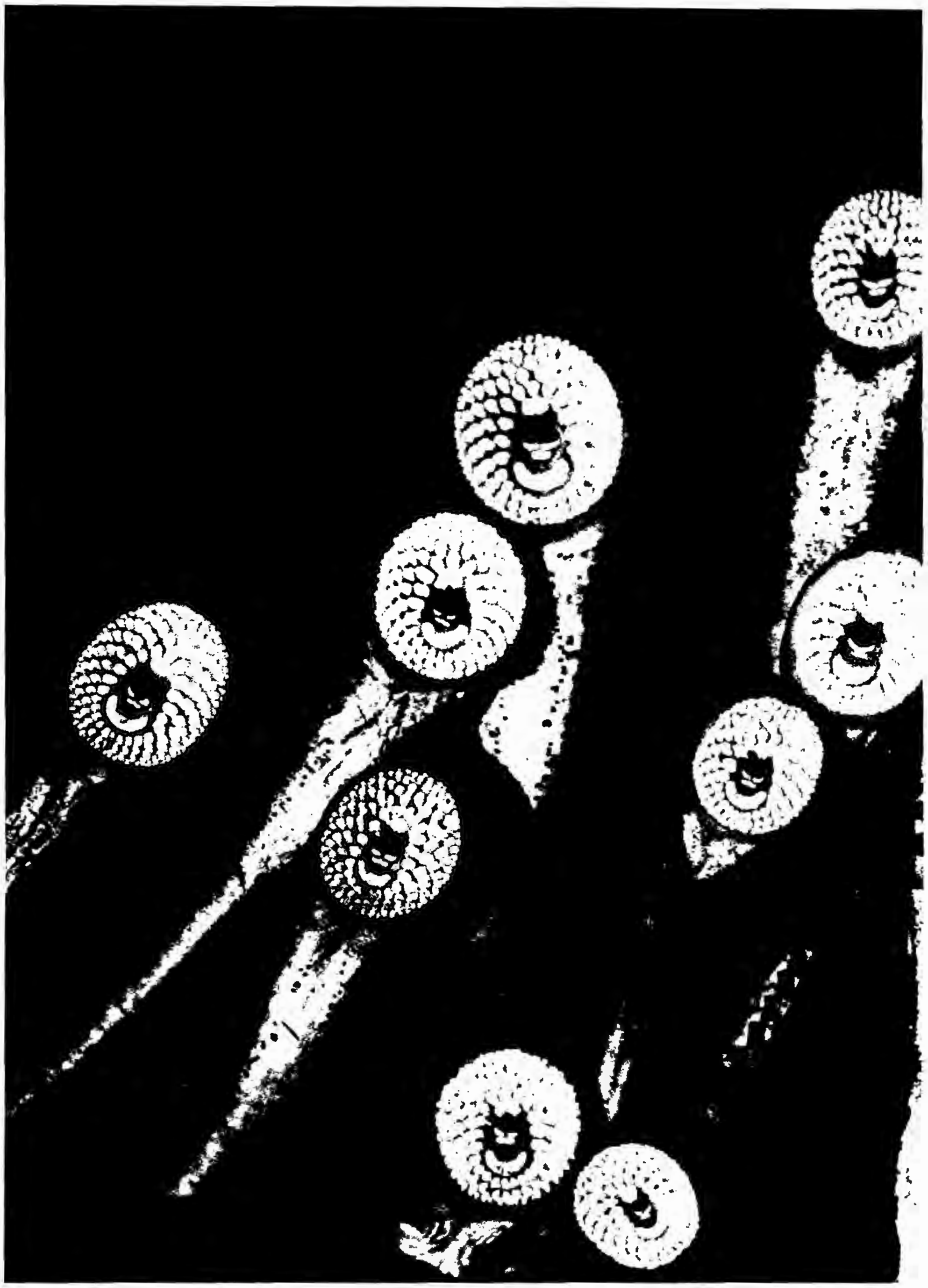
AN ECOLOGICAL STUDY OF THE CHESTNUT LAMPREY IN THE MANISTEE RIVER, MICHIGAN

JAMES DANE HALL

1963



Frontispiece.--Adults of the chestnut lamprey in an aquarium. Photograph by L. N. Allison.

ABSTRACT

AN ECOLOGICAL STUDY OF THE CHESTNUT LAMPREY, ICHTHYOMYZON CASTANEUS GIRARD, IN THE MANISTEE RIVER, MICHIGAN

By James D. Hall

The purpose of this study is to supply quantitative life history data for an unusually abundant population of the parasitic chestnut lamprey and to estimate the magnitude of its predation upon the associated rainbow and brook trouts. Research involved primarily the adult phase of lamprey in the upper Manistee River of Michigan. The population in the river was studied by direct observation with skin diving equipment and by capturing feeding adults in baited traps in a mark-and-recapture program extending from October 1960 to March 1962. Feeding of the adult lamprey and its effect on host fishes were studied in aquariums periodically from July 1959 to January 1962.

The population study was most intensive in a one-mile stretch of the river (marking area), but traps were also set as far as 18 miles upstream and 24 miles downstream from the marking area. Between May and November 1961, 1,911 adult lampreys were marked individually. Of 11,066 captures made in this interval, 2,785 were recaptures of marked lampreys (many individuals were recaptured more than once).

In the Manistee River the adult lamprey lived about 18 months in the parasitic phase, but fed actively for only about 5 months near the middle of its adult life span (May through October). During the peak of the feeding season, in June and July 1961, about 30 percent of the trout

(7 inches and longer) had lampreys attached. Almost all lamprey predation in the Manistee River was directed at the trouts.

Many of the lampreys used in aquarium experiments died from furunculosis (the first record of a bacterial disease from any species of lamprey). Limited data from remaining lampreys suggested that the destructive potential (grams of fish killed per gram of growth) of the chestnut lamprey was directly related to the size of the lamprey and was similar to that of the sea lamprey of comparable size. For the size range of adults of the chestnut lamprey in the Manistee River, the estimated fish-kill averaged about 20 grams per gram of growth by the lamprey.

In May 1961 there were approximately 2,000 adult lampreys in the marking area. The mortality rate of these lampreys was high; only 200 were present by October 1961. During this interval the average length of the lampreys increased from about 105 mm to 175 mm (average weights 1.8 and 9.1 grams respectively).

From the product of instantaneous growth rate and average biomass during each trapping period of about 12 days, net production of the chestnut lamprey population in the marking area from May through October 1961 was calculated to be 4.44 kg (1.32 pounds / acre). Production was negligible during the rest of the year.

The trout mortality caused by lamprey predation in the one-mile marking stretch of the Manistee River, estimated from the product of destructive potential and net production for each period, could have been as much as 70 kg (21 pounds/acre), about one-third of the trout available to anglers during the 1961 trout season.

Net production of the lamprey population was much lower per unit area than any previous measurement of production of a single fish species, but none of these species was at as high a trophic level. Total lamprey production in 1961 was about 1.3 times the weight of the standing crop in May. Because the growth rate did not keep pace with the very high rate of mortality of the adult lampreys, there was a steady decrease in the standing crop to about one-half of its initial value by the end of the season. There were indications that the mortality rate for adults of the chestnut lamprey in the Manistee River is substantially greater than that for larvae of the species.

AN ECOLOGICAL STUDY OF THE CHESTNUT LAMPREY, *ICHTHYOMYZON CASTANEUS* GIRARD, IN THE MANISTEE RIVER, MICHIGAN

by
James Dane Hall

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University of Michigan
1963

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INTRODUCTION

This is an ecological study of an unusually abundant population of the parasitic chestnut lamprey, *Ichthyomyzon castaneus*, and the impact of its predation upon the associated population of rainbow trout, *Salmo gairdneri*, and brook trout, *Salvelinus fontinalis*. Research involved primarily the adult phase of the lamprey in the upper Manistee River of Michigan. Data were gathered in both field and laboratory experiments.

Vital statistics of the lamprey population in the stream were determined by trapping lampreys in a mark-and-recapture program extending from October 1960 to March 1962. Marking was continuous between May and November 1961, when I marked 1,911 adult lampreys. Of 11,066 captures made in this interval, 2,785 were recaptures of marked lampreys (many individuals were recaptured more than once). Net production of the lamprey population was computed from its vital statistics.

Feeding by adult lampreys and its effect on host fishes were studied in aquariums periodically from July 1959 through January 1962. An estimate of the destructive potential (grams of fish killed per gram of lamprey growth) of the chestnut lamprey was obtained. From the product of net production and destructive potential, I calculated that the mortality of fish in the Manistee River due to attacks by the lamprey could have approximated one-third of the legal-sized trout (7 inches and longer) available to anglers.

Background

The lamprey

Distribution.--The chestnut lamprey inhabits a large area in central North America, from the Hudson Bay drainage in Manitoba to the Gulf of Mexico (Fig. 1). However, the dearth of published records on any aspect of the life history of this species suggests that it is scarce throughout most of its range. In recent years, suitable lamprey habitat has been reduced by siltation and pollution (Bailey, 1959; Starrett, Harth, and Smith, 1960; Trautman, 1957).

In Michigan the chestnut lamprey is confined to waters of the Lower Peninsula that flow into Lake Michigan. The closely related silver lamprey, *Ichthyomyzon unicuspis*, is found in the other major drainages of the state (Fig. 2). Nowhere in Michigan are the two species known to occur together.

Though widespread in the state, the chestnut lamprey is apparently abundant only in the upper Manistee River. There, trout bearing either lampreys or fresh scars from lamprey attacks are often taken by anglers. Almost certainly, nowhere in its entire range is the population of this cyclostome so dense as in the upper Manistee River.

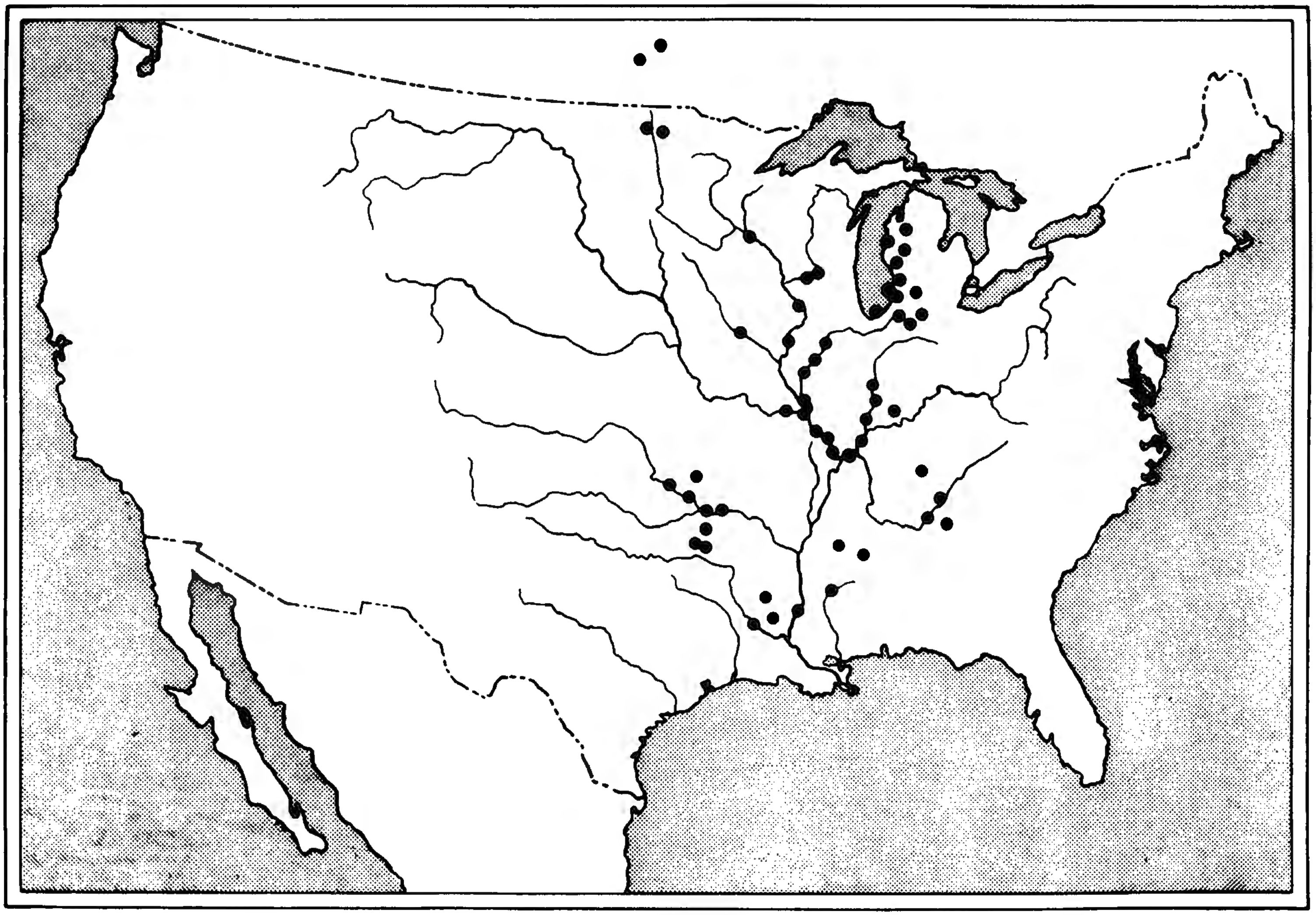

Figure 1.--Range of the chestnut lamprey in North America. Sources of data are: Hubbs and Trautman (1937), Gerking (1945), Knapp (1951), Hall and Moore (1954), Harlan and Speaker (1956), Bailey (1959), Cook (1959), Starrett et al. (1960), and records of the University of Michigan Museum of Zoology (courtesy of Dr. Reeve M. Bailey).

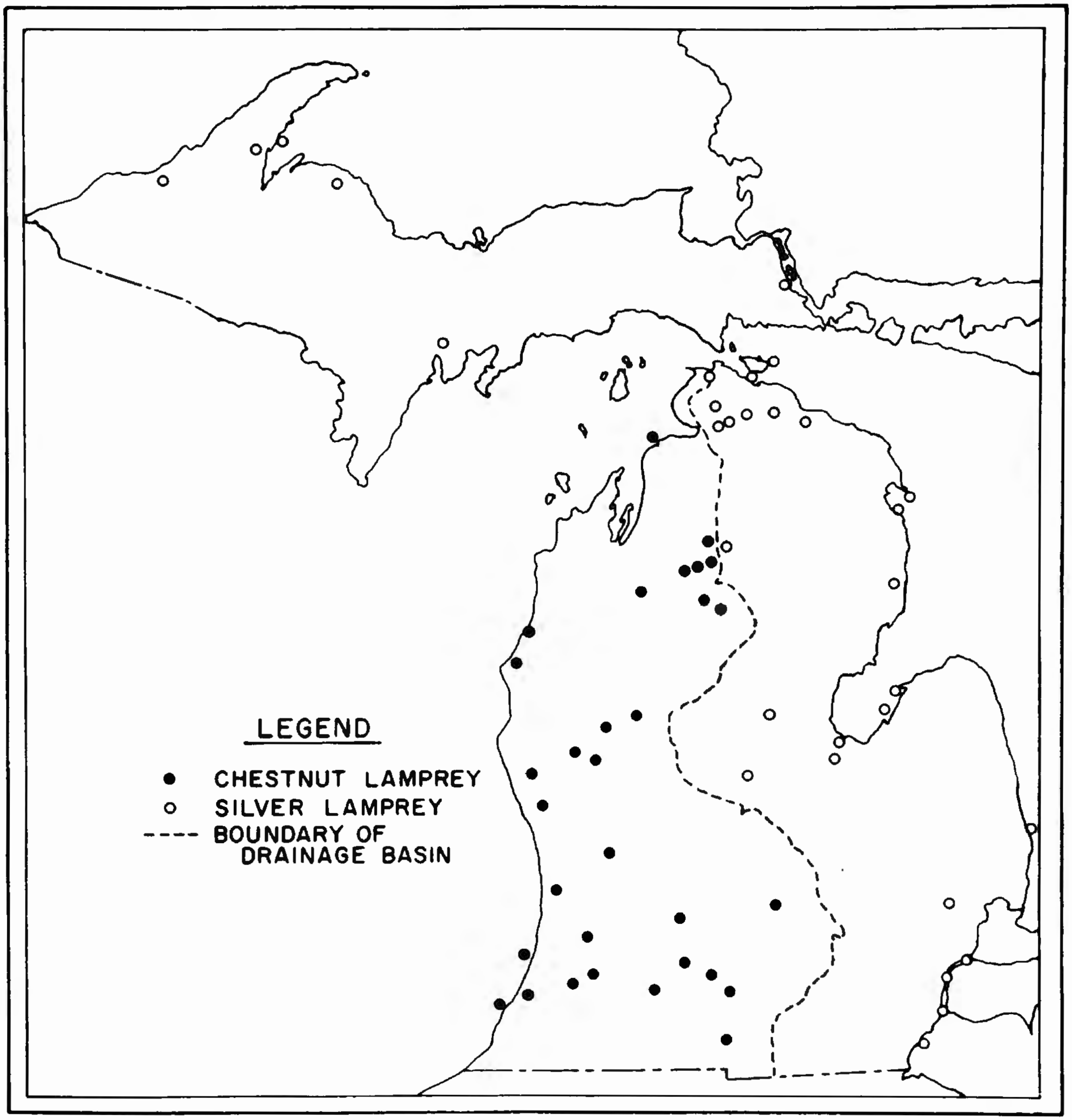

Figure 2.--Distribution of the chestnut and the silver lampreys in Michigan. Sources of data are: Hubbs and Trautman (1937), and records of the University of Michigan Museum of Zoology (courtesy of Dr. Reeve M. Bailey).

Life history and ecology.--The life history and ecology of the chestnut lamprey have received brief mention in taxonomic studies (Hubbs and Trautman, 1937; Hall and Moore, 1954; Starrett et al., 1960), but no field study of the species has been reported. The life history of the northern brook lamprey, *Ichthyomyzon fossor*, has been more fully investigated (Reighard and Cummins, 1916; Okkelberg, 1922; Leach, 1940; Churchill, 1947; and Vladykov, 1949). Field studies on other species of *Ichthyomyzon* have concerned the Allegheny brook lamprey, *I. greeleyi*, (Raney, 1939) and the southern brook lamprey, *I. gagei*, (Dendy and Scott, 1953).

Lamprey life history investigations in North America date from the pioneering studies of Gage (1893, 1928) on the sea lamprey, *Petromyzon marinus*, and the American brook lamprey, *Lampetra lamottei*. Work on lamprey biology has received considerable emphasis in recent years due to invasion of the Great Lakes region by the sea lamprey and the consequent decline in number of the lake trout, *Salvelinus namaycush*, (Applegate, 1950; Wigley, 1959).

A brief summary of the life history of a typical parasitic lamprey, compiled from several sources, is as follows: There are two stages, larval and adult. The larvae (also called ammocoetes) are blind and live in burrows constructed in deposits of sand and silt. They feed principally on diatoms and also on other microscopic drift in the stream water (Newth, 1930; Schroll, 1959). The length of the larval period is not definitely known, but is probably at least 7 years. Several striking changes occur at metamorphosis into the adult stage. Most significant of these involves the feeding mechanism, which becomes adapted for a life of sucking blood and body fluids from other fishes--the only food source in the adult stage. Thus the adult lamprey lives two or three trophic levels above its larva. Its method of feeding is undeniably that of a parasite, but by virtue of its large size and lethal effect on fishes attacked, it might better be classified as a predator. Its precise designation as a parasite or predator seems lost in semantics. In the spring, after 1 to 2 years in the feeding stage, the adults spawn and die.

Identification.--There are two species of *Ichthyomyzon* in the Manistee River, the chestnut and the northern brook lampreys. Investigation of the larval life of the chestnut lamprey was hampered by difficulty in distinguishing between larvae of these two species. There is no confirmed key to larvae of the genus; one is in preparation by Dr. V. D. Vladykov (personal communication).

The pattern and intensity of external and internal pigmentation is used to distinguish the larvae of eastern American lampreys with two dorsal fins, *Lampetra* and *Petromyzon* (Vladykov, 1950 and 1960). In collections from the Manistee River I was able to recognize about one-half of the large *Ichthyomyzon* larvae (longer than 70 mm) as separate species, based on patterns of pigmentation described by Crowe (1959), but small larvae could not be identified. Dr. Vladykov examined a series of 116 Ichthyomyzon larvae from the Manistee River and found some "intermediate" specimens (personal communication).

The river

Physical characteristics.--The Manistee River is the northernmost of five large rivers draining the western half of the Lower Peninsula of Michigan (Fig. 3). Its drainage basin, slightly over 100 miles long, covers some 1,780 square miles. The river originates in several small lakes in a glacial outwash plain northwest of Grayling (Fig. 4). It flows through this plain for about 180 miles before emptying into Lake Michigan. Two hydroelectric dams block upstream movement of fishes from Lake Michigan into the headwaters. Various sands dominate the soil of the drainage basin, particularly in the headwaters. (U. S. House of Representatives, 1931).

A survey of the distribution of the chestnut lamprey in the Manistee River (Crowe, 1959) served to define the geographic boundaries in my study. I selected approximately 45 miles of the river near the headwaters, from Deward to Sharon (Fig. 3).

In this area the Manistee River has the most stable flow of any stream of comparable size in the St. Lawrence River basin. A common measure of stream stability is the ratio of maximum to minimum flow (Wisler and Brater, 1959). In 18 years of records, this ratio for the Manistee River was 388:122 cubic feet per second (U. S. Geological Survey, 1961). The stability of the river is due largely to

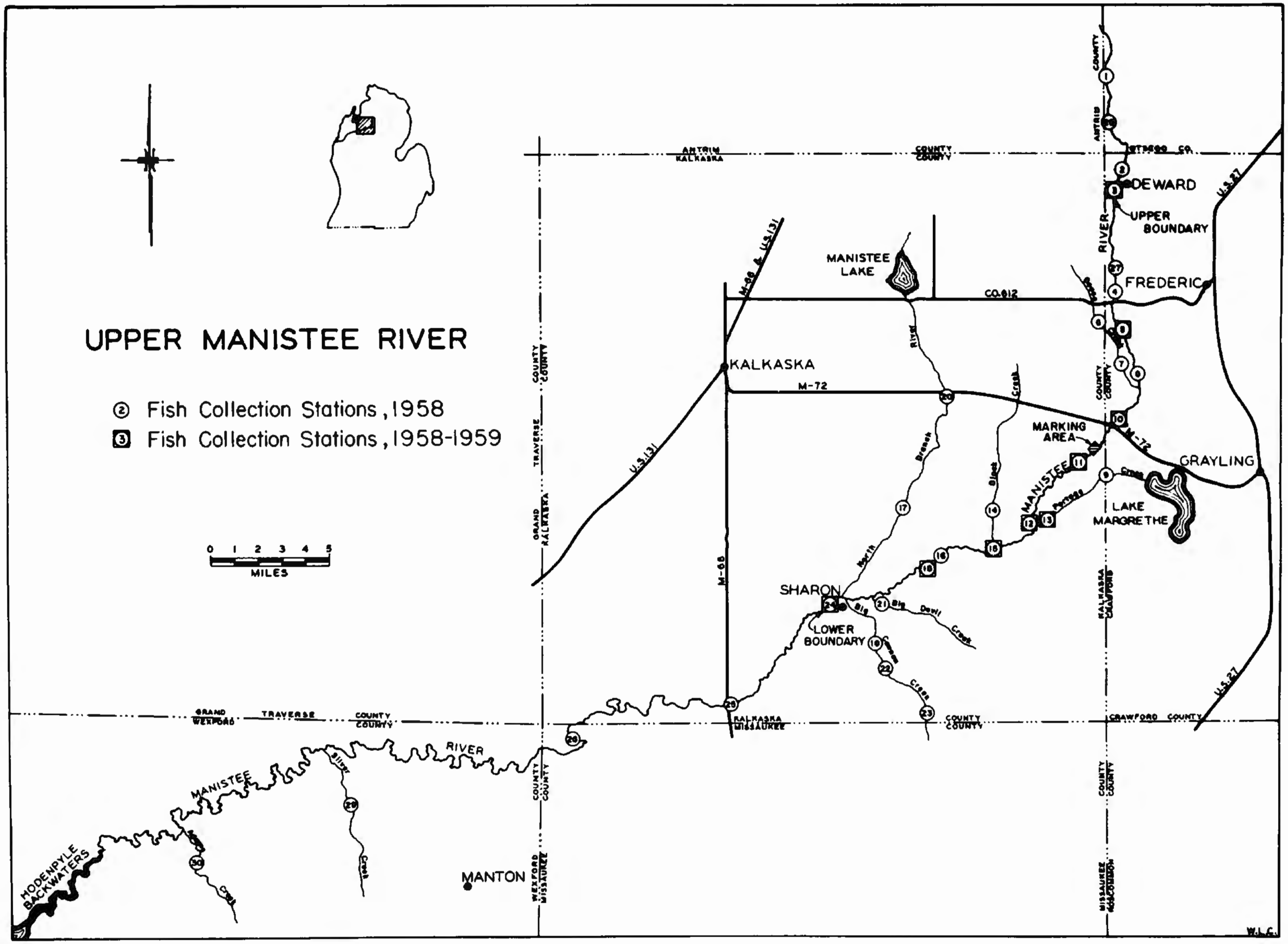

Figure 3.--Map of the upper Manistee River system showing location of fish collection stations and area of the trapping study (modified from Crowe, 1959).

Figure 4.--The upper Manistee River: Upper--near Deward; Lower--in the marking area.

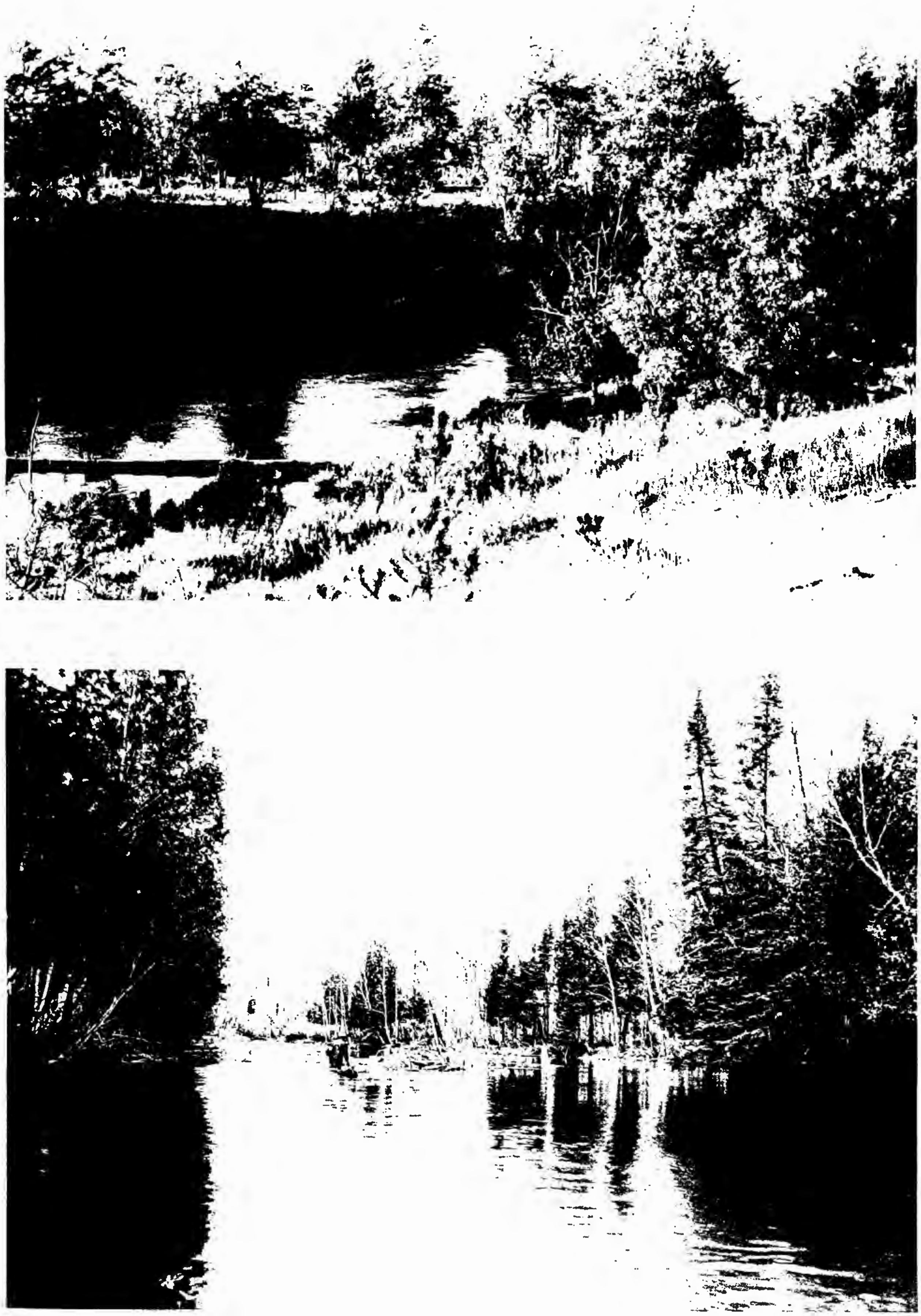

Figure 4

both the soil type and the extensive ground-water resource of the region (Wisler and Brater, 1959). In the area I studied, base flow of the stream in August 1954 increased from about 65 cfs at Deward to 350 cfs at Sharon. Of this increase, 60 percent was supplied by ground water, the remainder by tributaries (U. S. Geological Survey, 1957). In addition to stabilizing stream flow, ground water also moderates the stream temperature.

In the area studied, the gradient is about 3.3 feet per mile. Because of the low gradient and a surface soil vulnerable to erosion, much of the stream bed is composed of unstable banks of sand. The water conductivity is about 290 μmho at 18° C. The stream is free of pollutants in the headwaters.

Man's activities have caused considerable change in the Manistee River. The watershed was once forested with high quality pine and hardwood (U. S. House of Representatives, 1931). Most of the timber on the upper watershed was cut between 1885 and 1910. Many logs were skidded over the sand banks and floated downriver in large spring drives (Vincent, 1962), thus accelerating erosion. The logs dragged sand into the river and gouged the stream bottom, altering its character. Many logs that had lain in the stream since the early drives were salvaged around 1930; this further disturbed the stream bottom (Esbern Hanson and Hans Peterson, personal communications).

Biological history.--No mention of lampreys was made in the more than 20 personal accounts of fishing trips on the Manistee River between 1874 and 1904 (Vincent, personal communication). Two men who fished the stream around the turn of the century observed only a few lampreys on fish at that time (Esbern Hanson and Arthur Johnson, personal communications). This scarcity of lampreys could have been apparent rather than real because of the great numbers of other fishes then present.

The arctic grayling (Thymallus arcticus), which vanished around 1900, was the only salmonid fish in the Manistee River system prior to 1850 (Vincent, 1962). Today the introduced trouts--rainbow, brook, and brown (Salmo trutta)--constitute the game fish population in the headwaters of the stream. This situation in which the lamprey is native and the trouts are introduced, presents an interesting contrast to the relationship between the sea lamprey and the lake trout in the Great Lakes. Other fishes common in the upper Manistee are the creek chub (Semotilus atromaculatus), the blacknose dace (Rhinichthys atratulus), the white sucker (Catostomus commersoni), and the mottled sculpin (Cottus bairdi). Three species of lamprey are present--the chestnut, the northern brook, and the American brook lampreys (Crowe, 1959). Before construction of the hydroelectric dams, runs of rainbow trout from Lake Michigan provided a substantial sport fishery in the headwaters. Today this fishery is supported principally by hatchery-stocked rainbow trout.

Methods

Field procedure

A one-mile stretch of the Manistee River, near the middle of the 45-mile study section, was selected for intensive work and designated the "marking area" (Fig. 4). It was chosen to include the area of greatest apparent abundance of the chestnut lamprey, and also to be easily accessible throughout the year. Conditions for survival of trout appear to be above average compared with the stream as a whole. There is considerable gravel in the stream bed and less sand than in most of the river. Overhanging banks and deep pools provide cover superior to that in many other areas of the stream. The average width of this one-mile section is about 60 feet (mean of 28 tape measurements) and its area 7.4 acres.

The marking area was divided into 30 equal sections by pacing in mid-stream or along the stream bank. The 30 sections were grouped. Sections 1-6 were designated group A (A1-A6), sections 7-12 group B (B1-B6), etc. Two trap sites were chosen in each section. Most of these sites were in slack water or near cover, where fish were likely to rest. For comparison a few sites were in fast water near mid-stream.

Two types of traps were used to catch adults of the chestnut lamprey. A cylindrical frame about 4 feet long by 1 1/2 feet in diameter was covered with chicken wire of 1-inch hexagonal mesh to form a cage

(Fig. 5). This wire trap was baited with a live white sucker. Lampreys entered through the mesh and attached themselves to the sucker. When the trap was pulled from the water, with rapid elevation of the upstream end, the lampreys released their hold and fell into a removable cone of 1/8-inch mesh screen on the rear end of the trap. Lampreys were free to drop off the sucker and leave the trap while it was in the stream, but the traps were lifted frequently to minimize this loss. This trapping method was suggested to me by Mr. Fred Bromwell, a long-time resident along the river. A similar procedure had been proposed for capturing feeding sea lampreys (Vladykov, 1949). The other trap I used was an unbaited glass minnow trap made from a gallon jar (Fig. 5). A "set" consisted of one wire trap with a glass trap anchored on either side. A total of 12 wire and 24 glass traps were used in the trapping study.

Two sets of traps were placed in one section of each group. The traps were lifted every two days (with a few exceptions) and moved at each lift to another section in the same group. Each of the 30 sections was sampled once in every cycle of 6 lifts. The sequence of sections to be sampled in any one group was determined by drawing numbers from a random table. Thus there was equal trapping effort at each of the 30 sections throughout the season.

By moving traps upstream and downstream from the marking area, I found that marked lampreys moved rapidly out of the area. After several weeks of trapping, I took half of the traps from the

Figure 5. -- Traps used to catch adult lampreys: Left--the wire trap; Right--the glass trap.

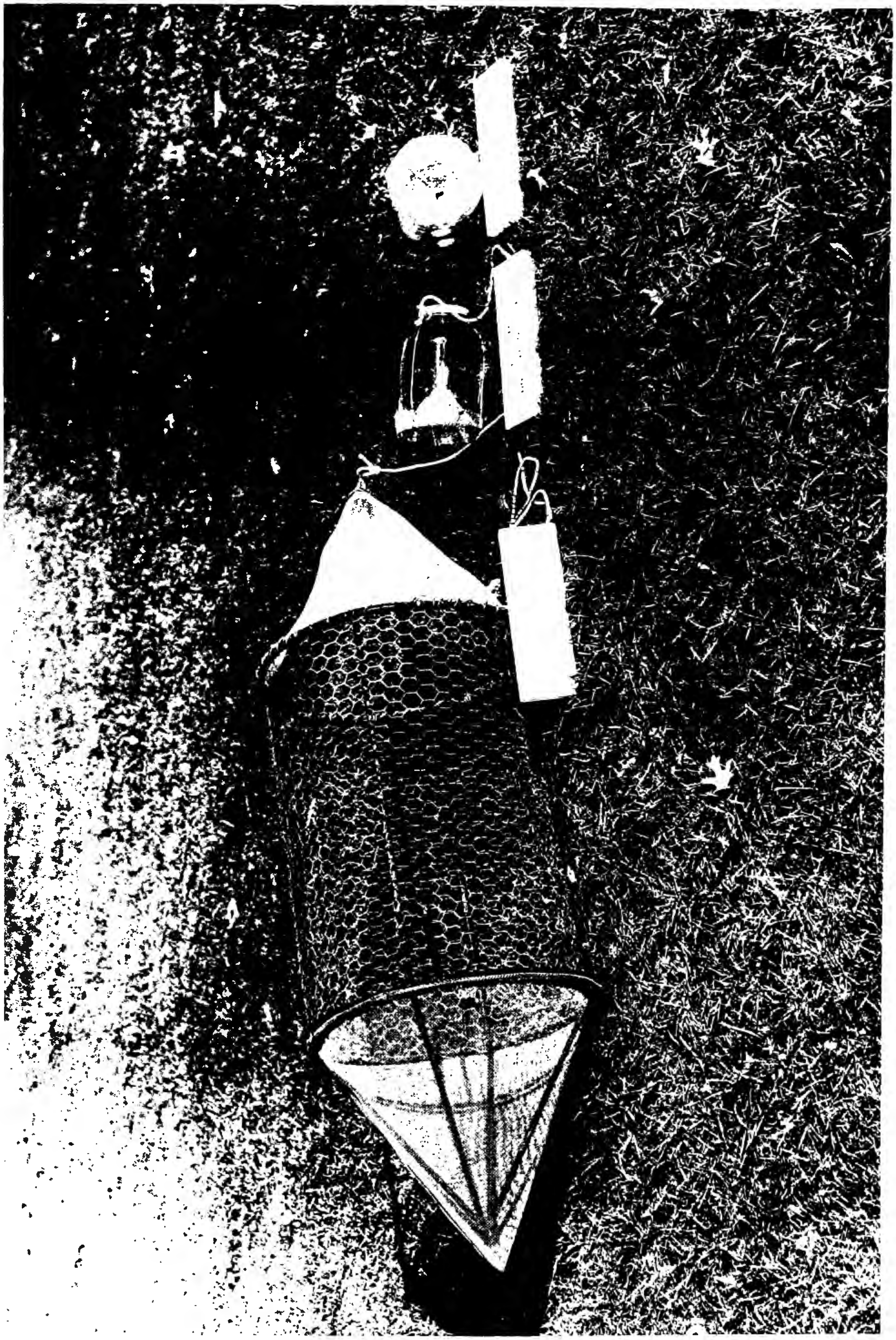

Figure 5

marking area (leaving one set in each group) and trapped simultaneously upstream and down. The seven trap sets outside the marking area were first placed upstream at 1/2, 1 1/2, 3, and 4 miles and downstream at 1/2, 1 1/2, and 3 miles. The stretch of river sampled was later enlarged to include 6, 9, 12, and 18 miles above, and 4, 6, 9, 12, 18, and 24 miles below the marking area.

In May and June I used a single sucker 15 to 20 inches long to bait each wire trap. Few of these bait fish lived more than 4 to 6 days in a trap. From July until October large suckers were difficult to collect, and I substituted several smaller suckers, 10 to 12 inches long, as bait in many of the sets. Late in the feeding season large suckers were again available for use.

I used a continuous mark-and-recapture format in which unmarked lampreys caught in the marking area were marked and released. Because of large catches in June and early July, time limitations prevented me from marking all of each day's unmarked fish. Unmarked lampreys were measured and released along with the marked ones. Since an unknown number of unmarked lampreys were undoubtedly trapped several times, the exact number of individual lampreys handled during the trapping season could not be determined.

An adult lamprey to be marked was immobilized in Tricaine methanesulfonate (MS-222 Sandoz) and its total length measured to the nearest millimeter on a fish measuring board. The lamprey was then placed on a damp sponge, and a drop of cadmium sulfide was injected under the skin (Wigley, 1952) at 2 of 20 pre-assigned points. Also the fin was notched with a pig ear notcher in 2 of 6 pre-assigned places (Fig. 6). These four marks provided 2,850 possible combinations. When the group of marked lampreys had revived in a bucket of fresh water, they were returned to the stream at the location of capture.

To determine patterns of distribution throughout the stream, fish and lampreys were collected with a 220-volt D. C. electric shocker. Crowe (1959) made such collections at 30 stations in the upper Manistee River system during September 16-24, 1958. I made additional collections at 9 of these stations during August 5-12, 1959 (Fig. 3). During January 10-17, 1961, collections were made within the marking area.

In 1961 I made direct observations on lampreys and fish in the river by floating downstream equipped with a rubber skin-diving suit, face mask, and snorkel. Approximately 23 hours were spent on 12 trips between May 10 and September 26. Most of the trips were made in May and June, when I was searching for spawning activity of the chestnut lamprey. Similar float trips were also made later in the season to determine the incidence of lamprey attachment on fish in the marking area.

Laboratory procedure

To study predatory feeding, I confined adult chestnut lampreys in aquariums during several periods from July 1959 to January 1962.

Figure 6.--An adult chestnut lamprey showing the two marks employed, fin notching (A) and pigment injection (B). The scale bar equals 1 inch. Photograph by Paul M. Earl.

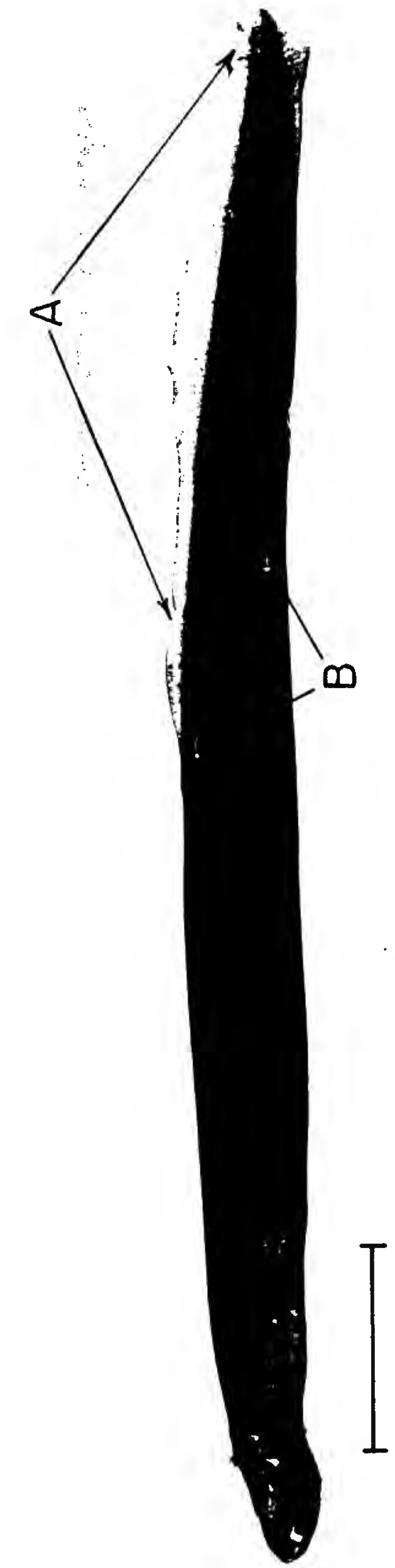

Figure 6

At first, two 50-gallon aquariums were used in the Pathology Laboratory, Grayling State Fish Hatchery. These "laboratory aquariums" were supplied with well water that remained constant at 50° F. When it became evident that temperature affected feeding by the lamprey, I built a shed (10 x 14 feet) on the grounds of the hatchery, where four 50-gallon aquariums were installed. They were supplied with water from the East Branch of the Au Sable River via a hatchery raceway. The flow of water directly from the stream provided a natural temperature fluctuation throughout the year. In these "raceway aquariums" the deviation from stream temperature was no more than 1°or 2° F. An oil stove in the shed prevented water from freezing during periods of severe winter cold. Methods of investigation and record-keeping were similar to those used by Parker and Lennon (1956).

Brook and rainbow trouts and the white sucker were used as host fishes. Most of the trout were from the Grayling Hatchery. Some trout and all of the suckers were collected from the East Branch of the Au Sable River with an electric shocker. All fish in the aquariums were fed a standard hatchery diet. Lampreys used in the feeding experiments were taken from fish caught by anglers, from traps, or with an electric shocker. From 7 to 16 lampreys were placed in each aquarium. They were first measured, marked, and weighed on a triple-beam balance sensitive to 0.01 gram. Occasionally during the trapping season, samples of lampreys taken in the traps were also weighed live on this balance to determine their length-weight relationship.

In both 1960 and 1961 the experiments had to be prematurely terminated because most of the lampreys died. Bacteriological diagnosis and subsequent inoculation confirmed that death had been caused by furunculosis. This was the first record of a bacterial disease from any species of lamprey. Many of the prey fishes also succumbed to this disease, and some others contracted fin rot and fungus infection--confounding the analysis of mortality caused directly by the chestnut lamprey.

BIOLOGY OF THE LAMPREY

General distribution

The center of abundance of the chestnut lamprey in the Manistee River appeared to be within the 45-mile stretch of the river where my study was conducted (Crowe, 1959). The upstream limit of its distribution seemed to be near the old town of Deward. No *Ichthyomyzon* larvae were taken above Station 5, and no adult lampreys were taken with the electric shocker above Station 3 (Fig. 3). Only 5 lampreys were taken in 18 trap-days at the uppermost trapping station, near Deward.

The downstream limit of distribution of the chestnut lamprey was more difficult to fix than the upstream limit. No adults were taken with the electric shocker below Station 25, and only one ammocoete was taken at Station 26 (Crowe, 1959). Twenty-four lampreys were taken in the traps at Sharon; no trapping was done downstream from there. Guides who fish the Manistee River below Sharon reported that lampreys are commonly taken on trout in most of Kalkaska County, but are uncommon below Missaukee County.

Reproduction

Season and location

I observed only one instance of spawning of the chestnut lamprey in the Manistee River, in spite of repeated searching over a three-year period in both tributaries and in the main stream. In the mid-afternoon of June 15, 1961 I watched a group of 8-10 spawning lampreys on one nest about 1 1/2 miles above the marking area. The nest was in 2 feet of water and well hidden beneath a log. This was apparently the first observation ever reported on spawning of this species. Spawning and nest-building behavior appeared similar to that reported for other lampreys (cf. Applegate, 1950; Hagelin and Steffner, 1958; Hagelin, 1959).

In addition, 8 ripe and 5 spent chestnut lampreys of both sexes were taken in traps and with an electric shocker during June 1961. The first ripe individuals were taken on June 8, the first spent one on June 18. On June 8, 1960 I observed a single chestnut lamprey engaged in nest-building activity in the marking area--the only mature adult seen that year.

I have concluded that the chestnut lamprey in the Manistee River spawns in June and perhaps July, depending somewhat upon water temperature. Spawning must occur over a wide expanse in the stream, but may well be centered in the vicinity of the marking area. These conclusions are based on: the single observation of spawning, the distribution of <u>Ichthyomyzon</u> larvae and of newly transformed adult chestnut lampreys, and the location of apparently suitable spawning areas (fast water, gravel bottom, and log cover).

The Manistee is a large stream--without underwater observations I probably would not have seen even the one instance of spawning activity. Nonetheless, it is surprising that so little activity of the chestnut lamprey was seen. Several hundred of the smaller brook lampreys (both the American and the northern species) were seen building nests and spawning during the three years that I made observations.

Dr. Milton B. Trautman suggested that the parasitic species of Ichthyomyzon may spawn more at night than do the other lampreys. He has seen very little spawning of parasitic Ichthyomyzon, in spite of many attempts to locate such activity (personal communication). I saw several chestnut lampreys building a nest after dark on June 16, 1961. The observation was made by flashlight between 9:30 and 10:30 PM at the same location where spawning had been seen the day before. Such nocturnal activity by the chestnut lamprey may well be the explanation for the scarcity of observations on its spawning habits.

Sexual dimorphism

There are obvious external differences between the mature males and mature females of the chestnut lamprey. These differences, which clearly distinguished the mature lampreys of both sexes from the immature feeding adults present at the same time (Fig. 7), are similar to those reported for other lampreys (Vladykov, 1949; Hagelin and Steffner, 1958).

In mid-July feeding females of the chestnut lamprey taken from traps were slightly longer than the males. By late August this difference had become statistically significant. The differential growth rate could explain the bimodal length-frequency distribution in early

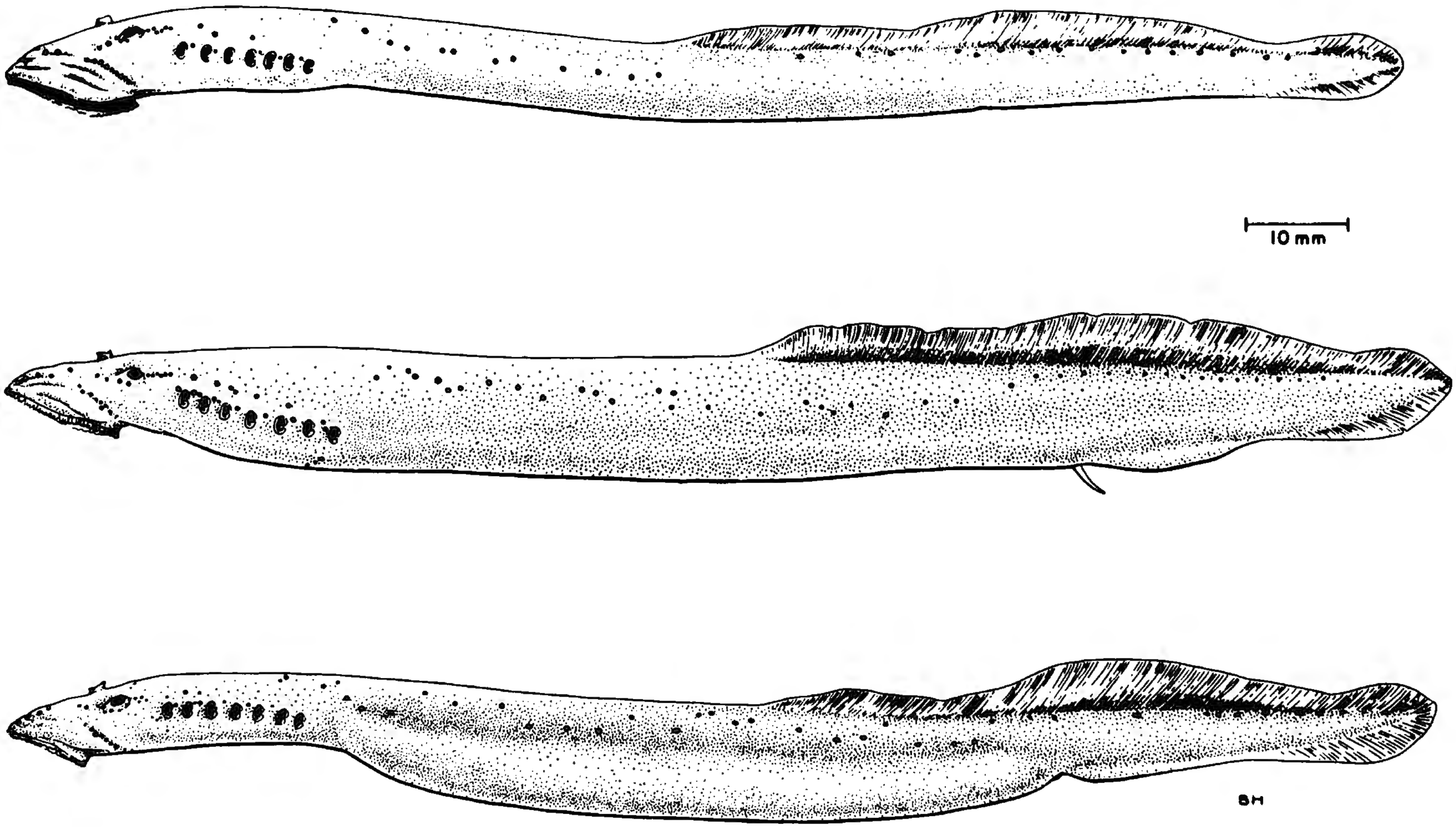

Figure 7.--Sexual dimorphism in the chestnut lamprey: Upper--Immature adult, 140 mm; Middle--Mature male, 145 mm; Lower--Mature female, 143 mm. Figure drawn by Bonnie Hall.

September (Fig. 8). Too few spawning lampreys were found to determine whether or not there was still a size difference the following spring.

There is conflicting evidence on differences in length between males and females of other lampreys. Females of the sea lamprey on the spawning run were from 0.62 to 3.8 percent longer than the males in all but one of the samples taken for 5 years from 2 streams tributary to Lake Huron (Applegate, 1950; Applegate and Smith, 1951; Applegate and others, 1952). A large number of lampreys were sampled from each run (629 to 4,619) so that even such small differences in length were statistically significant. Females of the sea lamprey taken on spawning runs into Cayuga Inlet, New York, from 1950 through 1952 were consistently smaller (0.63 to 2.6 percent) than the males (Wigley, 1959). The samples were small, however, and the differences non-significant.

Females of the northern brook lamprey exceeded males in average length in two samples (68 transforming larvae and 17 adults) from the Brule River, Wisconsin, by 13.6 and 13.9 percent respectively (Churchill, 1947). Here the difference in length was evident earlier in the life cycle than it was in the chestnut lamprey in the Manistee River. Females of the silver lamprey were also found to be longer throughout their adult life than were the males (Vladykov and Roy, 1948).

Sex ratio

The sex ratio in two collections (July 18 and August 30, 1961) of immature adults of the chestnut lamprey did not differ significantly

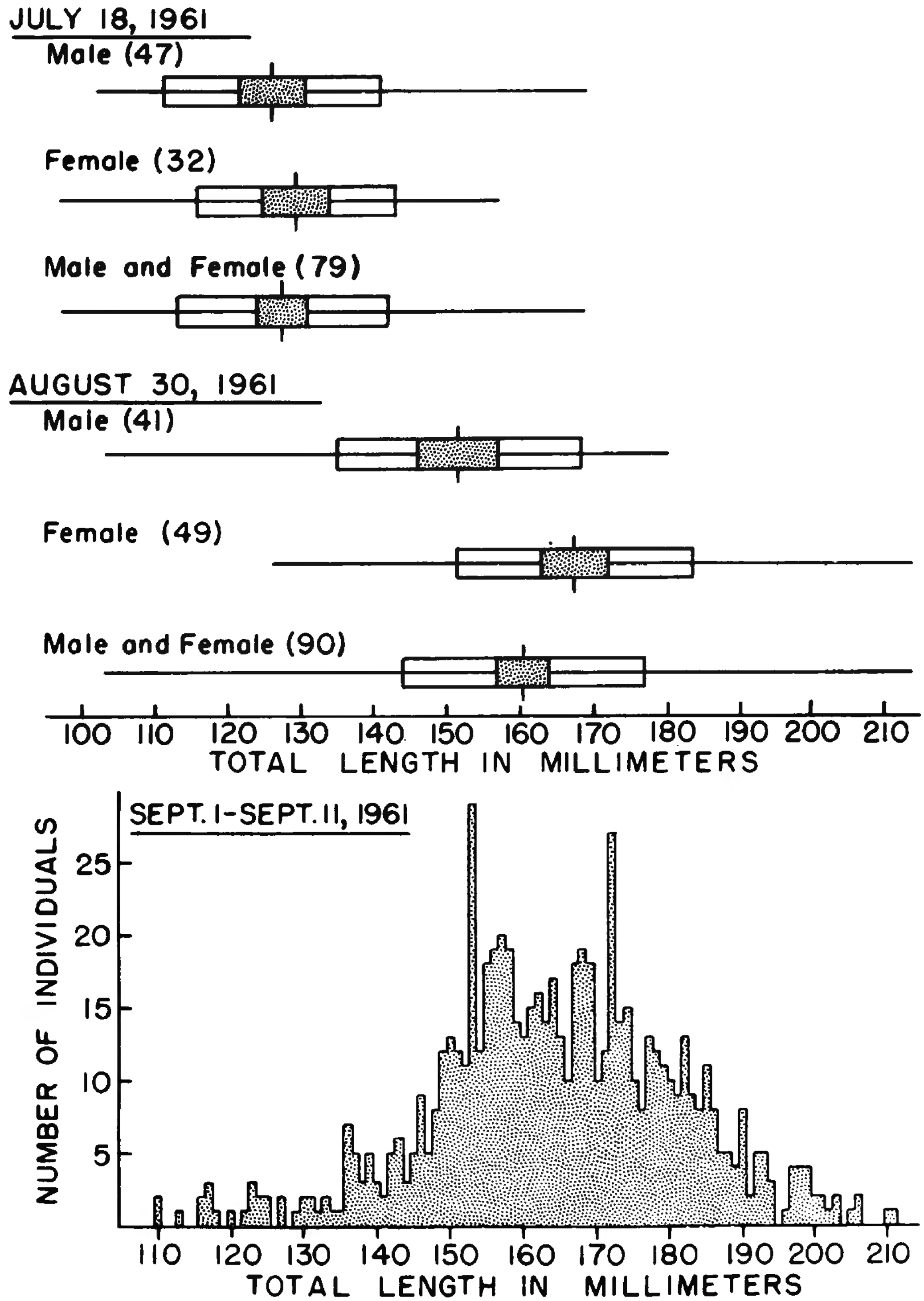

Figure 8.--Differential growth in length between males and females of the chestnut lamprey: Upper--Length of 79 adult lampreys collected July 18, 1961; Middle--Length of 90 adult lampreys collected August 30, 1961; Lower--Length-frequency distribution of 690 captures of unmarked lampreys, September 1-11, 1961. In the upper two graphs the vertical line shows the mean length, the solid rectangle represents twice the standard error of the mean, the open rectangle one standard deviation, and the single line the range (cf. Hubbs and Hubbs, 1953).

from 50:50 (47♂♂:32♀♀ and 41♂♂:49♀♀ respectively). Too few mature lampreys were found to determine whether the excessive imbalance of males reported for spawning populations of other lampreys was evidenced in the Manistee River.

The sex ratio of large ammocoetes was approximately 50:50 in populations of the sea lamprey from the Ocqueoc River, Michigan, and *Lampetra planeri* from the River Yeo in Great Britain (Hardisty, 1960). However, males greatly outnumbered females in the spawning runs of both populations. In both species the sex ratio was related to population level--the larger the population, the greater the proportion of males in the spawning run (Hardisty, 1961).

Feeding

Adult lampreys gain their entire sustenance from the blood, body juices, and liquefied flesh of fish that they attack (Lennon, 1954). To determine the impact of lamprey predation upon the trout population in the Manistee River, I studied the seasonal and daily pattern of lamprey feeding, food selection in the stream, and the amount of feeding that led to death of host fishes.

Feeding season

Nearly all predatory feeding in the stream occurred from May through October. Feeding began in April, built to a peak in July, and then declined until October. This conclusion is based on observations described in the following paragraphs:

Incidence of lamprey attachment.--About 30 percent of the trout seen in underwater observations in the marking area on June 7 had lampreys attached. Most of these fish had a single lamprey attached, but some had two. There was a decline in the incidence of attachment in that area throughout the rest of the summer (Fig. 9). I saw many trout in other parts of the river during May and June while I was searching for lamprey spawning activity. There seemed to be a large number of trout in the stream early in the feeding season, and they were heavily attacked. Few trout were seen as autumn approached, and the incidence of lamprey attachment was low.

When the sunlight was bright and the stream clear, direct observation proved a more effective means of sampling the fish population in this stream than did shocking, which was impossible in the deep pools and fast water. While floating downstream, I was able to approach many fish without frightening them. Almost all fishes seen could be identified to species.

Scarred fish in anglers' catch.--The percentage of trout in the anglers' catch of 1952 that had been scarred by lampreys[1] also indicated seasonal variation in feeding of the chestnut lamprey (Fig. 9).

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[1]These unpublished data from a creel census taken that year were kindly furnished to me by Dr. D. S. Shetter. Fish were checked for lamprey scars, but this was not an object of the census and was done only because of a personal interest of the census clerk. Some inconspicuous marks may have been overlooked; the observed percentage of scarring should be considered minimal.

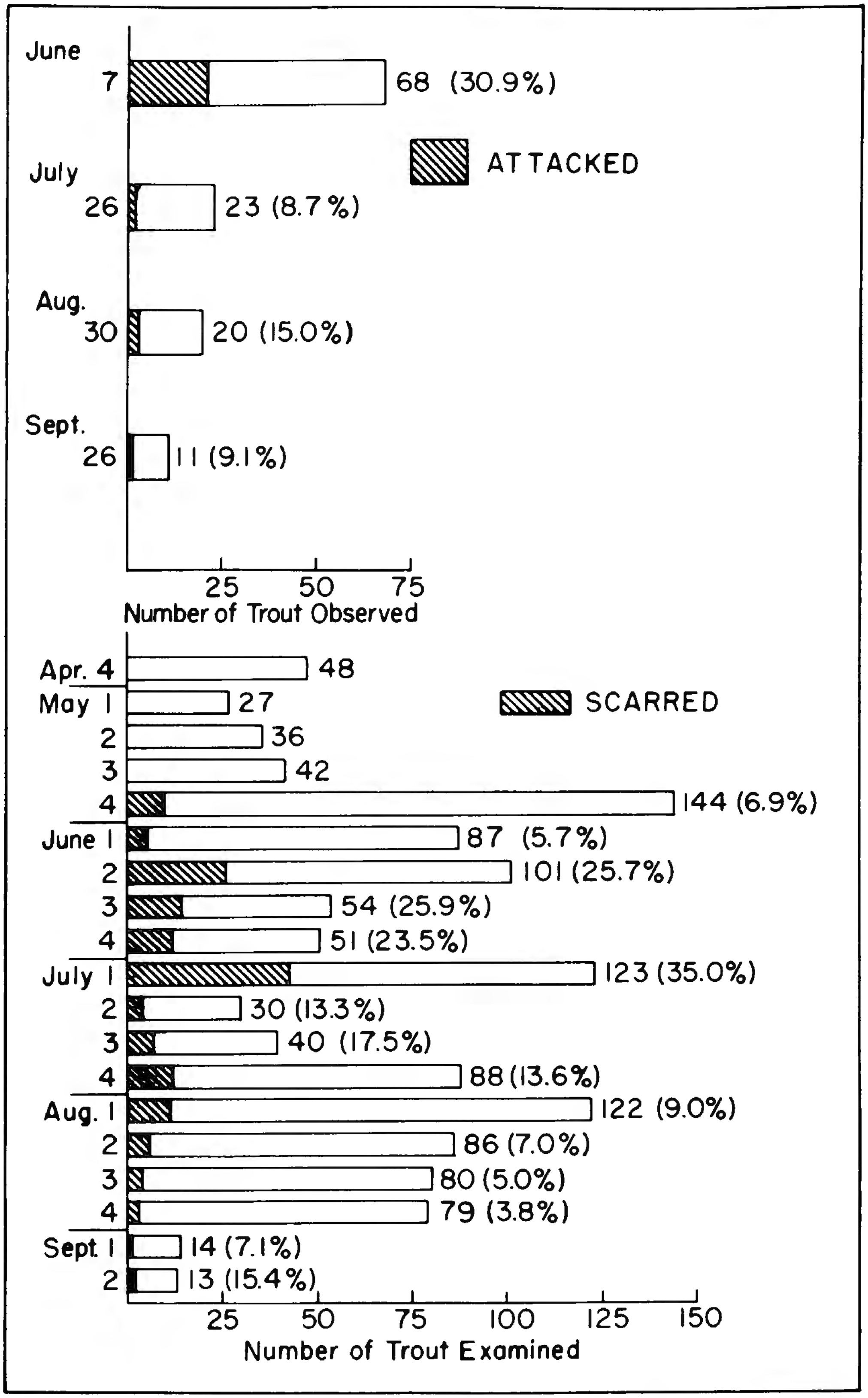

Figure 9.--Seasonal differences in the incidence of attacks by the lamprey: Above--Number of trout seen in underwater observations in the marking area during 1961, and percentage carrying lampreys at each date. Below--Number of trout examined in the anglers' catch in 1952 and the percentage bearing lamprey scars. Data are grouped by quarters of each month. In both graphs the number of observations and percentage attacked by lampreys (in parentheses) are to the right of the bar.

No scarred fish were taken until the last week of May, but early in July about 35 percent of the trout caught bore one or more lamprey scars. Of 1,265 trout examined during the 1952 fishing season, 160 (12.6 percent) had been attacked by one or more lampreys. This census was centered near my marking area (Shetter, 1962).

In a census taken from May 29 to June 17, 1939 in about the same area, 78 of 219 trout examined (35.6 percent) either had lampreys attached to them when caught or bore recent scars (Crowe, 1939).

Catch from traps.--Seasonal variation of the catch of lampreys in baited traps (where capture depended upon feeding) revealed the same pattern of extensive feeding in the summer and little or no feeding in late fall, winter, and early spring as suggested in the two previous sections. Traps baited with suckers were maintained rather consistently throughout the year (Fig. 10).

Part of the reduction late in the summer of the lamprey catch per unit of trapping effort was undoubtedly due to substantial mortality of lampreys from May to November (Fig. 17). However, their failure to enter traps in the winter was apparently due to inactivity of the lampreys rather than to their complete absence. Two mature and 79 newly transformed adults were collected from the marking area with an electric shocker in January 1961. The newly transformed adults were all taken from burrows in sand and silt, the same type of habitat where larvae were collected; location of the mature adults could not be determined.

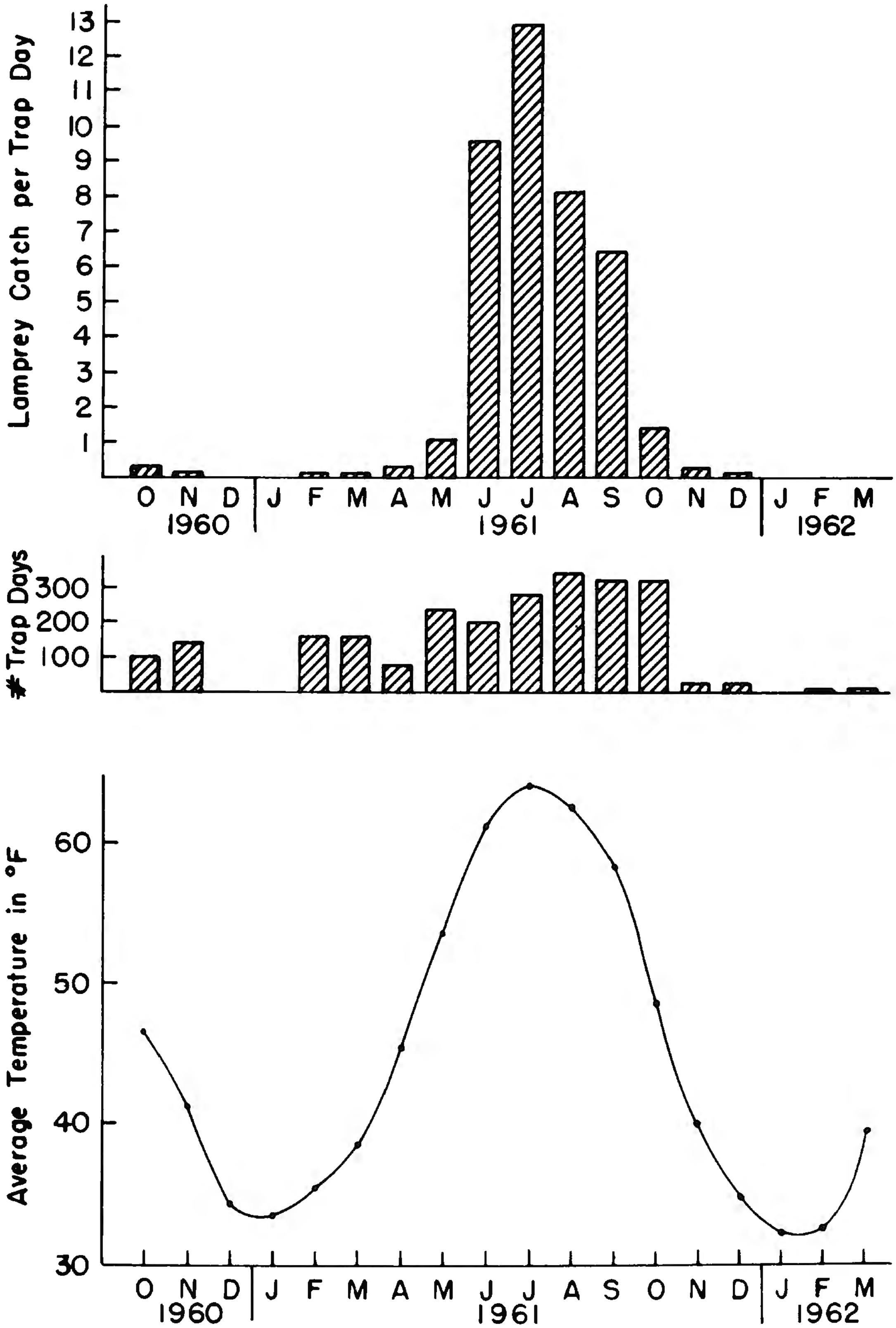

Figure 10.--Number of lampreys caught per trap-day, number of trap-days, and monthly mean water temperature, Manistee River, October 1960 to March 1962. Temperature data are from unpublished records of the U. S. Geological Survey.

Feeding in aquariums.--Adult lampreys in the river were largely inactive from November through April. Lampreys in the laboratory aquariums (constant temperature at 50° F) continued to feed during this period, suggesting that winter inactivity in the stream was primarily due to low water temperature.

The 79 newly transformed adults collected from the stream in January 1961 were placed in the raceway aquariums. On March 6, 1961, 10 of these were moved to one of the laboratory aquariums. On March 27 they were provided with live trout as prey and began to feed immediately. Twenty-two of the 79 lampreys were placed in three of the raceway aquariums and also supplied with prey trout during the same period. By May 12, when the experiment was terminated, both the feeding activity and growth of lampreys in the laboratory aquariums had greatly exceeded activity and growth of lampreys in the raceway aquariums (Fig. 11).

A similar test was conducted in the fall. On October 20, 1961 I collected from traps 24 adults that had fed throughout the summer. Twelve were placed in one of the laboratory aquariums, the remainder in one of the raceway aquariums. At each observation I recorded the identifying number of each lamprey feeding at that time. Until early November most of the lampreys in both raceway and laboratory aquariums were feeding. Then, both the stream temperature (Fig. 11) and the number of lampreys feeding in the raceway aquarium began to

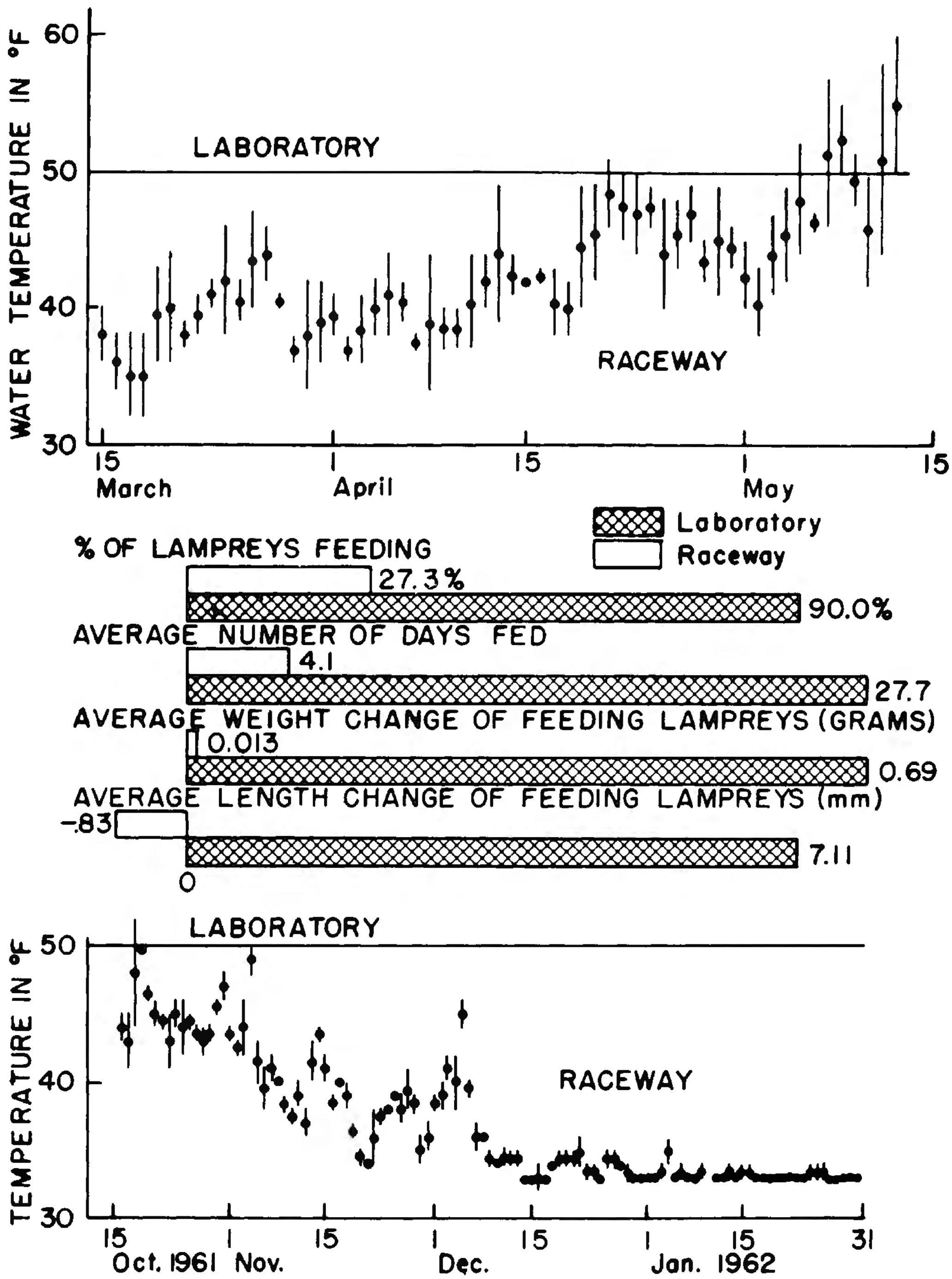

Figure 11.--Effect of water temperature on feeding and growth of the chestnut lamprey in aquariums: Upper--Water temperature in the laboratory and raceway aquariums, March 15 to May 12, 1961; Middle--Amount of feeding and growth by lampreys held in laboratory and raceway aquariums, March 15 to May 12, 1961; Lower--Water temperature in the laboratory and raceway aquariums, October 15, 1961 to January 31, 1962. In the temperature graphs the dot represents the mean of readings taken at 8:00 AM, 12:00 M and 5:00 PM. The vertical line represents the range. Temperature data are from records of the Grayling Fish Hatchery.

decline. From December 4 until termination of the work on January 30, 1962 no lampreys were seen to feed in the raceway aquarium, but most of the lampreys in the laboratory aquarium continued to feed during the entire period. Unfortunately the experiment was complicated by an outbreak of furunculosis that killed 8 of the 12 lampreys in the laboratory aquarium.

No measurements were made on the lampreys feeding in the laboratory aquarium to determine their rate of growth. Four lampreys used in another experiment in the laboratory aquariums did make substantial growth through the fall and winter (see Table 3).

The most apparent difference between the two groups of aquariums was in water temperature (Fig. 11). There were other slight differences between the two, related to differing water supply. Low water temperature appeared to be a major cause for the dormant period of the chestnut lamprey in the stream from November to April.

Cessation of growth and feeding of the brown trout in fall and winter was attributed to lowered water temperature (Swift, 1961). That another factor in addition to temperature may also be involved is shown by work on the bluegill, Lepomis macrochirus, (Anderson, 1959). Some bluegills were fed for 16 months in cages in a southern Michigan lake, and others were fed in the laboratory at uniform temperatures (50°, 60°, 70°, and 80° F) in all four seasons. The individuals in the laboratory fed and grew considerably more from November through

April than did fish in the lake, but showed significantly less feeding and growth in the late summer, fall, and winter than in May and June. The decrease in feeding and growth in the lake was attributed to an interaction of temperature and a seasonal factor independent of temperature. From the observations of others, Anderson concluded that the seasonal factor was most likely an endocrine mechanism. Temperature and the seasonal factor appeared to operate together by regulating the rate of food consumption.

Daily pattern of feeding attacks in the stream

During September 2-5, 1961 I checked 5 trap sets at approximately 7:00 AM and 7:00 PM each day. Of 140 lampreys captured in wire or glass traps in 4 days and 3 nights, 136 (97.1 percent) entered the traps at night. Only one of all these lampreys attacked a fish in the wire traps during daylight hours (Table 1). This evidence pointed to a definite nocturnal habit of attack.

Table 1.--Number of adult lampreys caught in traps during daylight and darkness, Manistee River, September 2-5, 1961.

	Sept. 2		Sept. 3		Sept. 4		Sept. 5	Totals		
	Day	Night	Day	Night	Day	Night	Day	4 days	3 nights	All
Wire	0	14	0	38	0	23	1	1	75	76
Glass	1	9	1	37	1	15	0	3	61	64
Total	1	23	1	75	1	38	1	4	136	140

↑ traps set at 7:00 AM (Sept. 2, Day); ↑ traps moved and reset at 7:00 PM (Sept. 3, between Day and Night)

Food of the lamprey in the stream

Composition of the fish population.--Data from the 1952 creel census and from my underwater observations in 1961 were used to estimate the species composition and the size of the fish population in 1961. I estimated that about 9 of every 10 fish of approximately legal size (7 inches and larger) seen in all the underwater observations were trout. The rainbow predominated over the brook trout in the ratio of 120:8 among fish seen in the marking area. The other large fish seen were nearly all white suckers. I have assumed that this sample of fish seen was a true representation of the stream population. Several species of small minnows were abundant, but most were too small to be considered as an important food source for the lamprey.

No direct estimate of the size of the trout population was made in 1961, but some inferences were drawn from the stocking rate of hatchery trout and data collected in the 1952 creel census. In that year, when the stocking rate was about 160 pounds of trout per mile, about 75 percent of the trout caught were hatchery-reared fish. In 1961 the stocking rate was much greater (about 260 pounds per mile). No creel census was attempted in this year, but I have assumed that the proportion of stocked trout in the catch during 1961 was not less than 75 percent, and was probably greater. On that basis, in 1961 no more than 350 pounds of both stocked and native trout would have been available to anglers per mile of stream.

Species attacked.--In 6 hours of diving observations within the marking area I saw 32 lampreys attached to fish; 30 of these were on trout. Although exact records were not kept for lampreys seen or fish in other parts of the river, the conclusion was the same--nearly all lamprey predation in the upper Manistee River during 1961 was directed at the trout population.

Early in the season, up to 62 lampreys were taken from a single large sucker confined to a wire trap for two days. This very high rate of attack did not occur among suckers free in the stream. The few large suckers I saw had from 0 to 3 lampreys attached. Presumably, fish swimming free in the stream were able to evade many approaching lampreys, but lost this advantage when in the traps.

The lamprey attacked several other species of fishes in the stream, but there was no noticeable selection for any one of these. Particularly surprising was the sight of several blacknose dace about 3 inches long carrying lampreys twice their length.

Source of trout attacked.--There was some suggestion that trout stocked from a hatchery were more vulnerable to lamprey attack than were wild trout. Among the fish examined in the 1952 creel census, there was no significant difference in the percentage of scarring among the three species of trout present (Table 2). So for further analysis by source, all species were combined. The percentage of scarring was greater among stocked fish than among wild

Table 2.--Numbers of trout, examined in the anglers' catch during 1952, that had been scarred by lampreys. All the 160 scarred fish were not recorded by species or origin; only those so identified are listed.

	Species				Origin		
	Brook	Brown	Rain-bow	Total	Hatch-ery	Wild	Total
Observed number of scarred fish	8	26	50	84	63	13	76
Total number of fish checked during season	169	364	732	1, 265	918	347	1, 265
	chi square = 1.08 d.f. = 2 $0.50 < p < 0.75$				chi square = 3.57 d.f. = 1 $p \cong 0.06$		

fish, but the difference was not quite significant at the 5 percent level (Table 2).

These data, however, may have been biased by an element common to many such studies--only the trout surviving to be caught by anglers were examined. Fish from one source may have died from lamprey attack more rapidly than did those from the other source. Since both stocked and wild fish in the sample were of about the same average length, I would expect any difference of this sort to be in the direction of more rapid mortality among stocked trout (Miller, 1958; Vincent, 1960). If differential mortality occurred, the true proportion of scarred stocked fish would have been greater than that indicated by the sample from the anglers' catch.

<u>Destruction of fish in aquariums</u>

How many grams of trout were destroyed by an individual chestnut lamprey in the course of its growth? The destructiveness of the sea lamprey was estimated by experiments in aquariums (Lennon, 1954; Parker and Lennon, 1956). I was able to get very little information on feeding of the chestnut lamprey in aquariums because of outbreaks of furunculosis. The limited information obtained was used to see whether data on the destructiveness of the sea lamprey could be applied to the chestnut lamprey. All the following comparisons are of sea and chestnut lampreys of approximately equal weight, unless otherwise noted. All data on the sea lamprey are from the 22 survivors reported by Parker and Lennon (1956).

<u>Growth rate.</u>--The sea lamprey in aquariums grew to a terminal weight nearly ten times that of the chestnut lamprey in the Manistee River (Fig. 12), but a more meaningful comparison is between the daily instantaneous rates of growth (Brody, 1945). These differed by a factor of 2, with some seasonal variation (Fig. 12). During the period when the two lampreys were of approximately equal size, the average daily instantaneous rate of growth in weight for the sea lamprey was 0.0232; for the chestnut lamprey it was 0.0117 (see later section on growth).

<u>Fish-kill per hour of feeding.</u>--Twenty-two trout and suckers used in my feeding experiments in the fall of 1959 and 1960 were judged

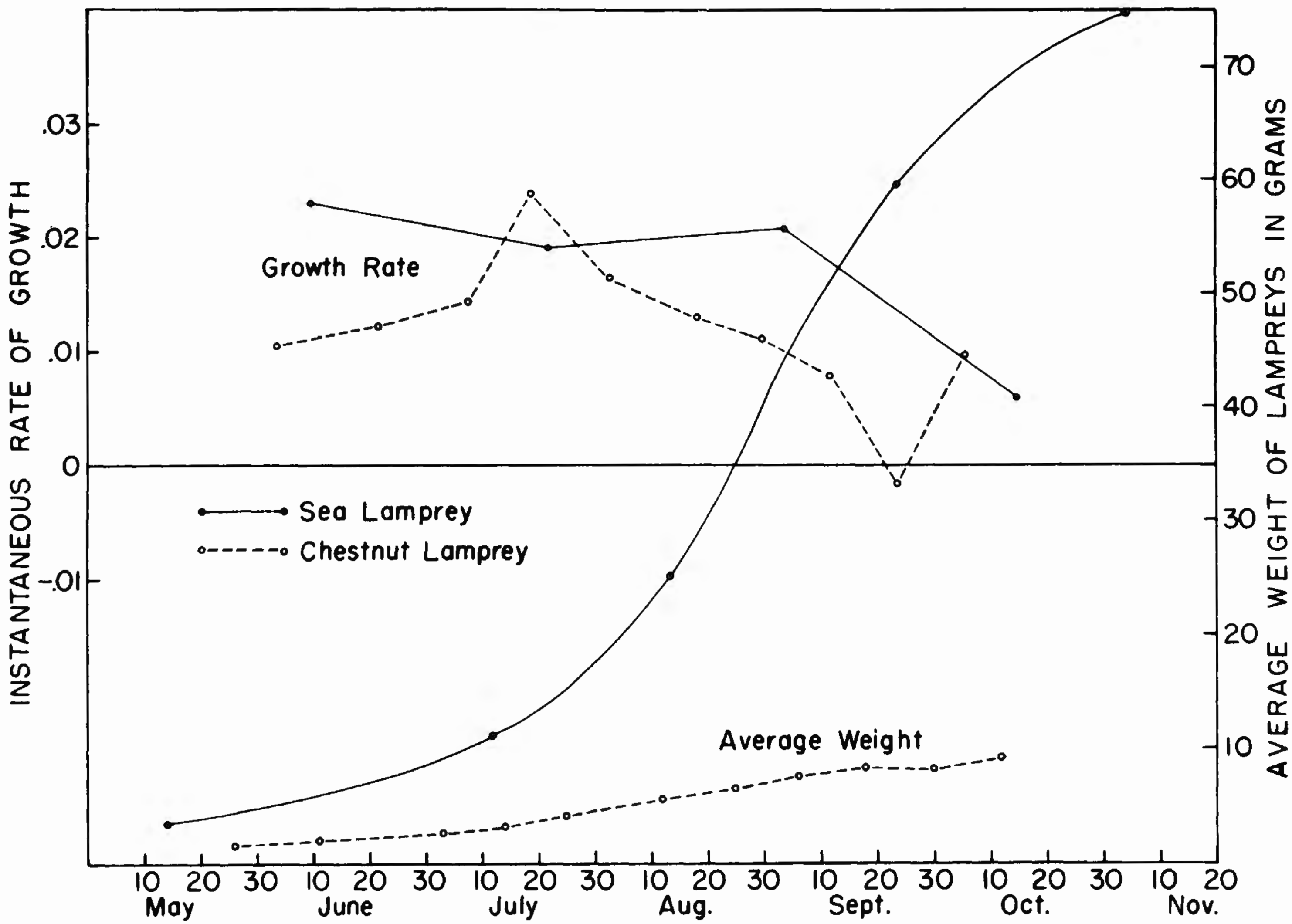

Figure 12.--Comparison of the daily instantaneous rate of growth in weight (upper) and absolute growth (lower) for the sea lamprey in aquariums and the chestnut lamprey in the Manistee River. Data on the sea lamprey are from Parker and Lennon (1956).

to have died solely from the effect of chestnut lamprey predation. They were apparently not affected by furunculosis or other diseases (based both on gross and on bacteriological examination). Although the lampreys in each of the three series (July to September 1959, September to October 1960, and October 1960 to February 1961) were of different average weight (7.3, 8.2, and 9.7 grams respectively), there seemed to be no significant difference in their destructiveness. Therefore all three groups were combined to estimate the fish-kill per day of feeding (Fig. 13). Large fish were able to survive lamprey attack for a longer period than small ones, but there was little difference in the grams of fish killed per hour between the large and small fish. The average chestnut lamprey (8.5 grams) killed 0.27 grams of fish per hour of feeding. An average sea lamprey of 7.6 grams killed 0.31 grams per hour.

Growth per hour of feeding. --Only four chestnut lampreys survived to be weighed twice during their destructive period. Their average gain in weight per hour of feeding (0.0040 gram, range 0.0030-0.0052) was about half that for the average sea lamprey (0.0085 gram). Nine smaller chestnut lampreys (average 1.9 grams) feeding from March 27 to May 12 gained an average of 0.0010 gram per hour of feeding (Table 3).

Destructive potential. --The statistic necessary to convert production to fish-kill is the grams of fish killed by the chestnut lamprey per gram of its growth. I had no direct estimate of this ratio.

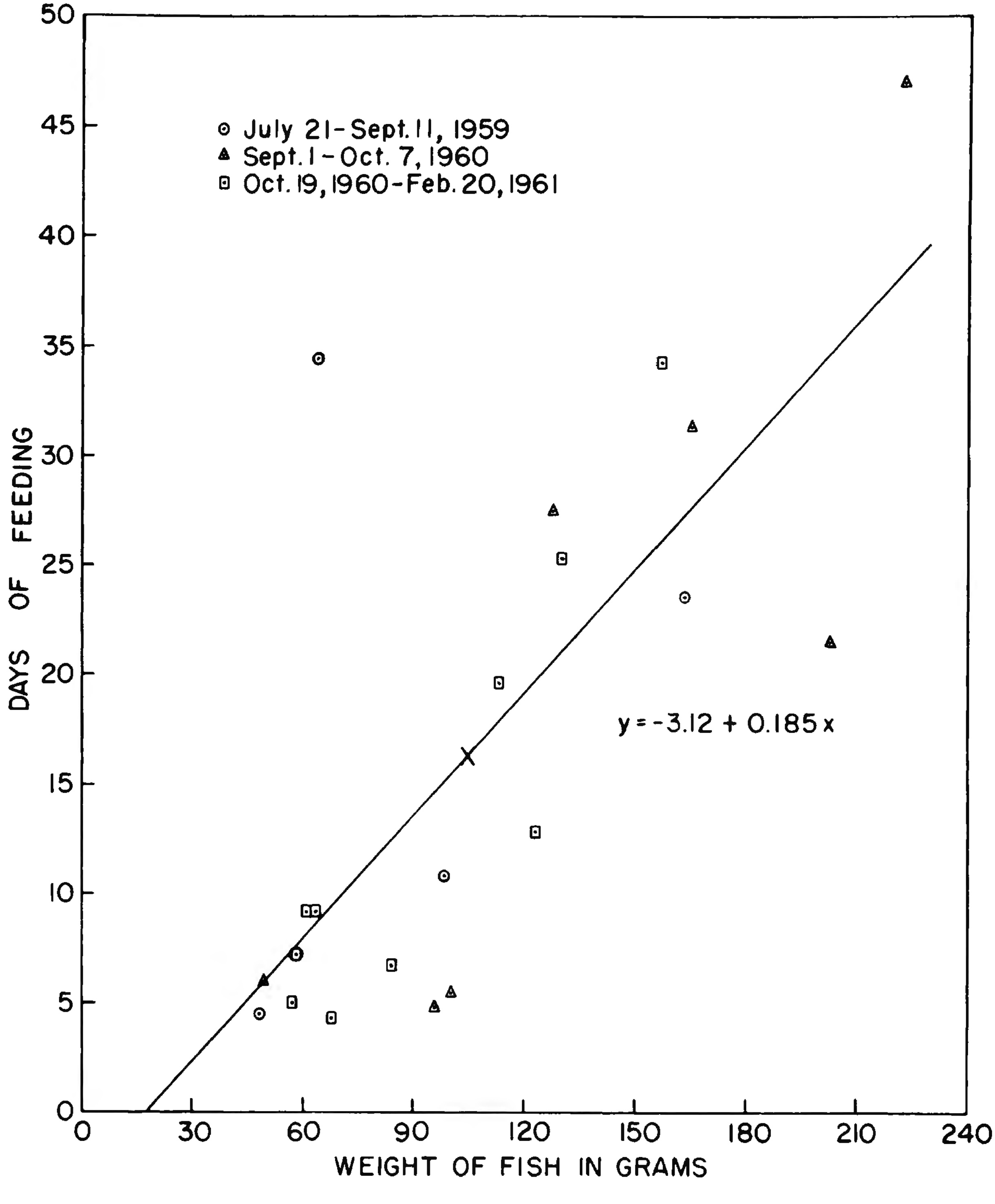

Figure 13.--Relationship between size of host fish and the days of feeding required by the chestnut lamprey to kill the fish. Data are combined for three series of experiments. The average weight of all 22 lampreys used was 8.5 grams.

Table 3.--Comparison of feeding, daily instantaneous growth rate (g), and effect on host fishes (in aquariums) of the sea lamprey and the chestnut lamprey. Data for the sea lamprey from Parker and Lennon (1956).

1	2	3	4	5	6
Interval	Average weight during interval (grams)	g	Grams fish killed per hour of feeding	Grams growth per hour of feeding	Grams fish killed per gram growth
Sea lamprey[a]					
May 15-July 2	7.6	0.0232	0.31	0.0085	36.3
July 3-Aug. 13	18.2	0.0190	2.90	0.0371	78.2
Aug. 14-Sept. 24	42.3	0.0208	8.00	0.0891	89.8
Sept. 25-Nov. 5	67.4	0.0060	8.50	0.0710	119.7
Nov. 6-Dec. 17	76.7	0.0005	3.50	0.0269	130.1
Chestnut lamprey[b]					
March 27-May 12	1.9	0.0076	--	0.0010	--
Sept. 1-Nov. 11	7.5 11.4	0.0119 0.0064	0.27[c] 0.27	0.0046 0.0034	59[d] 79
Oct. 19-Jan. 30	14.0 11.4	0.0036 0.0027	0.27 0.27	0.0052 0.0030	52 90

[a] Average values for 22 specimens.

[b] March-May group composed of 9 lampreys. The other observations were of a single lamprey.

[c] Average value determined for all 22 chestnut lampreys from the data of Fig. 13.

[d] Value for each of the 4 lampreys determined indirectly by dividing column 4 by column 5.

Very small chestnut lampreys were able to achieve some growth without killing the host fish. From March 27 to May 12, 1961, nine chestnut lampreys (average initial weight 1.6 grams) each gained an average of 0.69 grams feeding on two brook trout (115 and 150 grams) without causing death of the host.

In the sea lamprey the destructive potential, expressed as grams of fish killed per gram of growth, was directly related to the size of the lamprey (Fig. 14). Presumably, this was also true for the chestnut lamprey.

By dividing one by the other, I combined my estimate of fish-kill per hour of feeding (for all the chestnut lampreys used in the feeding experiment, Fig. 13) with the estimate of grams of growth per hour of feeding (for the four chestnut lampreys weighed twice) to get an indirect estimate of the fish-kill per gram of growth for these four lampreys (Table 3):

$$\frac{\text{fish-kill/hour}}{\text{grams growth/hour}} = \text{fish-kill/gram of growth}$$

The value for each of these four lampreys was in reasonable agreement with those for the sea lamprey (Fig. 14).

Confounding effects.--The water temperature in experiments with the chestnut lamprey was constant at 50° F. For those on the sea lamprey it varied with the temperature of the surface water of Lake Huron, but averaged near 60° F during the period of comparison.

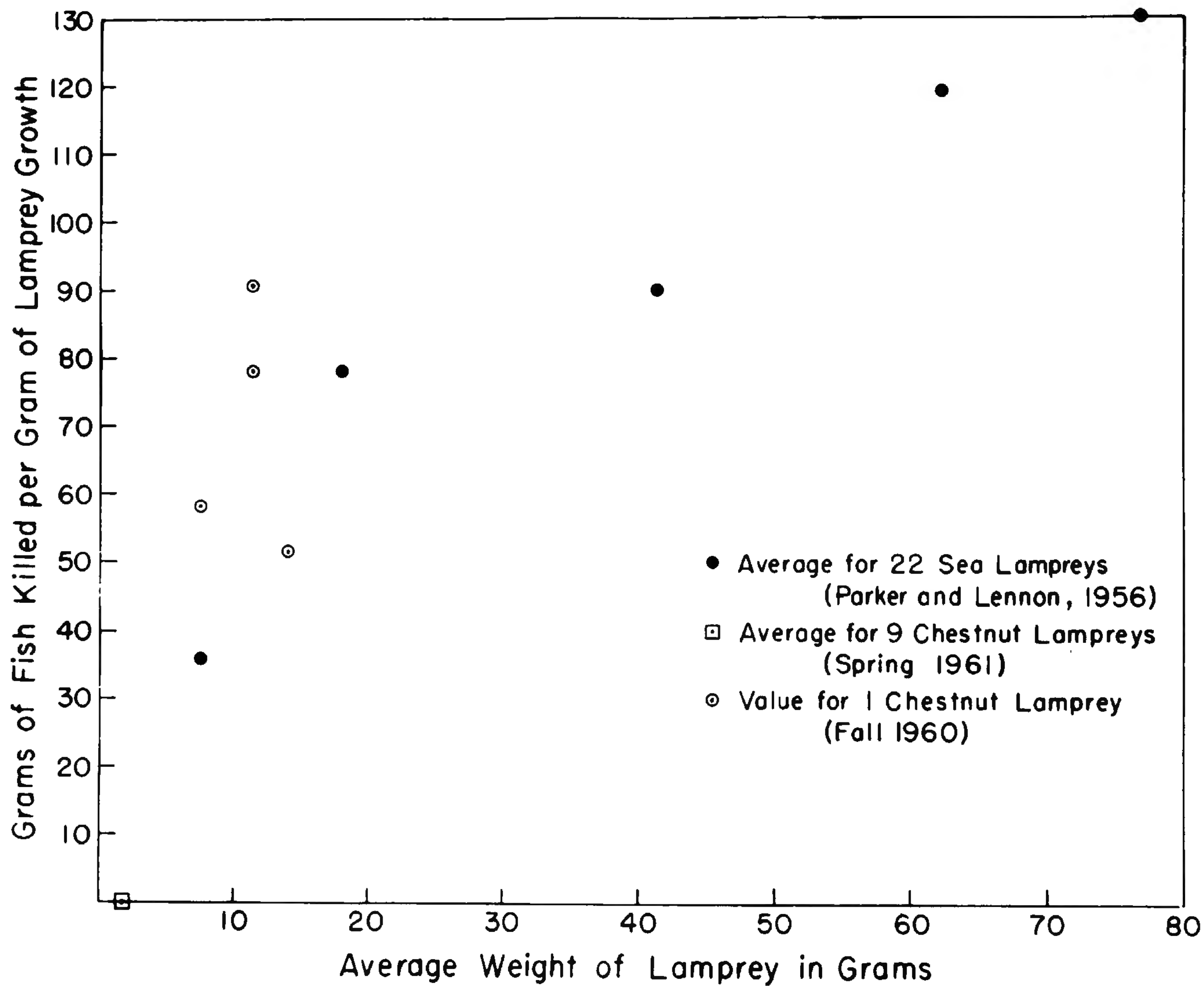

Figure 14.--Relationship between the average weight of a lamprey and the grams of fish killed per gram of growth by the lamprey.

Since water temperature had a significant effect on its feeding, the chestnut lamprey would likely have been more destructive at 60° than it was at 50° F.

Most of my work was done in the fall and winter, when the adult lampreys in the stream fed little or not at all. The warm water in the aquarium was probably responsible for continued feeding there, but the efficiency of food conversion may have been less than that during the summer. Such a seasonal decrease in the food conversion coefficient has been shown for the bluegill (Anderson, 1959; Gerking, 1962).

Since very small chestnut lampreys can feed and grow without killing the host fish, the question arises as to the size at which the lamprey becomes able to kill. In Fig. 13 I have plotted the point of zero fish-kill at the average size of the lampreys during this feeding experiment (1.9 grams), but perhaps lampreys of somewhat larger size would also feed without killing the host.

Lampreys confined in the aquariums were required to do little or no work to maintain their position or to seek prey, in contrast to those in the stream. Their efficiency of food conversion should therefore have been greater than that of lampreys in the stream. In addition, prey fish presumably succumbed more readily to lamprey attack in the stream, where energy was expended in maintaining position and procuring food, than they did in the aquarium. For these two reasons, a gram of growth by a lamprey in the stream should represent a greater kill of fish than would a corresponding gram of growth in the aquarium.

To summarize this complex situation: The instantaneous rate of growth of the sea lamprey in aquariums was about twice that of the chestnut lamprey in the Manistee River. The sea lamprey killed more fish per hour of feeding than did the chestnut lamprey. The latter grew somewhat slower per hour of feeding, with the result that the fish-kill per gram of growth appeared to be about the same for the two lampreys when they were of equal size. As the best estimate of the destructive potential of the chestnut lamprey, I have used linear interpolation between the three lowest average points on Fig. 14 (chestnut lamprey 1.9 grams, sea lamprey 7.6 and 18.2 grams), plotted on an enlarged scale. Several extraneous factors confounded the analysis. Clearly, any estimate of the fish-kill ascribed to the feeding of the chestnut lamprey in the Manistee River must be made in general terms.

DYNAMICS OF THE ADULT POPULATION

What impact does the lamprey have on the trout population in the Manistee River? Because it was difficult to determine the number of dead fish in as large a stream as the Manistee, I devised an indirect method to estimate the loss of trout due to lamprey predation. The net production[2] of the lamprey population was computed from its vital statistics for the feeding season, which extended from May through October. The production was multiplied by grams of fish killed per gram of lamprey growth, determined in aquariums, to estimate the mortality that could have occurred due to feeding of the lamprey.

Vital statistics of the lamprey population

Methods

The length of each lamprey and the dates and places of its recapture were coded and punched on IBM cards. An IBM 402 tabulator and an IBM 709 computer were used in analysis of the data. For purposes of population estimation it was not always desirable to merge returns from adjacent days, because I occasionally moved traps to

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[2]The term is used in the sense of Ivlev (1945) and Clarke (1946) as the total quantity elaborated by a population during a stated interval, regardless of whether or not all of it survives to the end of that time (the sum of growth made by all the members of a population).

new areas or temporarily ceased trapping. Since lampreys had been marked individually, recaptures could be segregated. I divided the trapping season from May 19 to October 27 into 12 periods of between 9 and 15 days duration (Table 4). Captures were grouped into these periods for estimation of population size and growth rate.

The net production was calculated by the method of Ricker and Foerster (1948). The statistics needed for its computation are: 1) the population size at some time during the season, 2) the rate of mortality during successive short periods throughout the season, and 3) the rate of growth during the same periods. Reliable information was obtained for each, and the resulting estimate of production is thought to be accurate.

Since the actual computation involves the product of the instantaneous rate of growth during a period and the average weight of the population during the same period,[3] I used instantaneous rates in all preliminary computations:

$$X = \frac{\ln A_2 - \ln A_1}{t_2 - t_1}$$

where X is the daily instantaneous rate of growth or mortality, A_1 and A_2 are successive estimates of the parameter (length, weight, population size, etc.), ln is the natural logarithm, and $t_2 - t_1$ is the

[3] The periods used were those described in Table 4. They were short enough to allow the assumption of a constant rate during the period, an important consideration in the use of instantaneous rates.

Table 4.--Division of the trapping season into periods, with pertinent results for trapping in each period within (in) and outside (out) the marking area.

Period number	Inclusive dates	Number days in period	Number trap lifts In	Number trap lifts Out	Total captures[a] In	Total captures[a] Out	Recaptures In	Recaptures Out	Catch per trap lift In	Catch per trap lift Out	Percentage of recapture In	Percentage of recapture Out
1	May 19-June 2	15	70	--	202	--	25	--	2.9	--	12.4	--
2	June 4-June 18	15	70	--	1,463	--	176	--	20.9	--	12.0	--
3	June 29-July 7	9	50	--	1,441	--	145	--	28.8	--	10.1	--
4	July 9-July 19	11	50	--	1,606	--	182	--	32.1	--	11.3	--
5	July 18-Aug. 1	15	--	42	--	1,081	--	131	--	25.7	--	12.1
6	Aug. 5-Aug. 19	15	30	35	562	629	200	156	18.7	18.0	35.6	24.8
7	Aug. 20-Aug. 31	12	30	42	454	984	205	361	15.1	23.4	45.2	36.7
8	Sept. 1-Sept. 11	11	--	42	--	1,000	--	308	--	23.8	--	30.8
9	Sept. 12-Sept. 24	13	30	28	469	367	224	141	15.6	13.1	47.8	38.4
10	Sept. 25-Oct. 5	11	25	41	139	351	102	219	5.6	8.6	73.4	62.4
11	Oct. 7-Oct. 17	11	20	28	103	167	81	96	5.2	6.0	78.6	57.5
12	Oct. 19-Oct. 27	9	--	35	--	32	--	23	--	0.9	--	71.9
13[b]	Oct. 30-Nov. 3	5	15	14	7	9	3	7	0.5	0.6	42.9	77.8
Totals			390	307	6,446	4,620	1,343	1,442	16.5	15.0	20.8	31.2

[a] Some unmarked lampreys were captured more than once; the number of individual lampreys captured was somewhat less than the figure indicated.

[b] Recaptures in this period were disregarded in population estimates.

number of days between the successive estimates of A. This rate estimates the percentage change in the population parameter per day (cf. Macfadyen, 1957; Ricker, 1958).

Validity of assumptions

A mark-and-recapture procedure such as I have used involves a number of assumptions: 1) mortality occurs at the same rate among marked and unmarked fish, 2) the marked and unmarked fish are equally vulnerable to the gear employed, 3) the mark is not lost, 4) the marked fish become randomly mixed in the population or subsequent sampling is at random with respect to the population structure, and 5) all of the marks are recognized and reported (Ricker, 1958). In the following analysis I determined that these assumptions were generally valid when applied to my work. Assumptions of some of the methods regarding mortality and recruitment are discussed later in the section treating population size.

Mortality.--The two marks used in the present study (pigment injection and fin notch) were inconspicuous and apparently did not interfere with swimming. The marks themselves should not have caused any mortality (Wigley, 1952). It seemed that any mortality due to marking would have been caused by the injection procedure, which was somewhat difficult when the lampreys were very small. Of 1,915 lampreys marked in the field program, however, only 4 failed to revive after marking. The mortality rate for marked lampreys, shown in Fig. 19, was not significantly different from that for the entire population.

A similar injection procedure did not result in any unusual mortality in experiments with larval sea lampreys, once experience was gained with the technique (Martin Hansen, personal communication). Injection of latex under the skin did not affect survival of several fish species (Gerking, 1958, 1962). The injection mark did not have any obvious adverse effect on survival of adult chestnut lampreys in aquariums.

Vulnerability.--My limited information suggested that there was no significant difference in vulnerability between marked and unmarked lampreys. It did not appear that feeding by lampreys was inhibited by marking; of the 1,015 lampreys recaptured at least once, 420 were taken on the next trap lift following marking. Lampreys marked and placed in aquariums began to feed immediately, as did unmarked lampreys, and there was no obvious difference in the feeding of the two groups.

Increased or erratic movement for a time after marking has been reported for some fishes (Ricker, 1958). Extensive movement shown by marked lampreys suggested this occurrence here, but movement of unmarked lampreys was also considerable. There appeared to be no systematic difference in the rate of recapture related to time after marking (Fig. 19).

Retention of marks.--Both types of marks appeared to persist well on lampreys in the stream during the entire trapping season from May to November. Late in the season the pigment spots on several lampreys had been lost, but the location of injection could still be easily determined. In a few cases, fin notches regenerated several months after marking, leaving a clear band visible at the location of the notch.

Injection of pigment as a marking method has not been reported for adult lampreys, but such marks have persisted for several years on larval lampreys (Wigley, 1952; Martin Hansen, personal communication). There was neither loss of marks nor unrecognizable regeneration of notches among 150 lampreys used in aquariums for feeding experiments lasting up to six months.

Distribution.--Either the distribution of marked fish into the unmarked population or the subsequent fishing effort for recaptures should be at random (Ricker, 1958). My plan for trap placement and release of marked lampreys was designed to provide for both of these requirements.

In practice the plan had some limitations. The large number of lampreys taken only two days after marking suggested that these individuals may not have become randomly mixed in the marking area. Because of their extensive movement, however, the marked lampreys probably became rapidly mixed with the unmarked population. The similarity of the ratio of marked to unmarked lampreys 1 1/2 miles above and below the marking area (Table 5) suggested that the lampreys marked were in fact a random sample from the population in the marking area (Ricker, 1958).

Table 5.--Percentage of lampreys marked in the marking area and recaptured at traps 1 1/2 miles upstream and downstream from the area, by period of recapture.

Period	Total captures		Percentage of recaptures		
	Above	Below	Above	Below	Chi-square
6	66	150	27.3	11.3	7.44[a]
7	119	193	25.2	24.4	0.001
8	160	120	21.9	18.3	0.33
9	78	68	28.2	36.8	0.86
10	60	108	26.7	30.6	0.13
11-13	24	50	41.7	32.0	0.31
Totals	507	689			9.07 (d.f. = 6, $0.10 < p < 0.25$)

[a] Significant at the 1 percent level.

Recognition of marks.--Since no outside observers were involved and I examined all lampreys, the chance of missing any marked animals was minimized. Notches in the fin caused by injury or deformity were present in a small fraction of lampreys caught. They were distinguishable from my clips and did not cause confusion.

Age structure

No reliable method has been reported for determining the age of any larval or adult lamprey, nor is the length of larval life known

for certain (Stauffer, 1962). Nevertheless, from the following observations I concluded that chestnut lampreys feeding as predators during the 1961 season were nearly all of a single year-class:[4]
1) The length-frequency distribution of all unmarked lampreys taken during June 4-18 resembled that for a homogeneous population (Fig. 15). The bimodal shape of this distribution in September has been attributed to a differential growth rate for males and females (Fig. 8). 2) A steady upward progression in the mean length, its standard deviation, and upper and lower range occurred from May to October (Fig. 16). The curve drawn through the mean length resembled growth typical of a single individual (Brody, 1945). 3) Growth of many of the marked lampreys paralleled growth estimated for the unmarked population in Fig. 16. Some of the smallest lampreys marked in May grew to approximate the maximum length observed for any unmarked individual.
4) Two morphologically distinct groups were present in the spring, mature adults and feeding adults (Fig. 7). The length of each of 19 mature adults measured in the spring of 1961 was more than 2 standard deviations above the mean length of the feeding adults (Fig. 16).
5) After the spawning season in June, no mature lampreys were seen, and all the feeding adult lampreys seemed morphologically similar.

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[4] I will restrict use of the term "year-class" in this paper to all lampreys which transformed to the adult feeding stage in one given year. No decision is yet possible on whether or not these lampreys all hatched in the same year.

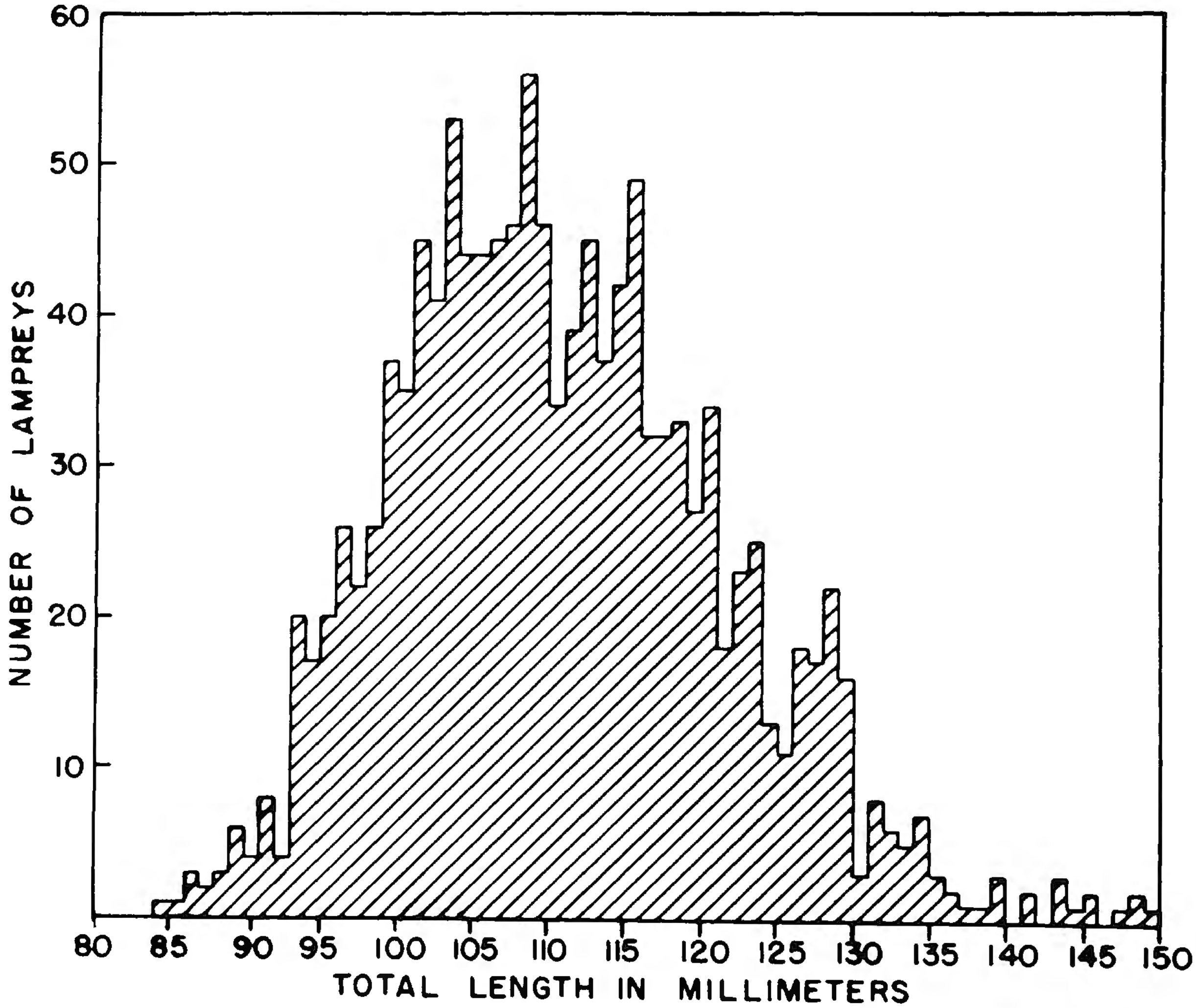


Figure 15.--Length-frequency distribution of 1,273 captures of unmarked adults of the chestnut lamprey made June 4-18, 1961.

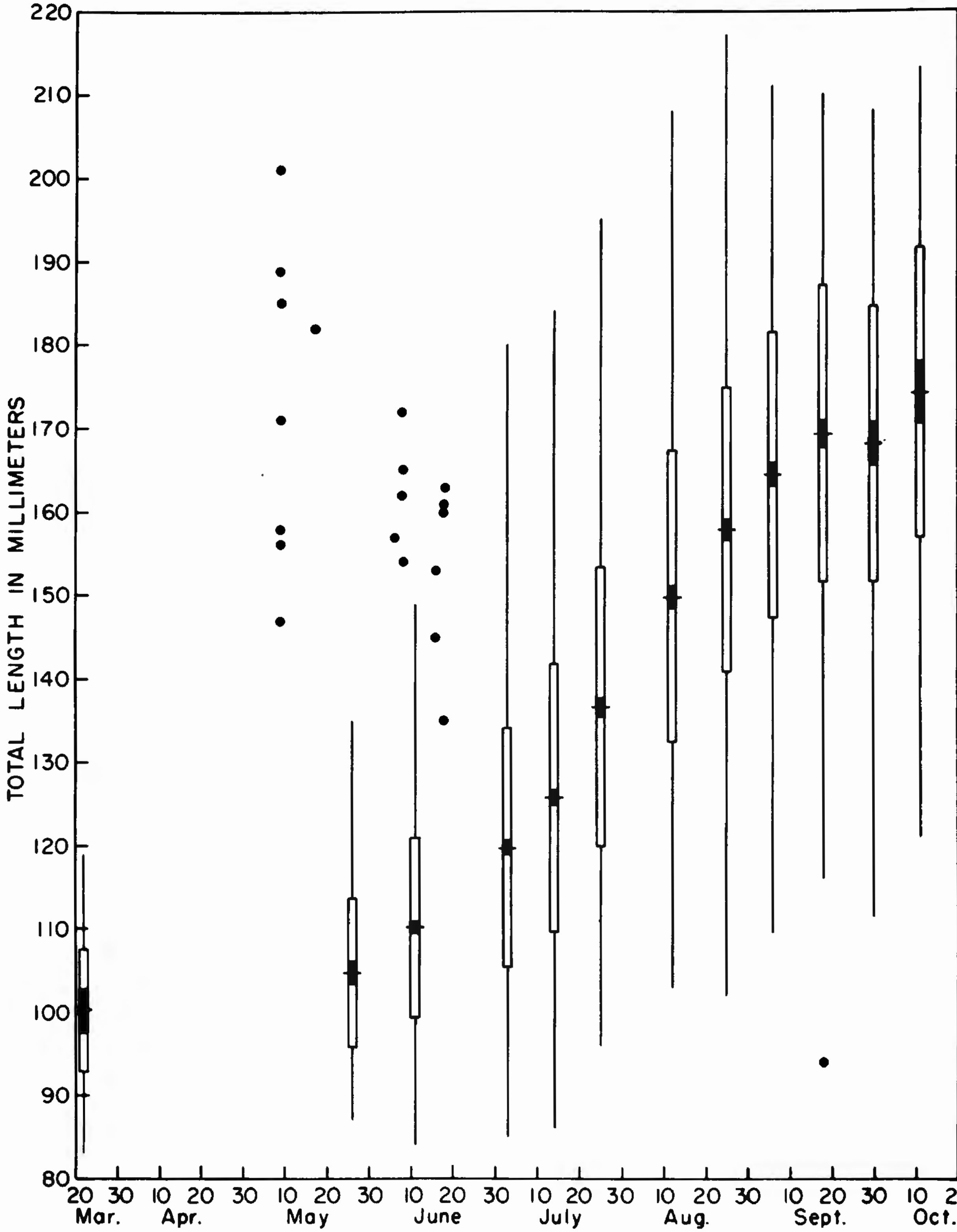


Figure 16.--Estimated growth of the chestnut lamprey in the Manistee River, based on measurement of 8, 234 captures of unmarked feeding adults made from March to October 1961. The single dots in the upper left are for the individual mature adults measured in the spring of 1961. The single dot in the lower right is for the newly transformed adult collected on September 18. Other symbols are described in the caption of Fig. 8. The average length shown for March is from 34 of the specimens collected in the marking area with an electric shocker in January 1961 and held in raceway aquariums until March.

6) On September 18 I trapped a single individual much smaller than the other feeding lampreys (Fig. 16). On the basis of its length and poorly developed mouth, I assumed it was a newly transformed adult. It resembled those captured with the electric shocker in the marking area in January 1961.

From my work on the chestnut lamprey and that of others on related species, the following generalized life cycle for the adult chestnut lamprey in the Manistee River is proposed:

Metamorphosis from the larval stage begins during the summer and is completed by January (Table 6). The sequence of events in metamorphosis appears to be similar to that in the closely related silver lamprey (Vladykov, 1949). The newly transformed adult may feed as a predator briefly in the first fall, but it is inactive over the winter. The following May this lamprey begins to feed, at a length of about 100 mm and a weight of 1-2 grams. It preys actively until

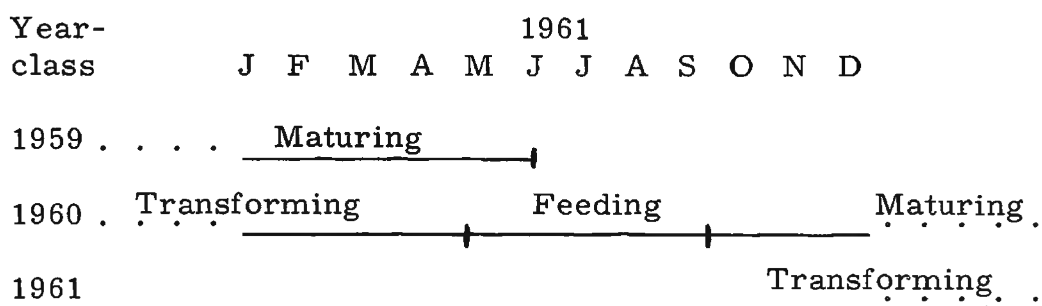
Table 6.--Occurrence of transforming larvae and newly transformed adults of the chestnut lamprey in collections made with an electric shocker in the Manistee River. Each collection included several hundred Ichthyomyzon larvae.

	Aug. 5-12, 1959	Sept. 19-26,[a] 1958	Jan. 10-17, 1961
Newly transformed adults	Absent	Absent	Present
Transforming larvae	Present	Present	Absent

[a] Data from Crowe (1959).

October, at which time its length is about 180 mm and its weight about 10 grams. From November until the following spring it is again inactive, and there is some decrease in both length and weight. The now mature adult lamprey may feed briefly in the spring. Sometime in June, after about 18 months in the adult phase, it spawns and then soon dies.

Thus at one time or another during any one calendar year there may be three year-classes of the adult present in the stream: the newly transformed adults (only in the fall), the intermediate feeding stage (throughout the year), and the mature adults (only in the spring). The only extensive feeding during the year is done by the intermediate stage and occurs from May through October.



Population size

Methods.--The marking area of the Manistee River was the only place in which trapping was consistent throughout the season. Accordingly, for purposes of population estimation, only lampreys marked and recaptured in this area were considered. I had designed the mark-and-recapture plan for analysis by the method of Schumacher-Eschmeyer (1943), shown by DeLury (1958) to be superior to the Schnabel (1938) method. However, both these methods of population estimation depend strongly upon the assumption that the population is unchanging throughout the period of marking. Clearly, this assumption was not met for the population within the marking area, even during a period as short as two weeks. Marked lampreys were moving out of the area rapidly, and I assumed that unmarked ones were moving in at about the same rate. In addition, some natural mortality was occurring. Two modifications of established methods of population estimation seemed appropriate to this situation.

DeLury (1958) proposed a multiple regression modification of the Schumacher-Eschmeyer method that allows an estimate of initial population size and instantaneous rates of mortality (emmigration and natural mortality in my data) and recruitment (immigration of unmarked lampreys). The unmodified Schumacher-Eschmeyer estimate was calculated for comparison. In both of these methods recaptures were accumulated for one or two trapping periods.

Parker (1955) proposed a linear regression modification of the Petersen method that corrects the initial population estimate for recruitment. The Petersen method is not affected by mortality, so long as mortality is equal between marked and unmarked fish.

The 95 percent confidence limits for the Schumacher-Eschmeyer and Parker methods were calculated as described by

Ricker (1958). For the DeLury method, calculations followed Snedecor (1956, p. 418).

Results.--Early in the season, estimates of the population in the mile-long marking area derived from the Parker method were significantly larger than those from the DeLury method (Table 7). Late in the season they were in closer agreement (Fig. 17). Although the 95 percent confidence limits for most estimates overlapped, the consistent difference between estimates from the two methods was significant.

The DeLury method utilized the maximum available information (it was based on all 6,446 captures made in the marking area, of which 1,267 were recaptures of lampreys that had been marked in the area (see Appendix A). Thus I favored it over the Parker method, for which I could effectively use only 60 percent of the 1,758 lampreys marked in the marking area and 60 percent of the recaptures (Appendix B).

Each of the conditions that violated assumptions of the Schumacher-Eschmeyer method (immigration, emmigration, and mortality) should have reduced the proportion of marked lampreys in the marking area and thus inflated the population estimate. The true value for the population size should always have been below the Schumacher-Eschmeyer estimate.

Four of the nine Parker estimates exceeded the Schumacher-Eschmeyer estimate for the corresponding time. This divergence

Table 7.--Estimates of the population of adult chestnut lampreys in the marking area, 1961, by three methods, with their 95 percent confidence limits. The daily instantaneous rates of mortality (μ) and recruitment (β) are shown for the DeLury method, except where the coefficients were not significantly different from zero.

Interval	Schumacher-Eschmeyer method: Estimate	Schumacher-Eschmeyer method: 95% conf. limits	DeLury method: Estimate	DeLury method: 95% conf. limits	μ	β
May 19-June 18	3,525	2,631-5,337	629[a]	346-3,472	--	--
June 4-June 18	2,868	2,034-4,860	1,460	652-[b]	--	--
June 29-July 19	2,261	1,814-3,000	945	831-1,096	0.0266	0.0144
Aug. 5-Aug. 31	1,191	940-1,624	662	384-2,390	0.0068	0.0046
Aug. 21-Aug. 31	546	479- 633	529	302-2,141	--	--
Sept. 12-Oct. 5	457	388- 566	368	260- 625	0.0230	0.0080
Sept. 26-Oct. 17	162	134- 205	141	88- 352	0.0753	0.0305

Parker method

Date	Estimate	95% conf. limits	Date	Estimate	95% conf. limits
May 25	366[a]	226- 741	Aug. 7	969	678-1,524
June 4	2,698[a]	1,396- 7,360	Aug. 11	962	649-1,593
June 8	5,296	2,840-13,306	Aug. 25	875	554-1,619
June 14	5,168	2,362-19,568	Sept. 14	617	447- 920
July 3	1,750	1,180- 3,111	Sept. 20	245	174- 394
July 9	1,354	860- 2,459			

[a] The lampreys had to be feeding actively to be sampled effectively. Early in the trapping season they were not, and these population estimates were inconsistent with those for later periods. These estimates have been omitted from the later calculations.

[b] The coefficient that estimated 1/N was below the 5 percent level of significance, so the upper confidence limit on this estimate was not meaningful.

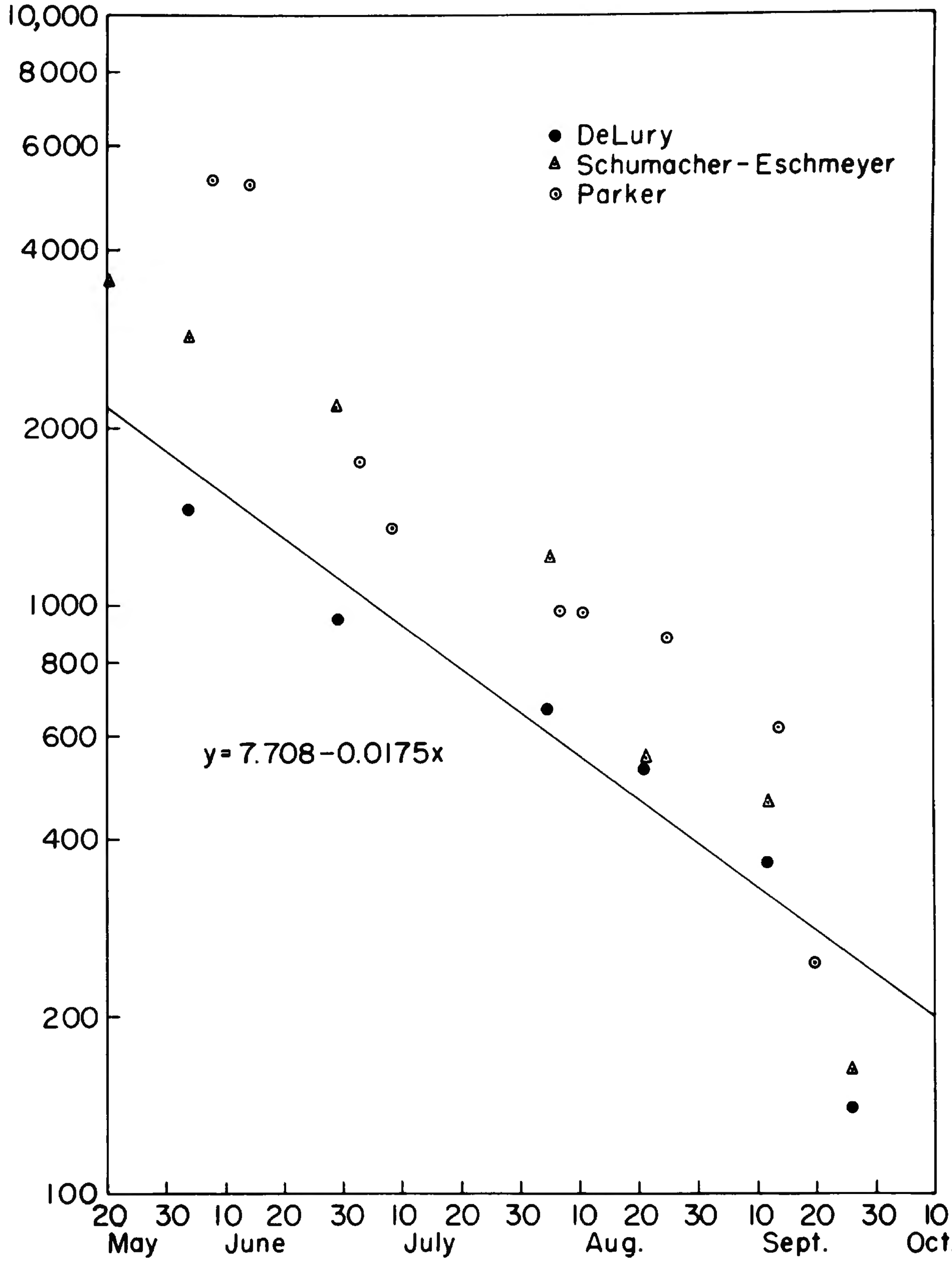


Figure 17.--Population estimates for the marking area made from the DeLury, Schumacher-Eschmeyer, and Parker methods. The regression line is fitted to the points for the DeLury estimate. The slope of the line (sign reversed) estimates i, the daily instantaneous rate of mortality.

was large early in the season, indicating that the Parker method had some unanticipated bias when applied to my data. The bias may have been due in part to the high rate of movement of unmarked lampreys into the marking area. The Parker method was designed for use when a large number of fish are marked during a short period. Since too few lampreys were marked on most days to result in a significant number of returns, I grouped lampreys marked on two successive trips (every two days). There may have been enough dilution of the marked population before the third trip (at which time recaptures were first recorded for this estimate) to cause a systematic upward bias in the method.

To test this possibility, I analyzed recaptures from two single days (June 6 and 8) when large numbers were marked. The separate estimates for these two days were significantly lower than the estimate made from recaptures from the two days combined (3, 659 and 3, 463 compared to 5, 296). These lower estimates still exceeded the Schumacher-Eschmeyer estimate, however.

In several of the experiments the ratio of marked lampreys declined rapidly and then increased, suggesting a curvilinear relationship (Fig. 18). By following the movement of marked lampreys, I was able to show that this increase was sometimes due to return into the marking area of lampreys which had been marked there and subsequently caught outside of it. This return would cause additional

Figure 18.--Relationship between the days after cessation of marking, and the arcsin of the square root of the ratio of marked lampreys to the total sample for each day. The number of lampreys initially marked is shown in parentheses after each two-day interval.

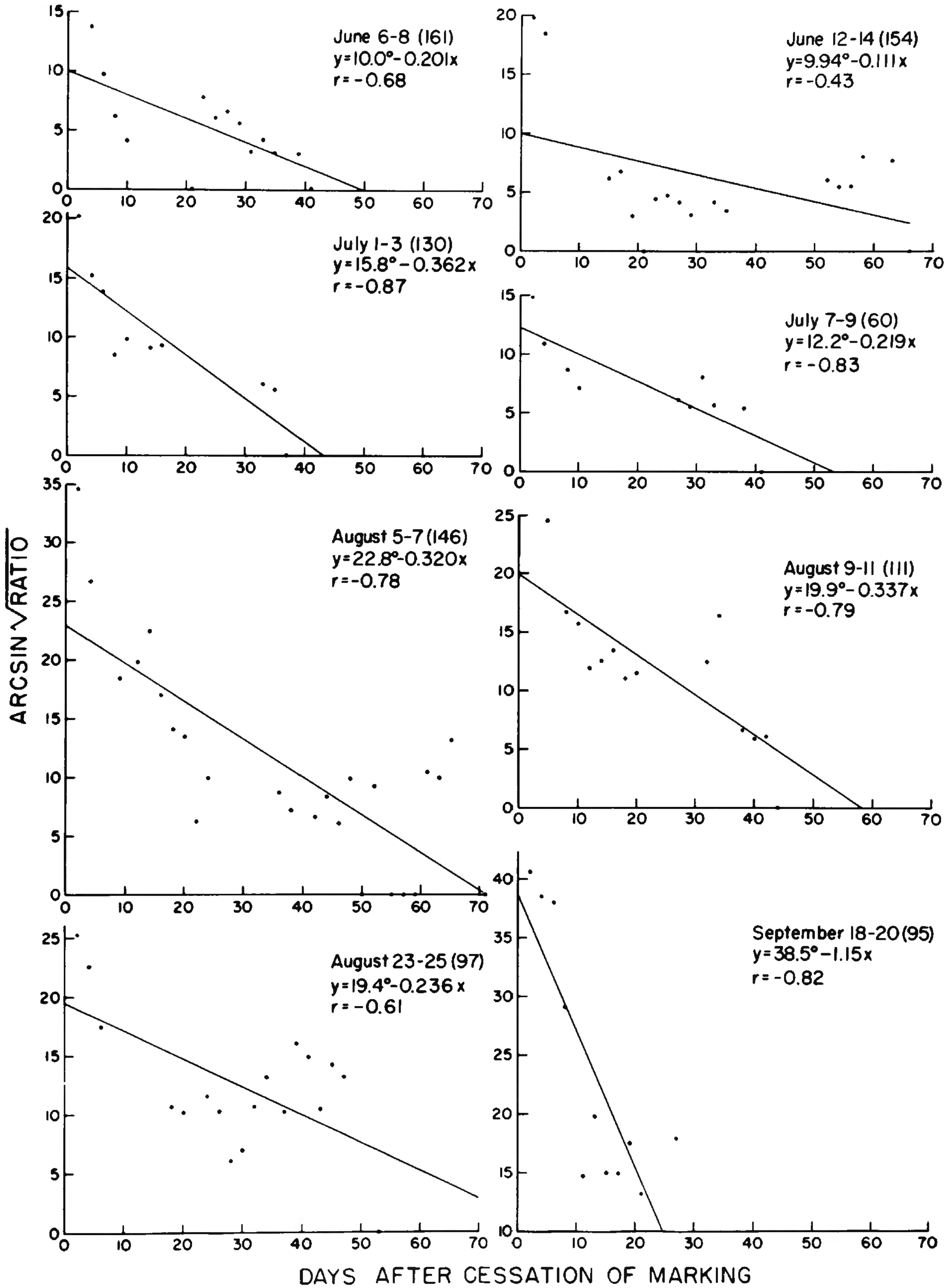

June 6-8 (161)
y=10.0°-0.201x
r=-0.68
June 12-14 (154)
y=9.94°-0.111x
r=-0.43
July 1-3 (130)
y=15.8°-0.362x
r=-0.87
July 7-9 (60)
y=12.2°-0.219x
r=-0.83
August 5-7 (146)
y=22.8°-0.320x
r=-0.78
August 9-11 (111)
y=19.9°-0.337x
r=-0.79
August 23-25 (97)
y=19.4°-0.236x
r=-0.61
September 18-20 (95)
y=38.5°-1.15x
r=-0.82
ARCSIN √RATIO
DAYS AFTER CESSATION OF MARKING

Figure 18

upward bias in the Parker method, as the estimate of the intercept made by least-squares would be too low.

For these reasons I have concluded that the Parker method of estimation was unsuitable for use with my data. Accordingly, I have relied entirely upon the DeLury method for estimates of the lamprey population present in the marking area throughout the season. I have retained the plots of percentage recaptured against time as indirect evidence of substantial movement of unmarked lampreys into the marking area (Fig. 18).

Mortality rate

Three methods that were used to estimate the rate of mortality of the lamprey population throughout the feeding season produced comparable results. In the first of these, successive estimates of the population in the marking area (derived from the DeLury method) were plotted on a semi-logarithmic graph. Satisfactory fit to a straight line suggested a constant rate of mortality throughout the season. A least-squares regression line was fitted to the natural logarithm of population size at the date of each estimate (Fig. 17). Each point was weighted by the degrees of freedom remaining from the multiple regression equation. The slope of the regression line (sign reversed) estimated i, the daily instantaneous rate of mortality, to be 0.0175.

As the second method, a catch curve (Ricker, 1958) was constructed by plotting, again on a semi-logarithmic graph, the number of lampreys that were marked in a given trapping period and recovered in each successive period (Fig. 19). Only those recaptures within the marking area were used. Many of the lampreys were recaptured several times in a single trapping period. In these instances I tallied each individual only once, disregarding additional recaptures in the same period. To adjust for unequal effort among the periods, the number of recaptures in a period was divided by the number of trap lifts in that period. One line was plotted for recaptures from each of the periods in which lampreys were marked.

The marked lampreys apparently did not die at a rate greater than did the entire population. I calculated the mortality rate to be 0.0153 (95 percent confidence limits 0.0063 to 0.0243) from the common slope of these lines (Snedecor, 1956, p. 398). Because this estimate of the mortality rate from the catch curve included both actual mortality and emmigration of marked lampreys from the marking area, I expected it to exceed the previously determined daily instantaneous rate of mortality (0.0175). It was in fact slightly less, but considering the confidence limits just noted, the agreement is satisfactory.

Finally, a check on the two previous estimates of mortality rate was available from the DeLury multiple regression equation. I had assumed that movement in and movement out of the marking area should be about equal, and that the coefficient for "mortality" in the DeLury equation should exceed that for "recruitment" by the amount of the actual mortality rate. DeLury (1958) suggested that the sampling

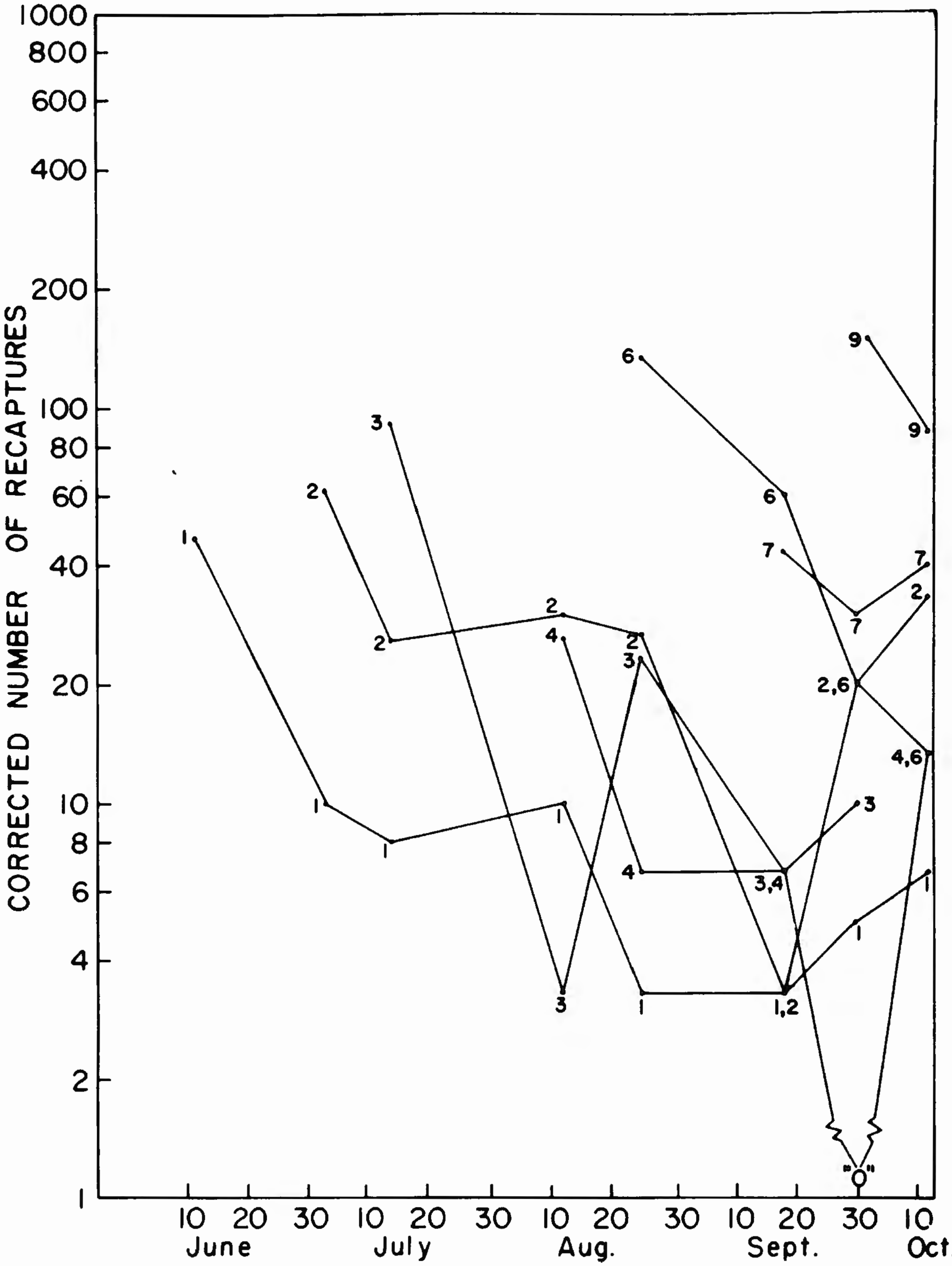


Figure 19.--Catch curves constructed for lampreys marked in each period and recaptured in subsequent periods. The lines are numbered according to the period of marking. The number of recaptures in each period was corrected by dividing it by the number of trap lifts made in the period and multiplying by 100. Points are plotted at the mid-point of each trapping period. The common slope of the seven lines, 0.0153, estimates the daily instantaneous rate of mortality for the marked lampreys.

error of estimates of the mortality and recruitment rates would probably be large, and this is true of most of my estimates (Appendix C). However, in the results for trapping periods beginning June 29 and September 12, the estimates of the daily instantaneous rate of mortality obtained by subtraction were 0.0122 and 0.0150 (Table 7).

Because the plot of the DeLury population estimates used the greatest amount of information, I consider the estimate of the mortality rate derived from it (0.0175) the best of the three. It is the one used in further calculations.

Movement

In a recent review of the restricted movement of fish populations, Gerking (1959) has reiterated that any quantitative description of the size of home range and the degree of straying describes the techniques of the investigator as much as the behavior of the fish. This was particularly true of my work, where all captures were made in traps. No information was available on the distribution of marked lampreys between traps, many of which were set several miles apart. From the present study I could make only general statements about the extent, rate, and direction of movement.

Extent of movement.--Movement by the marked lampreys was definitely not restricted in the sense reported by Gerking (1953, 1959), where some stream fishes remain within the space of a few hundred feet for several years. The mean total distance (calculated on the basis of the straight-line distance between traps) travelled by the 1,015 lampreys that were recaptured, was more than 2 miles. Four of 43 lampreys caught at the trap 12 miles above the marking area were recaptures; none of 5 lampreys trapped at 18 miles above was a recapture. There were 2 recaptures among the 24 lampreys taken 24 miles below the area, but no trapping was done below this point. Many marked lampreys were taken as far as 6 miles from the marking area. Among 1,041 captures made during July 18-31 at 1 and 2 miles above and below the marking area, the percentage of recoveries (11.5 percent) was actually higher than it had been up to that time among 4,712 captures within the marking area (11.2 percent).

Presumably the extensive movement of the lampreys was due almost entirely to their own swimming, since the fish to which they attach would be expected to move very little (Gerking, 1959). One unusual instance of movement was seen--a dead trout with one marked and two unmarked lampreys attached to it was observed floating downstream.

Rate of movement.--The mean rate of movement of all 2,255 recaptures was 0.18 mile per day. Of the 1,015 lampreys recaptured at least once, 97 moved at a rate in excess of 1.0 mile per day. One lamprey travelled 25.5 miles downstream in only 6 days--the maximum observed rate of movement.

A progressive increase in distance travelled with time at large was indicated by analysis of the movement of all recaptured lampreys that had been at large 2, 4, 6, 8, and 10 days since last captured (Table 8). The standard deviation of distance travelled increased regularly from 2 to 6 days but was erratic after that, possibly due to the small number of recaptures for the last two groups. Movement upstream and downstream was apparently about equal. The slight trend toward greater movement upstream could have been influenced by placement of the traps. Early in the season, when most of the lampreys were recaptured, slightly more trapping effort was expended upstream from the marking area than downstream from it.

Table 8.--Average distance moved from location of release, upstream (+) or downstream (-), and its standard deviation, for all recaptures of marked lampreys that had been at large for 2, 4, 6, 8, and 10 days.

Days at large	Number of recaptures	Average distance moved (miles)	Standard deviation (miles)
2	862	-0.02	0.70
4	243	+0.10	1.63
6	111	+0.002	3.18
8	50	+0.27	2.60
10	40	+0.55	2.52

Direction of movement.--No trend, either upstream or down, was apparent in movement of the marked lampreys. The average movement by all the 2,255 recaptures was slightly upstream (0.13 mile), but this again could have been influenced by placement of the traps.

No systematic pattern was suggested from an analysis of movement of the 20 most frequently recaptured individuals (Table 9). These lampreys moved both upstream and down, frequently changing direction. Many travelled several miles but were not far from the point of marking when recaptured for the last time. The extreme example was No. 794, which was recaptured 12 times. It made 9 changes in the direction of travel, and had moved at least 12 miles when it was recaptured for the last time--at the exact location where it had been marked 77 days earlier.

Movement of unmarked lampreys could not be confirmed by underwater observations, because most movement probably occurred at night. Indirect evidence did confirm that unmarked lampreys moved extensively. The slope of the regression lines in the Parker analysis (Fig. 18) could only have been caused by extensive movement of unmarked lampreys into the marking area, or by more rapid mortality of the marked than unmarked lampreys. The mortality rate of marked lampreys was apparently no greater than that of unmarked lampreys (Fig. 19); therefore, immigration of unmarked individuals must have been the cause of the progressive decrease in the percentage of marked lampreys in the samples.

In studies of some stream fish populations in which movement was slight, correction of population estimates for this limited movement was made by sampling at sites above and below the area studied

Table 9.--Summary of movement of the 20 most frequently recaptured lampreys.

Lamprey number	Times recaptured[a]	Significant changes of direction[b]	Total distance travelled (miles)	Net distance from point of marking (miles)[c]	Days elapsed since marking
		At time of last capture			
106	6	1	4.40	+1.40	89
486	9	3	11.37	-2.17	113
546	7	4	8.12	+0.20	68
611	13	5	7.33	+0.33	134
648	15	9	8.45	-1.63	64
697	12	5	13.27	-6.47	96
794	12	9	12.46	0.00	77
799	7	2	6.59	-2.13	106
926	6	2	4.52	+1.50	31
1093	8	2	4.77	-0.63	25
1131	15	6	10.10	-0.70	71
1193	6	1	14.97	-12.03	63
1275	9	4	11.61	-1.47	64
1368	7	3	9.36	-5.50	60
1407	6	2	8.50	-1.50	19
1463	12	4	4.87	-2.13	37
1622	13	6	3.96	-2.40	52
1726	11	2	1.74	-1.20	29
1798	6	4	5.83	-2.03	21
1842	9	4	7.98	+2.40	19

[a] Recaptures at the point of release were not counted.

[b] Movement of less than 4 sections (240 yards) in an opposite direction was not considered a significant change of direction.

[c] + = upstream, - = downstream.

(Scott, 1949; Gerking, 1953). I made no attempt at a correction from such data in this study because movement was so extensive.

Growth rate

The best estimate of growth rate in the adult feeding population was provided by estimates of the average length of the unmarked group of lampreys throughout the trapping season in 1961. The lengths of unmarked lampreys were averaged by trapping periods (Fig. 16). There were from 88 to 1,410 measurements in each period, and a total of 8,200 in the 11 periods (too few measurements were made in periods 12 and 13 to provide a reliable estimate).

To convert average length for each period to average weight, I calculated the linear regression of $\log_e$ weight on $\log_e$ length. The relationship, based on 669 measurements made throughout the season, was:

$$\log_e W = -14.338 + 3.207 \log_e L \text{ (computer solution)}$$
$$r = 0.986$$

I also calculated the relationship by the standard method of grouping (Lagler, 1956). The interval used was 5 mm. Disregarding the 4 intervals containing fewer than 5 observations, the result was:

$$\log_e W = -14.306 + 3.201 \log_e L$$

The close correspondence of the two results was probably due to the fact that I weighed about the same number of lampreys in most of the 5 mm length groups.

The final calculations of the instantaneous rate of growth in weight for each period of the feeding season were part of the computation of production (Table 10). The daily growth rate of the chestnut lamprey varied substantially from May to October (Fig. 12). It showed a steady increase from May until mid-July and then declined until October. This pattern was in contrast to the steadily declining rate of growth predicted by theory (Brown, 1957). The change in food source upon transformation to the adult stage and the typical seasonal increase in rate of feeding probably account for the temporary increase in growth rate. An increase in instantaneous growth rate occurs in fishes that leave fresh water to feed in the sea (Brown, 1957). A seasonal rise and fall in growth rate, superimposed upon a generally declining rate, was shown for a population of the brown trout (Allen, 1951) and the brook trout (McFadden, 1961).

There was a slight decrease in average length of lampreys trapped in late September (Fig. 16). The decrease was small compared with the standard error of the mean and may have been due only to sampling error. However, there was a severe rainstorm in the western half of the Lower Peninsula early in September, and during September 12-15 the flow of the normally stable Manistee River doubled (from 161 to 326 cfs). This flood flow was the maximum recorded in 1961 (U. S. Geological Survey, 1962). The river was turbid and highly colored with runoff from adjacent cedar swamps for more than a week following this storm. The sudden rise in water level and increase in suspended material in the stream could have disrupted feeding of the lampreys, causing loss in length and weight. In aquariums, lampreys have decreased in both length and weight when they did not feed (Parker and Lennon, 1956).

Rapidly rising water is known to cause newly transformed adults of the sea lamprey to leave their burrows and move downstream (Applegate and Brynildson, 1952; Applegate, 1961). Examination of length-frequency diagrams for periods 9 through 11, however, indicated that the decrease in average length for the chestnut lamprey in the Manistee River during late September was not caused by an influx of small individuals into the feeding population.

Most of the recaptures of marked lampreys were made within a few days of release; only a small proportion of the total were at large for sufficient time to provide a reliable estimate of growth. Only 478 of the 2,785 recaptures were at large for more than 10 days. Because there were more data from the unmarked lampreys (8,200 measurements) than from the marked group, data from the unmarked population were considered superior as an estimate of growth rate for use in the production computation. Only a limited analysis was attempted on the growth of the marked lampreys.

Of 38 lampreys marked in May and at large for 10 days or more before recapture, 15 equalled or exceeded the growth estimated for the unmarked population in Fig. 16, and 23 showed a reduced rate. As noted earlier, some of the smallest lampreys marked grew during the feeding season to approximate the maximum length attained by any individual in the population. A number of the marked lampreys decreased slightly in length; a few shrank substantially. This could have been caused by some aspect of the marking procedure, but such reduction in length may not be abnormal.

Net production

Although the chestnut lamprey lives for approximately 18 months in the parasitic adult phase, the evidence is overwhelming that its growth and feeding in the Manistee River are confined to about 5 months in the middle of this span. Production by a year-class of the lamprey was computed for only that 5-month interval, from mid-May through mid-October, but this can also be regarded as the total annual production. The method used in this computation was that of Ricker and Foerster (1948), in which the instantaneous rate of growth is multiplied by the average standing crop. Production was calculated for each of the trapping periods and summed for the entire feeding season (Table 10). (cf. Ricker and Foerster, 1948; Ricker, 1958 for details of calculation.)

For the year-class studied in the Manistee River, there was little relationship between the standing crop and production (Fig. 20), illustrating the limitation of standing crop as an estimate of production.

Table 10.--Computation of production of the chestnut lamprey in the marking area of the Manistee River, 1961, including instantaneous rates of growth (g), mortality (i), and change in biomass (g-i). The indicated dates are midpoints of trapping periods 1-11.

Date	2 Average length (mm)	3 Average weight (grams)	4 g	5 i	6 g-i	7 Change in biomass	8 Bio-mass (kg)	9 Average biomass (kg)	10 Produc-tion (grams)	11 Mortal-ity (grams)
May 26	104.7	1.78					3.45			
			0.167	0.279	-0.112	0.894		3.26	544	910
June 11	110.3	2.11					3.08			
			0,266	0.384	-0.118	0.889		2.91	774	1,120
July 3	119.8	2.75					2.74			
			0.157	0.192	-0.035	0.966		2.69	422	516
July 14	125.8	3.22					2.65			
			0.263	0.192	+0.071	1.074		2.74	721	526
July 25	136.6	4.18					2.84			
			0.295	0.314	-0.019	0.981		2.82	832	885
Aug. 12	149.8	5.62					2.79			
			0.167	0.227	-0.060	0.942		2.71	453	615
Aug. 25	157.8	6.64					2.63			
			0.132	0.210	-0.078	0.925		2.53	334	531
Sept. 6	164.4	7.57					2.43			
			0.093	0.210	-0.117	0.890		2.29	213	481
Sept. 18	169.2	8.31					2.16			
			-0.022	0.210	-0.232	0.793		1.93	-42	405
Sept. 30	168.0	8.13					1.71			
			0.115	0.210	-0.095	0.910		1.64	189	344
Oct. 12	174.1	9.12					1.56			
Totals			1.633	2.428	-0.795	0.452			4,440	6,333

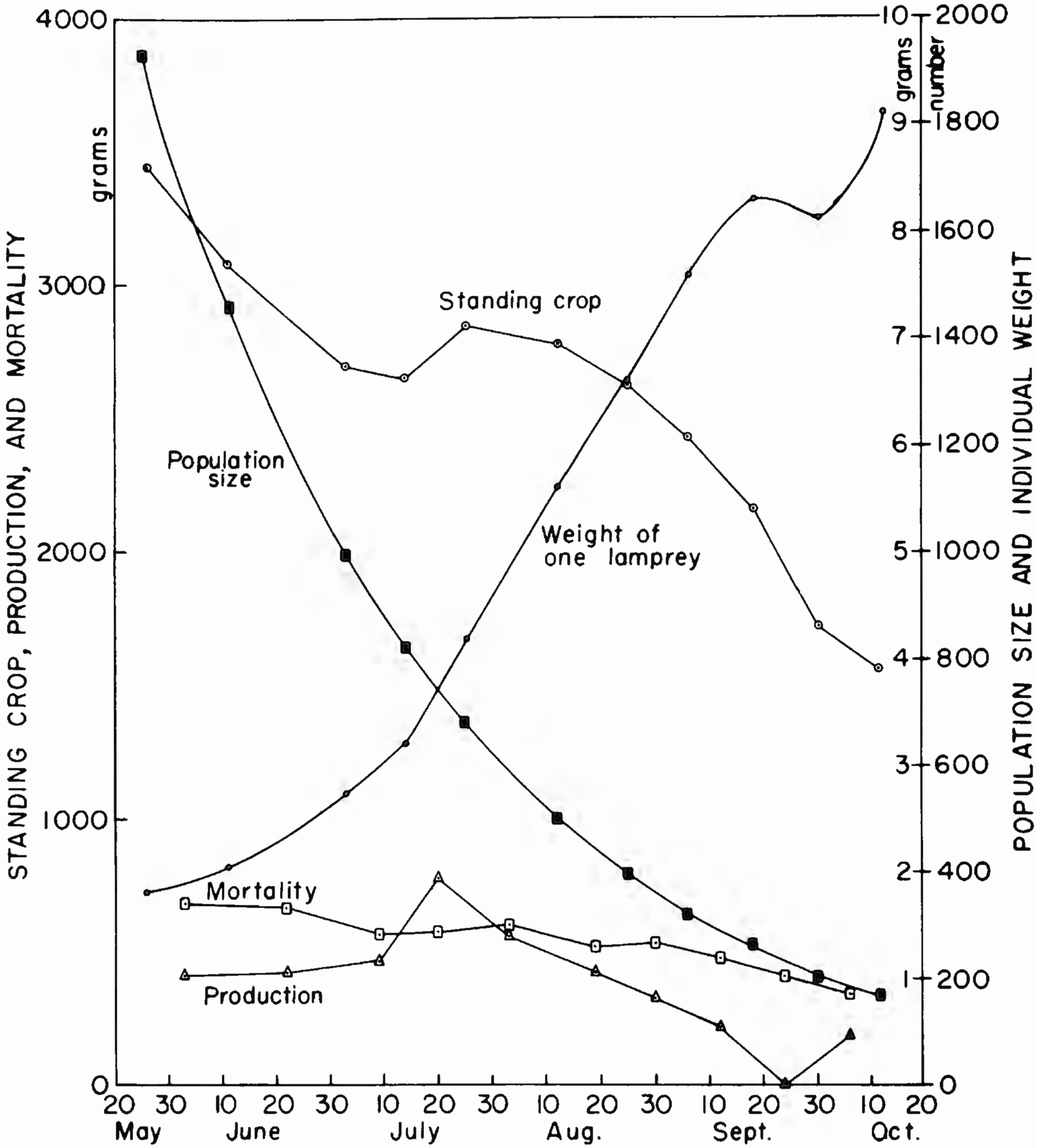


Figure 20.--The interrelations of abundance, individual weight, standing crop, production, and mortality for the chestnut lamprey population in the Manistee River, 1961 (after Ricker and Foerster, 1948). To show the seasonal trend in rates, production and mortality in each interval are corrected to a 12-day base.

During the period when the standing crop declined from 3.45 kg to 1.56 kg, net production of 4.44 kg was achieved. For the entire feeding season the production of the chestnut lamprey was about 3 times the final standing crop, or 1.8 times the average standing crop. Mortality was very rapid--in only one period did accretion of biomass by growth exceed the loss to mortality, and the final standing crop was only half of its initial value (Fig. 20).

Destruction of fish

The data are now at hand to estimate the loss of trout that could have been due to attacks by the chestnut lamprey in the Manistee River. The destructive potential (grams of fish killed per gram of growth) was determined from Fig. 14 according to the average size of the lampreys. Since this destructive potential varied greatly with size of a lamprey, an estimate of fish-kill was made for each trapping period. The method of calculation for each period was:

grams fish killed/gram growth x production = potential fish-kill

This potential fish-kill for the entire feeding season in the mile-long marking area was calculated to be approximately 70 kg, or about 155 pounds per mile (Table 11).

If the earlier assumption on the size of the trout population in 1961 (not over 350 pounds/mile of stream) is correct, the potential mortality attributed to lamprey predation was quite substantial. It

Table 11.--Potential destruction of fish in the marking area of the Manistee River resulting from lamprey predation in 1961.

Interval	Production (grams)	Grams fish killed per gram lamprey growth	Destruction of fish (kg)
May 26-June 11	544	0	--
June 11-July 3	774	3.5	2.7
July 3-July 14	422	7.0	3.0
July 14-July 25	721	12	8.7
July 25-Aug. 12	832	20	16.6
Aug. 12-Aug. 25	453	28	12.7
Aug. 25-Sept. 6	334	34	11.4
Sept. 6-Sept. 18	213	38	8.1
Sept. 18-Sept. 30	-42	37	--
Sept. 30-Oct. 12	189	41	7.7
Totals	4,440	--	70.9

amounted to about 21 pounds/acre--about half the annual stocking rate and over one-third of the trout available to anglers. For several reasons this estimate of potential mortality must be considered only approximate.

Sources of error in the estimate of fish-kill per gram of growth made in aquariums have been discussed. There is further complication; some trout partially weakened by lamprey feeding are taken by anglers. In addition, a number of trout not taken by anglers probably survive some lamprey predation throughout the season, recouping losses between attacks by the lamprey. Thus the lamprey population gains an unknown proportion of its growth from fish not actually killed.

All probable sources of error considered, there still seems no doubt that predation by the chestnut lamprey was a significant cause of mortality for that trout population within the marking area in the Manistee River in 1961.

DISCUSSION

The high density of parasitic adult lampreys found in the marking area at the beginning of the trapping season was surprising. There are no population data on other stream-dwelling lampreys for comparison, but almost certainly the population of the chestnut lamprey in the Manistee River is the most dense of this species anywhere in its range. The extensive sand beds in the stream bottom and the stable water level, both providing excellent conditions for the larvae, are undoubtedly of prime importance among factors contributing to the high population level.

Severe interaction between predator and prey populations is most common when the association is of recent origin, or when changes have occurred in the ecosystem (Odum, 1959). In fact, no instance of limitation of a population of native fish by a native lamprey has been noted. When construction of the Welland Canal allowed the sea lamprey to invade the upper Great Lakes, predation by this lamprey caused a precipitous decline in numbers of the lake trout there (Hile, Eschmeyer, and Lunger, 1951; Applegate and Moffett, 1955). Because the chestnut lamprey and the trouts have only recently become associated in the Manistee River, their relationship may not yet have become stabilized.

The net production of 4.44 kg by the chestnut lamprey in the one-mile stretch of the Manistee River is equivalent to 1.32 pounds/acre (1.48 kg/ha). This is a low value compared with previous measurements of production of single fish species, reviewed by Gerking (1962), but none of these was on a comparable species or at as high a trophic level. Only the work of Allen (1951) was in flowing water. In the Horokiwi Stream, New Zealand, Allen found annual net production of a very successful population of the brown trout to be 485 pounds/acre. So few data are available for comparison, however, that it would be premature to attach any biological significance to a particular value for production. The possible range of these values cannot yet be predicted.

Total elaboration of biomass by the chestnut lamprey population in the Manistee River in 1961 was 1.3 times the initial standing crop of adults in May of that year. This relationship of annual production to initial standing crop has varied considerably in other studies, depending largely upon the age distribution of the population. Production of young-of-the-year sockeye salmon, Oncorhynchus nerka, in Cultus Lake varied from 3.7 to 18.1 times the initial weight of fry (Ricker and Foerster, 1948). Annual production of the bluegill in a population composed of six age groups was slightly less than the initial summer standing crop (Gerking, 1962).

The continual decrease in standing crop of the chestnut lamprey in the Manistee River was a consequence of a very high rate of mortality in the adult population. In spite of the fact that the average lamprey grew to about five times its initial adult weight, in only one trapping period did addition of biomass to the standing crop by growth exceed the loss to mortality. This excess of mortality over production could obviously not have persisted throughout the life span; production exceeding mortality must have occurred for a time during the larval stage to bring the standing crop to the level found at the beginning of the adult feeding season.

The mortality rate was computed on the assumption that movement into and movement out of the marking area were equal. The consistent decrease in biomass suggests another possibility--that the marking area was part of a nursery area and that lampreys produced here dispersed to other parts of the stream. The possibility of such dispersal cannot be completely discounted, since a few adult lampreys have been found several miles upstream from the location of Ichthyomyzon larvae. But the strongest evidence is for approximately equal movement into and out of the marking area. The pattern of movement of marked lampreys did not indicate any regular dispersal, and Ichthyomyzon larvae are abundant in a stretch of the river about 20 miles long (Crowe, 1959).

Unfortunately, no data on survival of the adult lampreys before or after the trapping season could be obtained. If no mortality had occurred during the rest of the year, the instantaneous rate observed during the trapping season ($i = 2.43$, Table 10) would be equivalent to an annual survival rate, s, of 9 percent. If mortality had occurred throughout the year at the rate observed during the trapping season, the appropriate annual survival rate would be 0.2 percent. Either of these rates is too low to prevail over the entire life span of the lamprey, if a life span of 9 or 10 years and an average egg production of about 20,000 per female are assumed (these assumptions are discussed below). Thus, the mortality rate for adults of the chestnut lamprey in the Manistee River must be greater than that for larvae of the species.

Comparison of the life histories of the parasitic silver lamprey (closely related to the chestnut lamprey) and the non-parasitic northern brook lamprey provides another estimate of survival rate in the adult and larval stage. The reasoning used was suggested by Organ (1961) in a study of salamander population dynamics.

The number of eggs produced by females of the silver and the brook lampreys averaged about 19,000 and 1,500 respectively (Vladykov, 1951). The larval life of these two species is apparently quite similar, and probably lasts about 7 to 8 years in both (Wigley, 1959; Stauffer, 1962). Larvae of the two species have not yet been studied in detail, however, and criteria for their identification have not yet been established. The major differences in their life histories are in the adult stage. The parasitic adult lives for about 18 months, much of the time free in the stream. The non-parasitic adult lives only 4 to 8 months, feeds not at all, and spends most of this time in a burrow, emerging only to spawn in the spring (Leach, 1940; Vladykov, 1949).

Under steady state conditions a slightly greater average annual survival rate is indicated for the non-parasitic species than for the parasitic one:

$$i = \frac{\ln 1,500 - \ln 2}{9 \text{ years}} = 0.736, \quad s = 48 \text{ percent (non-parasitic)}$$

$$i = \frac{\ln 19,000 - \ln 2}{10 \text{ years}} = 0.916, \quad s = 40 \text{ percent (parasitic)}$$

These are average rates which, if they persisted, would result in maintenance of the population at a constant size. Actual rates are undoubtedly variable.

It seems reasonable to assume that mortality rates for such diverse forms as the larval and adult parasitic lamprey would differ because of contrasts in their habitats and food sources. By the same token, the mortality rates for larvae and adults of the non-parasitic species should be about equal, and survival of larvae of the parasitic and non-parasitic species should be similar.

If one applies the predicted average annual survival rate of the non-parasitic species (48 percent) to the number of eggs produced by a female of the parasitic species (19, 000) for 9 years, the survival rate predicted for the final year of parasitic life is 7 percent. This estimate falls within the rather wide range (9 to 0. 2 percent) suggested earlier, but the agreement may well be fortuitous.

A number of speculative assumptions have been made in this analysis, and the conclusions reached must be regarded as tentative. For example, if the larval period of the non-parasitic species has been reduced along with egg production, some of the conclusions would have to be modified. It is hoped that age determination and species identification of Ichthyomyzon larvae will soon be possible so that survivorship studies can be made over the entire life span of these unusual animals. When these data are at hand, further studies on the causes of mortality may establish the interrelationship of the trout and lamprey populations and the methods whereby each is limited in size.

Appendix A. --Data used in population estimates made for the marking area by the Schumacher-Eschmeyer and DeLury methods. Recaptures are from lampreys marked only in the listed periods.

Date		Number caught	Recaptures	Marked lampreys at large
Periods 1-2				
May	19	19	0	0
	21	11	0	18
	23	51	1	29
	25	37	7	79
	27	16	3	109
	29	16	6	122
June	2	52	8	132
	4	69	7	174
	6	199	20	222
	8	202	37	312
	12	302	26	383
	14	242	24	458
	16	260	37	537
	18	189	25	567
Periods 3-4				
June	29	254	0	0
July	1	211	1	20
	3	361	31	90
	5	301	38	150
	7	314	22	150
	9	293	26	175
	11	361	34	210
	13	335	32	239
	17	356	35	269
	19	261	27	299
Periods 6-7				
Aug.	5	88	0	0
	7	104	23	73
	9	102	33	146
	11	99	38	207
	16	109	30	257
	19	60	18	323
	21	41	13	361
	23	93	19	387
	25	84	28	437
	27	55	20	484
	29	81	28	513
	31	100	45	550

Date		Number caught	Recaptures	Marked lampreys at large
Periods 9-10				
Sept.	12	86	0	0
	14	62	13	71
	18	74	18	105
	20	93	31	151
	22	87	46	200
	24	67	41	229
	26	29	19	243
	28	38	19	249
Oct.	1	31	9	257
	3	26	10	268
	5	15	7	275
Periods 10-11				
Sept.	26	29	0	0
	28	38	1	6
Oct.	1	31	2	14
	3	26	4	25
	5	15	3	32
	7	30	7	36
	9	33	10	45
	11	19	8	50
	17	21	4	52
Period 2				
June	4	69	0	0
	6	199	7	48
	8	202	29	138
	12	302	21	209
	14	242	20	284
	16	260	33	363
	18	189	22	393
Period 7				
Aug.	21	41	0	0
	23	93	4	26
	25	84	16	76
	27	55	10	123
	29	81	22	152
	31	100	35	189

Appendix B.--Data used in population estimates made for the marking area by the Parker method. The number of lampreys marked in each two-day interval follows the dates in parentheses

Days after marking ceased	Number caught	Recaptures
May 23-25 (80)		
2	16	3
4	16	5
8	52	5
10	69	2
12	199	6
14	202	2
18	302	3
20	242	2
22	260	2
24	189	2
June 2-4 (92)		
2	199	13
4	202	12
8	302	5
10	242	2
12	260	0
14	189	1
25	254	3
27	211	1
29	361	2
31	301	2
33	314	0
35	293	1
37	361	0
June 6-8 (161)		
4	302	17
6	242	7
8	260	3
10	189	1
21	254	0
23	211	4
25	361	4
27	301	4
29	314	3
31	293	1
33	361	2
35	335	1
39	356	1
41	261	0
June 12-14 (154)		
2	260	30
4	189	19
15	254	3
17	211	3
19	361	1
21	301	0
23	314	2
25	293	2
27	361	2
29	335	1
33	356	2
35	261	1
52	88	1
54	104	1
56	102	1
58	99	2
63	109	2
66	60	0
July 1-3 (130)		
2	301	36
4	314	22
6	293	17
8	361	8
10	335	10
14	356	9
16	261	7
33	88	1
35	104	1
37	102	0
July 7-9 (60)		
2	361	24
4	335	12
8	356	8
10	261	4
27	88	1
29	104	1
31	102	2
33	99	1
38	109	1
41	60	0

Appendix B. --continued

Days after marking ceased	Number caught	Recaptures
August 5-7 (146)		
2	102	33
4	99	20
9	109	11
12	60	7
14	41	6
16	93	8
18	84	5
20	55	3
22	81	1
24	100	3
36	86	2
38	62	1
42	74	1
44	93	2
46	87	1
48	67	2
50	29	0
52	38	1
55	31	0
57	26	0
59	15	0
61	30	1
63	33	1
65	19	1
71	21	0
August 9-11 (111)		
5	109	19
8	60	5
10	41	3
12	93	4
14	84	4
16	55	3
18	81	3
20	100	4
32	86	4
34	62	5
38	74	1
40	93	1
42	87	1
44	67	0
August 23-25 (97)		
2	55	10
4	81	12
6	100	9
18	86	3
20	62	2
24	74	3
26	93	3
28	87	1
30	67	1
32	29	1
34	38	2
37	31	1
39	26	2
41	15	1
43	30	1
45	33	2
47	19	1
53	21	0
September 12-14 (105)		
4	74	18
6	93	11
8	87	9
10	67	7
12	29	4
14	38	4
17	31	3
19	26	2
21	15	1
23	30	2
25	33	1
27	19	1
33	21	2
September 18-20 (95)		
2	87	37
4	67	26
6	29	11
8	38	9
11	31	2
13	26	3
15	15	1
17	30	2
19	33	3
21	19	1
27	21	2

Appendix C.--Solutions for the DeLury (1958) multiple regression equations computed by the General Motors Stepwise Regression Program, IBM 709 computer. The equation used was:

$$Y = b_1 X_1 + b_2 X_2 + b_3 X_3$$

Interval	Degrees of freedom	Mult. corr. coeff.	X_1		X_2		X_3	
			Coefficient	Standard error	Coefficient	Standard error	Coefficient	Standard error
May 19-June 18	11	0.8625	0.001590	0.000592	-0.000286	0.000365	0.000054	0.000248
June 4-June 18	4	0.9469	0.000685	0.000306	-0.000277	0.000786	0.000042	0.000335
June 29-July 19	7	0.9975	0.001058	0.000062	0.000591	0.000118	-0.000319	0.000052
Aug. 5-Aug. 31	9	0.9608	0.001511	0.000483	0.000278	0.001472	-0.000187	0.000598
Aug. 21-Aug. 31	4	0.9915	0.001891	0.000513	-0.000052	0.000310	a	--
Sept. 12-Oct. 5	8	0.9882	0.002721	0.000486	0.001499	0.000811	-0.000525	0.000191
Sept. 26-Oct. 17	6	0.9879	0.007103	0.001742	0.011762	0.003881	-0.004762	0.001514

[a] The estimate of population size including the coefficient for recruitment exceeded the corresponding Schumacher-Eschmeyer estimate, so the coefficient was omitted (it was not significant at the 5 percent level).

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