrifuge tube, sealed, and stored at 40° F. Overnight, a precipitate appeared on the bottom of the tube to an extent of 25 percent of the original volume. The supernatant fluid was clear and light amber. Through the following days, the volume of the precipitate and debris in the bottom did not increase, but the color of the top fluid darkened strikingly. At the end of a week, the supernatant fluid and the settled substance were dark brown, and the deterioration was marked by an order of putrefaction.

Examination of a sample taken from the tube after agitation to mix the settled and liquid portions revealed no marked changes except in color. Another sample was mixed with an equal amount of fresh blood from the heart of a white sucker. The blood in the mixture clotted in normal time (3 minutes). No evidences of anticoagulant action or hemolysis could be observed. When the ratio of the storage-altered lamphredin to blood was increased to 2:1, the results were the same.

Drying.—To determine the effect of drying on the anticlotting properties of lamphredin, three samples of the material were collected from spawning-migrant sea lampreys on August 4, 1950. A quantity of 0.5 milliliter was placed in each of three centrifuge tubes, which were then held and rotated in the warmth (100° F.) of a space heater. The material was still liquid 2 hours after control tubes holding 0.5 milliliter of distilled water were dry. In 4 hours the lamphredin was dry and had a clear, greenish-yellow appearance. The loss in volume was estimated at 50 percent. On August 8, 1950, a 0.3-milliliter specimen of lamphredin was collected, placed in a centrifge tube, and held by hand in the heat (not in excess of 120° F.) of an alcohol burner. The material in the tube dried after 2½ hours. Its appearance was similar to the other dried samples, and again the volume had been reduced an estimated 50 percent. Each of the four tubes of dried lamphredin was sealed on the date of its desiccation and was stored immediately at approximately 40° F.

The dried lamphredin was tested 5 months later, in January 1951. Small amounts of distilled water were added successively to the tubes in the attempts to reliquefy the material. Not until a 2:1 ratio of water to lamphredin was used did the mixture become liquid; that is, the total volume of the redissolved lamphredin was 50 percent greater than that of the original solution. With smaller proportions of water, part of the lamphredin remained solid.

When blood from white suckers and the solution of redissolved lamphredin were mixed on clean glass slides in equal proportions, the coagulation of the blood was delayed only 2 to 3 minutes longer than the clotting time of the control slides containing an equal volume of undiluted blood. In 10 minutes, the hemolyzing action of the lamphredin had affected only 50 percent of the red cells in the blood. When the lamphredin solution and blood were mixed in a 2:1 ratio, coagulation of the blood once more took place after a short delay. Microscopic examination of the slides after a 10-minute interval showed only an estimated 50 to 60 percent of the erythrocytes destroyed.

These results, which indicate a reduction in the potency of lamphredin reclaimed from the dried state, are not conclusive. There is a possibility that the method of desiccating the lamphredin by gentle heating may have damaged it.

The foregoing experiments have shown that the anticoagulant and hemolyzing properties of lamprey buccal-gland secretion are easily lost under storage. The facilities at the Hammond Bay Fishery Laboratory did not permit the biochemical analysis of the secretion that would be needed to explain the nature and reactions of the lamphredin or its various fractions.

Lytic properties of lamphredin

The study of numerous wounds created by sea lampreys on fishes in laboratory aquariums and in nature indicated that cytolysis or autolysis were involved, as well as mechanical injury. The damage to muscle tissues often appeared greater than that which could have been caused by the rasping tongue and/or suction pressure exerted over the wound. Microscopic examination of fresh and stained sections of tissue from typical wounds on white suckers and rainbow trout were disappointing. Evidences of possible lysis due to lamphredin were by their nature largely destroyed during the processing of the mounts. The marks of cellular erosion that appeared on the slides could have been the result of the mechanical action of the tongue of the lamprey and/or suction pressures exerted on the wound. The injection of lamphredin into live fish yielded more definite results.

Injections of lamphredin in fish

Brook trout.—On May 27, 1952, two 8-inch eastern brook trout from the hatchery-reared supply in the laboratory holding tank were anesthetized in urethane, and the first fish was injected with 0.20 milliliter of lamphredin. The injection was made on the right side of the fish into the dorsal musculature at a point well above the lateral line and midway between the dorsal fin and the head. A small hypodermic needle was inserted through the skin and then directed anteriorly for 1 inch so that the secretion could be released at a location away from the insertion hole in the skin, and yet not too deeply into the muscle. The latter precaution was taken so that any reaction of lamphredin in the fish might be reflected on or near the skin and thereby observed. In spite of precautions, at least half of the injected lamphredin oozed from the hole as soon as the needle was withdrawn.

The second trout was injected in the same manner and in the same body area with 0.20 milliliter of distilled water as a control.

Both fish were put into a 50-gallon aquarium supplied with running lake water, where they rapidly recovered from the anesthesia. The fish had been fin-clipped for identification. Lamphredin produced a positive reaction in brook trout No. 1. The dark-green skin became discolored and edematous; it changed to jet black, then to gray, and back to black. After 2 days the fish refused food placed in the aquarium. It appeared sluggish. Eleven days after the inoculation, the size of the swelling was reduced, the mouse-gray discoloration became black, and the fish again accepted food. After about 3 weeks, recovery was sufficiently advanced to permit the assumption that it would eventually have been complete. The small injection puncture in the skin persisted unhealed until the fish was discarded. Owing to the temporary failure of the water system which necessitated the removal of the fish from the aquarium, the degree of recovery from the injection of lamphredin remains unknown. The control fish showed no abnormal reaction to the injection of distilled water. The puncture remained pale for a day and then became obscure and disappeared. This trout was normal in every respect, and fed normally.

Longnose sucker.—The next fish to be inoculated with lamphredin was a male longnose sucker, 15.0 inches long and weighing 580 grams. On June 3, 1952, a 0.20-milliliter sample of lamphredin, collected from sea lampreys on the same date, was introduced into the musculature of the fish on the left side, at a point midway between the dorsal fin and the posterior limit of the head, and about 1 inch above the lateral line. A hypodermic needle was directed anteriorly for 1.5 inches at a depth not more than 0.3 inch below the skin. The buccal-gland secretion was slowly released as the needle was carefully withdrawn. Again part of the lamphredin—at least 0.05 milliliter—escaped from the injection hole as soon as the needle was removed.

Within 3 hours after the inoculation, there was a whitish discoloration of the skin at the site of injection. The discoloration became more and more pronounced in the next 2 days, although its area increased only a little. During this time, all else about the fish appeared normal.

On the third day, the discoloration began to spread, and a rapidly increasing swelling of the area was noted. An area 2 inches in diameter was affected, and the maximum height of the protuberance was estimated at 0.5 inch above the normal skin level. The skin over this swelling had turned a pale yellow.

The distention involved such an area and pressures that the fish became contorted; its body was flexed as if it were making a shallow, right-hand turn. The specimen did not move at all during the day, and its rate of respiration was more rapid than that of other longnose suckers in the aquariums. On the fifth day, the sucker died, presumably as a result of the injection. It was removed from the aquarium, examined in detail, and photographed (figs. 5 and 6).

The normally dark fish was very pale just before death and remained the same after death. The gills, too, were blanched. The swelling now appeared reddish, owing to the contamination of the mucous on the surface with a small amount of blood residue that issued from the injection hole. Beneath the stained mucous, the skin tone was jet black except for a whitish-yellow area in the center of the swelling. The distention measured 3.0 inches long, 2.5 inches wide in dorsoventral direction, and 0.8 inch high at the maximum; it was not peaked, but appeared high and rounded. The injured region was soft and rubbery, indicating that the distention was edematous.

Any slight pressure on the area caused a bloody issue from the injection hole.

When a small incision was made in the swelling with a scalpel, a large quantity of murky, purplish liquid poured out, as if under internal pressure. The exact volume of the issue could not be determined, but 5 milliliters were collected in a syringe and 2 to 3 milliliters were lost. There is no way to estimate how much of this material had previously escaped by oozing through the injection hole.

The liquid in the vesicle exceeded the total volume of blood found in normal longnose suckers of this size. It was more labile than normal whole blood and contained no clots or lumplike aggregations. The odor was sweetish, but unpleasant, and resembled that of flesh in the initial stage of decomposition.

Two smears of the exudate were examined under high- and low-power magnification. The purplish color of the liquid was due probably to the hemolysis of erythrocytes, but no red blood cells were present. Leucocytes were abundant and appeared normal, though generally of small size. Cellular debris was prominent, which perhaps included unidentifiable remains of destroyed red-blood cells and muscle and connective-tissue cells. Numerous, sharply pointed rods were piled like jackstraws which exhibited the characters noted in drying samples of lamphredin (fig. 4). There was no evidence of clotting. The liquid remained free flowing for 20 minutes, at which time it was discarded.

No flesh or connective tissue remained attached to the skin in the affected area. The skin was blackish and had suffered a loss of elasticity. When the skin covering the entire affected area was trimmed away, a deep, blood-red crater was revealed, from which the fluid had escaped (fig. 6). The lining of the cavity consisted of soft, reddish, mushy material which averaged 5 millimeters in depth. A smear of this substance, though showing no definite cell structures, was interpreted as a mass of muscle-tissue cells in an advanced stage of cytolysis. Immediately beneath the mushy layer, the flesh was white, firm, and apparently normal.

Figure 5.—Vesicle produced by a subcutaneous injection of lamphredin into a longnose sucker 15.0 inches in length (fish No. 3 in table 4). See also figure 6.

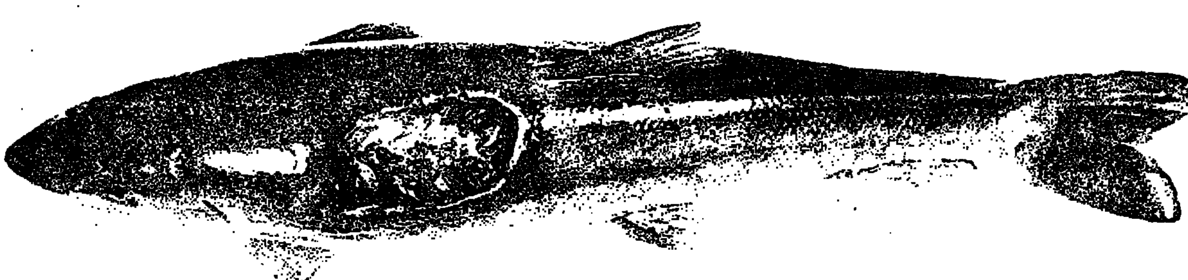

Figure 6.—Tissue lysis produced by the action of lamphredin in a longnose sucker 15.0 inches in length (fish No. 3 in table 4). See also figure 5.

The crater had many stringlike fragments of connective tissue extending into it, all revealing apparently severe erosion which we may presume to have been caused by the lamphredin. Several strands were traced into the surrounding, unaffected flesh to prove their identity. No traces of the vascular-system structures could be found within the excavation.

The depth of the hole was measured downward from the normal level of the skin, and the greatest reading of 0.8 inch extended over a wide area. The total dimensions of the vesicularized area were recorded as follows: Length, 3.0 inches (long axis of fish); width, 2.25 inches (dorsoventral); and total depth, 1.6 inches (surface of swelling to bottom of cavity).

The results of this experiment indicate that the lamphredin acted as a lytic agent on the flesh of the longnose sucker. Of the four affected tissues, the integument was the most resistant and the muscle and vascular tissue the least resistant. The reaction of the fish was positive, and its death was directly attributable to the effects produced by the injection of 0.20 milliliter of lamphredin. The viscera of the fish appeared normal, but blood was notably lacking in the atrium and ventricle of the heart. The color of the ventricle was light rather than the normal red.

Trouts and suckers.—The results of the preceding and other experiments with lamphredin injections performed in June and July 1952 are summarized in table 4. The fish used in the tests, except for the brook trout and rainbow trout, were delivered alive from our trap nets in Hammond Bay. The eastern brook trout were supplied by the State Fish Hatchery at Oden, Mich., and the rainbow trout by the Federal Fish Hatchery at Northville, Mich. The specimens were held in large aquariums supplied with running lake water, and there were never more than 2 fish in a 50-gallon aquarium.

Reaction of a fish to lamphredin injection was considered positive when dissection of the affected area disclosed evidence of cytolysis and hemolysis. These conditions were usually accompanied by swelling and discoloration of the skin over the site of the reaction. The severity of a positive reaction was arbitrarily rated as 1+ for the least degree of effect that could be considered positive, and 4+ for the maximum reaction. Ratings of 3+ and 4+ were ascribed to those reactions whose results approached or reached fatal proportions. Values of 1+ and 2+ indicate that recovery from the injection effects was not only possible but likely.

Most injections of lamphredin into the muscle of 4 species of fish produced extensive damages. It is not known whether these effects on fish tissue are due to the direct enzymatic action of a cytolytic constituent or to autolysis induced by a histotoxic element in the lamphredin. Positive lytic reactions were recorded in all but 3 of the 17 tests performed. Although a wider range of volumes might have been used in injections, we chose to deal with quantities that approximate the normal content of buccal glands in living lampreys (aver-

TABLE 4.—*Reactions produced in fishes by injections of lamphredin, June and July 1952*

[M=male; F=female. See text for explanation of the several degrees of positive reaction]

Fish No.—	Species	Length	Weight	Sex	Lamphredin injected	Location of inoculation	Reaction	Degree
		Inches	*Grams*		*Milliliters*			
1	Eastern brook trout	8.0			0.20	Dorsal muscle	Positive	3+
2	Rainbow trout	16.0	794	F	.25	do	do	4+
3	Longnose sucker	15.0	580	M	.20	do	do	4+
4	do	15.2			.20	do	do	4+
5	do	14.1			.10	do	do	2+
6	do	14.9			.20	do	do	4+
7	do [1]	14.3		M	[2] .20	do	do	4+
8	White sucker	13.1	366	M	.20	do	do	2+
9	do [1]	15.3	660	F	[3] .20	do	Negative	
10	do	14.0	486	M	[3] .20	do	Positive	2+
11	do	13.3	330	M	[4] .20	do	do	1+
12	do [5]	15.5	740	F	[4] .20	Right side	Negative	
					.25	Left side	Positive	4+
13	do	13.9	448	F	[4] .25	Dorsal muscle	do	1+
14	do	13.0	312	M	.25	do	do	4+
15	do	14.1	476	M	[4] .10	Pericardial cavity	Questionable	
16	do	14.0			.10	Dorsal muscle	Positive	4+

[1] Fishes bore healed scars resulting from attacks by sea lampreys in the lake.
[2] Lamphredin was frozen and stored for 5 days.
[3] Lamphredin was frozen and stored for 2 days.
[4] Lamphredin was frozen and stored for 1 year.
[5] Fish injected twice as indicated.

age yield, 0.15 milliliter, and ranging upward to 0.25 milliliter per pair of glands in larger individuals). Two things at least are not known about the volumes used by feeding lampreys: (1) The total amount employed in a feeding attack; (2) the rate of production of the fluid.

Inoculations ranging from as little as 0.10 up to 0.25 milliliter produced 9 severe reactions—1 rated as 3+ and eight as 4+ (figs. 7 and 8). Of this number, 2 resulted in the deaths of subjects: Longnose sucker, 15.0 inches, 5 days after injection of 0.20 milliliter of fresh lamphredin; longnose sucker, 14.9 inches, 9 days after receiving 0.20 milliliter of fresh lamphredin. The observations on the other 6 fish that showed responses were terminated for various reasons before death due to the lamphredin could occur. Death was not a necessary criterion in determining the lytic powers of the lamphredin, however; the extent of necrotic tissue provided an adequate, though only roughly quantitative, measurement.

Only 2 fish giving a 2+ reaction had been injected with fresh lamphredin, and in 1 of these the amount was small (specimen No. 5, 0.10 milliliter).

It appears that buccal-gland secretion that has been frozen and stored for some time suffers a loss in its cytolytic or histotoxic power, as well as in the

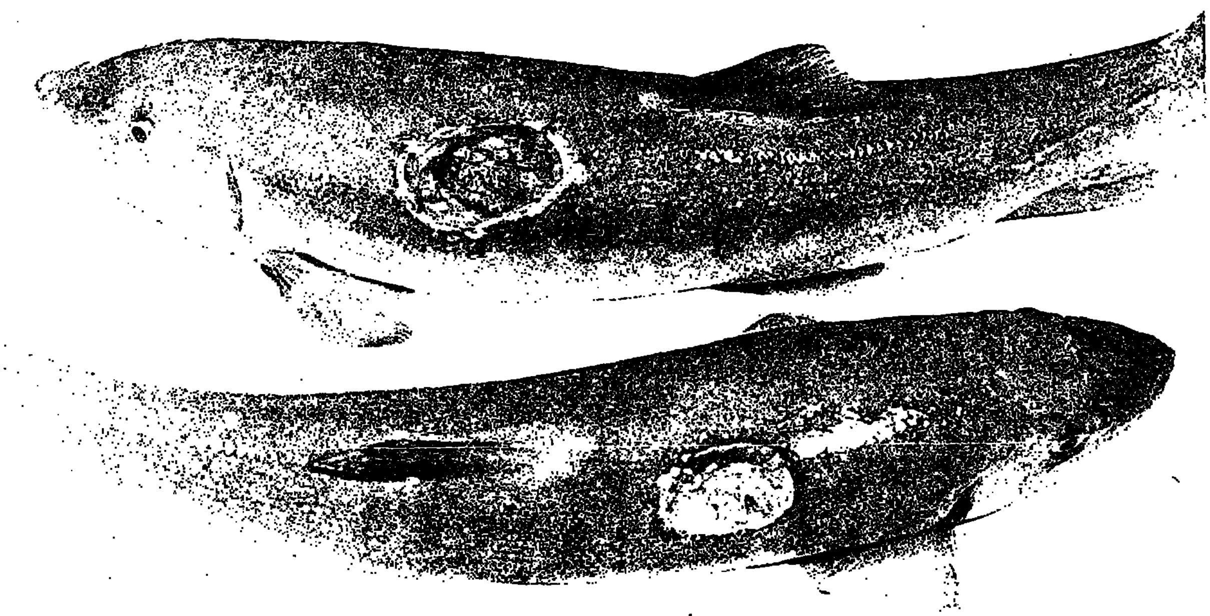

FIGURE 7.—Lytic reactions produced in longnose suckers by subcutaneous injections of lamphredin. Top fish was 14.9 inches long (fish No. 6 in table 4); lower fish was 14.3 inches long (fish No. 7 in table 4). The skin and fluid contents of the vesicles were removed immediately before photographing.

FIGURE 8.—Lytic reaction produced in dorsal muscles of a rainbow trout by an injection of lamphredin (fish No. 2 in table 4). The skin and fluid content of the vesicle were removed immediately before photographing.

hemolytic and anticoagulant properties previously described. Material collected from spawning-migrant lampreys in June 1951 and kept frozen for 1 year was thawed and injected into the dorsal muscles of three white suckers and into the pericardial cavity of a fourth. Two of the muscle tests were called positive but rated only 1+; the other was considered negative. The results of the heart test were recorded as questionable. The quantities of lamphredin used in these experiments were comparable to those that produced strong, positive reactions in hosts when fresh material was used.

A 0.20-milliliter sample of lamphredin that had been frozen and stored for 5 days caused a 4+ reaction when injected into the dorsal muscles of a longnose sucker 14.3 inches in length. Two 0.20-milliliter samples of secretion that had been frozen and stored only 2 days were introduced into two white suckers, one 15.3 inches and the other 14.0 inches long. The effect in the first fish was entirely negative, but lysis in the second one was called positive and rated 2+.

The observed variation in reactions of hosts to injections of lamphredin may be attributed to individual differences in the fishes, to the species involved, to the location of the point of inoculation, to the quality of the secretion, either fresh or frozen, to the size of the injection, and to the amount of secretion that escaped from the subject as the hypodermic needle was withdrawn. In every test, an undetermined quantity of lamphredin oozed from the hole in the skin of the fish immediately after the inoculation. In some cases the loss of lamphredin from the test fish was estimated at one-quarter to one-half of the total volume injected. If the whole amount of fluid introduced into the subject had remained there, the effects unquestionably would have been greater.

We now have the evidence that lamphredin from sea lampreys exerts a lytic action on the skeletal muscle, blood vessels, connective tissue, and integument of living fish. Add to this injury the action of the rasping tongue, abrasion of circumoral cusps, and suction pressure, and the explanation of feeding penetrations is basically in hand.

Attachment and Feeding

Attachments on fish

Gage (1929) alone has reported on feeding experiments with "lake lampreys" (*P. marinus*) and fish. His work was carried out in aquariums at Cornell University and in a bathtub in his home during 1914 and 1915. Many of Gage's findings have been confirmed and extended at the Hammond Bay Fishery Laboratory where there was unparalleled opportunity to observe sea lampreys feeding on prey fishes. Twenty 50-gallon, glass-sided aquariums, supplied with running water from Lake Huron, were in operation from April 1950 to July 1952. During this time, several hundred sea lampreys ranging from 4.8 to 18.3 inches in length passed a part or all of their parasitic lives in the aquariums. A report is in preparation concerning the growth, food consumption, and maturity of some of the captive lampreys.

Eleven common species of fishes were used in the laboratory aquariums as prey for the sea lampreys: Brown trout (*Salmo trutta*), rainbow trout, eastern brook trout, lake whitefish, white sucker, longnose sucker, brown bullhead (*Ameiurus nebulosus*), northern pike (*Esox lucius*), burbot, yellow perch (*Perca flavescens*), and rock bass (*Ambloplites rupestris*). Most of these fishes have some angling or commercial importance in the Great Lakes. Two or three species usually were represented in each aquarium.

Of great value to the sea lampreys in their predatory, parasitic existence in the sea or in lakes are their acute vision and strong and rapid swimming. The lampreys have an additional and important advantage in the fact that the prey species of fishes are not ordinarily frightened by them. Even under aquarium conditions, prospective victims typically ignore the lampreys and take no actions to avoid them.

In a laboratory aquarium, the attack on a prey fish is often direct, swift, and accurate. The lamprey sights the fish, and as it closes for the attack the disk is opened and the head is elevated; this elevation brings the suctorial apparatus into a position that facilitates attachment. As soon as contact is made with the fish, the lamprey maintains its hold by suction. The reaction of the fish is usually violent, but its struggles to dislodge the attacker are almost always in vain.

Sometimes there is an amazing lack of coordination in an attempted attack on a fish. The approach is negotiated as just described, but the lamprey may overshoot or undershoot the fish and attach itself to the bottom, to the glass wall, or to

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the standpipe drain. The lamprey perceives its error within a few seconds, but at times as many as three or four attempts are made before contact with the fish is achieved. These clumsy attacks were not characteristic of particular lampreys; frequently a lamprey that attacked with accuracy on one occasion was inaccurate on a later one.

A moving fish or one that is struggling to dislodge a lamprey frequently draws other attacking lampreys to itself. Many times a fish in a laboratory tank was host to several lampreys simultaneously (fig. 9), while other fish of the same species in the tank remained untouched. If neglected fish became agitated by the frantic struggles of other fish bearing lampreys, they apparently became more subject to attack themselves.

The location of the fish in an aquarium did not affect its chances of being attacked. Fishes such as brook trout, brown trout, rainbow trout, yellow perch, rock bass, and northern pike, which usually maintain midwater positions in aquariums, were no more immune than species that typically remain on the bottom. The parasites have been observed to ignore suckers resting nearby on the bottom and to rise and attack unerringly the specimens hovering at a higher level.

The great tenacity with which a lamprey maintains its attachment on a fish was demonstrated repeatedly. Each aquarium was covered with fine-mesh, wood-framed copper screens of sufficient weight to prevent the specimens from escaping. A host engaged in a violent struggle to throw off its attacker frequently scraped the lamprey along the screen, causing an appreciable abrasion of the skin. Not once, however, was a lamprey dislodged when hurt in this manner.

Norman (1947) wrote that sea lampreys are able to attach themselves so firmly to victims that it is rare indeed for the fish to shake off its persecutor before succumbing from loss of blood. He also suggested that the great strength of the

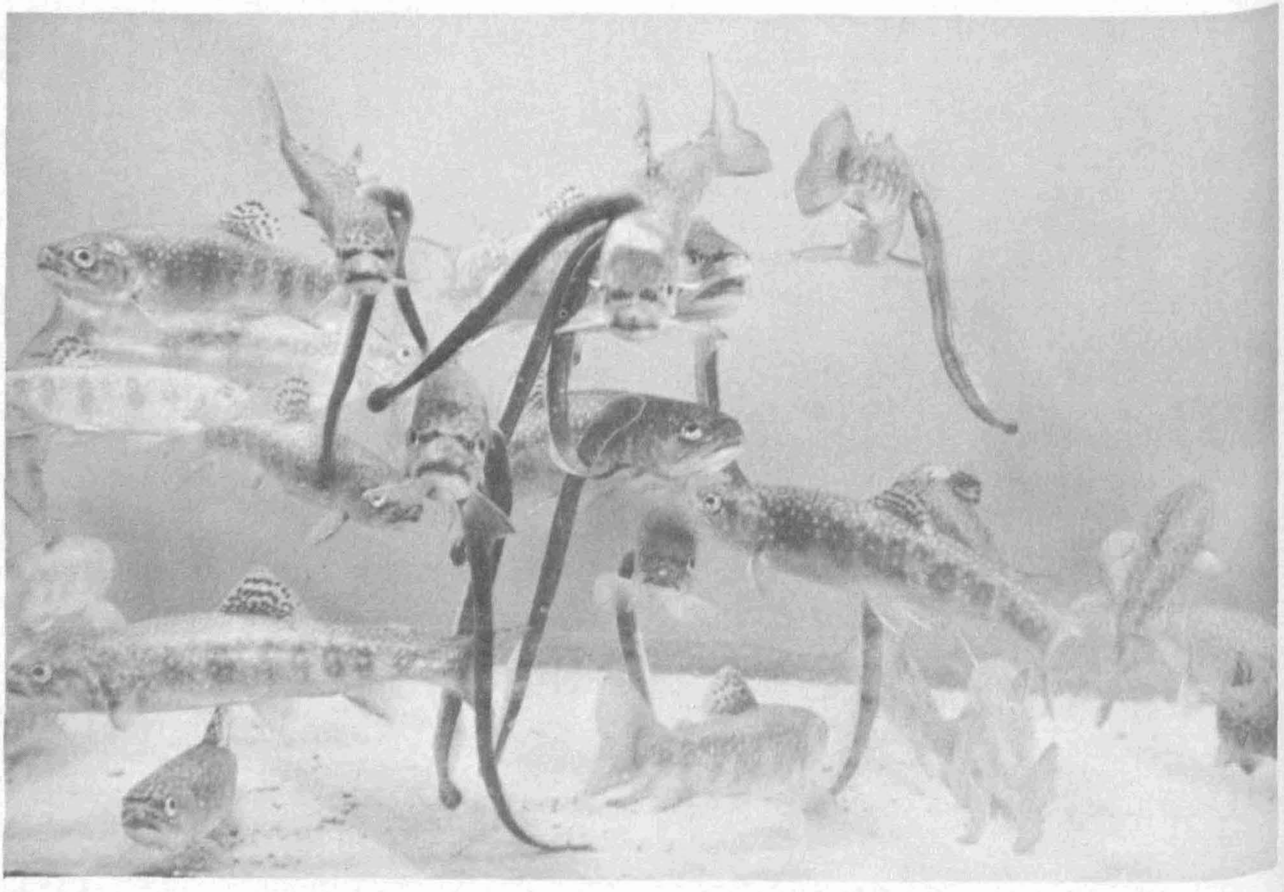

FIGURE 9.—Brook trout under attack by small, recently transformed sea lampreys in a laboratory aquarium, April 1951. Note multiple attachments on some fish.

sucking disk could be tested by allowing a lamprey to attach itself to one's hand or arm, whereupon it would be almost impossible to detach the organism without lifting it from the water. The power of the suction is also demonstrated by the large edema or hyperemia that appears at the site of attachment before the skin is broken. At times, suction is indicated by a noticeable indentation of the skin on the opposite side of the fish. Many observations were made on rainbow trout, brown trout, and white suckers in which suction pressure was reflected across the body through 1.5 to 2.0 inches of dorsal musculature.

In general, fish possess no means for ridding themselves of attached lampreys. The initial, excited reaction of a fish to attachment was typical of all the species observed. The more active kinds, such as the trouts and perch, gradually slowed in their struggles, but tended to remain in motion for the duration of the attack, with brief periods of struggle intervening between increasingly longer periods of passivity. The white suckers and longnose suckers usually returned to resting positions on the bottom after their initial battles for relief. At times during the attachment they were stimulated to new but brief periods of frenzy.

The wounding process

When the efforts of the fish to dislodge its attacker have subsided, the lamprey proceeds to create a wound. Many new wounds clearly reflect the application, pattern, and utility of buccal dentition. The suction exerted by the predator brings the disk teeth into close application with the surface of the host. There the cusps penetrate the scales or skin sufficiently to anchor the lamprey. To a lesser extent, these teeth may dislodge scales over the intended site of the feeding hole. Some of the loosened scales are ingested and pass out of the anus of the parasite, but most of them are cleverly forced aside, presumably by tongue action, and emerge beneath the marginal membrane of the funnel and fall away to the bottom. The process is particularly remarkable when observed on prey fishes that possess scales of considerable size. The coating of mucous on the victim obviously permits the passage of such scales between the marginal membrane of the lamprey and the surface of the fish with no interruption of the suction pressure.

Within the tooth-studded disk, the large, supraoral cusps, the eight circumorals, and the infraoral lamina encircle the zone of action of the lamprey's tongue. There they appear to hold the slippery and elastic surface of the fish sufficiently rigid so that the tongue can quickly make a penetration. The lingual retractor muscles are brought into play, and the tip of the tongue is hooked strongly in a dorsal and posterior direction which causes the flesh of the fish to be ripped by the transverse and longitudinal teeth of the tongue as they describe an arc upwards and backwards. About six or seven respiratory movements take place between drives of the tongue. The rasping action appears to continue at this rate until a flow of the fish's blood is obtained. Thereafter, the application of the tongue is normally less frequent. During the wounding process the secretion of the buccal glands is brought in contact with the torn flesh of the fish.

Gage (1929, p. 163) gave a colorful and accurate description of the wounding process as he observed attacks by sea lampreys on suckers and bullheads:

> After several minutes the fish seemed exhausted and thoroughly discouraged and remained rather quiet. On watching the lamprey it seemed to be working hard to get something from the fish. The movements of its head and body reminded one of the actions of a suckling pig or kitten. After some especially hard suck the fish would jump and struggle as if hurt.

Lamprey attacks on other lampreys

Sea-lamprey attachments on their own kind are not uncommon, but they rarely result in wounds. Numerous such attachments were observed in the laboratory. In individuals close to sexual maturity, such activities were interpreted as prespawning manifestations of the reproductive urge. Before maturity, the attack of one upon another of its kind is made in an attempt to feed.

Remarkable responses are elicited from the victim lamprey to prevent the creation of a feeding wound. The only successful penetration observed was on a spawning migrant captured in Ocqueoc River. In an aquarium, a host lamprey invariably dislodges the offender by tying itself into a knot in the immediate vicinity of the point of attachment. Thereby, pressure is applied directly on the attacking individual in such a way as to cause it to slide away from the original site. The knot-tying is repeated again and again until the attacker is forced to release its hold.

Attachments on humans

There have been numbers of authentic reports of sea lampreys attaching themselves to persons in the Great Lakes area. Creaser (1950) mentioned reports of such attachments on human swimmers in Lake Ontario and in Burt and Crooked Lakes in northern Michigan. Vladykov (1949) also recorded attachments on swimmers in Lake Ontario. Neither author mentioned any injuries sustained by the human hosts, and since such associations are rapidly terminated by the victims there is little likelihood that the lamprey would have the opportunity to create an injury.

Observations in the laboratory seem to indicate that sea lampreys are repelled by the warmth of human skin; all induced attachments on the hands, except one, were terminated by the lampreys within a matter of seconds. The "host" in the one exception was Oliver R. Elliott, a member of the laboratory staff. During the servicing of aquariums one day in August 1950, his hands became cold from the low water temperature, and a lamprey affixed itself to the back of one. Elliott was urged to allow it to remain thereon as long as it would. The parasite initiated a rasping action and the consequent discomfort caused Elliott to remove the animal. The attack lasted 5 minutes, and in this time the lamprey had lacerated the skin slightly. The site of the attack was markedly reddened, and apparently a flow of blood would have been started soon had the attachment continued.

EFFECTS ON HOST FISHES

The effects of sea-lamprey attacks on fishes were investigated to determine the following: The characteristics of wounds; whether wounds heal; where attachments are made on fish; whether wounds are more harmful in some loci than in others; and whether lampreys have host-species preferences. Later points deal with tissue destruction, the hematology of prey fish before and after lamprey attacks, and secondary pathology of vulnerable species.

Characteristics of Wounds

The study of sea-lamprey wounds was based on detailed observations made April 1950–July 1952 of 1,189 wounds on 18 species of fish in Lake Huron and 1,690 wounds on 11 species attacked in laboratory aquariums. The following data

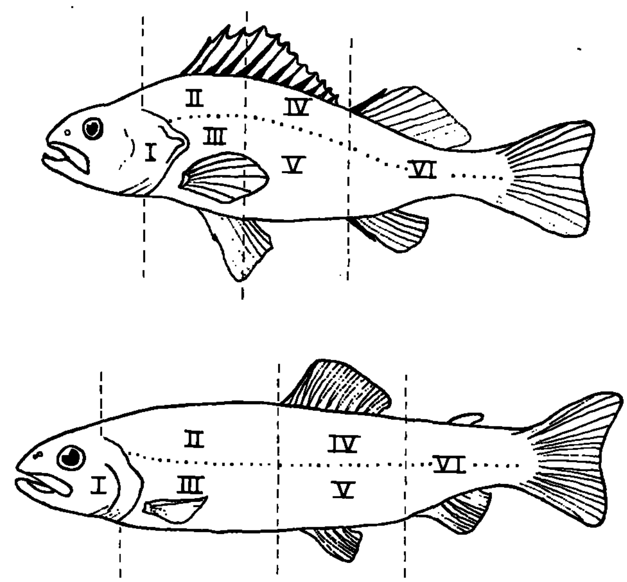

FIGURE 10.—Diagram of a typical spiny-rayed fish (above) and a soft-rayed fish (below) showing body regions used in plotting the location of sea-lamprey attacks.

were recorded for the wounds on lake and laboratory fish: Completeness; recentness; location on body of prey; duration of the attack; and dimensions of the wound. Each of these characters will be discussed in turn later in this section.

The form devised for recording the wound data included sketches of a fish, on which each lamprey injury was plotted. Certain regions were delineated on the bodies of both spiny-rayed and soft-rayed fishes, and each region included parts of the right and left sides of a fish (fig. 10). Region I included the head; regions II and IV included the dorsal section of the trunk; regions III and V included the ventral section of the trunk; and region VI included the caudal peduncle. A further designation was made of the number and types of wounds that occurred over either eye in region I, of those found in the immediate vicinity of the pectoral fins in region III, of those that occurred close to the pelvic fins in region V, and of those that penetrated the body wall into the coelomic cavity in regions III and V.

The white sucker was the most consistently available species for examination in the areas fished by our experimental nets in Lake Huron (fig. 11). Unblemished fish captured in trap nets were used in the laboratory feeding experiments; the many specimens bearing lake-incurred sea-lamprey injuries were studied for the wound characters. Of the total number of lamprey scars examined from both lake and laboratory sources, 68.8 percent were on white suckers and 31.2 percent were on the other 19 species.[2] Regrettably lacking in our data are records of wounds on lake trout, the principal victim of the sea lamprey. At the time these observations were made, the lake trout had disappeared as a commercial species in northern Lake Huron.

Completeness

Each wound was classed as complete or as incomplete. A wound was classed as complete if the skin of the prey fish was pierced and feeding took place. A wound was classed as incomplete if no feeding had occurred; incomplete wounds varied from wounds that showed only temporary marks on the surface of fish to those in which the scales had been torn but the skin had not been punctured. Of the 1,189 lake-incurred wounds, 93.4 percent were complete and 6.6 percent were incomplete (table 5). Of the 1,690 aquarium-incurred wounds, 89.8 percent were complete and 10.2 percent were incomplete. For our principal species, the white sucker, the percentages of complete and incomplete wounds were about the same as the percentages for all species. Of 979 lake-incurred wounds on white suckers, 93.4 percent were complete and 6.6 percent were incomplete; of 1,001 aquarium-incurred wounds, 88.0 percent were complete and 12.0 percent were incomplete. The percentages for the incidence of incomplete wounds on fish in the aquariums are probably more indicative of the true incidence in nature,

[2] Part of the study of scarring is reported in a paper on the relation of length of fish to incidence of sea-lamprey scars on white suckers in northwestern Lake Huron by A. E. Hall, Jr., and Oliver R. Elliott, to appear in *Copeia.*

FIGURE 11.—Examination of fish captured in experimental trap nets set under the ice in Duncan Bay, Lake Huron, 1953. Note the sea-lamprey mark on the white sucker below its dorsal fin and between the hands of the investigator.

TABLE 5.—*Numbers and percentages of complete and incomplete sea-lamprey wounds, and of new and healed wounds on prey fishes captured in Lake Huron*

Species	Total number of wounds	Complete wounds		Incomplete wounds		New wounds		Healed wounds	
		Number	Percentage	Number	Percentage	Number	Percentage	Number	Percentage
Rainbow trout	22	21	95.5	1	4.5	14	63.6	8	36.4
Round whitefish (*Prosopium cylindraceum quadrilaterale*)	4	4	100.0			1	25.0	3	75.0
Lake whitefish	10	8	80.0	2	20.0	5	50.0	5	50.0
Lake herring (*Coregonus artedii*)	10	10	100.0			8	80.0	2	20.0
Smelt (*Osmerus mordax*)	1	1	100.0			1	100.0		
White sucker	979	913	93.4	66	6.6	780	79.7	199	20.3
Longnose sucker	59	55	93.2	4	6.8	22	37.3	37	62.7
Carp (*Cyprinus carpio*)	4	3	75.0	1	25.0	4	100.0		
Lake chub (*Couesius plumbeus*)	1	1	100.0			1	100.0		
Channel catfish (*Ictalurus lacustris*)	6	6	100.0			6	100.0		
Brown bullhead	2	2	100.0			2	100.0		
Black bullhead (*Ameiurus melas*)	2	2	100.0			2	100.0		
Northern pike	6	6	100.0			6	100.0		
Burbot	1	1	100.0			1	100.0		
Walleye (*Stizostedion v. vitreum*)	6	5	83.3	1	16.7	6	100.0		
Yellow perch	72	69	95.8	3	4.2	62	86.1	10	13.9
Smallmouth bass (*Micropterus d. dolomieui*)	2	2	100.0			2	100.0		
Rock bass	2	2	100.0			2	100.0		
All species	1,189	1,111	93.4	78	6.6	925	77.8	264	22.2

since some of the incomplete wounds incurred in the lake may have healed without leaving an observable scar.

Recentness

All representative samples of prey fish captured in northern Lake Huron exhibit lamprey wounds of various ages, possibly including some only hours old and others one or more years old. The 1,189 lake-incurred wounds on 929 host fish were examined for evidences of recovery from the sea-lamprey attacks. These wounds were classified as new and open, or old and healed (table 5). The ratio of recent injuries to older ones may be used in estimating the recovery potential in attacked fishes.

For the present purposes, new wounds are those of recent origin on the fish, varying from hours to several weeks in age. They are characterized by a lack of any evidence of healing, and often by signs of recent hemorrhage and histolysis. Old ones exhibit scar tissue varying in extent to complete. closure, and any wound that showed healing tissue was classed as old. The system employed does not indicate the severity of the lesion, because major damages to structure or function of deeper tissues or organs may be obscured by superficial regeneration. Many feeding sites were entirely healed, and holes formerly very deep showed as mere surface indentations. Such areas were sometimes covered with new, irregularly arranged scales.

The rate and extent of healing in sea-lamprey wounds depends on the severity of the original damage. Some incomplete wounds heal quickly. Others are complete but the damage is slight, and these too may be repaired soon. Many prey fishes are debilitated to a point just short of death, and healing in their wounds is probably delayed until the victims regain vitality. Yet even these may heal.

Wounds were observed to begin formation of repair tissue sooner in summer than in winter. The higher metabolic rate of fishes in relatively warm water may explain this seasonal difference. On the other hand, the higher rate of metabolism in warm water undoubtedly works a disadvantage at times in prey specimens under attack by lampreys. The efficiency of the attack is presumably greater and the tolerance of the victim to injury is lower under such conditions. Furthermore, growth of any secondary invader of the site, such as bacteria or molds, may be favored by higher temperatures.

Of the 1,189 sea-lamprey wounds observed on 18 species of fish from Lake Huron, 77.8 percent were new wounds and 22.2 percent were healing or healed (table 5). Nearly all of the wounds were on white suckers and, of these, 79.7 percent were new marks and 20.3 percent were healed or in the process of healing.

The listing of the 199 old wounds on white suckers (table 6) by body region shows the highest percentages of recovery from lamprey damage in body regions IV (27.7 percent), II (27.6 percent), and V (21.7 percent). Lower values were found for regions VI (16.0 percent), III (12.1 percent), and I (5.9 percent). Although the total number of 979 wounds on white suckers included 66 incomplete attacks which might be expected to heal more readily than complete ones, the ratio of old wounds to incomplete ones was 3 to 1.

Among the reasons for the greater percentage of new than of old wounds on white suckers may be listed the strong probability that most suckers attacked by sea lampreys die as a direct or indirect result of the attacks. Secondary infections by fungus are known to kill some of the fish that are not fatally injured by the lampreys. In addition, the incidence of healed wounds is modified to an unknown extent by subsequent mortal attacks by lampreys on the recovered fish.

TABLE 6.—*Distribution of 780 new and 199 healing or healed sea-lamprey wounds observed among the 979 wounds on white suckers from Lake Huron*

[See fig. 11 for definitions of body regions]

Body region	Total number of wounds	New wounds		Healed wounds	
		Number	Percentage	Number	Percentage
I	17	16	94.1	1	5.9
II	163	118	72.4	45	27.6
III	313	275	87.9	38	12.1
IV	184	133	72.3	51	27.7
V	277	217	78.3	60	21.7
VI	25	21	84.0	4	16.0
All regions	979	780	79.7	199	20.3

Material concerning new and old lamprey injuries on trout species in nature is sparse, but Royce (1950, p. 75) observed wounds made by landlocked sea lampreys on male lake trout, 22.4 to 33.3 inches in length, in Seneca Lake. He reported that—

When the incidence of recent and old attacks is compared it is found that the lake trout averaged 2.8 total lamprey marks per fish and (in another group of fish) 1.0 unhealed sores. If we assume again that a sore remains unhealed only 1 month, then it appears that these lake trout possessed more unhealed sores in proportion to healed scars than would be expected from a random distribution of incidence of attack throughout the year. A random distribution of two attacks each year should cause about one-sixth of the marks to be unhealed rather than more than one-third. Possibly the concentration of spawning lake trout attracts lampreys and the spawning urge makes a fish take less notice of attacks.

In April and May 1951, 11 scarred rainbow trout, 18.3 to 25.0 inches long and 4 to 6 years of age, were trapped by lamprey weirs during their upstream, spawning migrations in tributaries of northern Lake Huron. Their sea-lamprey injuries numbered 1.9 scars per fish; of these, 1.2 were new and unhealed and 0.7 were healed. Most of the injuries were so severe that it was presumed that few of the trout would live to reach their spawning grounds. These limited data on large rainbow trout in Lake Huron indicate that, in contrast to Royce (1950), the paucity of healed wounds in comparison with unhealed ones is attributable to the high mortality, direct or indirect, from sea-lamprey wounds.

Distribution of wounds

The patterns of the distribution of sea-lamprey wounds on the bodies of host fishes were observed on 1,111 complete marks on 18 species of fish in Lake Huron and on 1,518 complete attacks on 11 species in the laboratory (table 7). The differences in the two sets of data were considerable. More than 60 percent of the lake-incurred wounds were in regions III and V, whereas 45 percent of the laboratory-incurred wounds were in regions II and IV. Only 2.1 percent of the lake wounds occurred on the heads of the fishes, but in the laboratory 18.5 percent of the attacks were in this region.

TABLE 7.—*Locations of complete sea-lamprey wounds according to body region on lake and laboratory fishes*

[See fig. 11 for definition of regions. Data for all species have been combined; see table 8 for information on individual species]

Body regions	Lake-incurred wounds		Laboratory-incurred wounds	
	Number	Percentage of total	Number	Percentage of total
I Entire region	23	2.1	281	18.5
Eye	5	.5	98	6.5
II	166	14.9	362	23.8
III Entire region	377	33.9	313	20.6
Pectoral fins	75	6.8	52	3.4
Body cavity [1]	172	15.5	72	4.7
IV	198	17.8	321	21.2
V Entire region	318	28.6	175	11.5
Pelvic fins	98	8.8	41	2.7
Body cavity [1]	68	6.1	33	2.2
VI	29	2.7	66	4.4
All regions	1,111	100.0	1,518	100.0

[1] Wounds that penetrated the body.

It is believed that the differences between laboratory and lake fish with respect to distribution of sea-lamprey wounds on the body can be attributed to the fact that all wounds were available for study in the laboratory, whereas the scarred fish from the lake included only fish that had survived sea-lamprey attacks. Observations on the mortality rate from attacks on different body locations in laboratory fish strongly supported this view.

The data on lake-incurred scars may have been biased by the fact that some of the marks were created while the fish were confined alive in trap nets. On many occasions when the nets were being lifted, lampreys detached themselves from prey and dropped through the meshes into the water. Although the nets were usually tended every third day, there is no way of determining the number or percentage of victims that suffered lamprey attacks while confined, but it is estimated that they did not exceed one-quarter of the total number of scarred fishes in the catch. Therefore, it was presumed that the pattern of lake-incurred injuries was not modified greatly by sea-lamprey attacks in the nets.

Laboratory data on the location of attacks are open to criticism in that conditions, at best, were artificial. Whether the habits of the sea lampreys in aquariums were typical is not known, but their growth, though considerably slower, paralleled that of lampreys in the wild. This similarity was considered indicative that the feeding habits of the animals was not particularly affected by confinement. The lampreys did feed in captivity; the prey fishes provided them were typical; and the water conditions in the tanks were satisfactory. The aquarium did limit movements, but no influence due to these space conditions could be detected in the pattern of lamprey attacks. In the lake, a lamprey may approach a fish without limitations imposed by lack of space.

The average size of hosts used in the experiments may have had some influence on site selection. The tank fishes, other than the longnose suckers, averaged slightly smaller (table 8) than the lake fish (table 9) but among the species that contributed most of the wound records, the differences were small.

TABLE 8.—*Mean lengths and weights of fishes used in the sea-lamprey feeding experiment and examined for wound locations from August 1950 to February 1952*

Species	Number of specimens	Mean length	Mean weight
		Inches	*Grams*
Brown trout	26	10.7	200
Rainbow trout	385	9.6	129
Eastern brook trout	70	8.7	111
Lake whitefish	1	12.1	238
White sucker	858	12.4	350
Longnose sucker	36	15.4	702
Brown bullhead	1	8.2	66
Northern pike	2	14.4	290
Burbot	2	19.6	860
Yellow perch	15	8.9	140
Rock bass	1	7.2	120

TABLE 9.—*Mean lengths and weights of fishes captured in northern Lake Huron and examined for wound locations from August 1950 to February 1952*

Species	Number of specimens	Mean length	Mean weight
		Inches	*Grams*
Rainbow trout	11	21.4	1,631
Round whitefish	3	14.1	392
Lake whitefish	8	17.7	886
Lake herring	9	10.6	145
Smelt	1	7.0	------
White sucker	759	12.9	406
Longnose sucker	46	15.2	683
Carp	2	15.1	1,186
Lake chub	1	5.3	20
Channel catfish	1	24.3	2,752
Brown bullhead	1	8.2	66
Black bullhead	4	12.0	357
Northern pike	7	20.7	1,193
Burbot	2	19.6	860
Yellow perch	65	9.3	158
Walleye	3	17.4	851
Smallmouth bass	2	11.6	400
Rock bass	3	9.2	279

On white suckers.—The distribution of sea-lamprey attacks[3] by body regions on host fishes from Lake Huron and the laboratory tanks is best seen in the white sucker. For this species, we have the locations of 913 complete wounds from natural water (table 10) and of 881 from the feeding experiment. The suckers bearing these injuries were nearly of the same size, since the individuals used in aquariums were from the same catches that provided the data on scarring in the lake (tables 8 and 9).

The areas of the six body regions used to designate the locations of the lake and laboratory wounds were by no means equal. The actual dimensions of each region were measured on a white sucker, 15.3 inches long and 537 grams in weight (fig. 12). A comparison of the percentage distribution of the total body surface among the different regions with the percentage distribution of the total numbers of wounds reveals certain marked discrepancies (table 11).

[3] The points of attack discussed in this section should not be interpreted as descriptive of the points of original attachment. Lampreys commonly shifted considerable distances from the point of original attachment before starting the wounding process.

TABLE 10.—*Location of complete sea-lamprey wounds according to body regions for various species of fish in the laboratory and in the lake*

[See fig. 11 for definition of regions]

Species and body region	Laboratory-incurred wounds		Lake-incurred wounds	
	Number	Percentage	Number	Percentage
Brown trout:				
I	3	2.3		
II	40	31.2		
III. Entire region	31	24.2		
Pectoral fins	9	7.0		
Body cavity	5	3.9		
IV	32	25.0		
V. Entire region	12	9.4		
Pelvic fins	2	1.5		
Body cavity	1	.8		
VI	10	7.8		
All regions	128	100.0		
Rainbow trout:				
I. Entire region	8	2.7		
Eye	6	2.0		
II	90	29.8	1	4.8
III. Entire region	72	23.9	1	52.4
Pectoral fins	11	3.6	3	14.3
Body cavity	11	3.6	1	4.8
IV	64	21.2	3	14.3
V. Entire region	39	12.9	5	23.8
Pelvic fins	8	2.7	1	4.8
Body cavity	3	1.0	1	4.8
VI	29	9.3	11	3.7
All regions	302	100.0	21	100.0
Brook trout:				
I. Entire region	2	2.0		
Eye	2	2.0		
II	47	47.0		
III. Entire region	21	21.0		
Pectoral fins	4	4.0		
Body cavity	3	3.0		
IV	21	21.0		
V. Entire region	7	7.0		
Pelvic fins	1	1.0		
Body cavity	1	1.0		
VI	2	2.0		
All regions	100	100.0		
Round whitefish:				
III			1	25.0
V. Entire region			3	75.0
Pelvic fins			1	25.0
All regions			4	100.0
Lake whitefish				
II	1	50.0		
III			3	37.5
V. Entire region	1	50.0	5	62.5
Pelvic fins			3	37.5
All regions	2	100.0	8	100.0
Lake herring:				
II			1	10.0
III			2	20.0
IV			2	20.0
V. Entire region			5	50.0
Pelvic fins			4	40.0
Body cavity			1	10.0
All regions			10	100.0
Smelt:				
V			1	100.0

TABLE 10.—*Location of complete sea-lamprey wounds according to body regions for various species of fish in the laboratory and in the lake*—Continued

[See fig. 11 for definition of regions]

Species and body region	Laboratory-incurred wounds		Lake-incurred wounds	
	Number	Percentage	Number	Percentage
White suckers:				
I. Entire region	244	27.7	17	1.9
Eye	80	9.1	5	0.6
II	160	18.2	152	16.7
III. Entire region	173	19.6	300	32.9
Pectoral fins	25	2.8	61	6.7
Body cavity	49	5.6	140	15.3
IV	180	20.4	170	18.6
V. Entire region	106	12.0	253	27.7
Pelvic fins	25	2.8	67	7.3
Body cavity	25	2.8	52	5.7
VI	18	2.0	21	2.3
All regions	881	100.0	913	100.0
Longnose suckers:				
I. Entire region	22	23.2	1	1.8
Eye	10	10.5		
II	24	25.3	2	2.7
III. Entire region	14	14.7	10	18.2
Pectoral fins	3	3.2	1	1.9
Body cavity	3	3.2	1	1.9
IV	22	23.2	17	30.9
V. Entire region	6	6.3	23	41.8
Pelvic fins	4	4.2	6	10.9
Body region	1	1.1	2	3.6
VI	7	7.4	2	3.6
All regions	95	100.0	55	100.0
Carp:				
III. Entire region			2	66.7
Pectoral fins			1	33.3
Body cavity			1	33.3
IV			1	33.3
All regions			3	100.0
Lake chub:				
II			1	100.0
Channel catfish:				
I			1	16.7
III. Entire region			3	50.0
Pectoral fins			1	16.7
Body cavity			2	33.3
V			2	33.3
All regions			6	100.0
Brown bullhead:				
V. Entire region	1	100.0		
Body cavity	1	100.0		
Black bullhead:				
III. Entire region			2	50.0
Pectoral fins			2	50.0
Body cavity			2	50.0
IV			1	25.0
V			1	25.0
All regions			4	100.0
Northern pike:				
II			1	16.7
III. Entire region			3	50.0
Pectoral fins			1	16.7
IV	1	33.3	1	16.7
V	1	33.3	1	16.7
VI	1	33.3		
All regions	3	100.0	6	100.0

TABLE 10.—*Location of complete sea-lamprey wounds according to body regions for various species of fish in the laboratory and in the lake*—Continued

[See fig. 11 for definition of regions]

Species and body region	Laboratory-incurred wounds		Lake-incurred wounds	
	Number	Percentage	Number	Percentage
Burbot:				
I	2	66.7		
II			1	100.0
IV	1	33.3		
All regions	3	100.0	1	100.0
Yellow perch:				
I			3	4.4
II			8	11.6
III. Entire region	2	100.0	34	49.3
Pectoral fins	1	50.0	3	4.4
Body cavity			22	31.9
IV			2	2.9
V. Entire region			18	26.0
Pelvic fins			16	23.2
Body cavity			12	17.4
VI			4	5.8
All regions	2	100.0	69	100.0
Walleye:				
I			1	20.0
III. Entire region			3	60.0
Pectoral fins			1	20.0
Body cavity			2	40.0
V. Entire region			1	20.0
Pelvic fins			1	20.0
All regions			5	100.0
Smallmouth bass:				
III. Entire region			1	50.0
Body cavity			1	50.0
VI			1	50.0
All regions			2	100.0
Rock bass:				
III			1	50.0
V. Entire region	1	100.0	1	50.0
Body cavity	1	100.0		
All regions	1	100.0	2	100.0
Total number of wounds	1,518		1,111	

TABLE 11.—*Comparison of distribution of 913 lake-incurred and 881 laboratory-incurred complete sea-lamprey wounds on white suckers with percentage of total body surface contained in each region*

[See fig. 11 for definition of regions]

Body region	Percentage [1] of total area	Lake-incurred wounds		Laboratory-incurred wounds	
		Number	Percentage of total	Number	Percentage of total
I	15.8	17	1.9	244	27.7
II	15.5	152	16.7	160	18.2
III	18.8	300	32.8	173	19.7
IV	14.3	170	18.6	180	20.4
V	18.2	253	27.7	106	12.0
VI	17.4	21	2.3	18	2.0
All regions	100.0	913	100.0	881	100.0

[1] Exclusive of all fin surfaces.

In the laboratory fish, the only group in which all wounds inflicted were available for examination, the discrepancies were particularly large for the peduncular region (region VI, 17.4 percent of the total area but only 2.0 percent of the wounds) and the head (region I, 17.8 percent of the area and 27.7 percent of the wounds). In the central part of the body, the percentage of wounds was greater than the percentage of area in regions II, III, and IV, but was less in region V. If this observed distribution reflects the true behavior of the lamprey (that is, if we may assume that the artificial conditions in the laboratory did not lead to a distribution pattern different from that which would have occurred in nature) the parasite can be said to exhibit a strong preference for the head as a point of attack and a similarly strong avoidance of the peduncle. Possible preferences among other regions seem less clear-cut, although there is some indication of preference for region IV and avoidance of region V.

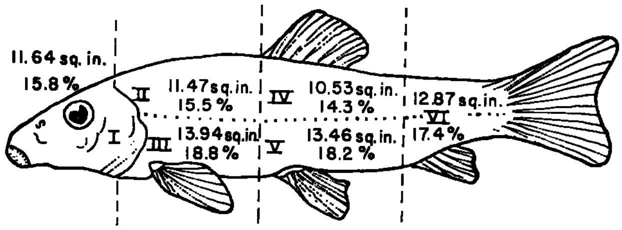

FIGURE 12.—Diagram of a white sucker showing actual sizes and percentage distribution of total body surface among the six regions used in recording the locations of lamprey wounds. Measurements taken from a female fish, 15.3 inches in length, 537 grams in weight, captured in Hammond Bay, Lake Huron, July 25, 1952. The total area of the fish, exclusive of fins, was 73.90 square inches.

The distribution of wounds on white suckers captured in the lake differed sharply both from the area percentages (on a regional basis) and from the observed distribution on laboratory fish. The disagreements among the three sets of percentages were not particularly large for region II (range from 15.5 to 18.2) but elsewhere amounted to at least 6.1 percent (the range for region IV). On the whole, therefore, both patterns of wound distribution differed from the area percentages and from each other.

The most striking difference between the lake and laboratory data was in the percentage of wounds on the head (27.7 percent in region I for the lake fish but only 1.9 percent for the laboratory fish). The percentages for the lake fish were much higher in regions III and V (values of 32.9 and 27.7, as compared with 19.6 and 12.0 for laboratory fish). The differences between the two groups of fish were relatively small for other regions; it is to be noted especially that they agreed in showing extremely few scars in region VI.

It is believed that the differences in wound distributions on laboratory and lake fish are attributable to the fact that wounds are more likely to bring about early death if inflicted on one body location than if inflicted on another. As was explained earlier, all wounds on laboratory fish were available for examination whereas the suckers examined from the lake were survivors of past attacks—some made a considerable time earlier and others recent.

Among the cranial wounds (region I) there were about 17 times as many in the eyes of the aquarium hosts than in the eyes of lake fish. Considering the size of the eyes of white suckers, it is noteworthy that these organs should attract as many as 9.1 percent of the total number of attacks studied in the laboratory. The small percentage (0.6) of eye wounds in the lake samples makes it appear that the fishes attacked in such a vital area do not usually survive the lamprey attachments.

A comparison of the percentages of wounds that penetrated into the coelomic cavity (in regions III and V) showed that 8.4 percent of all attacks in the laboratory and 21.0 percent of all attacks on the lake fish pierced the body wall. Severe damages to visceral organs and disruptions of vital physiological processes frequently resulted from wounds that punctured the body wall, but it was also observed that such wounds were less likely to prove immediately fatal than others located elsewhere on the fish (regions I, II, and IV). Many white suckers attacked by sea lampreys in the lake survived their eventually mortal, body-cavity wounds long enough to become captured in our trap nets.

The contention of Gage (1929) that sea lampreys usually attach themselves on fishes in the vicinities of the paired fins does not appear valid. Injuries that occurred beneath the normal, retracted positions of these fins or closely approached or included fin insertions were recorded. Only 5.7 percent of the complete wounds on white suckers in aquariums were proximal to the pectoral and pelvic fins. Among the suckers attacked in Lake Huron, 14.0 percent of the complete wounds were located in the neighborhood of the paired fins.

On trout.—The pattern of sea-lamprey attacks on salmonids was plotted for the most part from data obtained in aquariums at the laboratory. Numbers of complete wounds recorded were 128 on brown trout, 302 on rainbow trout, and 100 on eastern brook trout (table 10). Twenty-one additional wounds were observed on rainbow trout from Lake Huron. The trout used in the sea-lamprey feeding experiment were mostly provided by Wolverine Rearing Station and Oden Hatchery of the Michigan Department of Conservation. Additional specimens were furnished by the Fish and Wildlife Service Hatchery at Northville, Mich.

One or more species of trout were employed as hosts in aquariums from December 1950 to July 1952. The majority of the attack records were compiled from April through August 1951. During this period, the parasitic lampreys in the same tanks averaged 5.5 inches long on May 3, 1951, and 11.0 inches on September 1, 1951. It is believed that the relatively small size of the lampreys that created most of the marks on trout in no way altered the pattern of attacks.

The data collected in the laboratory on the rainbow trout may be more representative than those listed for brown trout and brook trout. The larger total number of complete wounds on the rainbow trout and their better distribution throughout the lamprey-feeding experiment lend advantage to the data. However, the patterns of wound distribution on the brown trout and brook trout support the findings on the rainbow species.

The six body regions used to plot the locations of wounds on the rainbow trout were not equal in extent. The actual dimensions of each region were measured on a rainbow trout, 8.2 inches long and 90 grams in weight (fig. 13). The percentage distribution of the total body surface among the different regions closely resembled that determined for the white sucker (fig. 12). Further, as was noted with the white sucker, a comparison of the percentage distribution of the total body surface with the percentage distribution of the total numbers of wounds reveals some marked discrepancies.

A large discrepancy exists in region I, the head, which contained 16.0 percent of the total surface area but only 2.7 percent of the wounds. The percentage distribution of head wounds on the three species of trout ranged from 2.0 to 2.7 percent in contrast with the 27.7-percent incidence

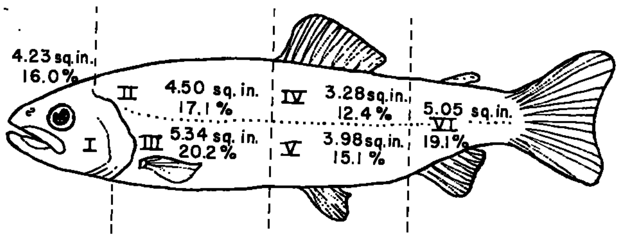

FIGURE 13.—Diagram of a rainbow trout showing actual sizes and percentage distribution of total body surface among the six regions used in recording the locations of lamprey wounds. Measurements taken from a male fish, 8.2 inches in length, 90 grams in weight, captured in the Ocqueoc River, Presque Isle County, Mich., August 18, 1952. The total area of the fish, exclusive of fin surfaces, was 26.38 square inches.

on the heads of white suckers attacked in aquariums and a 23.3-percent incidence in region I on laboratory longnose suckers. No explanations can be given for this difference. In the central part of the body on rainbow trout, the percentage of wounds exceeded the percentage of area in regions II, III, and IV, but was less in region V. The difference between area and incidence in region VI on the trout (19.0 percent of the area and 9.3 percent of the wounds) was not as large as that found in the same region on white suckers (17.4 percent of the area and 2.0 percent of the wounds). The percentage incidence of attacks on the peduncular region of brown trout approached that of the rainbow trout, whereas only 2.0 percent of the wounds in brook trout were in region VI. Except for the lampreys' avoidance of attaching on region I on trout, the pattern of their attacks on these species was similar to that on white suckers in aquariums.

The percentage distribution of 21 sea-lamprey wounds on rainbow trout from Lake Huron roughly followed the pattern for lake-incurred attacks on white suckers. More than 75 percent of the 21 wounds occurred in the lower middle third of the body (regions III and V) and the upper middle third contained only 14 percent of the scars.

On yellow perch.—A total of 69 complete wounds were studied on yellow perch captured in Lake Huron (table 10). The distribution of these attacks fell into the pattern already discussed for white suckers, longnose sucker, and rainbow trout which bore lake-incurred sea-lamprey marks. The preponderance (75 percent) of feeding attachments on perch occurred on the lower middle third of the body, and wounds on other regions were seen with less frequency, presumably because they were more quickly fatal.

Two complete wounds were obtained from yellow perch used as prey in lamprey-feeding experiments. Both attacks occurred in region III, and one of them was adjacent to a pectoral fin. The other penetrated the coelom. The perch that were held in aquariums were largely ignored by the sea lampreys when other species such as white sucker or rainbow trout were available. Only when the perch was alone did the lampreys seem inclined to attack.

It has been suggested that the yellow perch is relatively more immune to lamprey attack than soft-rayed fishes because it is more heavily scaled. This view is untenable, however, because prowling lampreys do not attach themselves to the perch and test the covering; the lampreys usually take no notice of them except when they are the sole prey available. No explanation can be offered for this selection. The midwater position maintained by the yellow perch in aquariums was shared by brook, brown, and rainbow trout, which were very susceptible to sea-lamprey attacks.

The commercial fishery for yellow perch in northern Lake Huron collapsed in the winter of 1950–51. Until that time, the perch was largely disregarded by sea lampreys in the lake, but early in the winter, the incidence of lamprey wounds on yellow perch suddenly increased to as much as 75 percent of the entire catch in some lifts of the laboratory trap nets. By the following spring, the species in the northwestern part of the lake apparently ceased to exist in commercial proportions. Since other species had become extremely scarce during immediately preceding years (Moffett 1950; Hile, Eschmeyer, and Lunger, 1951), it appeared to workers at the laboratory that the sea lampreys had turned to the yellow perch as a last resort.

On other species.—Records on sea-lamprey wounds were obtained in small numbers from 15 additional species of fish captured in Lake Huron (table 10). The material provides further evidence that the majority of scars on prey fish in Lake Huron are in regions III and V. Attacks were recorded in the laboratory on eight of these hosts, but their numbers were so small that discussion is not warranted.

Duration of attack

Observations on sea lampreys in aquariums showed that, in general, the parasites are quick to perceive an insufficient food return from wounds. They are then likely to move to other sites on their hosts (this behavior was also observed by Gage, 1929). If the host is dead or dying, they usually detach themselves and immediately seek fresh victims, a habit mentioned by Bigelow and Welsh (1925).

In this experimental work, it was possible to record the duration of a number of parasitic attacks on the various body regions of host fishes. Records were kept on the sizes and kinds of fish, the dates when they were placed in aquariums. the dates and time when attacks were initiated by the lampreys, the locations of the attachments on the bodies of the victims, the number of hours of feeding at each wound, the date and time of death of the hosts, and the sizes of the lampreys.

The time that the lampreys spent attached to individual fish appeared to depend to a large extent on size of the lamprey, size of the host, site of attack, and proximity of blood vessels to the site. Obviously important but largely conditioned by the factors just listed is the length of time the victim survives. A lamprey seldom remains long attached to a dying or dead fish. Still another seemingly significant but unmeasurable factor was the vigor with which the individual lamprey fed.

Among the attacks by sea lampreys on host fishes observed in aquariums, the lengths of lampreys responsible for 435 attacks of certain durations were known (table 12). The relation between the size of a lamprey and the mean duration of its attack on a host (fig. 14) shows that the longest attacks (220.2 hours) were made by newly transformed feeders that averaged 5.5 inches long, whereas the shortest attacks (38.7 hours) were made by lampreys that averaged 12.9 inches. Attacks by lampreys of still larger size could be described as even more brief if we could accurately measure the time that efficient feeding continued. With the approach of sexual maturity and attendant degeneration of the feeding mechanism, more total hours though less hours of feeding were spent per attack. Hence the mean durations for lampreys that averaged 15.2 and 16.5 inches long (43.0 and 42.3 hours respectively) showed slight increases over the minimum (38.7 hours).

TABLE 12.—*Duration of 435 attacks by sea lampreys of known length on 11 species of prey fish in laboratory aquariums*

Number of lampreys	Length of lampreys		Average duration of attack
	Range	Mean	
	Inches	*Inches*	*Hours*
58	4.0– 5.9	5.5	220.2
80	6.0– 7.9	6.6	90.2
27	8.0– 9.9	8.8	57.4
42	10.0–11.9	11.3	50.7
64	12.0–13.9	12.9	38.7
121	14.0–15.9	15.2	43.0
43	16.0–17.9	16.5	42.3
435		11.3	76.2

The records of attack durations on various body locations for 614 complete sea-lamprey wounds on white suckers in aquariums (table 13) showed that attachments averaged longest on region II (35 hours), followed in decreasing order by body regions IV, VI, III, I, and V. On the basis of both duration and number of attacks, regions II, IV, and I and III in that order provided the most used feeding sites.

Region I was included among the best feeding sites on this species owing to the high incidence of attacks, and in spite of the more rapid lethality of the wounds in this region. Attachments over

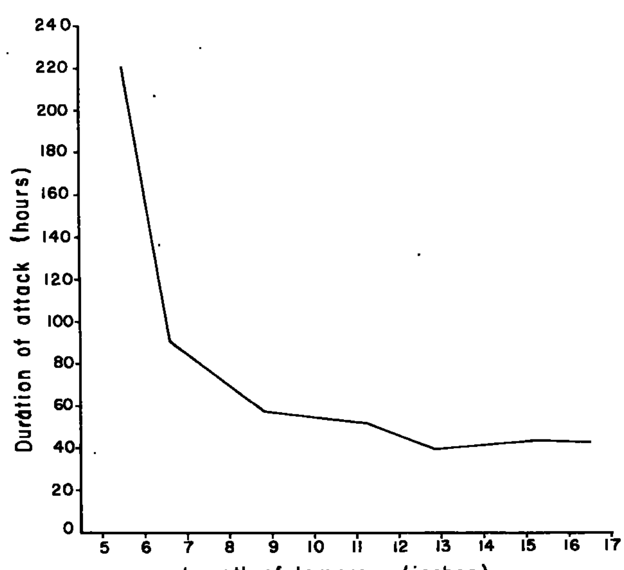

FIGURE 14.—Relation of length of lamprey to duration of attack. Data obtained from study of 435 wounds on 11 species of fish attacked by lampreys of known length in aquariums.

the eyes, which comprised 32.1 percent of the 168 wounds recorded on the head, had an average duration of 19.1 hours compared with the grand average of 22.4 per attack in region I as a whole.

The total amount of feeding time logged in aquariums for 512 complete sea-lamprey wounds on the three trout species was 22,281 hours (table 14). The data for brown, rainbow, and brook trout were combined since no large differences were noted between them. The majority of the attacks occurred in regions II, III, and IV, which regions combined supported 392, or 76.9 percent of the total wounds and 79.8 percent of the total hours; the average duration of attack was 45.3 hours.

Region I, the head, contained 14 wounds, or 2.7 percent of the total number. The average duration of attachment here was 15.1 hours. The six attachments on the eyes had an average duration of only 9.0 hours. In most of these attacks, the eyeball injuries were fatal before the detachment of the attacker. Head wounds generally led to death more rapidly than attacks on other parts of the body.

TABLE 13.—*Locations and attack durations for complete sea-lamprey wounds on white suckers from laboratory aquariums*

[Data represent 614 attacks by lampreys 5.5 to 17.0 inches long]

Body region	Wounds		Hours per attack	
	Number	Percentage of total	Number	Percentage of total
I. Entire region	168	27.4	22.4	23.0
Eye	54	8.8	19.1	6.3
II	128	20.9	35.4	27.8
III. Entire region	118	19.2	24.9	18.0
Pectoral fins	26	4.2	26.3	4.2
Body cavity [1]	41	6.7	22.5	5.7
IV	120	19.5	28.8	21.2
V. Entire region	69	11.2	19.3	8.2
Pelvic fins	21	3.4	20.8	2.7
Body cavity [1]	12	2.0	10.2	.8
VI	11	1.8	26.7	1.8
All regions	614	100.0	26.5	100.0

[1] Wounds that penetrated the body wall.

TABLE 14.—*Locations and attack durations for the combined complete sea-lamprey wounds on brown, rainbow, and brook trout in aquariums*

[Data represent 512 attacks by lampreys 5.5 to 17.0 inches long]

Region	Wounds		Hours per attack	
	Number	Percentage of total	Number	Percentage of total
I. Entire region	14	2.7	15.1	1.0
Eye	6	1.2	9.0	.2
II	168	32.8	49.5	37.3
III. Entire region	99	19.4	43.1	19.1
Pectoral fins	21	4.1	33.5	3.2
Body cavity [1]	28	5.5	27.0	3.4
IV	125	24.4	41.6	23.3
V. Entire region	65	12.7	41.5	12.1
Pelvic fins	14	2.7	17.9	1.1
Body cavity [1]	10	2.0	40.1	1.8
VI	41	8.0	39.0	7.2
All regions	512	100.0	43.5	100.0

[1] Wounds that penetrated the body wall.

The duration of lamprey attacks on trout was longest on region II. The 168 feeding attacks made in this locale averaged 49.5 hours. As was true for the white suckers, more injuries penetrated the body cavity in region III than in region V, but in the later region these attachments consumed more time individually.

The determination of the incidence and average durations of sea-lamprey attacks according to body regions on host fish demonstrates that feeding attachments may be more satisfactory to the parasites on certain sites than on others. The regions favored by lampreys, as indicated by the numbers and durations of attachments, on white suckers were I, II, III, and IV, whereas on the three species of trout the attackers created the most wounds and spent the longest times in regions II, III, and IV.

The data on hours per lamprey attack on white suckers and brown, rainbow, and brook trout are not directly comparable. The durations of attachment were longer on trout because the majority of wounds on these species were made by relatively small sea lampreys. When the sea lampreys reached greater size, the normal length of attack was shorter and suckers were the main prey available. The hours per attack on white suckers can therefore be considered more typical than those on trout since they represent lampreys of greater size range.

Observations made in the laboratory on the parasites themselves offer some explanation for the seeming preference for certain body regions. For example, lampreys that attacked fish briefly on regions V and VI usually made only small wounds and then shifted anteriorly and/or dorsally to new regions where more efficient feeding took place.

Dimensions of wounds on fishes

Three dimensions of 2,629 sea-lamprey wounds on 20 species of fishes from Lake Huron and laboratory sources were measured and recorded: Diameter of the oral-disk mark; diameter of the hole rasped in the fish tissues; and depth of the hole.

Accurate measurements of wounds were sometimes difficult. The exact dimensions of many of the marks of both complete and incomplete wounds were obscured by healing or by closely adjacent or overlapping attacks by other lampreys. The parasites often moved somewhat on the attachment sites, thereby distorting or obliterating the original boundaries. Some attachments were of too short duration for the marks to be sharply defined.

Oral-disk marks.—The imprint of the oral disk on a fish forms the largest measurable dimension of a sea-lamprey wound. On some fish this imprint is clearly defined, but on the majority of hosts the oral-disk mark is distorted slightly (1 to 2 millimeters) by edema at the wound site or by the effects of the oral-suction pressure on the fish skin or flesh. The marks made by newly transformed lampreys and those that are close to sexual maturity are often greatly distorted owing to changes of position at the wound sites. Scrapelike marks up to 100 millimeters long are sometimes produced, and the dimensions of the original wounds are obliterated.

The diameters of the oral-disk marks were measured on 832 complete and incomplete wounds incurred by 18 species of fish in Lake Huron (table 15) and on 1,630 wounds examined on 11 species of hosts in aquariums (table 16). The measurements were obtained between July 1950 and July 1952, and when they were plotted by calendar months the existence of a 16-month wound cycle was demonstrated. This cycle of wounds is created by a single year class of lampreys and supports the conclusion by Applegate (1950) that sea lampreys spend 12 to 16 months in their parasitic phase of life. Captive lampreys in aquariums were slaughtered after 15 months of parasitic living; nearly all were sexually mature.

The smallest wounds in both groups of hosts were observed during the first month (April) of parasitic feeding by newly transformed lampreys. By the seventh month of the parasitic phase (October), the diameters of the oral-disk marks on lake and laboratory fishes had doubled. Thereafter the mean diameters of marks on Lake Huron hosts increased more rapidly than those on prey fish in aquariums. The maximum mean diameters occurred in both sets of data during the eleventh month (February), at which time the disk marks averaged 40.2 millimeters (270-percent overall increase) on lake fish, and 36.8 millimeters (230-percent overall increase) on hosts in aquariums. Thereafter, from the twelfth to sixteenth month (March to July), the mean sizes of the disk marks on lake and laboratory fishes decreased sharply for several reasons: the largest lampreys were generally the first to cease feeding and become sexually mature, therefore a larger proportion of the wounds each month were made by smaller lampreys; most of the parasites reduce their feeding activities and undergo considerable shrinkage in length (from 1 to 3 inches in aquariums) and

TABLE 15.—*Minimum, average, and maximum dimensions of new, complete sea-lamprey wounds as they occurred during 16-month wound cycle of fish in Lake Huron*

Month	Diameter of oral-disk mark				Diameter of wound hole				Depth of wound hole			
	Number	Minimum	Average	Maximum	Number	Minimum	Average	Maximum	Number	Minimum	Average	Maximum
		Millimeters	*Millimeters*	*Millimeters*		*Millimeters*	*Millimeters*	*Millimeters*		*Millimeters*	*Millimeters*	*Millimeters*
April [1]	1	15	15.0	15	1	5	5.0	5	1	3	3.0	3
May	5	15	18.8	21	5	6	6.2	7	4	1	1.5	2
June	9	14	18.7	23	7	3	4.1	7	5	1	1.8	3
July	10	16	19.2	24	8	4	5.8	11	8	1	1.4	2
August												
September	27	20	29.3	42	25	2	9.3	22	47	1	3.3	10
October	89	22	30.7	39	74	4	9.8	25	48	1	4.2	9
November	175	24	35.6	50	180	3	11.3	28	136	1	4.1	15
December	71	25	38.1	50	94	3	16.5	43	77	1	4.9	10
January	102	26	38.8	50	111	2	14.9	40	100	1	4.5	12
February	66	30	40.2	53	76	3	15.4	40	78	1	4.3	12
March	102	25	39.6	55	116	2	13.2	35	90	1	5.0	13
April	118	22	36.9	50	105	3	12.6	25	122	1	3.3	13
May	38	30	35.9	48	42	3	15.0	25	41	1	2.7	7
June	12	27	32.1	42	15	4	9.9	26	8	1	2.5	2
July [2]	7	27	30.0	39	9	2	6.2	16	3	1	2.0	3
Total number	832				868				768			

[1] Start of parasitic feeding.

[2] End of parasitic feeding.

TABLE 16.—*Minimum, average, and maximum dimensions of new, complete sea-lamprey wounds as they occurred during 15-month wound cycle on 11 species of fish in laboratory aquariums*

Month	Diameter of oral-disk mark				Diameter of wound hole				Depth of wound hole			
	Number	Minimum	Average	Maximum	Number	Minimum	Average	Maximum	Number	Minimum	Average	Maximum
		Millimeters	*Millimeters*	*Millimeters*		*Millimeters*	*Millimeters*	*Millimeters*		*Millimeters*	*Millimeters*	*Millimeters*
April [1]	47	10	15.9	18	56	2	4.2	12	55	1	2.0	4
May	113	12	16.7	21	125	1	4.0	8	119	1	2.1	4
June	253	10	18.7	23	257	1	6.5	20	251	1	2.4	6
July	235	13	20.0	27	211	1	4.2	15	202	1	2.4	6
August	282	10	26.1	36	274	1	6.0	17	233	1	3.0	10
September	174	13	27.5	37	154	3	6.3	26	125	1	3.1	10
October	243	18	30.8	39	234	2	6.7	18	186	1	3.7	12
November	48	22	34.4	41	46	2	7.8	25	32	1	4.4	12
December	47	22	34.5	42	48	2	8.3	30	39	1	3.8	14
January	28	28	34.6	42	28	2	7.5	13	25	2	5.1	8
February	46	30	36.8	45	39	2	10.4	23	36	1	3.9	12
March	35	29	34.5	40	35	2	11.4	30	27	1	3.6	8
April	42	26	33.9	38	38	3	8.7	23	34	1	3.0	8
May	34	30	34.8	39	34	3	7.4	18	30	2	4.0	9
June [2]	3	28	32.7	35	4	5	9.8	10	3	3	4.3	6
Total number	1,630				1,583				1,397			

[1] Start of parasitic feeding. [2] End of parasitic feeding.

weight as their gonads ripen; the smaller lampreys of the year class may continue to feed actively until the fifteenth or sixteenth month before becoming sexually mature, but their increase in size, if any, is small.

The terminal average of oral-disk marks on lake fishes was 30 millimeters, a reduction by 40 percent from the maximum mean size recorded in the eleventh month. The final average disk mark obtained on laboratory hosts in the fifteenth month was 32.7 millimeters, a reduction of 20 percent from the maximum mean size listed for this group. During the period from April to July the wounds made by the outgoing year class (thirteenth to sixteenth month) of sea lampreys were readily separable by their dimensions from those of the incoming year class (first to third month).

The curves showing the development in sizes of oral-disk marks on fishes during certain calendar periods (fig. 15) may be useful in estimating the growth of sea lampreys in the lake and in aquariums. This view is supported by data obtained on individually identifiable lampreys held in aquariums; their lengths were periodically determined, and the measured diameters of their oral disks were found to be equal to the diameters of their individual disk marks on host fish. These feeders doubled their lengths by the seventh month and reached maximum average length in the eleventh month of parasitic habit. Thereafter most of the specimens shrank in length and weight as they tended to cease feeding and become sexually mature. It is therefore likely that a similar direct relation exists between the growth of lampreys in the lake and the size development of their oral-disk marks on host fishes.

In order to compare the growth of lampreys in the lake and in the laboratory, the mean diameters of fresh oral-disk marks on wounds from both sources were converted to mean lengths of lampreys by referring to table 4 which lists length groups of lampreys with the mean diameters of their oral disks. These lengths-by-conversion are included in table 17 along with some actual lengths of sea lampreys captured in the Great Lakes by Applegate (1950) during certain calendar periods in 1948. In considering these data, it is necessary to keep in mind the fact that a decline in the average size of spawning-migrant lampreys in Lake Huron is in progress (Applegate et al. 1952); spawning lampreys in Carp Lake River, a tributary to Lake Huron, averaged 17.4 inches long in 1947 and 15.8 inches long in 1951. Nevertheless, it appears that the growth trends of lampreys in the Great Lakes, in Lake Huron, and in laboratory aquariums are comparable.

The lampreys listed by Applegate (1950) were longer at the start of their parasitic phase than the ones which made the lake- and laboratory-incurred wounds studied in 1950 through 1952, but the differences in monthly increments of mean growth in the three sets of data in table 17 were small (0.2 to 1.8 inches). By the seventh month of parasitic life, the three groups of lampreys had at least doubled their lengths. Applegate's last measurement for the Great Lakes lampreys was 17.3 inches in the ninth month; at the same stage, the lengths-by-conversion of lampreys in Lake Huron and in the laboratory were 18. 5 and 16.3 inches. The parasites seem to grow until the eleventh month, at which time the lampreys in the lake (20.3 inches) averaged 2.5 inches longer than those held in the aquariums (17.8 inches).

TABLE 17.—*Mean lengths of sea lampreys from the Great Lakes measured by Applegate (1950) during calendar months of 1948, and average lengths-by-conversion of sea lampreys in Lake Huron and aquariums during corresponding calendar months of 1950 through 1952*

Month	Mean lengths of sea lampreys		
	In Great Lakes [1]	In Lake Huron [2]	In aquariums [2]
	Inches	*Inches*	*Inches*
April	7.5	6.4	6.7
May	8.1	7.6	7.0
June	8.2	7.6	7.6
July	10.0	7.8	8.0
August	12.6	---------	11.4
September	13.6	12.8	12.1
October	16.0	13.6	13.7
November	16.7	17.0	16.1
December	17.3	18.5	16.3
January	---------	19.3	16.4
February	---------	20.3	17.8
March	---------	19.8	16.3
April	---------	17.7	16.0
May	---------	17.1	16.6
June	---------	14.8	15.3
July	---------	13.2	---------

[1] Applegate (1950, p. 175).
[2] Mean lengths obtained by conversion from average oral-disk diameters (table 4).

Thereafter, the mean lengths of lampreys in the three groups of data decreased and the final average lengths were smaller than those for the ninth month.

Wound-hole dimensions.—The wound hole which lies within the oral-disk mark on a fish represents the actual penetration point into the tissues of the host. The diameter and depth of the wound hole were measured on lake and laboratory fishes (tables 15 and 16). These measurements do not necessarily have a clear-cut relation to the sizes of the lampreys that made the wounds, since the area and depth of a wound hole depend also on the duration of the attack, the amount of rasping by the tongue, the extent of tissue lysis caused by the action of the buccal-gland secretion, the location of the attack on the fish, and the extent of movement by the lamprey from the original site.

The smallest wound holes on fish from the lake and aquariums were made by recently transformed lampreys during the first month (April) of feeding; the mean diameter of holes was 5.0 millimeters on lake fish and 4.2 millimeters on aquarium hosts. The greatest mean diameter occurred on fish from the lake in the ninth month (December) (16.5 millimeters) and on fish in aquariums in the eleventh month (February) (11.4 millimeters).

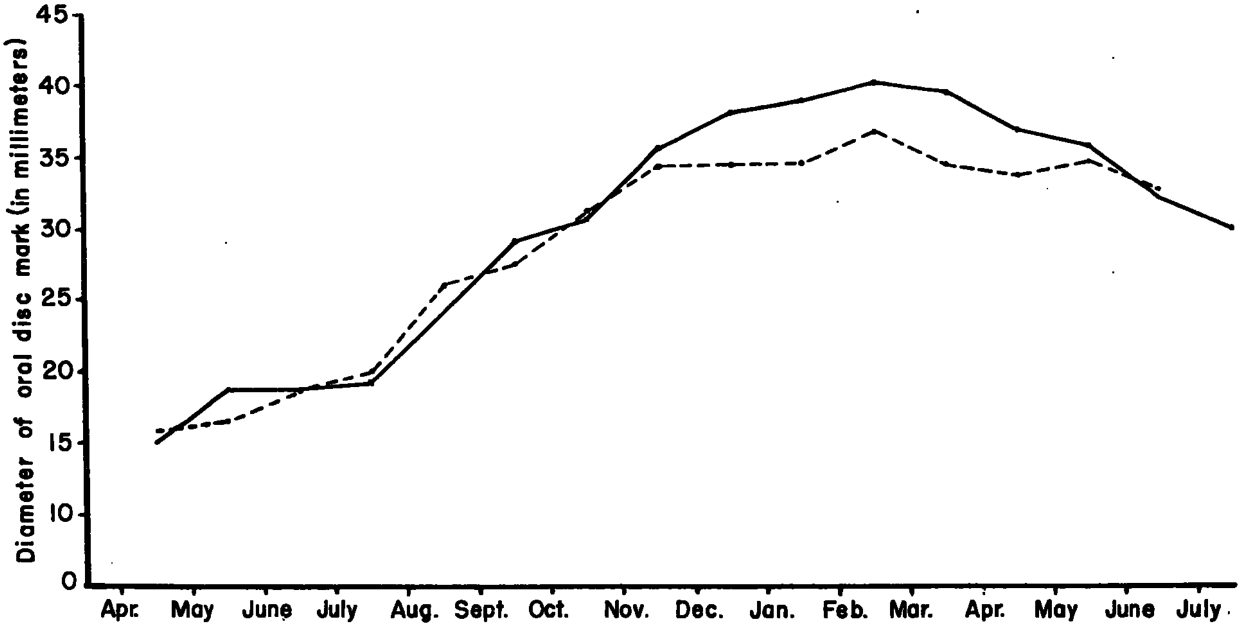

FIGURE 15.—Curves showing seasonal changes, 1950–52, in the mean diameter of oral-disk marks on fishes that bore sea-lamprey wounds. Solid line represents 832 measurements of marks on 18 species of host fish attacked in Lake Huron, broken line represents 1,630 oral-disk marks on 11 species of fish in aquariums.

The mean diameters of holes in both groups of hosts then decreased as the lampreys in the lake and aquariums approached sexual maturity and death.

The mean depths of wound holes listed in tables 15 and 16 for lake and laboratory fishes include only those wounds in which accurate measurements of depths could be made. Many wounds were observed which penetrated the body wall and extended into the viscera of hosts. No depths could be recorded for such penetrations, but they undoubtedly exceeded the depths measured in other wounds. The mean depths expressed for the holes in fishes from lake and laboratory are therefore smaller than they should be. The holes on lake-incurred wounds ranged from 1 to 15 millimeters in depth, with a maximum mean of 5.0 millimeters recorded in the twelfth month (March) of the lampreys' parasitic phase. The range of wound depths on fish in aquariums was 1 to 14 millimeters, with a maximum average depth of 5.1 millimeters recorded in the tenth month (January).

Significance of wound dimensions.—The dimensions of sea-lamprey wounds are not reliable criteria for evaluating the deadliness of attacks on host fishes. In general, wounds of small dimensions made by newly transformed feeders have the same mortal consequences for their hosts as the more extensive wounds made by large lampreys.

One of the largest fatal sea-lamprey wounds examined was on a white sucker, 12.0 inches long and 340 grams in weight, captured in Lake Huron. The injury was new and located on the right side of the fish, slightly below the lateral line in region III. The diameter of the distinct oral-disk mark was 50 millimeters, which indicated that the length of the attacker exceeded 23 inches. The wound hole had a diameter of 42 millimeters and extended deep into the body cavity. Portions of many myomeres were missing and the viscera were exposed. The margins of the hole on skin and muscle were smoothly chiseled as the result of lysis and suction as well as erosion by the tongue.

Among the smallest wounds seen was one created in a laboratory aquarium by a 5.3-inch sea lamprey on a white sucker, 6.6 inches in length and 40 grams in weight. The parasite remained attached to the host for 24 hours in region II. The diameter of the oral-disk mark was 13 millimeters and the wound hole was 2 millimeters in diameter and 1 millimeter deep.

Pathology of Sea-Lamprey Injury

Destruction of tissue and organs

Sea-lamprey wounds, either complete or incomplete, always entail injuries to the host fishes. The extent of damage to the tissues or organs depends on the size of the attacking lamprey, the duration and intensity of its attack, the size of the host fish, and the site of the attachment. The effects of damage were indicated by Surface (1898) who stated that the injured fish do not always die, but in every case they are seriously weakened and reduced in flesh, in blood, and in their ability to reproduce.

Integument.—The skin of the prey fish, with its protective coverings of mucus and usually of scales, is always affected in attacks by sea lampreys. Incomplete attachments involve interruptions in the mucous coat and scales, and the skin may be scored, even though unbroken. Where feeding by the lampreys takes place, the skin is eroded away. The extent of the skin disruption varies from a spot 1 millimeter in diameter to patches as long as 75 millimeters in cases where the parasite progressively moved from the original site.

The injury to, or the destruction of, the integument at the point of attachment renders the host fishes susceptible to various types of infection or disturbs the osmotic balance between exposed tissues and the lake water. The fungi *Saprolegnia parasitica* and *Leptomitus lacteus* were observed as secondary invaders of wounds. Their effects are described later in this paper (p. 288).

A waterlogged condition was noted frequently in white suckers and at times in trout species in the laboratory aquariums. The suckers bearing open wounds from which the lampreys had recently departed gained as much as 100 grams in weight in the hours or few days before death. The increase in weight was attributed to an influx of water into the tissues through the site of attack. Pincher (1948) reported that damage to the waterproof covering of scales and slime of a fish is followed by serious trouble. A fresh-water fish becomes waterlogged and dies when water streams into the body faster than it can be excreted.

The greatest increase in weight due to waterlogging was recorded in a female white sucker, 13.8 inches in length, which weighed 527 grams when first placed in a laboratory aquarium on August 31, 1951. The fish suffered three lamprey attacks almost immediately. The diameters of the holes in the flesh were 6 (region IV), 5 (region III), and 6 (region I) millimeters. The lampreys remained on the wounds 47, 48, and 31 hours, respectively. Immediately after the death of the fish on September 4, 1951, after less than 5 full days in the tank, its weight was 630 grams, a gain of 103 grams or nearly 20 percent of the original body weight.

A typical case of waterlogging in trout was noted in a female brook trout, 10.8 inches long, which weighed 192 grams when placed in the aquarium. The fish was attacked on region II, starting January 11, 1951, for 28.5 hours. A hole 6 millimeters in diameter and 6 millimeters deep was cut into the dorsal muscles by a sea lamprey 16.1 inches long. The dying trout weighed 208 grams a few hours after the lamprey left the wound. The fish died slightly less than 48 hours after the detachment. The weight was 223 grams immediately after death, a gain of 31 grams or about 16 percent.

Muscular tissue.—The skeletal muscles were often penetrated and damaged to a considerable extent by the rasping tongue and the lysis-producing secretions of the lampreys (fig. 16). Wounds located near the pectoral fins at times involved injuries to the fin musculature, resulting in impairment of action in the appendage thus afflicted. The greatest amount of tissue, other than blood, ingested by the lampreys was skeletal muscle.

Connective tissue and cartilage.—The connective tissues lying beneath the skin and between the segments of the body muscles suffered damages in the wounding process. Cartilages in the head and in the paired fins were also destroyed on occasion. Complete wounds were observed on the "lips" of white suckers in which the tough tissue and cartilage had been efficiently cut, disrupted, or dissolved.

Vascular system.—The capillaries in areas under lamprey attack were destroyed within the confines of the wound. Veins and small arteries in certain organs, such as the eyes and liver, were often severed during feeding attachments involving these parts. Some wounds continued to hemorrhage for various intervals of time, usually short, after the lampreys left the fishes.

Blood and lymph.—Blood and lymph are pumped from the wounds on fishes and ingested by the sea lampreys as food. Studies of the blood remaining in host fishes after attacks revealed, in some instances, that the erythrocytes had been altered, perhaps by lamphredin which entered the ruptured blood vessels. The red cells were distorted into odd shapes, suggestive of the first stages of hemolysis, and the blood contained much unidentified debris. The white cells, generally abundant during and after attacks, seemed resistant to adverse effects. A detailed account of studies on the blood of host fishes is given on page 284.

Gills.—A lamprey wound was occasionally located partly under the operculum; in others the operculum had been penetrated. In some such cases, the gill filaments were torn extensively on one or more gill arches. The irritation in so vital an area usually evoked a rapid and copious secretion of mucus in the gill chamber, with the result that the fish then suffered a pneumonialike condition, which possibly contributed to death.

Lateral-line system.—Pincher (1948) mentioned that the lateral-line system functions mainly in the perception of sound waves of low frequency. The canals, sense organs, and nerves included in the system are at times interrupted and destroyed in wounds. The degree to which the hearing and balance of the fish is disturbed by such an attack is difficult to evaluate.

Nerve tissue.—No sea-lamprey wounds were observed that penetrated into the brain of a host fish. Injuries were recorded, however, that in-

FIGURE 16.—Damage created on a rainbow trout by a sea-lamprey attack of short duration. The trout died after 5 hours, but the lamprey remained an additional 6 hours on the wound. The actual hole was 26 millimeters in diameter and 6 millimeters deep. Several neural processes of the vertebrae were exposed and damaged.

volved parts of main trunks or major rami or one or more of all cranial nerves except the auditory. Deep penetrations located on the eyes, over the nasal apertures, on the ventral side of the head, in the gill area, or extending into the viscera certainly affected many branches of both cranial and spinal nerves. Severe attacks sometimes appeared to cause a degree of paralysis in the host fishes. Some of these attacks were quickly lethal, possibly owing in part to nerve damage.

Bone tissue.—Bones of a host fish were ineffective as barriers to penetrations by sea lampreys. Among the wounds examined on fish from Lake Huron and in laboratory aquariums, were some that involved injury to, including complete severance of, one or more of the following bones of the head: Premaxillary, maxillary, mandible, nasal, lacrimal, circumorbital, frontal, parietal, supraoccipital, opercular, supracleithrum, cleithrum, gular, and the branchiostegals. On the body proper, bones damaged by lampreys included neural processes of vertebrae (fig. 16), ribs, and bony rays of the pectoral, pelvic, dorsal, anal, and caudal fins.

An example of severe bone destruction was seen on a female white sucker 17.7 inches in length and 992 grams in weight. The fish, captured in Duncan Bay in Lake Huron on March 11, 1952, was close to death due to a pair of new and complete wounds which probably were inflicted in the trap net. The most damage was over the left eye where the well-defined disk mark measuring 46 millimeters across indicated that the attachment was made by a lamprey approximately 22 inches long. The wound hole, which included the eye, was 19 millimeters across the center, or at least 8 millimeters greater than the normal socket diameter on a fish of this size. The eyeball was missing, the circumorbital bone was largely destroyed, and parts of the lacrimal and frontal bones near the eye were naked and their margins eroded. The socket was full of newly coagulated blood.

The second wound on this fish was on the base of the caudal fin on the left side. An oral-disk mark 39 millimeters in diameter indicated a sea lamprey about 19 inches long. The wound hole was 5 millimeters across the center and 3 millimeters deep. Two fin rays were severed or broken. This attachment appeared to have been of shorter duration than the one over the eye.

Eyes.—Attachments over the eyes of the fishes by sea lampreys invariably resulted in the destruction of vision in those organs, and usually in the death of the hosts. Damage varied from mere excoriation of the conjunctiva and cornea to the complete removal of the eyeball. Wounds of intermediate severity penetrated the eyeballs, tapping both aqueous and vitreous humors, in addition to the richly supplied blood vessels that overlie the ventral part of the retina. The lens was usually missing after a puncture of the eyeball. The optic nerve, blood vessels, and eye muscles attached to the ball were often severed or otherwise damaged.

Fish do not always succumb immediately or directly from wounds over the eyes. Many grievous eye injuries from recent lamprey attacks were observed, but only one healed eye wound occurred among the total of 264 healing or healed injuries examined on fishes from Lake Huron. It is likely that the weakened condition and impaired vision of the host fish make it easy prey for other enemies or to disease even if it does survive the attack.

Nasal apertures.—Deep and effective sea-lamprey wounds were observed which included nostrils of fishes. The blind passages and the olfactory sense cells were often destroyed, and the hemorrhage attending such attachments was usually profuse. Very few healed wounds on this area of the head were seen.

Intestine.—The intestines were at times damaged in attacks that penetrated the body wall of host fishes. The digestive tube was punctured, or severed completely, which allowed the intestinal contents to escape into the body cavity or to the exterior through the wound hole. Many of the live hosts bearing such injuries were bloated to some degree and the materials in their body cavities were foul, sometimes with attendant peritonitis.

Several white suckers and yellow perch taken in Lake Huron exhibited body-wall perforations in advanced stages of healing. The gonads or intestine in some fish had adhered to the body wall. Suction pressure exerted by the lamprey apparently drew parts of the organs close to the excavation, and during the healing the intestinal or gonad tissues became firmly bound to the body wall by the scar tissue.

The only case of a healed fistula was found in a yellow perch which displayed unusual recovery from a severe lamprey wound. The 10.2-inch fish, a spawned-out female in good condition, was captured in Hammond Bay on July 3, 1951. Its injury was located just posterior to the left ventral fin and was almost fully healed about its margins. The oral-disk mark was 30 millimeters in diameter, and the hole which penetrated the body wall was 7 millimeters in diameter. The intestine had been severed at a point 158 millimeters of gut length posterior to the pylorus, and the ruptured end had been pulled through the wound hole. During the process of healing, the margin of the wound hole and the wall of the protruding intestine became firmly joined. Any portion of the intestine exterior to this point sloughed off. The lumen of the tube at the point of adhesion with the body wall was open and was apparently a functional anal opening. There was no trace in the coelom of the posterior part of the ruptured organ. The vent was nearly blocked off by adhesions. The stomach and short pieces of intestine contained no food at all but the good condition of the fish attested its ability to handle food.

Leach (1951, p. 215) reported a similar case of "accidental and unintentional colostomy" performed by a sea lamprey on a pike in Cayuga Lake, N. Y. The wound served as the new outlet of the perforated intestine, and the original anus appeared to be nonfunctional.

The pyloric caeca.—The pyloric appendages in trout species and yellow perch were extensively lacerated in some body-cavity penetrations. Doubtless the production of trypsin by the caeca was reduced by such wounds. Whether leakage of this enzyme about the injury had a harmful effect is not known.

Liver.—The vital functions of the liver were reduced in the several fish in which a lobe of the organ was damaged by sea-lamprey attacks. The more serious effects of injuries to the liver are perhaps the attendant hemorrhage and reduction in the victim's hemopoietic, excretory, and digestive efficiency.

Pancreas.—The pancreas, an organ important to a fish in the manufacture of digestive enzymes and the hormone insulin, was badly lacerated in a few perch and rainbow trout whose body walls were pierced by sea lampreys.

Spleen.—Several lamprey attacks resulted in direct erosion of the spleen of rainbow trout and yellow perch. Aside from the hemorrhage, there was a possible reduction of the host's hemopoietic and blood-storage capacities.

Airbladder.—One yellow perch taken in a trap net in Lake Huron had suffered a deep lamprey wound which punctured the airbladder. The direct effects of the deflation of this organ are difficult to assess. The primary function of the bladder in the physoclistous perch is presumably hydrostatic, although Pincher (1948) reported that an accessory respiratory function has been both claimed and denied for it in this species.

Gonads.—Ova of coregonid fishes have been observed in the intestines of parasitic sea lampreys. The eggs were probably ingested when the body walls and gonads of the fishes were perforated by the attackers. In the study of lake- and laboratory-incurred lamprey wounds, damages to ovaries and testes were observed in rainbow trout, yellow perch, and white suckers.

Anus.—Some severe, open wounds were observed in the anal area of host fishes, but no healed ones involving this site were found on hosts captured in Lake Huron. The destruction of the anus could be fatal to the victim.

Significance of injuries to tissue and organs.—The rasping tongue, the lamphredin, and the suction pressure employed by the sea lamprey to create feeding attachments on fish cause injuries to many tissues and organs with consequent impairment of functions in the hosts. Fish that do not succumb directly to the effects of their lamprey wounds are more subject to the lethal or detrimental influences of fungi, other parasites, predators, and the possible malfunction of their own vital processes. The extent and nature of injuries received in the attacks often render surviving hosts unfit for commercial marketing.

Effect of Lamprey Injury on Blood of Prey

Of the tissues affected by sea-lamprey wounds on host fishes, the blood was usually the most drastically altered. The severe hemorrhage attending the attacks of this largely sanguivorous parasite brings death to most of the victims. The importance of fish blood in the diet of sea lampreys indicated the necessity for some hematological observations on prey fishes.

The blood of normal fishes

The blood of a bony fish, like that of other vertebrates, is a circulating tissue. The major constituents are the plasma, a fluid combination of water, proteins, and inorganic salts; erythrocytes; and leucocytes. The erythrocytes of fishes are flattened, oval, nucleated cells whose cytoplasm contains hemoglobin. The leucocytes include agranulocytes and granulocytes, both of which show varying degrees of ameboid motion.

Blood plasma is contributed by the liver, and the blood cells develop in the reticular connective tissues of the blood-forming organs. In fishes, the spleen is the fundamental blood-cell contributor, while in some species the development of the leucocytes, especially the granulocytes, is held to take place in the mesonephros (Cole 1941).

Fishes, in common with all vertebrates, possess hemoglobin in the blood for the transport of oxygen. The capacity of fish blood for carrying oxygen depends on the individual specimen, on the species, and on some environmental conditions. For example, the load capacity is reduced by increases in water temperature or in the concentration of dissolved carbon dioxide.

Bony fishes have a small supply of blood. In spite of the efficiency of their circulatory system, the low volume of blood places them at a disadvantage when attacked by parasitic lampreys. Prosser et al. (1950) noted that teleosts have the least amount of blood of any of the vertebrate groups. The quantity was listed as 1.5 to 3 percent of the body weight as compared with 7 to 10 percent in mammals. The volume of lymph in fishes is not known.

The respiratory exchange between fishes and their environment takes place in the gills. Considering their respiratory area, the gills of teleosts have been regarded as surpassing lungs in efficiency (Prosser et al. 1950).

White suckers.—The sea-lamprey feeding experiments at the Hammond Bay Fishery Laboratory afforded an opportunity to study the blood levels in lamprey-wounded prey fishes. The determination of blood values in normal specimens of the same species provided the comparative material for evaluation of the effects of lamprey attacks.

The white sucker was the species best suited for the accumulation of hematological data in quantity, because of its local availability, its favorable average size, and its physiological characteristics. Furthermore, the sucker is a typical host fish for sea lampreys in Lake Huron and the properties of its respiratory pigments are comparable to those of the Salmonidae. Black (1940) pointed out that fish blood with a high sensitivity to carbon dioxide and low affinity for oxygen was associated with cold-water habit. In Prosser et al. (1950), the sucker was grouped with the brook, brown, and rainbow trouts with respect to its sensitivity to temperature and to carbon-dioxide tension. The effects of temperature and carbon dioxide on the availability of oxygen for these species is certainly a factor in their distribution. They characteristically seek cold, highly oxygenated waters, although the suckers have a wider distribution in warmer waters than do trout. In view of the similarity of the blood in suckers and salmonids the data given here on the former may be held descriptive, in a general way at least, of conditions in trouts and coregonids.

Twenty-three white suckers captured in good condition in Lake Huron were anesthetized and sampled for their total blood volumes by the caudal-severance technique.[4] The amount of blood in them averaged 1.5 percent of the total body weight (table 18). On the basis of a conclusion by Gage (1928) it appears that the blood volume of an average-sized white sucker would hardly satiate an active and hungry lamprey and still leave enough to sustain life in the host fish. He determined that a full-grown lake lamprey (12 to 13 inches long) required about 25 milliliters of fish blood to fill its intestine.

To obtain information on white-cell counts, blood samples were obtained from 119 white suckers by a cardiac-puncture method described by McCay (1929) and Field, Elvehjem, and Juday (1943). The white counts computed on a hemocytometer averaged 3,869 cells per milliliter of whole blood and ranged from 380 to 12,000 cells per milliliter (table 21).

The number of erythrocytes per milliliter of blood in white suckers was computed from the 119 specimens from which the white-cell counts were made. The mean count for these fish was 1,159,256 red cells per milliliter (table 20). Most of the 119 counts were made during the months of February, March, and April, 1951, when low

[4] Severance of the tail in nonanesthetized fish produced a state of shock that inhibited bleeding.

TABLE 18.—*Mean blood volumes in 23 white suckers from Lake Huron*

Weight range of fish (grams)	Number of fish	Mean length	Mean weight	Mean blood volume	Ratio, weight of blood [1] to total weight
		Inches	*Grams*	*Milliliters*	*Percent*
200-299	9	11.9	270.3	4.1	1.6
300-399	7	13.6	328.5	4.9	1.6
500-599	2	14.6	521.0	6.4	1.3
600-699	1	14.8	607.0	8.7	1.5
800-899	1	17.1	866.0	12.5	1.5
900-999	3	17.9	941.3	11.8	1.3

[1] Specific gravity of the blood estimated at 1.05 (average for human blood is 1.055).

water temperatures (34° to 41° F.) prevailed in the lake and in the laboratory holding facilities.

Katz (1950) reported an apparent correlation between the increase and decrease in the average blood counts in silver salmon, *Oncorhyncus kisutch*, with an increase and decrease in water temperatures. He demonstrated that the erythrocyte counts in silver salmon were higher in summer than in the spring and autumn, and suggested the possibility that the increase of water temperature in summer may have lowered the oxygen content of the water enough to cause a slight, compensatory increase in erythrocytes. On the other hand, the work of Hart (1943) suggested that the concentration of carbon dioxide may be a major factor in the blood count of white suckers. Prosser et al. (1950) further observed that in the presence of very small amounts of dissolved carbon dioxide, the oxygen-carrying capacity of sucker blood is reduced, causing the fish to seek waters with lower carbon-dioxide concentrations or with a greater supply of dissolved oxygen.

The suckers upon which the blood counts were made were held in the laboratory tanks and aquariums. Periodic chemical analyses of water and continuous temperature records demonstrated oxygen concentrations approaching saturations at all times. The low temperatures which prevailed during the period when the counts were made, however, may have tended to depress the red-cell counts. Nevertheless, the holding facilities registered carbon-dioxide concentrations which, while very low, were invariably 1 to 2 p. p. m. higher than in Lake Huron. It is reasonable to suppose that lake fish introduced into the tanks would effect a compensatory increase in their erythrocytes to offset the influence of the carbon dioxide. In fact, increases up to 15 percent in erythrocytes were observed in white suckers after 4 days in captivity in the tanks. After 8 days, the erythrocyte counts on this species declined but still continued to average slightly higher than counts made on blood samples from fish freshly caught in Lake Huron.

It appears reasonable to conclude that the red-cell determinations as made in the blood of white suckers are representative of normal levels. Influences which tend to affect the numbers of erythrocytes were in force simultaneously and were to a degree compensating.

The hemoglobin content in the red cells of 119 white suckers was determined by an acid-hematin method, in which a hemoglobinometer was used as described in Todd and Sanford (1948). The mean value was 8.24 grams of hemoglobin per 100 milliliters of normal fish blood, or about half the amount contained in the blood of humans.

Observations on the clotting time of the blood of 119 white suckers confirmed the views of Gage and Gage (1927) and Smith, Lewis, and Kaplan (1952) that fish blood normally coagulates rapidly outside the blood vessels of the animal. The blood clotted in less than 1 minute in capillary tubes; or, when several drops of blood were placed on greased glass slides, solid clots were formed in about 3 minutes at room temperatures of 68° to 70° F.

Trout.—Only a few values on the normal blood of trout were obtained (table 19), because the fish were usually too small to make possible satisfactory sampling by cardiac puncture.

Three brown trout had mean counts of 1,379,167 red cells and 8,120 white cells per milliliter, and averaged 8.0 grams of hemoglobin per 100 milliliters of blood. Wunder (1936) listed average counts of 1,140,000 red cells and 25,000 white cells per milliliter for this species.

Two rainbow trout had mean values of 1,107,500 red cells and 7,980 white cells per milliliter, and an average of 7.5 grams of hemoglobin per 100 milliliters of blood. These figures were lower than those found by Marsh and Gorham (1906) who reported that 11 domestic rainbow trout sampled by them had an average of 1,487,000 red cells per milliliter whereas hemoglobin content in 19 individuals averaged about 9.0 grams per 100 milliliters of whole blood.

No determinations were made on brook trout, but Marsh and Gorham (1906) listed an average red-cell count of about a million and a hemoglobin content of slightly less than 8.0 grams per 100 milliliters of normal blood (based on 35 individuals). Field, Elvehjem, and Juday (1943) found means of 1,013,000 erythrocytes and 3,910 leucocytes and 8.5 grams of hemoglobin. Little difference was noted by these workers in the red-cell levels of domestic and of wild trout.

TABLE 19.—*Blood levels in healthy wild brown trout and in hatchery-reared rainbow trout*

Length (inches)	Weight (grams)	Blood cell counts (per milliliter)		Hemoglobin (grams per 100 milliliters)
		Red	White	
Brown trout				
10.9	220	1,437,500	3,180	9.0
12.8	311	1,340,000	14,800	8.0
15.2	536	1,360,000	6,380	7.0
	----------	1,379,167	8,120	8.0
Rainbow trout				
9.5	114	1,002,500	7,960	7.5
10.4	152	1,212,500	8,000	----------
	----------	1,107,500	7,980	7.5

The blood of wounded fishes

White suckers.—The hematological data treated in this section are only from fishes that were dying as a direct result of attacks by sea lampreys in aquariums. The blood of each wounded fish was sampled near death by cardiac puncture. Certain obvious symptoms made it possible, with experience, to identify dying victims. Among these symptoms were the slowed and shallow respiratory movements, the pale pink or whitish color of the gill lamellae, the loss of equilibrium and departure from customary level or position in the tanks, the lack of response to visual and tactile stimuli, and the paled color of the body.

Many of these fishes that suffered lingering deaths demonstrated a gradual progression of body rigor from the caudal region towards the head. The tetany was due possibly to accumulated metabolic wastes, and the affected regions of the fish became stiff and immobile and at times contorted. Death invariably occurred before the anterior third of the body became thus affected. Interestingly, the muscles relaxed their tension soon after the fishes died. So far as I could determine, this reaction is without parallel in humans or other mammals subjected to fatal hemorrhage.

The mean red-cell count in 119 mortally wounded white suckers [5] (table 20) was 189,705 per milliliter of blood. This figure represents a net loss of 83.6 percent from the mean of 1,159,256 red cells per milliliter in uninjured fish of the same species. Curves showing the distribution of red-cell counts in the wounded and in the healthy white suckers are presented in figure 17. The gross loss of erythrocytes is the quantity of these cells which pass from the fish's blood stream during an attack by a lamprey; therefore the net-loss value as given represents a smaller portion than that actually consumed by the parasite. Hemopoiesis makes an unknown contribution but obviously cannot keep up with the rate of loss.

[5] The identity of number (119) in the groups examined to obtain normal and pathological blood data was accidental; only 6 fish were common to the groups. Data on these 6 suckers are discussed in the next section.

TABLE 20.—*Number of erythrocytes per milliliter in blood specimens drawn from hearts of 119 healthy white suckers and 119 white suckers fatally wounded by sea lampreys*

Number of erythrocytes	Number of fish	
	Healthy	Wounded
0–99,999	----------	37
100,000–199,999	----------	36
200,000–299,999	----------	20
300,000–399,999	----------	17
400,000–499,999	----------	6
500,000–599,999	----------	3
600,000–699,999	----------	----------
700,000–799,999	3	----------
800,000–899,999	7	----------
900,000–999,999	8	----------
1,000,000–1,099,999	17	----------
1,100,000–1,199,999	33	----------
1,200,000–1,299,999	30	----------
1,300,000–1,399,999	13	----------
1,400,000–1,499,999	6	----------
1,500,000–1,599,999	2	----------
Total	119	119

Average count for healthy white suckers, 1,159,256.
Average count for fatally wounded white suckers, 189,705.

The lowest hemoglobin level that could be read on the hemoglobinometer was 3.75 grams per 100 milliliters of whole blood. The acid-hematin content of the blood tested in mortally wounded suckers was invariably too low to register on the scale of the instrument. Consequently, the hemoglobin values were listed as "less than 3.75" grams per 100 milliliters, which represents a reduction of at least 54 percent in the oxygen-carrying capacity of the blood. The actual reduction of hemoglobin in the blood of the suckers is estimated to range as low as 20 percent of normal.

The numbers of white cells were counted in the blood samples from 115 suckers of this series. The average per milliliter of blood was 8,514 cells or 2.2 times the normal mean of 3,869 leucocytes (table 21); but in many dying individuals the white-cell counts were below normal. Curves showing the distribution of counts in the 115 dying white suckers and in the 119 healthy fish are presented in figure 18. The gross increase of white cells in the blood as a defensive mechanism apparently exceeds the loss of cells due to hemorrhage. It was concluded that, in general, the suckers were able to manufacture leucocytes faster than the cells were removed by the lampreys.

The blood samples from the hearts of wounded suckers clotted more rapidly than normal blood. A solid clot usually formed on a glass slide in 1 minute at room temperature. Frequently it was impossible to obtain cell counts on dying fish owing to the extremely rapid coagulation of the blood specimens. Even blood samples that were very pale and of low viscosity retained the ability to clot within a few minutes.

The ability of the blood in a wounded prey fish to coagulate rapidly is a protective response designed to arrest further hemorrhage. This defense mechanism is probably provoked by reactions in the liver which produce fibrinogen and/or by thrombokinase picked up in the blood stream at the site of tissue damage. Apparently the positive actions of these materials overcame any opposite influence of lamphredin which may have diffused away from the wound site; alternatively, this anticoagulant does not leave the lamprey's point of penetration in any appreciable quantity.

No measurements were made on the volumes of residual blood in dying suckers. Many dissections were performed on specimens that were dying or dead as the result of sea-lamprey attacks and the volume of blood was always much reduced. Rapidly fatal attacks on suckers usually resulted in the greatest reduction of the fluid in the vascular

TABLE 21.—*Number of white cells per milliliter in blood specimens drawn from hearts of 119 healthy white suckers and 115 white suckers fatally wounded by sea lampreys*

Number of white cells	Number of fish	
	Healthy	Wounded
0–1,999	45	8
2,000–3,999	35	16
4,000–5,999	12	22
6,000–7,999	11	15
8,000–9,999	8	11
10,000–11,999	5	14
12,000–13,999	3	9
14,000–15,999	----------	7
16,000–17,999	----------	6
18,000–19,999	----------	1
20,000–21,999	----------	2
22,000–23,999	----------	1
24,000–25,999	----------	3
Total	119	115

Average count for healthy white suckers, 3,869.
Average count for mortally wounded white suckers, 8,514.

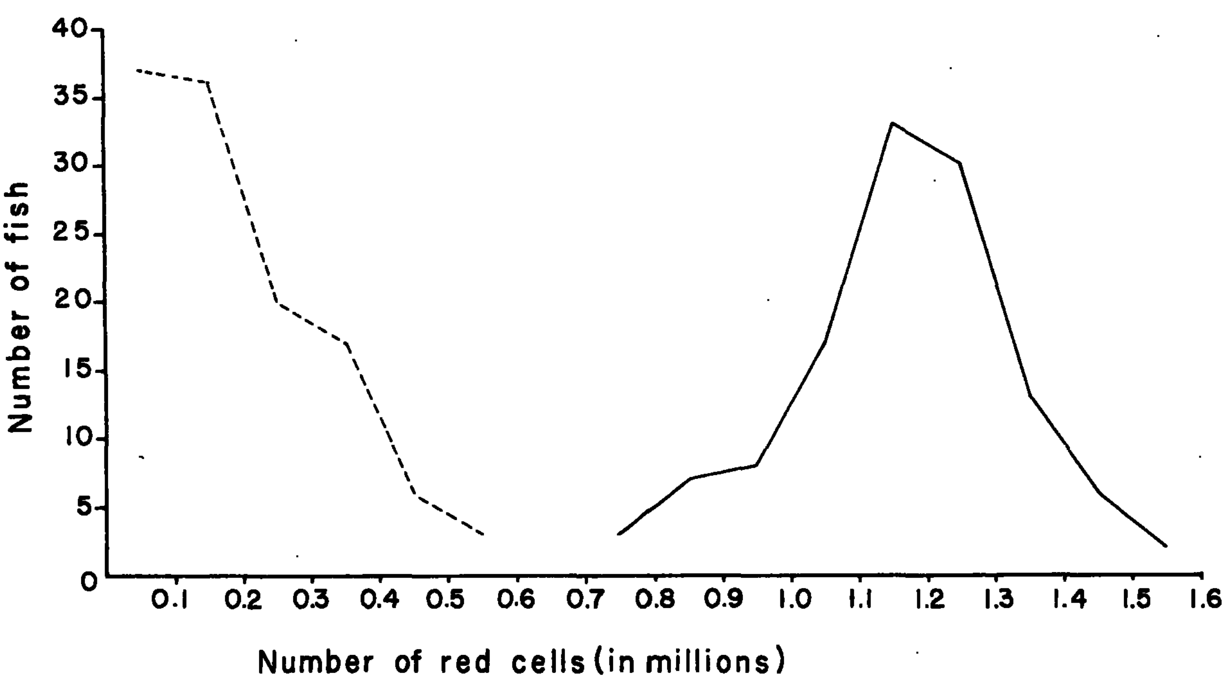

FIGURE 17.—Distribution of red-cell counts in 119 white suckers that were dying as a result of sea-lamprey wounds (broken line) and in 119 healthy white suckers (solid line).

system. It was sometimes impossible to obtain blood in sufficient quantity from these fish to perform hematological tests. Those fish that suffered lingering deaths from attachments of longer duration more often contained larger volumes of very dilute blood, closely resembling water in color and viscosity.

Changes in individual white suckers.—It was possible to obtain both preattack and postattack samples of blood from 6 white suckers (table 22). The data on the red cells, white cells, and hemoglobin in the blood of these fish do not differ greatly from the values for the same characters in blood samples taken from the 119 normal and 119 mortally wounded white suckers previously discussed. There were average reductions of 81.3 percent in red-cell counts and 52 percent in hemoglobin contents between the preattack and postattack blood samples from the 6 white suckers as compared with mean decreases of 83.6 percent in red-cell counts and 54 percent in homoglobin contents between the blood samples drawn from 119 normal and 119 mortally wounded white suckers. It was only after repeated attempts failed to secure preattack and postattack blood samples on many individual fish, that average values for the blood of normal white suckers were established for comparison with levels measured in mortally wounded fish.

The cardiac puncture employed to collect blood specimens apparently was not injurious, and no effects could be detected in the fish used as controls and hosts that would alter significantly the values of subsequent samples. White suckers were bled as many as three times at intervals of 1 to 4 days, with no mortalities. Field, Elvehjem, and Juday (1943) bled brook trout and carp as many as eight times with the same technique and experienced a total mortality of only 5 percent for repeated treatments.

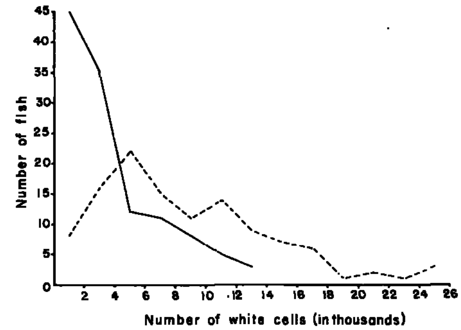

FIGURE 18.—Distribution of white-cell counts in 115 white suckers that were dying as a result of sea-lamprey wounds (broken line) and in 119 healthy white suckers (solid line).

Trout.—The blood values were recorded for 1 brown trout, 12 rainbow trout, and 3 brook trout which were dying as a result of sea-lamprey wounds incurred in the aquariums (table 23).

The brown trout had 76,457 red cells, which indicates a net loss of 94.5 percent from the mean of 1,379,167 cells listed (table 19) for healthy fish of the same species. The number of white cells was 58.1 percent less than the mean value for normal fish. The hemoglobin content had declined from a normal mean of 8.0 to less than 3.75 grams per 100 milliliters of blood, a loss of at least 53.1 percent.

Twelve dying rainbow trout had an average count of 165,167 erythrocytes, which is 85.1 percent less than the mean count of 1,107,500 in 2 healthy fish. White cells decreased 49.2 percent as indicated by a comparison of 4,052 cells in the wounded trout with the average of 7,980 leucocytes

TABLE 22.—*Preattack and postattack hematological data obtained from white suckers that were mortally wounded by sea lampreys in aquariums at the Hammond Bay Fishery Laboratory*

Length (inches)	Weight (grams)	Sex	Hours under attack	Red cell counts (per milliliter)		Percentage decrease of red cells	White cell counts (per milliliter)		Percentage change of white cells	Hemoglobin [1]		Percentage reduction of hemoglobin [3]
				Preattack	Postattack		Preattack	Postattack		Preattack	Postattack [2]	
12.6	330	M	54	1,100,000	192,500	82	2,640	7,900	199	8.0	<3.75	>53
13.0	380	M	11	1,287,500	207,500	84	7,640	5,200	−32	8.0	<3.75	>53
13.1	418	F	69	1,225,000	105,000	91	8,340	1,740	−79	8.0	<3.75	>53
13.3 [4]	357	F	11	822,500	365,000	56	7,100	1,960	−72	6.0	<3.75	>38
13.9	450	F	30	1,157,500	130,000	89	7,440	10,320	38	8.5	<3.75	>60
14.3	518	F	96	1,500,000	210,000	86	----------	----------	----------	9.0	<3.75	>58

[1] In grams per 100 milliliters.
[2] <3.75 indicates values less than lowest reading possible on the hemoglobinometer used.
[3] >indicates that the reduction of hemoglobin actually exceeds percentages listed.
[4] The attack on this fish was already in progress and thus the preattack levels listed are less than normal; the number of hours given refers to time after the preattack blood determinations.

in healthy rainbow trout. The hemoglobin in the blood was reduced by at least 90 percent.

The 3 blood samples obtained from mortally wounded brook trout had an average of 86,667 red cells, which represents a net loss of 91.4 percent from the mean count of 1,013,000 cells recorded by Field, Elvehjem, and Juday (1943). The average number of 2,030 white cells in the dying trout was 48.1 percent less than the mean of 3,910 leucocytes found by the same authors in healthy brook trout. The reduction of hemoglobin content in the host fish again exceeded 50 percent.

TABLE 23.—*Blood levels in wild brown trout, hatchery-reared rainbow trout, and wild brook trout fatally wounded by sea lampreys in aquariums at the Hammond Bay Fishery Laboratory*

Length (inches)	Weight (grams)	Blood cell counts (per milliliter)		Hemoglobin (grams per 100 milliliters) [1]
		Red	White	
Brown trout				
12.6	297	76,457	3,400	<3.75
Rainbow trout				
15.0	622	200,000	9,320	<3.75
10.0	158	400,000	4,220	<3.75
10.0	132	30,000	300	<3.75
10.6	174	52,000	1,440	<3.75
10.6	132	60,000	440	<3.75
12.0	260	397,500	6,020	<3.75
11.0	178	170,000	9,920	<3.75
9.2	114	50,000	2,120	<3.75
9.0	114	110,000	2,400	<3.75
9.4	124	67,500	10,000	<3.75
8.9	114	185,000	1,320	<3.75
9.8	122	260,000	1,120	<3.75
Average	----------	165,167	4,052	<3.75
Brook trout				
7.8	71	60,000	2,280	<3.75
6.5	42	170,000	----------	<3.75
5.9	27	30,000	1,780	<3.75
Average	----------	86,667	2,030	<3.75

[1] <3.75 indicates values less than lowest reading possible on the hemoglobinometer used.

Phillips (1947) demonstrated that under the stimulation of asphyxia, eastern brook trout increase the number of erythrocytes in their blood by 17.2 percent in 1 hour. This figure indicates a considerable hemopoietic potential which is possibly overcome or exhausted when a specimen suffers hemorrhage and is killed by a feeding sea lamprey. The gross loss of blood in the fish is presumably greater than a comparison of the normal and postattack counts of erythrocytes would show.

Significance of hematological tests.—Comparison of blood data obtained from examinations of healthy fish and those close to death from the effects of sea-lamprey attacks revealed profound differences. The numbers of erythrocytes, the hemoglobin content, and the total volumes of blood in prey fishes were often reduced to small fractions of their normal values. The deaths of many host fishes no doubt occur as direct results of the hemorrhages.

The lethal factors in extensive hemorrhage cannot be identified exactly for fish. The reduction of the oxygen-carrying capacity of the blood causes some degree of anoxia and accumulation of metabolic wastes in the tissues. The distribution of essential endocrine secretions via the blood may be greatly reduced. The decrease in blood volume is probably attended by a fall in arterial pressure, which according to Carlson and Johnson (1948) constitutes an immediate danger to life in humans during sudden and severe hemorrhage.

A condition akin to shock was observed in many fishes dying from lamprey-feeding attacks. The specimens were pale, largely immobile; respiratory movements were slow and weak. They were mostly powerless to perceive or respond to tactile, sonic, or visual stimuli. The hemorrhage also produced disruptions in other physiological mechanisms of the host fishes such as in the osmotic balance between the blood and tissues and probably in the function of the kidneys.

Although the white suckers, rainbow trout, brown trout, and brook trout included in the hematological study represent only a fraction of the fish killed by lamprey attacks in laboratory aquariums they were typical of the group, and hence the data are believed to be truly descriptive of the effects of lamprey predation. The mean values listed for the fishes at the point of death are considered the minimum levels. The critical blood levels, below which the fish are doomed, are undoubtedly higher. It is believed that the trout species and white suckers are in mortal danger when their counts of erythrocytes fall below 300,000 cells per milliliter during lamprey-induced hemorrhages.

The wounded white suckers and trout for which the mortal blood losses were determined are typical of the prey species for sea lampreys in the Great Lakes. The suckers were of average size for northern Lake Huron. They were shown to be susceptible to extensive and lethal hemorrhages caused by the attacks of sea lampreys of all parasitic-phase sizes.

The trout species used in the aquariums averaged smaller (table 8) than the suckers, and their blood supplies were frequently exhausted beyond critical levels in a short time. Many of the victims in the aquariums suffered multiple attachments which usually brought about quicker death. Attacks by more than one lamprey on a host fish in the lake are also common (fig. 19). Single wounds, however, may be equally deadly.

Secondary Infection of Sea-Lamprey Wounds

The fungi *Saprolegnia parasitica* and *Leptomitus lacteus* were the only common secondary invaders observed on sea-lamprey wounds on fishes. Both infectious species, representatives of the aquatic Phycomycetes, were found on wounded fishes in the aquariums and from Lake Huron.

Saprolegnia parasitica, well known as "fish mold", belongs to the order Saprolegniales.

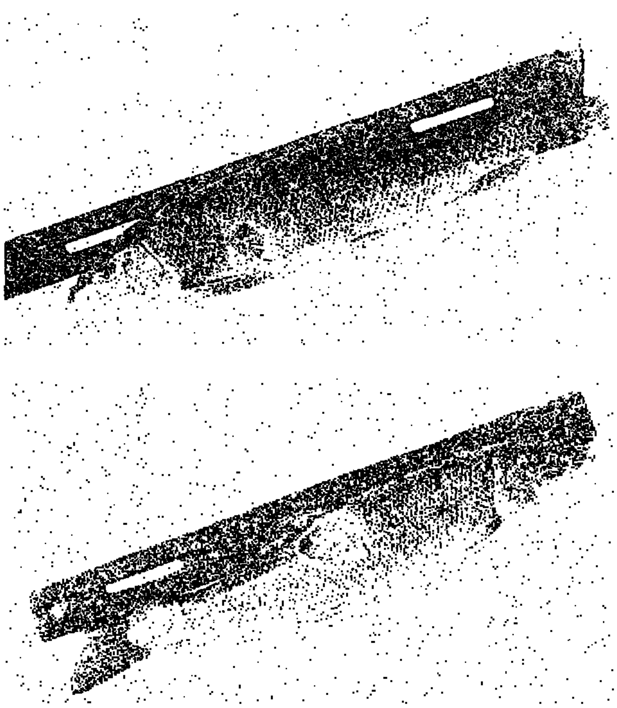

FIGURE 19.—Two complete sea-lamprey wounds on a single white sucker captured in Lake Huron, March 13, 1951. The specimen in both photographs was a male, 11.4 inches in length and 254 grams in weight. The fish was close to death as a result of the attacks. Top picture, wound on region III (note the exposed ribs); bottom picture, wound on region IV.

Sparrow (1943) listed the members of this order primarily as saprophytes of plant and animal debris in fresh water or damp soil; some species are parasitic on microscopic and macroscopic animals (fish, amphibia) and roots of higher plants. Allison (1950) reported that a heavy infection of *S. parasitica* may cause the death of the fish. When fish are injured, perhaps by external parasites, careless anglers, or spawning activity, the wounds provide openings for attack by bacteria and fungus. One zoöspore of the fungus is sufficient to initiate an extensive growth.

It was necessary on several occasions to arrest outbreaks of "fish mold" on the sea lampreys and host fishes in the laboratory aquariums. Solutions of malachite green-oxalate in 1:15,000 dilutions were used. The treatment proved selective for *Saprolegnia*, but any *Leptomitus* present on specimens in the tanks was unaffected.

Leptomitus lacteus, of the order Leptomitales, occurred more often than *Saprolegnia* on lamprey wounds on fish from Lake Huron and in the aquariums. The large, tough mats of gray-brown, foul, and odorous growth were found directly over the sites of lamprey attacks on the hosts.

Our first identification of *Leptomitus* was based on an infection observed on a white sucker, 11.1 inches long and weighing 233 grams, captured in Duncan Bay, Lake Huron, on January 16, 1951. This fish bore an open sea-lamprey wound on its right side in region III, near the insertion of the pectoral fin. During the lamprey's attack, the pectoral fin was pinned to the side of the fish by the sucking disk and was partially eroded away. The subsequent fungus infection over the wound area involved the fin; the growth adhered in part to the inserted portion and in part to the naked, eroded fin rays. Fin tissues beyond the limits of the original lamprey wound also appeared to be affected adversely by the secondary invader. The large growth of fungus was removed from the fish and sent to Dr. Frederick K. Sparrow, who identified it (personal communication) as—

> almost wholly *Leptomitus lacteus*. Occasional filaments of *Saprolegnia* mixed in, but 99.44 percent is the *L. lacteus*. It is rather unusual in my experience to find *Leptomitus* so dominant on this type of material. It is entirely possible that the *Saprolegnia* initiated the action after the wounding, but that conditions favored the growth of the other fungus. From what we know of the physiology of *Leptomitus*, I would suspect that this fish had lain in quiet water under conditions of very little dissolved oxygen.

Additional fungus specimens from host fishes were also identified by Sparrow as almost entirely *L. lacteus*.

In 1943 Sparrow wrote that *Leptomitus* is saphrophytic on debris and occurs often in heavily polluted fresh waters but rarely in purer waters. It typically forms large, turflike masses on organic detritus. The fishes in Lake Huron that bore infections of this fungus were captured mostly alive in the Straits of Mackinac, Duncan Bay, and Hammond Bay. None of these waters can be considered polluted to any appreciable extent, nor is organic debris present in quantity except in Duncan Bay. In a later, verbal communication, Dr. Sparrow expressed surprise at the sources of our fungus samples, i. e., living fishes from the laboratory aquariums and Lake Huron.

It is not known whether *Leptomitus lacteus* is parasitic alone or whether it must be preceded by or exist in combination with *Saprolegnia* over wound areas on fish. The numerous observations on infections by this fungus indicate that the invader is detrimental to fishes. The sizes of many fungus growths on lamprey wounds suggests parasitism. These growths, in a form resembling a dark-gray, raglike streamer, were often 10 to 20 inches long, and trailed from their points of attachment over the wounds. The tissue beneath the fungus colonies was often soft and creamy, or charged with blood.

In laboratory aquariums, many fish that contracted infections of *L. lacteus* following nonfatal attacks by sea lampreys, died after 2 or 3 weeks of gradual decline in vitality. For example, a male rainbow trout, 9.0 inches in length and 114 grams in weight, was attacked by two lampreys on November 27, 1951, for a total of 24 hours. Both incomplete attachments, made in region II, resulted in slight hyperemias, but no feeding took place. Within 3 days, *L. lacteus* was observed to grow rapidly and extensively over the lamprey marks. The fish died on December 10, 1951, 13 days after the lamprey attack. The death was chiefly attributed to the secondary infection. The skin was unbroken, but beneath it at the wound sites the flesh was semiliquid to a 5-millimeter depth.

Brown trout, rainbow trout, brook trout, white suckers, longnose suckers, yellow perch, and sea lampreys were subject to infections by both *Leptomitus lacteus* and *Saprolegnia parasitica* in laboratory aquariums. The incidence for both species of fungi was large during all seasons of the year, but *Leptomitus* (probably in combination with a small amount of *Saprolegnia*) was encountered more frequently than *Saprolegnia* alone.

The occurrences of the fungi in such proportions was surprising since the water used in aquariums was pumped from Hammond Bay. The bay area is devoid of aquatic vegetation except for periphyton on the rocks, and lacks any appreciable amount of organic debris. It has a sand, gravel, and boulder bottom. The usually clear, colorless, cold water in the aquariums was unpolluted, and periodic chemical analyses indicated high concentrations of dissolved oxygen and only small amounts of dissolved carbon dioxide. Since the water supply was of excellent quality in all respects, the zoöspores of the fungi must be considered omnipresent in the water or on the fishes.

In Lake Huron, *L. lacteus* and *S. parasitica* were observed at all seasons of the year on white suckers, longnose suckers, carp, yellow perch, and walleyes captured by trap nets fished in Duncan, Hammond, and Spens bays and in the Straits of Mackinac. *Leptomitus* was the more common of the two species.

In 715 complete and incomplete, unhealed, sea-lamprey wounds on white suckers from Lake Huron, growths of *L. lacteus* occurred on 6.2 percent and *S. parasitica* on 0.4 percent. The percentages of fungal incidence on the white suckers in nature actually are greater than given above since unknown numbers of growths on wounds were rubbed off the fish during the net-lifting operations. In addition, most of the fish were examined during the colder months of the year when the incidence of fungus infections may be less than during the warmer seasons.

OTHER PARASITES ON FISH

Ten forms of invertebrate parasites were observed in fishes from Lake Huron and hatchery sources which were studied for their sea-lamprey wounds or used as prey fish in aquariums. These parasites were as follows (for some parasites indicated by "sp." it is not known whether one or more species were present).

Scientific name	*Common name*
External parasites:	
Protozoa: *Ichthyophthirius multifilis.*	Itch.
Trematoda:	
Gyrodactylus sp	Anchorworm.
Neascus sp	Blackspot.
Hirudinea	Leech.
Copepoda:	
Argulus sp	Fish louse.
Salmincola sp	Gill louse.
Internal parasites:	
Cestoda: *Ligula intestinalis.*	Tapeworm.
Nematoda:	
Philometra sp	Red roundworm.
Cystidicola sp	Bladderworm.
Acanthocephala: *Echinorrhyncus* sp.	Spiny-headed worm.

Fishes harboring these animals usually exhibit no ill effects unless the host-parasite relations are modified by certain conditions, such as a lamprey attack on the fish. Such an attack might weaken a fish to the point where it is affected by an invertebrate parasite that normally would cause no appreciable damage. In no instance could it be determined that an invertebrate parasite followed a sea-lamprey attack on a host fish as a secondary invader.

SUMMARY

The studies reported herein are concerned with the structural characteristics of the sea lamprey that adapt it to a parasitic existence, the mechanism of its attacks on fish, and the consequences of the injuries inflicted.

The feeding mechanism of the adult sea lamprey includes the buccal-gland system, the rasping tongue, the toothed oral disk, and the suctorial mouth. All are peculiarly adapted for the procurement and ingestion of liquid materials from prey fishes. Although blood and body fluids are the primary food materials sought by the parasites, evidence was obtained that some liquefied flesh may be ingested.

The buccal glands of a parasitic-phase sea lamprey are a pair of prominent bean-shaped structures in the head. During feeding they drain into the mouth cavity through a pair of ducts. The glands and their accessories appear in an early stage of metamorphosis and function throughout the parasitic phase.

The capacity of the central reservoirs of the buccal glands varies according to the size of the animal. A pair of prime glands in an average sea lamprey, 15.5 inches long and 121 grams in weight, was found to contain a total of 0.14 milliliter of secretion. As the individual achieves sexual maturity, this exocrine system follows along the irreversible degeneration of other organs and tissues in the body. Nevertheless, liquid of good quality (that is, physiologically effective) was easily aspirated from the glands of many lampreys which were captured during their upstream spawning migration.

Lamphredin (a term applied to the fluid product of the buccal glands) bathes the wound on a prey fish under attack. It prevents the coagulation of the fish's blood, exerts a hemolytic influence on the erythrocytes, and induces a lytic action in the torn flesh. The presence of a cytolytic or histotoxic property in the secretion was strikingly demonstrated in experiments with living fishes into which small amounts of lamphredin were injected subcutaneously. Reactions were observed in brook trout, brown trout, rainbow trout, longnose suckers, and white suckers which brought death in certain of the test specimens. Attempts were made to preserve lamphredin by refrigeration, freezing, and desiccation, but postpreservation tests indicated that the material suffered a reduction of potency as an anticoagulant, hemolytic, and lytic agent. The least rapid deterioration took place in frozen samples.

The tongue of an adult lamprey, with its hinged tip bearing cutting armament of transverse and longitudinal laminae, serves as a powerful rasp to effect a penetration of the skin, scales, and flesh of a fish. No host tissues were found to be entirely impervious to the excoriation. The tongue appears during the process of metamorphosis from ammocoete to parasite and is one of the last of the feeding mechanisms to become fully developed. In newly transformed lakeward-bound sea lampreys, captured in Carp Lake River in November 1951, 73.9 percent exhibited lingual laminae in a state of incomplete development, a condition that rendered them incapable of feeding. Members of the same year class, lakeward bound in the following April, included only 10 percent with incomplete development of the tongue-teeth.

The oral disk of a parasitic lamprey, entrance to the mouth cavity, constitutes a part of the powerful suctorial apparatus. Its circular, tooth-studded, inner surface provides traction and a

measure of erosive action when applied closely to the skin of a prey fish. The imprint of the oral disk on a host usually furnishes the largest dimension of the typical "lamprey mark." From a knowledge of the regression of the diameter of the sucking disk on the length of a lamprey, it is possible to estimate closely the size of a parasite responsible for any given wound on a prey fish. The accuracy of an individual estimate is influenced by reason of a slight sexual dimorphism in the size of the oral disk. Males generally possess somewhat larger disks than females of the same length.

Eleven species of fish were employed as hosts in laboratory studies of sea-lamprey feeding. The fish showed no fear of and took no actions to avoid the lampreys. The approach of a lamprey on a host is usually direct and rapid. Once the attachment is secured, the frantic struggles of the victim to dislodge its persecutor are seldom successful.

Among the factors that determine effects of a lamprey's attack on a host fish are the species, size, and condition of the victim; the site of the feeding attachment; the size of the wound; the duration of the attack; the severity of blood loss; and the incidence of secondary invaders in the injury.

The sites of 2,629 complete sea-lamprey wounds (wounds in which feeding took place) were plotted for 20 species of fish attacked in the laboratory or in Lake Huron to determine the pattern of scar distributions on the surfaces of the hosts. The surface most used on the aquarium hosts was the upper half of the middle third of a fish's body. In contrast, wounds incurred in the lake were most common on the lower half of the middle third of the fish. Head and eye injuries were observed more frequently in the aquariums than in the lake samples; on the other hand, penetrations of the body cavity were relatively more frequent in natural hosts. The differences in wound distribution on laboratory and lake fish were attributed to the greater mortality from dorsal and head attacks over those on ventral surfaces of the prey. The data on wounds on fish from Lake Huron represented mostly the undetermined but possibly small percentage of fish that had survived their injuries long enough to be caught in our nets. In the laboratory, all lamprey attachments were available for examination. It is accordingly probable that the experimental data have less bias and present the truer picture of the distribution of wound in natural populations.

Three dimensions were measured on 2,629 "complete" wounds, (1) diameter of oral-disk mark, (2) diameter of the hole, and (3) the depth of the hole. Lampreys 5 to 23 inches long produced wounds that ranged from 12 to 50 millimeters in maximum diameter. Even the smallest of injuries frequently led to grievous injury or death. The smallest wounds, found in April, were caused by the attacks of recently transformed feeders. By the following October, the mean size of the wounds doubled. The maximum proportions, reached by the following February, represented a total increase of 262 percent over the size of the April wounds.

Lamprey attachments on fishes do not always result in feeding penetrations. Of 2,879 attacks studied, 9.2 percent involved occasional loss of scales but no skin ruptures or damages to underlying tissues. Nevertheless, hosts which bore such incomplete wounds were susceptible to invasions of fungi at the attachment sites.

In a sample of 1,189 complete wounds on 18 species of fish from Lake Huron, only 22.2 percent were classified as healing or healed. This low incidence of healed or healing wounds indicates strongly that a host subjected to an attack is usually doomed.

Fish under attack died in as little as 4 hours, whereas other attachments continued up to 9 days, or longer, before the fish died. The actual time a parasite remained on a fish depended usually on the length of time the fish lived. The durability of the fish in turn was affected greatly by its size and species, the size of the predator and the vigor with which it pressed the attack, and the site of the feeding penetration.

Accounts are given of the gross pathology of attacks on the following regions of the fish's body: the integument, skeletal muscles, cartilage and connective tissues, vascular system, blood, lateral-line system, nerve tissue, bones, eyes, nasal passages, gills, intestine, anus, pyloric caeca, liver, spleen, pancreas, and gonads.

The severe hemorrhage that attends the sanguivorous attacks of lampreys on fishes is the direct cause of death of most of the victims. At best, teleosts possess only a small quantity of blood which places them at a disadvantage when they are beset by parasitic lampreys. Hematological studies on dying brown trout, rainbow trout, brook trout, and white suckers showed that the volume, red-cell count, and hemoglobin content of their blood are drastically reduced in mortal attacks. The mean blood values for 119 normal white suckers were 1,159,256 erythrocytes and 3,869 leucocytes per milliliter, and 8.24 grams of hemoglobin per 100 milliliters of whole blood. In contrast, the average determinations made on postattack blood samples from 119 mortally wounded suckers were 189,705 red cells and 8,514 white cells per milliliter, and less than 3.75 grams of hemoglobin per 100 milliliters of blood. The erythrocyte and hemoglobin levels indicated net reductions of 83.6 percent and at least 54.0 percent, respectively, whereas leucocytes were increased 2.2 times in the injured fish. The differences between preattack and postattack values are not necessarily indicators of extent of blood consumption, for the net changes recorded do not take into consideration the hemopoietic potentials of the hosts. The prey suckers had a mean length of 13.0 inches; their deaths occurred in an average of 59.1 hours; and their attackers averaged 12.1 inches long.

The lethal factors in extensive hemorrhage could not be specifically defined in the host fishes. The large losses of erythrocytes, hemoglobin, and blood volume itself, as observed in dying specimens, were undoubtedly attended by serious physiological derangements, some of which in turn produced such conditions as shock, anoxia, loss of equilibrium, lack of responses to external stimuli, and lack of osmotic balance between exposed tissues and the surrounding water. The trout species and white suckers were considered to be in mortal danger when their erythrocyte counts fell below 300,000 cells per milliliter of blood.

Many fishes that fall prey to sea lampreys already harbor one or more invertebrate endoparasites or ectoparasites. Although 10 such organisms were found on hosts, no example was observed of penetration by any invertebrate into a wound as a secondary invader. However, the fungi *Leptomitus lacteus* and *Saprolegnia parasitica* did produce secondary infections in wounds. A sample of 715 complete and incomplete, unhealed, lamprey injuries on white suckers from Lake Huron showed 6.2 percent infected with *Leptomitus* and 0.4 percent with *Saprolegnia*. It is possible that the large growths of *Leptomitus* were contaminated to some extent by *Saprolegnia*. In the laboratory aquariums, fishes that survived their lamprey attachments often succumbed from subsequent infection by fungi.

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