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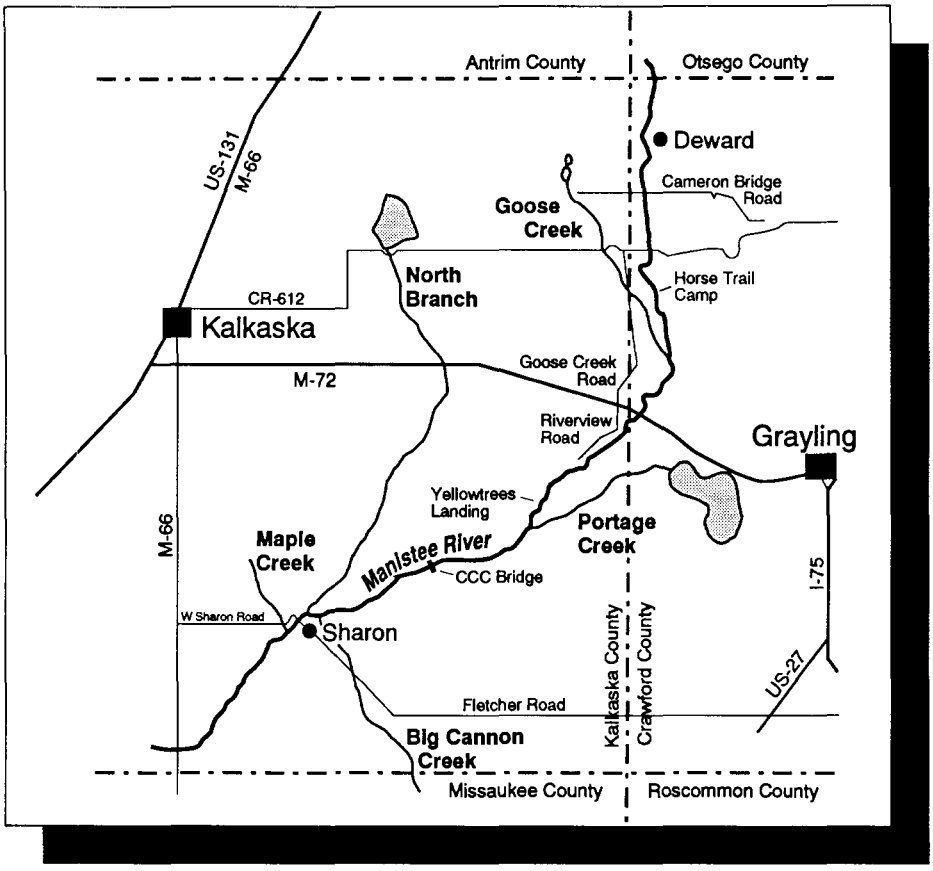

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FISHERIES DIVISION

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CHESTNUT LAMPREY PREDATION ON CAGED, AND FREE-LIVING BROWN TROUT IN THE UPPER MANISTEE RIVER, MICHIGAN

Andrew J. Nuhfer

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Chestnut lamprey predation on caged, and free-living brown trout in the upper Manistee River, Michigan

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Abstract.—From 1989-91 brown trout *Salmo trutta* of different sizes (15-41 cm) were caged in the Manistee River and exposed to predation attacks by chestnut lampreys *Ichthyomyzon castaneus* during spring and summer test periods. Fishery survey and angler catch data was used to estimate percentages of free-living trout attacked by lamprey. Larger trout were more likely to be preyed upon, both in cages, and in the wild. Larger trout in cages, or the wild, were also more frequently observed attacked simultaneously by more than one lamprey. From 0-100% of caged trout were attacked depending upon the test period. Attack rates on caged trout were generally highest during July. Over 76% of the lamprey marks on caged trout during 1990-91 were on the prey's dorsal region. Lamprey marks or attached lamprey were rarely observed on free-living trout in sections of the Manistee River upstream from the County Road 612 bridge in Crawford County. However, from 0-90% of trout observed in river sections between the M-72 bridge in Crawford County, and the Sharon Bridge in Kalkaska County, had been attacked by lamprey.

Mortality of caged trout due solely to lamprey attack could not be reliably estimated due to the confounding effects of such stress factors as confinement, intermittent high water temperatures, and disease. Depending on the year, test site, and test period, from 0 to 100 percent of trout attacked in various test groups died. However, from 4 to 80 percent of brown trout not attacked, also died during the same test periods.

Chestnut lamprey *Ichthyomyzon castaneus* inhabit at least 13 stream systems in Michigan's Lower Peninsula. They also occur in an additional 28 tributaries and are believed to occupy approximately 1,700 lineal miles of Michigan streams, all within Lake Michigan's drainage (Morman 1979). Chestnut lamprey occur primarily in the main branches of large streams and are rarely found in headwaters or small tributaries (Morman 1979). The five largest populations, based on distribution and density of larvae, occur in the St. Joseph, Muskegon, Pere Marquette, White, and Grand Rivers (Morman 1979). Hall (1963) believed, however, that the most dense population was in the Manistee River, based on estimated populations of the parasitic-phase chestnut lamprey. Crowe (1959) reported that chestnut lamprey were particularly abundant in waters of the Manistee River between the M-72 bridge in Crawford County and a point midway between Riverview and Sharon in Kalkaska County (Figure 1). The stable flow, good water quality, and extensive sand beds on the bottom of the Manistee River provide excellent habitat for chestnut lamprey ammocoetes (Hall 1963; Morman 1979). Scott and Crossman (1973) reported that these

ammocoetes are presumed to live for 5-7 years before beginning their transformation into adults during August or September, at a total length of 9-10 cm. Although these small adults may briefly feed during the fall that transform, they are inactive over the winter. The adults do their most active parasitic feeding during the following April-October period. They reproduce and die in June or July of the following year.

Because many trout anglers fish the Manistee River and because it is very clear, reports of fish observed or captured with attached lamprey or lamprey marks are common. Accordingly, anglers and fishery managers have focused more attention on chestnut lamprey in this system than on those in other Michigan rivers.

Hall (1963) stated that "mortality of fish in the Manistee River due to attacks by lamprey could have approximated one-third of the legal-sized trout (7-inches and longer) available to anglers". After Hall's findings were reported, both fishery managers and anglers decided that chestnut lamprey were seriously reducing the survival of wild and stocked salmonids in the upper Manistee River. In an effort to increase the quality of the salmonid sports fishery, the Michigan Department of Conservation treated approximately 90 kilometers of the Manistee River with Bayluscide during October 1966 (Jacob 1966). Trout were then restocked into the treated river section. The treatment began at Cameron Bridge in Crawford County and was intended to kill both fish and lamprey downstream to a point just upstream from the M-66 bridge in Kalkaska County (Figure 1). Five tributaries to the Manistee River, Big Cannon Creek, Goose Creek, Portage Creek, Maple Creek, and the North Branch of the Manistee River were also treated to remove fish and lamprey. Electrofishing surveys, and observations of caged fish, indicated that a complete kill of fish and lamprey was not obtained in the treatment zones (Jacob 1966). Data collected before, during, and after, the treatment were not adequate for determining the percentage of lamprey and fish killed in the treatment zone. However, for a number of years after the river was treated and restocked, trout fishing quality was reported to be very good. Although Hall (1963) estimated the population of adult chestnut lamprey in a section of the Manistee River in 1961, their population was not estimated after the lampricide treatment. Data on pre- and post-treatment trout populations, or angler catches, were not sufficient to quantitatively determine the effect of the lampricide treatment on trout survival or angler catch. Moreover, the number, size, and species, of trout stocked into the Manistee River has varied substantially over time (Table 1). Hence, even if good quantitative data on trout populations and catches were available, it would be difficult to differentiate between the effects of variable stocking rates and the 1966 chemical removal of a (presumed) majority of chestnut lamprey and competing fish species from a long segment of the river.

In 1987 members of the Upper Manistee River Association reported that the quantity and size of brown trout *Salmo trutta* caught had declined, while lamprey attacks appeared to be increasing. They asked what effect this lamprey predation was having on brown trout stocks in the Manistee River and if another lampricide treatment might be appropriate. In my review of literature on the chestnut lamprey I found only the study by Hall (1963) that specifically addressed the lethality of chestnut lamprey attacks. Unfortunately, Hall had few laboratory observations of lamprey attacks on fish confined at the higher water temperatures found in the Manistee River during the summer period when chestnut lamprey feeding and growth rates peak (Hall 1963). His estimates of the destructive potential of chestnut lamprey are based primarily on laboratory observations where water temperature was consistently near 10° C.

I hypothesized that brown trout mortality caused by chestnut lamprey might be higher at ambient spring and summer water temperatures in the Manistee River. I therefore designed a study to examine chestnut lamprey predation on brown trout in the Manistee River from May-August. I estimated lamprey attack frequencies on caged and free-living trout in sections of the upper

Manistee River. I tested the hypothesis that chestnut lamprey selectively prey on larger trout, and documented the frequency of lamprey attachments to different anatomical regions of caged brown trout. I estimated mortality of caged brown trout exposed to predation by chestnut lampreys. I attempted to link mortality of caged brown trout to such factors as lamprey wound frequency, size, and severity; to disease; and to tissue damage resulting from confinement.

Methods

Live-cage design and placement

Rectangular wooden frames with dimensions of 61 x 61 x 120 cm were constructed and covered with wire screen. Half the cages (control cages) were covered with fine mesh screen (3-mm square openings) to exclude chestnut lamprey. The other cages (treatment cages) were covered with larger mesh screen (12-mm square openings) that allowed free entry and exit of parasitic-phase chestnut lamprey. Before the 1991 tests began, all cages were modified by installation of a vertical screen to separate each cage into equal-sized upstream and downstream compartments. This modification was intended to reduce competition for space since observations made during 1989-90 indicated that all trout tended to occupy positions close to the upstream end of each cage.

The cages were anchored in the Manistee River at test sites in an irregular line, with their long axis parallel to the current in areas of slow to moderate current velocity at water depths ranging from 25 to 50 cm. Control and treatment cages were alternated, with a control cage at the most upstream position at each site. Half the cages at each site were control cages and half were treatment cages. During the 1989 test periods, 4 cages were placed at each of 3 sites (Figure 1). During the 1990-91 test periods 8 cages were placed at each of 2 sites (Figure 1). Electrofishing and visual surveys made during July 1989 indicated that chestnut lamprey were more abundant in some river sections than in others. Hence, to increase the exposure of test fish to lampreys, I selected a new study site for the second and third year of study, and eliminated the upstream and downstream sites used in 1989.

Experimental trout

Wild brown trout for the 1989 cage tests were collected by non-pulsed direct current electrofishing gear from the Manistee River and the East Branch of the Au Sable River. In 1990, half of the brown trout used were collected from the Manistee River and half were domestic fish from the Oden State Fish Hatchery. Brown trout from this hatchery were used because no fish diseases have been detected there during annual health inspections since 1985 (Hnath and Zischke 1991). In 1991, all brown trout confined in cages were from the Oden Hatchery. All hatchery trout were used in 1991 because analysis of the 1990 data showed no major differences between hatchery and wild fish in survival, or susceptibility to lamprey attack.

Trout were transported to the test sites in oxygenated fish planting units. They were anaesthetized with tricaine-methanesulfonate (MS-222) before their total lengths and weights were measured. Five trout were placed in each cage at the beginning of each 1989 test period (May 10-June 16, June 22-July 20, July 20-August 17). Small trout (15-25 cm long) and large trout (26-41 cm) were segregated for all 1989-91 tests, and randomly assigned to control and treatment cages at each site. In 1990, the number of trout placed in each cage was reduced to 4 fish. Hatchery and wild trout were segregated so that half the cages at each site contained hatchery fish. The 1990 test periods were June 25-July 16, and July 17-August 8. The same numbers of trout used in 1990 were used in 1991. However, these hatchery brown trout were split among the upstream and downstream compartments of the newly-modified cages. At the beginning of the first 1991 test period (June 24-July 12) all trout were tagged with color-coded jaw tags. Trout were assigned different tag colors so that each of the 4 fish

in each cage could be individually identified during daily observations. After the first test period, it appeared that severe jaw injury caused by abrasion of the tags against the cages was associated with trout mortality. Thus, during the second 1991 test period (July 15-August 5), color-coded Floy T-bar anchor tags (FD-68B) were injected at the anterior base of the dorsal fins to identify individual trout in each cage. Trout were not artificially fed during the time they were confined for 1989-91 observations.

Observations of caged trout

Volunteer observers living near the test sites opened the cage lids and visually examined the fish in each cage once every 24 hours during each of the 1989-91 test periods. They recorded the number of lamprey attached to each fish as well as time, air and water temperature, and general observations of fish vigor. During 1989, observers recorded temperatures at the time they observed the caged fish. During 1990-91 daily water temperature ranges at test sites were measured with Taylor maximum-minimum thermometers. If trout died, they were frozen in zip-lock bags with labels indicating date of death and cage number. Percentages of trout attacked by chestnut lamprey and percentages of fish dying were determined for each test period and fish size category.

All fish removed from the cages were weighed and measured. At the end of each test period, I carefully examined surviving and frozen fish for evidence of lamprey attack. In this paper I use the terms lamprey marks, wounds, and evidence of lamprey attack interchangeably. I was unable to positively identify healed chestnut lamprey wounds on 4 brown trout wounded during May 1989. These fish were stocked into a small pond and recovered 5 months later. Thus, I judged that evidence of lamprey attachments on trout observed during this study were most likely to have occurred the same year they were observed.

During 1990-91 I measured the distance between the outside margins of lamprey marks with a set of vernier calipers (diameter of circular marks, longest length and width of other marks). Lamprey wound area (cm^2) was computed from these measurements. During 1990-91, lamprey mark locations, and their size, were recorded onto the outline of a trout depicted in Figure 2. These data were used to determine the frequency distribution of lamprey attachments among trout body regions, the number of wounds, and wound area (cm^2). In 1991, I also classified marks as minor or severe. I classified marks as severe when at least a portion of the wound had penetrated the skin. However, I did not measure the outside dimensions of the portion of the mark that had penetrated the skin.

Smears of kidney tissue from trout were collected and cultured from trout that died during the 1990 tests to determine if furunculosis or other bacteria were present. In 1991, kidney tissue smears were cultured both from fish dying during the test periods, and from fish surviving at the end of test periods. The bacterial cultures and 13 of the caged trout that died during the study were examined and diagnosed by fish pathologists at the Wolf Lake Fish Health Laboratory.

In 1991, I began recording the presence of skin abrasions (raw skin) sustained during the holding period and measured their size (cm^2) in the same manner as described above for lamprey marks. Jaw damage caused by the cages or by the jaw tags was partitioned into two categories: absent to light (skin scraped off) or severe (eroded to the bone or broken).

Observations of free-living trout

Estimates of the frequency of chestnut lamprey attacks on free-living trout from 1988-91 were made from data collected by a group of volunteer anglers. They recorded observations of attached chestnut lamprey and lamprey attack marks. They kept fishing logs of their catch and effort on the Manistee River in a series of seven river sections between Mancelona Road in Otsego County and Sharon in Kalkaska County (Figure 1). Additional estimates of the frequency of chestnut lamprey attacks on trout, and some

other fish species, were gleaned from Michigan Department of Natural Resources (MDNR) fishery survey records.

During July 1988, visual surveys of approximately 20 kilometers of the Manistee River were made at night with underwater lights mounted beneath a boat that was drifted freely downstream. I did not count all trout observed since the primary purpose of this survey was to locate and count Arctic grayling. However, I did record approximate numbers of trout observed, and estimated the approximate percentage of trout with attached chestnut lamprey in some river sections.

Data Analysis

I used logistic regression techniques to identify variables most useful for predicting if trout would live or die in the holding cages (Hosmer and Lemeshow 1989). Because data collected during the 1989 pilot tests were limited, only 1990-91 data were analyzed by logistic regression. This regression technique can simultaneously consider effects of both categorical variables, such as lamprey attack (attacked or not attacked) or disease status (diseased or not diseased), and continuous variables, such as fish weight or number of days a fish was attacked by a lamprey. Logistic regression analysis was also used in an attempt to identify variables useful for predicting the probability that fish would develop furunculosis or fungal infections.

I used the forward stepwise procedure to select independent variables. Only variables that met a probability of F-to-enter of 0.05 were entered into the logistic regression models during this procedure. I also examined correlation matrices to determine if independent variables were significantly correlated, which would justify deleting them from the list of variables available for entry into the regression. For example, if a preliminary regression analysis to predict mortality (dependent variable) first selected the variable for wound area (cm^2), and if the correlation matrix indicated that wound area was significantly correlated with another independent variable, such as number of wounds, I deleted the "less important" number of wounds variable from the list of variables available for entry into the regression, and ran the analysis again. I used the significance level of the likelihood-ratio (LR) criterion ($P = 0.10$) to determine if variables should be removed from the logistic regression models. Selection of independent variables was terminated, either when the LR criterion was exceeded, or when the addition of more variables did not significantly improve the significance level or fit of the logistic equation. I also examined classification tables and histograms of observed versus predicted mortality (dead or alive) to determine if the addition of a variable to a logistic model significantly improved its fit to the data. Data were pooled among test sites and test periods within years before analysis. Most logistical regression analyses presented in this report are for either 1990 or 1991 pooled data. In this report statistical tests were judged to be significant at $P \leq 0.05$.

Independent variables examined for their relationships with mortality or furunculosis during 1991 included: number of wounds, total wound area (cm^2), severe wound area (total area of wounds where any part of the wound penetrated the skin), presence or absence of abrasions caused by the holding cages, size of abrasions (cm^2), jaw damage caused by the cages or jaw tags (absent-to-light or severe), presence or absence of furunculosis infection, presence or absence of fungus infection, an attack variable (attacked or not attacked), a fish size category variable (small or big), and length or weight of fish.

Fewer independent variables were measured in 1990. Independent variables not measured were: severe wound area, presence or absence of abrasions caused by the holding cages, size of abrasions, jaw damage caused by the cages, presence or absence of furunculosis infection, and presence or absence of fungus infection. In 1990, furunculosis diagnoses were made only for the dead fish and half could not be used because samples were damaged during shipment to the pathology lab. However, a fish origin variable (hatchery or wild) was included in the analysis of 1990 data.

Forward stepwise logistic regression analysis was also used to determine if the probability that a trout would be attacked was related to fish size. For this analysis, each lamprey mark was defined as an attack. The independent variables used in this analysis were fish length, weight, and estimated body skin surface area. The estimates of skin surface area were computed using the two equations given in Webb and Skadsen (1979) that related body surface area to body mass (g) of rainbow trout. Since these independent variables were highly inter-correlated, selection of independent variables was terminated after the best one was selected. Relationships between the number of lamprey marks and trout size were analyzed by linear regression. Regression analyses were done using procedures in the SPSS/PC+ software package (Norusis 1988; SPSS Inc. 1989).

Results

Percentages of caged-trout attacked

From 0-100% of the trout in treatment cages were attacked by chestnut lamprey during 1989-91 test periods (Table 2). In general, higher percentages were attacked in periods beginning near the middle of July. Only 1 of 30 trout accessible to lamprey was attacked during the earliest period (May 10-June 16, 1989). Fewer lamprey attacks occurred at the test sites used during 1989 than at those used in 1990-91.

Higher percentages of large brown trout (26-41 cm long) were attacked (one or more times) than small brown trout (15-25 cm) (Table 2). The percentage of small trout attacked during 1990-91 test periods ranged from 0-63 percent. By comparison, 13-100 percent of large trout were attacked during these tests. During 1990-91, 38% of small trout accessible to lamprey attack, and alive at the end of the test periods, had no lamprey marks. By contrast, only 9% of accessible large trout that were alive at the end of the test periods had not been attacked.

The probability that lamprey would attack accessible caged trout during 1990-91 was positively and significantly correlated with trout size. Logistic regression analysis indicated that estimates of body skin surface area were better for predicting attack probabilities than either trout length or weight. However, each of these size-related independent variables had significant positive relationships with the probability of attack. The logistic regression equation fitted to the 1990-91 data indicated that the predicted probability of an attack ranged from 14%, for the smallest accessible trout tested (40 g, skin surface area 77 cm^2) up to nearly 100% for the largest trout tested (616 g, skin surface area 434 cm^2).

Large trout were more likely to be attacked multiple times than small trout (Table 3). No small trout accessible to attack during the 1990-91 test periods had more than 4 lamprey marks, while 18 (28%) of the large trout acquired 4 or more marks. Linear correlation coefficients for the number of lamprey marks on accessible caged trout versus trout size (length or weight) were all positive and significant, regardless of whether or not trout survived to end of test period. The linear regression equation (r = 0.53) relating number of lamprey marks to trout weight was

$$N = -0.2080 + 0.0052\ W,$$

where N was number of wounds and W was weight in grams. The equation was derived for surviving trout exposed to predation for the same length of time.

Percentages of free-living trout attacked

Data collected by volunteer anglers indicated that the highest attack frequencies (percentage of trout with attached lamprey or lamprey marks) during 1988-91 occurred in the Manistee River sections downstream from M-72 (Figure 3). Only one trout out of 718 reported caught upstream from County Road 612 was observed with an attached chestnut lamprey. Thus, I did not include data from this river section in Figure 3. Except for 1988, attack frequencies on trout caught downstream

from M-72 have been 7.0% or less. One percent or less of the trout caught by anglers in the river section between County Road 612 and M-72 were reported attacked between 1989-91 (Figure 3).

Chestnut lamprey attacked higher percentages of larger angler-caught trout. The three species of trout caught from the Manistee River during 1988-91, listed in descending order of their mean lengths in angler catches, were rainbow trout *Oncorhynchus mykiss*, brown trout, and brook trout *Salvelinus fontinalis*. The percentages of angler-caught trout reported attacked by lamprey between Mancelona Road and Sharon were 4.8% of 1,445 rainbow trout, 3.7% of 2,629 brown trout, and 2.3% of 4,340 brook trout.

The percentages of trout observed at night during July 1988 with lamprey attached, varied from 4-90%, depending upon the river section. Lamprey were more frequently observed attached to larger trout. During a July 26, 1988 night survey of a 7.9 kilometer river section between the Horse Trail Camp and Long's Canoe Livery (Figure 1), I estimated that less than 4% of approximately 500 trout observed had visible attached lamprey. Most trout seen and observed with attached lamprey were about 17 cm long. By contrast, during a similar survey made on July 28, 1988 in a 12.1-kilometer river section between Yellowtrees Landing and CCC Bridge, chestnut lamprey were observed attached to an estimated 90% of approximately 50 trout observed within the first two kilometers of river downstream from the landing. Further downstream, an estimated 30% of approximately 150 trout observed had visible attached lamprey. Larger trout (30 cm +) were more frequently observed during the July-28 survey than during the July-26 survey. Simultaneous attachments of more than one lamprey were observed only on large trout (25 cm +). The abundance of visible trout varied markedly between segments of this 12.1-kilometer river section and in general the percentage of trout with attached lamprey was higher where more trout were observed.

The percentage of lamprey-marked trout collected during daytime electrofishing surveys from 1987-91 ranged from 0-8% depending upon the year and survey site. Data from 1987 fall surveys indicated that trout longer than 20 cm were more frequently attacked (Table 4). Although the exact length of the smallest trout attacked was not recorded, its length was between 12.7 and 15.0 cm. The distribution of lamprey marks among trout of different sizes was not recorded in 1988-91 daytime electrofishing survey records.

The percentages of lamprey-marked fish were higher among the fish collected during a night electrofishing survey, and larger fish bore more marks. Half of a small sample of trout (12 fish) collected downstream from Yellowtrees Landing during July 1989 exhibited lamprey marks. Lengths of these trout ranged from 17-34 cm, and averaged 23 cm. Multiple wounds were observed only on trout longer than 26 cm. Eight of eight large (37-58 cm) redhorse suckers Catostomidae sp. and three of five white suckers *Catostomus commersoni* (18-36 cm) collected during the same survey bore lamprey marks. Seventy-five percent of the redhorse suckers had two or more lamprey marks.

Electrofishing surveys from 1987-91 indicated that few trout were attacked at stations upstream from County road 612. These data corroborate those compiled from angler records.

Anatomical Attachment Regions

Over 76% of 250 lamprey marks acquired by trout in live cages were on the dorsal half of the fish (Table 5). With the exception of the first 1991 test period, lamprey most frequently attached to trout in the dorsal region II between the head and the leading edge of the dorsal fin (Figure 2). The next most common attachment site was in the dorsal region IV beneath the dorsal fin. Attachments were least frequent in regions V and VI.

Mortality of caged brown trout

From 1989-91 the percentage of test groups of brown trout dying in holding cages after being attacked by chestnut lamprey varied between 0 and 100 depending upon the year, site, and test period (Table 6). However, from 4 to 80 percent of trout not attacked also died during the same holding periods. Thus, it was unclear how much mortality of attacked fish was linked solely to the effects of chestnut lamprey attack.

Logistic regression analysis indicated that, during 1990 test periods, caged trout (all sizes combined) wounded by lamprey were more likely to die. The size of the lamprey wound area (cm^2) was significantly related to the probability of death during the time of confinement in cages. The predicted probability of death for attacked trout ranged from 20-100% depending upon the size of the wound areas measured (0.17-26.6 cm^2). The predicted probability of death for a caged trout with one mean-sized attack wound (0.83 cm^2) was 29%. However, the logistic regression analysis also indicated that nearly 18% of caged trout with no wounds would die. Addition of variables other than lamprey wound area to the logistic regression equation did not significantly improve the accuracy of mortality predictions.

Mortality of small trout (15-25 cm) alone, during 1990, was not significantly linked to lamprey attack, but mortality of large trout (26-41 cm) was significantly related to lamprey wound area. The logistic regression equation derived using the 1990 data for large-trout only, indicated that large trout were slightly less likely to die from wounds of a given size. For example, the predicted probability of death for a large trout with one average-sized attack wound (0.83 cm^2) was 23% versus 29% when all sizes of trout were used to derive the regression equation.

During 1991, mortality of caged trout (all sizes combined) was not significantly linked to chestnut lamprey attacks. Logistic regression analysis showed that the probability of death during the test periods was higher for trout that tested positive for furunculosis bacteria and had sustained severe jaw damage while in the cages.

Mortality of large trout (26-41 cm), during both 1991 test periods combined, was positively linked only to the presence of furunculosis, whereas small trout mortality was significantly (and positively) related to a combination of furunculosis infection, jaw damage, and the size (cm^2) of skin scrapes sustained in the cages. Small trout sustained jaw damage more frequently, due to tagging, during the first 1991 test period. Mortality of small trout during the second 1991 test period was significantly related only to the presence of furunculosis bacteria.

I could find no clear links between furunculosis infections contracted by caged trout during 1991 and lamprey attack or tissue damage sustained in the cages. The percentages of lamprey-attacked trout diagnosed as having furunculosis infections were 18% during the first test period and 32% during the second test period. Furunculosis infections were diagnosed in 26% and 19% of trout that were not attacked during the first and second 1991 test periods.

During 1991, only those trout diagnosed as being free of furunculosis infections survived lamprey attachments that lasted more than 10 days. Some furunculosis-free trout (4 fish) survived with chestnut lamprey attached for 16-19 days. However, absence of furunculosis infections did not assure survival, as only 36% of trout dying after a 1-day attack during 1991 tested positive for furunculosis bacteria.

Fungus infections *Saprolegnia sp.* were frequently observed during 1991, but could not be linked by logistic regression analysis to furunculosis infections or any of the variables related to lamprey attack or tissue damage. Obvious fungus infections were observed on 16 of 128 fish during 1991 and all but one of the fish known to be infected died before the end of the test periods. Almost exactly the same percentage of attacked and non-attacked fish developed obvious fungus infections.

Fungus infections probably were not detected on some fish that had substantially decomposed before they were frozen. Because fish were observed only once every 24

hours, fish that died shortly after an observation ended were significantly decomposed before the next observation, particularly during warm periods. Trout tested in 1991 were also found to have acquired other bacterial infections (*Aeromonas hydrophila, Aeromonas shigelloides,* and *Pseudomonas* sp.), but these infections could not be readily related to lamprey attacks or mortality because all fish were not tested for these diseases.

Mortality of some caged trout during 1990-91 was associated with episodes of high water temperature. During 1991, nearly half of the trout that died during the test periods died on days when maximum water temperatures reached or exceeded 70 °F. Some trout appeared to attempt to escape from the cages during these warm-water periods and presumably suffered more abrasions, jaw damage, and stress.

Discussion

Attack frequencies

Attack frequencies found for free-living trout in 1989-91 in Manistee River sections between the Mancelona Road and Sharon Bridges, suggested that contemporary chestnut lamprey populations have a similar density distribution as lamprey observed before the 1966 chemical treatment. Recent angler and electrofishing survey records clearly indicated that few trout were attacked upstream from County Road 612, while the percentages attacked were highest in river sections between M-72 and the Sharon Bridge. Chestnut lamprey adults and *Ichthyomyzon* larvae during the late 1950s and early 1960s were apparently most dense for a number of kilometers downstream from the M-72 bridge in Crawford County and were sparse in both the upper river near Deward and downstream from Sharon in Missaukee County (Crowe 1959; Hall 1963).

The finding that chestnut lamprey feeding activity in the Manistee River peaks near the middle of the summer (based on predation on caged fish) corroborates findings previously reported for Manistee River lamprey populations. Hall (1963) reported that chestnut predatory feeding began in April, was highest during the months of June, July, and August, and then declined until October.

Size selective attacks

Findings of this study supported the hypothesis that chestnut lamprey selectively attack larger trout in the Manistee River. This conclusion corresponds with the findings of other investigators that chestnut and sea lamprey *Petromyzon marinus* generally select larger hosts when they are available (Berst and Wainio 1967; Farmer and Beamish 1973; Pycha and King 1975; Beamish 1980; Farmer 1980; Cochran 1985; Henderson 1986; Noltie 1987; Swink 1991). Evidence of chestnut lamprey attacks observed on free-living trout, could be somewhat biased toward large fish since small fish are less likely to be observed or captured during surveys and angling. Moreover, only fish that had survived attacks were examined, and in general larger fish were less likely to die after an attack. However, the consistently higher frequency of multiple lamprey attacks observed on larger fish, both in the live cages, and in the wild, provides additional evidence that there was active selection for larger prey.

Anatomical attachment sites of chestnut lamprey

The tendency for chestnut lamprey to select dorsal attachment sites on prey, as I found during this study, has been previously reported. The distribution of attacks I found in this study was similar to the distribution of attacks on rainbow trout reported in laboratory studies (Cochran 1986). Dorsal attachment sites may be selected more frequently by lamprey in shallow lotic environments to avoid abrasion on the bottom, although ventral attachments may offer higher potential rates of feeding (Cochran 1986; Cochran and Kitchell 1986). Sea lamprey

most frequently attach to ventral regions of fish and can cause substantial mortalities (Berst and Wainio 1967; Davis 1967; Farmer and Beamish 1973; Cochran 1986; Kitchell 1990). Different feeding strategies used by parasitic lamprey have been modeled and investigated in detail relative to fish size, lamprey size, attachment sites, period of attachment, feeding and growth rates, temperature, and other factors (Kitchell and Breck 1980; Cochran 1986; Cochran and Kitchell 1986; Cochran and Kitchell 1989).

Mortality of attacked brown trout

Mortality of caged brown trout observed during this study could not be attributed solely to effects of lamprey attack. Although trout mortality during some test periods was significantly linked to lamprey attacks, such stress factors as intermittent high temperatures, disease, and injuries from confinement confounded analysis of mortality data. These stress factors could have acted alone, in combination, or sequentially to cause death. The high percentages of unattacked trout that died during some test periods was clear evidence of severe stress. Thus, even when trout mortality was significantly correlated with lamprey attacks, the stress from the attack was presumably an additive, rather than a primary stressor.

Kitchell (1990) reported that key factors for predicting death of salmonids following sea lamprey attack were the size ratio of host to lamprey and attachment time. My study design did not allow me to determine the average size ratio of host fish to chestnut lamprey. Most lamprey detached from fish before they could be captured and weighed. Several brown trout that suffered attacks that penetrated the body cavity in ventral regions died quickly. Hall (1963) estimated that chestnut lamprey (mean weight 8.5 g) killed 0.27 grams of fish per hour of feeding at 50 °F. If this kill-rate was applied to the 1990-91 data, it would have taken a single lamprey attachment lasting 16 days to kill the average small brown trout (103 g), and a 56-day attachment to kill the average large brown trout (360 g). Attacked trout died far more quickly than this during 1990-91. However, I could not accurately estimate the grams of trout killed per hour of attachment because my study design was different. Interpretation of mortality due to lamprey attacks during 1990-91 was further complicated by occasional observations of large numbers of lamprey (up to 20) attached to one fish.

Diseases, stress and mortality

Diseases contracted by caged trout, particularly furunculosis, appeared to be a major cause of mortality during 1991. Hall's (1963) analysis of mortality caused solely by chestnut lamprey was also confounded when his host fishes (rainbow and brook trout, and white suckers) contracted furunculosis, fin rot, and fungal infections. Brown trout are more likely to die from furunculosis than brook or rainbow trout (Wolf 1939; Cipriano and Heartwell 1986). Stressed trout have low resistance to disease and fish mortalities in the wild caused by furunculosis are not unusual when water temperatures are high (Allison et al. 1977). High water temperatures may have been the primary reason trout contracted furunculosis in 1991, because this disease could not be linked statistically to lamprey attacks or tissue damage sustained during confinement. Water temperatures at test cage sites frequently exceeded 70 °F during 1991 when furunculosis infections were prevalent (Appendix 1).

Fungal infections observed during 1991 were further evidence of stress, although they did not appear to be related to lamprey attack. Allison et al. (1977) reported that fungus can develop rapidly on stressed fish. Parker and Lennon (1956) reported that some fish in aquariums died of fungus infections after surviving sea lamprey attacks. Swink and Hanson (1989) found in laboratory tests that 5% of rainbow trout, and 14% of lake trout subject to a single attack by a sea lamprey died due to secondary fungal infections.

Management Implications

This study indicated that the present distribution of chestnut lamprey within the Manistee River between Mancelona Road and Sharon is similar to their distribution before the 1966 lampricide treatment. Contemporary lamprey abundance may be lower than in the past when large numbers of catchable sized trout (excellent prey) were stocked (Table 1). The Manistee River trout fishery was probably most famous during the period when large numbers of highly-catchable, legal-sized rainbow trout were stocked. These rainbow trout also undoubtedly increased the growth and survival of the brown trout that ate them, and hence produced a renowned trophy brown trout fishery.

This study failed to provide a good estimate of how many unstressed trout are likely to die from a lamprey attack. Although Hall's (1963) dissertation is frequently cited as evidence that chestnut lamprey could have a devastating effect on the Manistee River trout fishery, his mortality estimates were also confounded with other stress factors, and could be quite inaccurate. At a minimum, estimates of trout mortality per lamprey attack, attack frequencies, and lamprey populations are needed before potential lamprey effects on trout populations can be assessed. The high cost of a lampricide treatment of the Manistee River for a temporary reduction in lamprey populations can not be justified when the effect of lamprey predation on the trout population is uncertain.

I believe that alteration of the bed type and channel morphology of the Manistee River by historical logging practices and other anthropogenic effects have enhanced larval lamprey habitat in the river via increased sedimentation. Anglers who fished the Manistee River from 1874-1904 rarely reported observing chestnut lamprey (Hall 1963). The progress made to reduce excessive sand sediment delivery to the river in recent years by the 13-partner Upper Manistee River Restoration Committee is already enhancing the morphology of the river. Sediment control and removal is probably the best long-term treatment to enhance trout populations in the Manistee River. It has been proven to increase trout reproduction, habitat, and food. If sediment control also reduces habitat quality for chestnut lamprey some further enhancement of trout populations may ensue.

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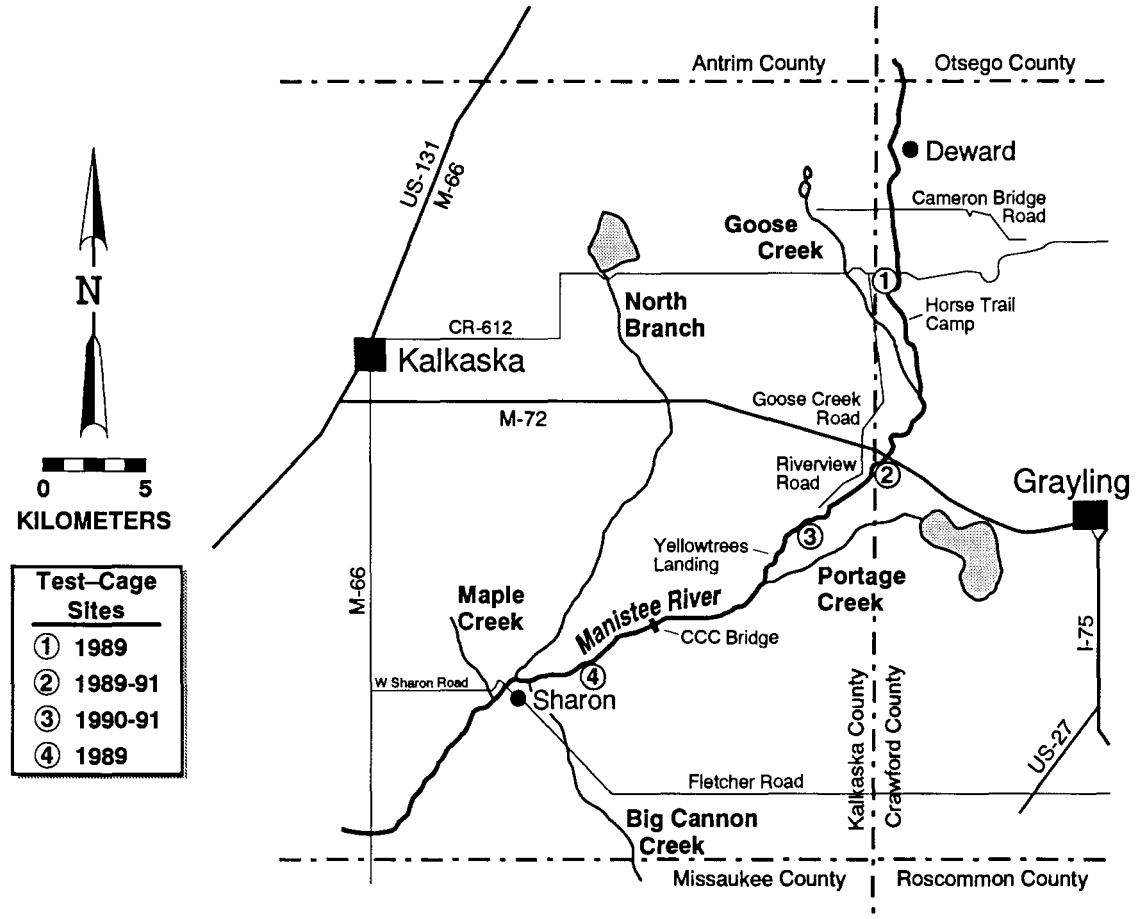

Figure 1.—Map of the upper Manistee River, Michigan, showing test cage sites, bridge crossings, survey sites, and tributaries referred to in the text.

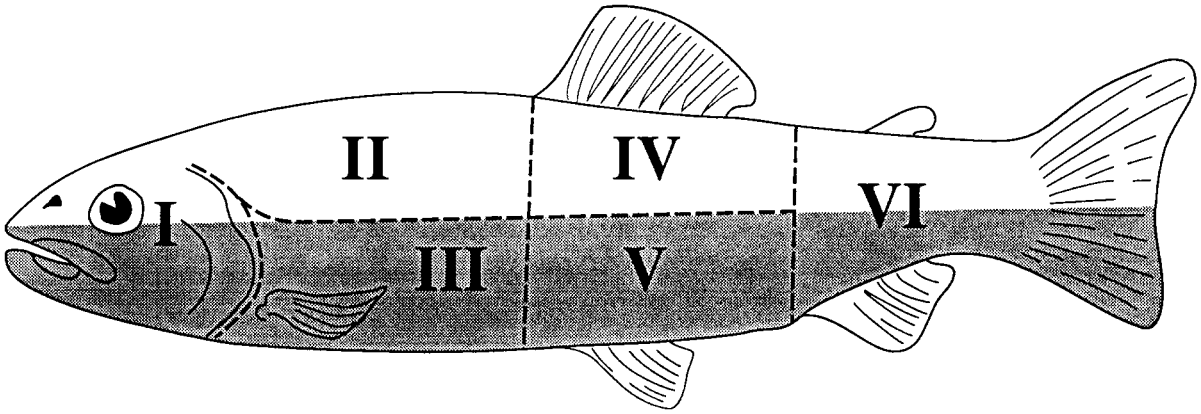

Figure 2.—Diagram showing body regions used in designating the location of chestnut lamprey attacks. Wounds within the shaded area were designated as ventral attacks and wounds above the shaded area were designated as dorsal attacks. (Figure modified from Cochran 1986).

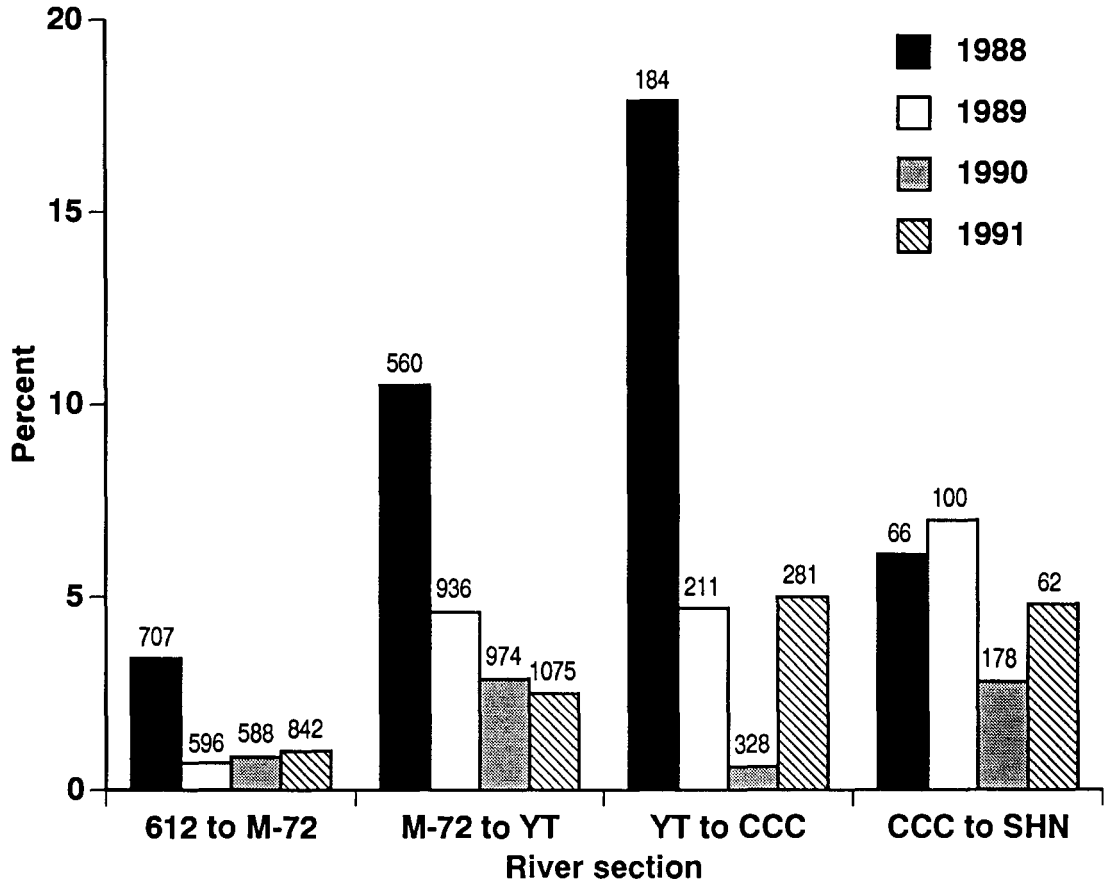

Figure 3.—Percentage of trout with attached chestnut lamprey or lamprey wounds as reported by volunteer anglers in sections of the Manistee River during 1988-91. The number of trout caught is shown above each bar. River sections are County Road 612 to M-72 (612 to M-72), M-72 to Yellowtrees Landing (M-72 to YT), Yellowtrees Landing to CCC Bridge (YT to CCC), and CCC Bridge to Sharon (CCC to SHN).

Table 1.—Number of brown trout, brook trout, and rainbow trout stocked in the mainstem Manistee River in Crawford and Kalkaska Counties from 1956—91.

	Brown Trout			Rainbow Trout			Brook trout	
Year	Finger-ling	Year-ling	Legal Sized	Finger-ling	Year-ling	Legal Sized	Year-ling	Legal Sized
1956	—	—	2,800	—	—	122,768	—	3,500
1957	—	1,150	1,612	—	—	97,947	—	3,500
1958	—	—	1,180	—	3,600	99,571	—	3,500
1959	—	—	150	—	—	84,166	—	6,300
1960	—	—	2,681	—	—	83,544	—	3,500
1961	—	—	—	—	—	66,059	—	4,500
1962	—	—	—	—	—	58,200	—	4,500
1963	—	—	7,500	—	—	46,000	—	4,500
1964	—	—	—	—	—	50,900	—	4,500
1965	—	—	18,176	—	—	35,200	—	3,176
1966	14,000	—	—	55,025	—	23,000	—	—
1967	252,761	40,725	5,520	1,500	11,950	7,881	—	—
1968	20,000	15,300	—	—	—	—	—	—
1969	—	33,723	—	—	—	—	—	—
1970	—	39,000	—	—	36,158	2,000	—	—
1971	—	31,140	—	—	55,190	—	—	—
1972	—	49,713	525	—	—	—	—	—
1973	—	46,775	—	—	12,800	—	—	—
1974	—	43,000	2,720	—	50,045	—	—	—
1975	—	42,765	—	67,553	—	—	—	—
1976	2,912	36,165	—	50,061	—	—	—	—
1977		25,215	—	—	—	—	—	—
1978	4,805	25,410	—	—	12,000	1,750	—	—
1979	4,287	16,500	—	61,188	4,017	4,521	—	—
1980	5,114	15,675	—	—	16,945	—	—	—
1981	—	18,500	—	—	2,000	—	6,000	—
1982	—	19,293	—	—	5,000	—	—	—
1983	70,073	30,500	—	—	5,000	—	—	—
1984	8,000	33,106	3,232	—	—	5,900	—	—
1985	3,000	16,430	—	—	—	2,000	—	—
1986	9,500	19,700	—	—	—	4,990	3,750	—
1987	—	21,500	—	—	—	—	4,500	—
1988	5,850	30,500	—	—	—	3,000	—	—
1989	24,000	49,109	—	—	1,500	—	500	4,600
1990	8,286	29,275	400	—	3,000	5,000	4,500	200
1991	1,980	30,500	600	—	—	—	5,000	400

Table 2.—Percentage of accessible small (15-25 cm) and large (26-41 cm) brown trout attacked in holding cages by chestnut lamprey in the Manistee River, 1989-91.

	Locations of holding crates							
	M - 72		Yellowtrees		County Rd. 612		Above Sharon	
Test Period	Small trout	Large trout	Small trout	Large trout	Small trout	Large trout	Small trout	Large trout
1989								
May 10-June 16	0	0	—	—	20	0	0	0
June 22-July 20	40	0	—	—	20	20	20	0
July 20-August 17	0	60	—	—	40	20	0	40
1990								
June 25-July 16	0	63	13	75	—	—	—	—
July 17-August 8	63	88	50	88	—	—	—	—
1991								
June 24-July 12	25	75	25	88	—	—	—	—
July 15-August 5	63	100	25	88	—	—	—	—

Table 3.—Number of chestnut lamprey wounds on small (15-25 cm) and large (26-41 cm) brown trout accessible to attack in holding cages in the Manistee River during 1990-1991. The percentage of trout in each test period with a given number of wounds is given in parenthesis. The first test period was June 25-July 16, in 1990 and June 24-July 12, in 1991. The second test period was July 17-August 8, in 1990 and July 15-August 5, in 1991.

Number of wounds	Small trout				Large trout			
	First Test Period		Second Test Period		First Test Period		Second Test Period	
	1990	1991	1990	1991	1990	1991	1990	1991
0	15 (93.8)	12 (75.0)	7 (43.8)	9 (56.3)	5 (31.3)	5 (31.3)	2 (12.5)	1 (6.3)
1	1 (6.2)	2 (12.5)	6 (37.5)	7 (43.8)	7 (43.8)	3 (18.8)	1 (6.3)	2 (12.5)
2	0 (0)	0 (0)	1 (6.3)	0 (0)	2 (12.5)	3 (18.8)	3 (18.8)	4 (25.0)
3	0 (0)	2 (12.5)	1 (6.3)	0 (0)	2 (12.5)	3 (18.8)	0 (0)	3 (18.8)
4	0 (0)	0 (0)	1 (6.3)	0 (0)	0 (0)	0 (0)	2 (12.5)	4 (25.0)
5	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (6.3)	1 (6.3)	1 (6.3)
6	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (12.5)	1 (6.3)
7	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (6.3)	0 (0)
8	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (6.3)	1 (6.3)	0 (0)
9	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (12.5)	0 (0)
20	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (6.3)	0 (0)

Table 4.—Numbers of brook trout and brown trout examined for chestnut lamprey marks during September 1987 electrofishing surveys of sections of the Manistee River. The number of trout examined that were marked by lamprey is shown in parenthesis adjacent to the number of fish examined in that size range.

	Trout length (cm)					
Location	50-12.5	12.6-20.1	20.2-27.8	27.9-35.4	35.5+	Total
Deward	253	128	34	7	9	431 (0)
County Rd. 612	118	108 (1)	38 (3)	6 (4)	4	274 (8)
Horse trail camp	116	67	20 (2)	—	—	205 (3)
M-72	148	29 (2)	5 (2)	1 (1)	—	183 (5)
River View Road site	37	10	—	—	—	47 (0)
Yellow Trees access site	8	4 (1)	—	—	—	12 (1)
CCC Bridge	10	8	6	—	—	24 (0)
Sharon Bridge	28	1	1 (1)	—	—	29 (1)

Table 5.—Distribution of 250 lamprey marks observed on brown trout by body region. Data were from Manistee River during 1990-91 test periods. The dorsal and ventral regions and the body regions referred to by the roman numerals are shown in Figure 2. Percentages of wounds by body region are shown in parenthesis.

	Percent of marks by body regions:							
Test period	I	II	III	IV	V	VI	Dorsal	Ventral
1990								
May 25-June 16	2.0 (11.8)	5.5 (32.4)	2.5 (14.7)	3.0 (17.6)	4.0 (23.5)	0 (0)	8.5 (50.0)	8.5 (50.0)
July 17-August 8	16.0 (16.3)	27.0 (27.6)	14.0 (14.3)	26.0 (26.5)	5.0 (5.1)	10.0 (10.2)	77.0 (78.6)	21.0 (21.4)
1990 tests combined	18.0 (15.7)	32.5 (28.3)	16.5 (14.3)	29.0 (25.2)	9.0 (7.8)	10.0 (8.7)	85.5 (74.3)	29.5 (25.7)
1991								
June 24-July 12	9.0 (15.0)	16.0 (26.7)	6.0 (10.0)	20.0 (33.3)	3.0 (5.0)	6.0 (10.0)	47.0 (78.3)	13.0 (21.7)
July 15-August 5	8.0 (10.7)	31.0 (41.3)	12.0 (16.0)	16.0 (21.3)	2.0 (2.7)	6.0 (8.0)	59.0 (78.7)	16.0 (21.3)
1991 tests combined	17.0 (12.6)	47.0 (34.8)	18.0 (13.3)	36.0 (26.7)	5.0 (3.7)	12.0 (8.9)	106.0 (78.5)	29.0 (21.5)
1990-1991 combined	35.0 (14.0)	79.5 (31.8)	34.5 (13.8)	65.0 (26.0)	14.0 (5.6)	22.0 (8.8)	191.5 (76.6)	58.5 (23.4)

Table 6.—Percentage of brown trout that died in holding cages during each 1989-91 test period as a function of chestnut lamprey attack. The number of fish is given in parenthesis.

Test period	Attacked by lamprey	Not attacked by lamprey
1989		
May 10-June 16	0 (3)	4 (57)
June 22-July 20	20 (5)	24 (59)
July 20-August 17	82 (11)	31 (49)
1990		
June 25-July 16	25 (12)	17 (52)
July 17-August 8	70 (23)	20 (41)
1991		
June 24-July 12	100 (17)	80 (47)
July 15-August 5	73 (22)	62 (42)

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Richard D. Clark, Jr. Editor
Jim Peck, Editorial Board Reviewer
Alan D. Sutton, Graphics
Barbara Champion, Word Processor

Appendix 1.—Daily maximum and minimum water temperatures (^{0}F) in the Manistee River at M-72 and Yellowtrees during the 1990 and 1991 periods when trout were confined in holding cages.

	Site								
	M-72		Yellowtrees			M-72		Yellowtrees	
Date	Max	Min	Max	Min	Date	Max	Min	Max	Min
6/25/90	—	—	—	—	6/25/91	69	57	68	60
6/26/90	—	—	—	—	6/26/91	—	—	72	64
6/27/90	—	—	—	—	6/27/91	73	60	78	68
6/28/90	65	57	63	59	6/28/91	74	67	78	72
6/29/90	65	59	62	59	6/29/91	70	63	73	69
6/30/90	67	59	63	59	6/30/91	71	61	72	64
7/01/90	69	59	65	62	7/01/91	70	58	64	60
7/02/90	68	59	64	62	7/02/91	—	—	—	—
7/03/90	70	60	—	—	7/03/91	65	58	64	60
7/04/90	75	65	72	68	7/04/91	66	60	64	60
7/05/90	77	64	71	68	7/05/91	67	60	68	62
7/06/90	67	55	71	62	7/06/91	69	61	68	62
7/07/90	66	55	61	59	7/07/91	72	64	72	64
7/08/90	61	56	—	—	7/08/91	73	62	72	64
7/09/90	67	56	62	59	7/09/91	72	57	68	58
7/10/90	68	60	68	62	7/10/91	67	58	69	60
7/11/90	70	59	69	62	7/11/91	69	58	68	64
7/12/90	69	59	66	60	7/12/91	—	—	68	62
7/13/90	69	57	72	60	7/13/91	—	—	—	—
7/14/90	67	57	66	60	7/14/91	—	—	—	—
7/15/90	61	56	62	59	7/15/91	69	57	—	—
7/16/90	—	—	—	—	7/16/91	—	—	68	62
7/17/90	—	—	—	—	7/17/91	—	—	70	65
7/18/90	—	—	—	—	7/18/91	71	63	72	66
7/19/90	—	—	64	60	7/19/91	72	65	73	68
7/20/90	68	59	68	62	7/20/91	73	63	73	70
7/21/90	69	60	69	64	7/21/91	69	63	70	64
7/22/90	69	59	68	62	7/22/91	68	63	66	64
7/23/90	63	59	64	60	7/23/91	69	61	68	62
7/24/90	65	57	66	59	7/24/91	70	60	68	64
7/25/90	67	58	66	59	7/25/91	63	59	64	60
7/26/90	67	59	68	61	7/26/91	65	55	64	56
7/27/90	66	59	68	62	7/27/91	64	55	62	56
7/28/90	65	59	66	62	7/28/91	64	55	62	58
7/29/90	65	59	66	62	7/29/91	60	54	60	54
7/30/90	63	60	62	60	7/30/91	62	54	62	58
7/31/90	65	58	64	60	7/31/91	64	57	63	58
8/01/90	66	57	66	60	8/01/91	66	57	66	60
8/02/90	67	58	69	62	8/02/91	69	59	66	60
8/03/90	68	59	68	62	8/03/91	65	56	66	58
8/04/90	61	57	62	59	8/04/91	68	60	66	62
8/05/90	59	57	60	58	8/05/91	65	52	—	—
8/06/90	60	55	60	56	8/06/91	—	—	—	—
8/07/90	60	52	59	54	8/07/91	—	—	—	—