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EFFECTS OF GILL LICE (SALMINCOLA EDWARDSII) ON BROOK TROUT (SALVELINUS FONTINALIS) IN LAKES [1]

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Abstract

Six small lakes (3-10 acres) stocked annually with brook trout at the Pigeon River Fisheries Research Station, Vanderbilt, Michigan, have well established populations of S. edwardsii. This parasite was considered a possible cause of natural mortality of fish in these lakes. Objectives were to measure parasitism of gill lice on brook trout in relation to condition and rate of natural mortality of fish, and possibly identify factors influencing development of gill lice populations. Annual trout population estimates were made. Monthly samples of fish were taken from each lake January through December, 1964. Gill lice on each trout were counted and classified as to stage of development. Reproduction continued throughout the year. No relationship was found between parasitism and condition and rate of natural mortality of brook trout. Development of gill lice populations was not influenced by a summer decrease in volume of water with suitable temperature and oxygen characteristics for trout. Degree of infestation was most influenced by degree of infestation of older

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fish in each lake. In four lakes gill lice populations developed exponentially, and the rate of increase was inversely related to initial number of gill lice on fish.

Introduction

Causes of natural mortality of trout stocked in lakes have not been definitely determined (Johnson and Hasler, 1954; Alexander and Shetter, 1961, 1969; Eipper, 1961; Hatch and Webster, 1961; Latta, 1963). Davis (1956) states, "Small ponds . . . may provide so favorable an opportunity for the multiplication and spread of copepods that they become exceptionally abundant and may cause great mortality." Six small lakes at the Pigeon River Fisheries Research Station, Vanderbilt, Michigan, have well established populations of the parasitic copepod *Salmincola edwardsii*. The causes of natural mortality of brook trout (*Salvelinus fontinalis*) in these lakes have not been identified (Latta, 1963). The gill louse appeared to be a likely source of mortality. The objective of this study was to measure the degree of infestation of the gill louse on the brook trout and to determine the effects of this infestation on the condition and the rate of natural mortality of the trout. A secondary objective was to possibly identify some of the factors influencing development of gill lice populations.

The lakes of the Pigeon River area are considered by geologists to be limestone sinks; i.e., they were formed through the solution of underlying limestone by groundwater, accompanied by a settling of the surface layer of sand and gravel which produced a cone-shaped pothole. The water surface in most of the lakes is 40 to 60 feet below the surrounding terrain. Eschmeyer (1938) and Tanner (1960) give a physical and chemical description of each lake.

Trout spawning was unsuccessful in these lakes and the fishery was maintained by annual plantings of fingerling trout. From 1957 through 1964 the rate of stocking was approximately 100 per acre. Each November, North Twin Lake received 550, West Lost 400, South Twin 430, Hemlock 600, Lost 460 and Ford 1, 170 fingerling brook trout. Trout 5 to 6 inches long (average about 5. 5 inches total length) of age-group 0 were selected for each planting. Each year class was identified by a distinctive fin clip. Although all lakes were poisoned in the early 1950's, the mudminnow (Umbra limi) was present in Ford Lake, the bluntnose minnow (Pimephales notatus) in Hemlock Lake and the white sucker (Catostomus commersoni) in Lost Lake.

Regulations for trout fishing in the lakes included a minimum size of 7 inches, a creel limit of 5 fish and with the exception of Ford Lake, no restriction as to lure or bait except that minnows could not be used. The same regulations applied to Ford Lake except that only the wet or dry fly could be used as bait. The fishing season extended from the last Saturday in April through the second Sunday in September.

A permit-type creel census was in operation at the station during the study. All anglers were required to report their catch at the end of each trip to each lake, which guaranteed a nearly complete record of the harvest.

Methods

Samples of trout were taken from each lake each month January through December 1964. Sample size was 10 fish per month per lake for the recently planted (November, 1963) year class and 5 fish from the older year classes. Fish from the older year classes were not collected after April. The dates and methods of collecting trout are given in Table 1.

Gill lice on each trout were counted and classified as to stage of development. The classification consisted of "very young"--the smallest individuals; "immature"--nearly the size of mature individuals but no egg sacs present; "early mature"--the individuals with egg sacs; "late mature"-- the individuals with egg sacs containing eggs about to be released as larvae (identified by the appearance of pigment in the eggs); and "senescent"--the large individuals essentially devoid of eggs (Fig. 1).

All trout in the samples were identified as to year class, measured to the nearest tenth of an inch total length and weighed to the nearest five thousandths of a pound. The coefficient of condition, C, which equals W (weight) x 10^5 divided by L (length) cubed, utilizing length and weight as described above, was calculated for each trout.

Estimates of the number of trout present in each lake in October 1963 and 1964 were calculated using the Bailey modification of the Petersen formula for mark-and-recapture estimates (Ricker, 1958). Confidence limits (95%) were calculated from Clopper and

Pearson's (1934) chart. Trout to mark were caught with hook and line and seines. The samples for recaptures were taken with a direct-current shocker (Latta and Myers, 1961). Latta (1963) described the method in detail. The estimates of population size, the catch by anglers and the number of trout removed in sampling from each lake are given in Table 2. Instantaneous mortality rates were calculated from the population estimates and other data of Table 2 following Ricker, 1958.

Temperature and dissolved oxygen of the waters of the lakes were measured the middle of each month, June through October, 1964. In this way the limits of the thermocline were defined and the water of the hypolimnion containing 4 ppm or less of dissolved oxygen was delimited. The stratum of water in each lake from the top of the thermocline to the water of the hypolimnion containing 4 ppm or less of dissolved oxygen was called the thermocline-oxygen stratum. From contour maps of the lake basins the volume of water in the thermocline-oxygen stratum was calculated for each month, June-September, that the thermocline was present. Total volume of water in each lake was calculated also. Some of the physical and chemical features of the lakes are given in Table 3.

Life history

Fasten (1921) reported the life history of the gill louse. The entire life cycle is completed in about two and a half months. Two or three weeks after attachment of the larvae to the trout the parasite becomes sexually mature. Salmincola edwardsii occurs only on brook trout. The larvae are liberated from the egg sacs about a month after fertilization. They are free swimming for about two days. If the specific host, the brook trout, is not found within this time the larvae die. Ordinarily each female produces two batches of eggs. According to Fasten this copepod reproduces only in the summer. In the fall the old females die and the young copepods remain inactive on the gills during the winter.

The mean number of gill lice per trout of the 1963 year class for each month and each lake is given in Table 4. In addition the percentage of the mean number in each stage of development is given.

This year class of trout was planted in the lakes in November 1963. We do not know how many gill lice they were carrying then except that it was probably low. All of the fish came from the same hatchery and whatever infestation they contained would have been similar for all individuals. In the fall of 1965, 100 trout of the same size and from the same hatchery as those used in this study were examined for gill lice. These trout carried a mean number of 3.8 ± 0.4 [1] gill lice in all stages of development.

By the time we started to sample the lakes for trout in January 1964, two months after the stocking in November 1963 the mean number of gill lice per trout varied from 0.7 ± 0.1 to 18.4 ± 1.5 (Table 4). The lowest mean of 0.7 which was observed in Ford Lake either represents the infestation at stocking or indicates

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[1] All limits on means are one standard error.

a loss of gill lice after stocking. The mean of 0.7 is considerably lower than the mean of 3.8 counted for a sample taken prior to stocking in 1965. From additional counts made in 1965-66 after stocking, it appears that the hatchery fish do have a decrease in infestation after stocking. In this year it was particularly apparent in Ford and Lost lakes. It is assumed that the same loss occurred in 1964 as in 1966, and that the actual infestation at time of planting in 1963 was about 3 or 4 gill lice per trout.

The "very young" stage of development of the gill louse, in comparison with the other life stages, was most abundant during the early months of 1964, as indicated by the percentage of the mean number in that stage (Table 4). Typically this "very young" stage reached a low in August and September and then started to increase again toward the end of the year. This is in direct contradiction to Fasten (1921) who indicated that the gill louse reproduced only during the summer months. The other stages complement the development of the "very young." The "senescent" stage was most abundant during the late summer, while the "very young" were least abundant and this stage was uncommon during the early months of the year. The intermediate stages of development between "very young" and "senescent" show the maturation of the gill louse population.

The mean number of gill lice per trout in the 1961 and 1962 year classes, the older residents in the lakes, is given in Table 5. Collections were made only in January through April because of the scarcity of the fish. The percentage of the mean number of gill lice in each stage of development for the 1962 year class is given in Table 6. In contrast to the newly stocked 1963 year class, the 1962 year class appears to be static with regard to changes in percentages of developmental stages. Typically in each lake there were small numbers of "very young" and "senescent" individuals on these older trout and large numbers of "early mature" individuals. There was little or no change in percentages during the months. Either the gill lice population was not developing or it was in balance with no changes in the numbers in each stage of development. Because the younger 1963 year class of trout had a developing gill louse population, it is assumed that the population on the older trout was essentially in balance during these months with the recruitment of "very young" equaling loss through "senescence."

Population growth

The following discussion of the growth of the gill lice population on each trout will be limited essentially to the 1963 year class. Not enough fish were examined from the older year classes to permit an extensive analysis (Table 5). However, from the few fish collected from the older year classes it appears that the mean number of gill lice per trout was usually greater on the older fish of the 1961 year class than on those of the 1962 year class. The mean numbers did not change from January through April. A comparison of the means for January 1964, the 1962 year class, with the means for December 1964, the 1963 year class, indicates that the means for trout in West Lost and South Twin are considerably greater in the 1963 year class (Table 4). In North Twin, Hemlock and Lost lakes the means for the two year classes were nearly identical. Ford Lake was not comparable for reasons to be discussed later.

The changes in the mean number of gill lice per trout per month for the 1963 year class in each lake can be followed in Table 4 and Figure 2. The pattern of increase was very similar in all lakes except Ford and Lost. In Lost Lake the mean number of lice continued at a low level of 3 or 4 per trout until in October through December there was a slight increase to about 12 per trout. In Ford Lake the means continued at a low level (6 gill lice per trout or less) until in August when they completely disappeared from the trout population. We do not have any explanation for this disappearance.

An analysis of variance of the gill lice means for North Twin, West Lost, South Twin and Hemlock lakes indicated that all were significantly different at the 95% level except North Twin and West Lost (Table 7). North Twin and West Lost had annual means of 46.8 and 46.6, while South Twin had 33.0 and Hemlock 23.1 gill lice per trout. Lost and Ford lakes were not included in the analysis because they were so obviously different from the other lakes. In December when we quit sampling, the mean number of gill lice per trout was still increasing. For West Lost it was 118, South Twin 98, North Twin 86, and Hemlock 57 gill lice per trout.

The rate of increase of the mean number of gill lice per month on each trout was examined by calculating a regression line for the logarithm of each mean. The intercept a for each line and the slope b are given in Table 7. All of the intercepts are significantly different at the 95% level and all the slopes are significantly different except South Twin and Hemlock. The intercept a is inversely related to the slope b , i.e., the trout with the fewest number of gill lice at the start of sampling in January had the fastest rate of increase in number of gill lice through the year. The number of gill lice per trout at the start seems to be directly related to the mean annual number of gill lice per trout.

In order to compare the reservoir of gill lice present on the holdover trout in the lakes in the fall of 1963, when the year class was stocked, with the mean infestation on the trout in January, when the year class was first sampled, the population of gill lice on older trout was estimated. The mean number of gill lice per trout for the 1962 and older year classes in January 1964, was as follows: North Twin, 100.3 ± 11.9, West Lost, 52.6 ± 7.7, Lost, 10.6 ± 2.0, Hemlock, 44.0 ± 7.3, South Twin, 46.3 ± 8.9 and Ford 7.3 ± 2.2. The mean times the estimated number of trout present in each lake in October 1963 (Table 2) gave an estimate of gill lice abundance at the time of stocking in the fall, 1963 (Table 7). A correlation coefficient r for gill lice abundance in the lakes versus the mean number of gill lice per trout of the 1963 year class in January 1964 was 0.89, significant at above the 95% level. Apparently the extant population of gill lice influences considerably the development of the infestation on newly planted trout, the level the infestation reaches and the rate at which the infestation progresses.

An attempt was made to relate gill lice abundance to some factors of the physical environment. A comparison of the annual mean number of gill lice per trout or other aspects of the gill lice population development (Table 7) with the alkalinity of the lakes (Table 3) indicates no relationship. The possibility that the volume of water available for each trout in each lake would influence the gill lice abundance was investigated by comparing the mean infestation with an estimate of the volume per trout in November 1963 (Table 8). The population estimates plus number of trout stocked that fall provided the total number of fish present in each lake (Table 2). The estimates of total volumes reflected the fact that Hemlock and Lost lakes are permanently stratified chemically and that there is only hydrogen sulfide below 36 feet in each lake (Table 3). The above calculations indicated that North Twin, West Lost and South Twin had a lesser volume per trout (about 5, 000 cubic feet) than Hemlock and Lost (with 7, 000 and 6, 000 cubic feet, respectively). The first three lakes had the higher infestations but Ford Lake had only 1, 000 cubic feet per trout and in Ford Lake the gill lice disappeared (Table 4). Ford Lake did not stratify during the summer as did the other lakes but what influence this would have is unknown.

Because of temperature limitations above the top of the thermocline and oxygen limitations below 4 ppm, it was hypothesized that trout would remain most of the time during the summer months in this stratum of the lake. The summation of the four volumes in this stratum (June through September) for each lake is given in Table 3. The mean numbers of trout from October 1963 to October 1964 for the 1963 and 1962+ year classes were added for an index to population abundance during the summer, 1964 (Table 2). The cubic feet of water per trout is given in Table 8. Again there was no close relationship between volume per trout and mean infestation of gill lice. The three lakes with the higher infestations had the lesser volumes--North Twin, West Lost and South Twin--but the volume per trout in Ford Lake was very close to those three and in Ford Lake the gill lice disappeared in late summer (Table 8). Also there was no apparent increase in rate of infestation during the period of stratification of the lakes (Fig. 2). We can only conclude that for our observations some factors had more influence than space on gill lice infestation.

Effects on trout

The condition factor, C, was determined for each trout taken in the monthly samples. The mean C for each month in each lake and the annual mean for the 1963 year class are given in Table 9. Typically in each lake the trout lost weight from January till March and April and then gained in weight till they reached a peak in early summer. Weight loss then began again in September and October. Although a comparison among lakes is not entirely acceptable because of differences in growth among lakes, there was no apparent relationship between annual mean condition factor and number of gill lice per trout. A better check of the relationship between condition and infestation of gill lice was made by comparing the infestation in December 1964 of individual trout of the 1963 year class, when the mean number of gill lice per trout was the largest (trout had been in the lakes for almost 14 months), with the condition factor for those trout. The correlation coefficients, r, indicated no relationship (Table 10). A similar comparison was made for the trout of the 1962 year class for January 1964, and again there was no correlation (Table 10). (These trout had been in the lakes for slightly more than 14 months.)

The relationship between infestation of gill lice and survival of trout was investigated by comparing the annual mean number of gill lice per trout with annual instantaneous total and natural mortality rates, i and q. For both the 1963 year class of trout and the 1962 and older year classes there was no obvious relationships between infestations of gill lice and survival of trout (Table 11).

It has been suggested that the act of attachment of the copepod larvae to the trout causes the most physical damage and because of this damage the trout are more susceptible to disease and thus mortality. In an effort to check this hypothesis a comparison was made of the mean number of "very young" gill lice per trout with the mortality rates. Although the percentage of "very young" per trout decreased from January through December, the actual numbers tended to increase (Table 4). The annual mean number of "very young" per trout was as follows: North Twin, 9.6; West Lost, 10.8; South Twin, 9.0; Hemlock, 6.5; Lost, 2.2; and Ford, 0.3. An analysis of variance indicated that there was no significant difference among North Twin, West Lost, South Twin and Hemlock lakes in numbers of "very young" gill lice per trout. There was no obvious relationship between the mortality rates and "very young" infestations.

Discussion

The effects of parasites on the condition and survival of fishes in the wild are not well known. Apparently whether the effects are detrimental or not to the fish is dependent upon not only the magnitude of the infestation, but also the kinds of parasites and the environmental conditions under which the fish are living (Freeman, 1964; Haderlie, 1953; Rabideau and Self, 1953).

Although it is well established that under hatchery conditions parasitic copepods can cause large mortalities (Fasten, 1921; Davis, 1956; Uzman and Rayner, 1958; Savage, 1935; Allison, 1950), there are few instances of these organisms causing mortalities in the wild (Allum and Hugghins, 1959; White, 1940).

We were unable to find any studies of the effects of Salmincola edwardsii on trout in the wild. The results of our studies indicate no measurable effect on the condition or survival of the trout. Although we found one trout with an infestation of 226 copepods, most of the trout had less than 100 copepods per fish. Perhaps an infestation considerably greater than this is needed to produce a measurable effect in growth or mortality. Fasten (1921) stated that it was not uncommon in his experience to find as many as 250 copepods on one trout. Allum and Hugghins (1959) reported in their description of the fish kill in Brant Lake, South Dakota, 300 to 400 Argulus per fish as common. Undoubtedly, more studies of the quantitative relationships between parasites and their hosts in the wild are desirable.

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Table 1.--Dates and methods of sampling brook trout for study of gill louse infestations in 1964

Month	Day	Method
January	14-17	Angling
February	14, 17, 18	Angling
March	18-19	Angling
April	15, 20-22	Shocking
May	12, 15, 18, 21, 22, 25-27	Angling, shocking, netting
June	15, 17-20, 22, 25, 26	Angling, shocking, netting
July	12, 17, 22-25, 27-31; Aug. 4	Angling, netting
August	18-20, 22-24, 26, 31	Angling, netting
September	28-30; Oct. 1, 2, 5	Angling
October	22, 26, 29, 30; Nov. 2	Shocking
November	25, 27; Dec. 3	Angling
December	28-30; Jan. 4	Angling

Table 2.--Number of brook trout estimated to be present, removed by sampling, and caught by anglers in six lakes, 1963-1964

Year class	Estimate Oct. 1963	Sample Jan.-Dec. 1964	Catch Apr.-Sept. 1964	Estimate Oct. 1964
North Twin Lake				
1963	550[a]	137	68	153
1962+ [b]	215	41	74	21
West Lost Lake				
1963	400[a]	118	103	124
1962+	164	33	59	22
South Twin Lake				
1963	430[a]	114	97	85
1962+	145	24	42	42
Hemlock Lake				
1963	600[a]	125	170	179
1962+	132	24	27	6
Lost Lake				
1963	460[a]	135	8	130
1962+	131	29	44	8
Ford Lake				
1963	1, 170[a]	120	80	137
1962+	335	27	124	23

[a] Number planted in November 1963.

[b] 1962+ indicates 1962 and older year classes.

Table 3.--Some physical and chemical characteristics of six lakes at the Pigeon River Fisheries Research Station

Lake	Surface area (acres)	Maximum depth (feet)	Methyl orange alkalinity (ppm)	Total volume (feet^3 x 10^3)	Summation of volume in thermocline-oxygen strata June-Sept. 1964 (feet^3 x 10^3)
North Twin	4.8	39	20	3,825	3,624
West Lost	3.5	41	116	2,870	2,460
South Twin	3.9	32	50	2,926	2,516
Hemlock	5.9	59	120	5,202[a]	7,161
Lost	3.7	50	130	3,684[a]	6,119
Ford	10.2	24	84	1,694	6,776

[a] Hemlock and Lost lakes are permanently stratified chemically. Hydrogen sulfide occurs below 36 feet in both lakes. The total volume estimates do not include the lower segments of these lakes that do not turn over.

Table 4.--Mean number of gill lice per trout of the 1963 year class and percentage of gill lice in each stage of development for each month in six lakes, 1964

Month	Number of trout	Mean number gill lice per trout		Percentage in each stage of development				
		Mean	Std. error	Very young	Immature	Early mature	Late mature	Senescent
North Twin								
Jan	8	18.4	1.5	77	20	2	1	0
Feb	10	24.2	3.8	17	80	1	2	0
Mar	10	25.4	2.6	7	67	25	1	0
Apr	10	23.8	4.0	11	21	53	14	1
May	10	33.2	2.7	16	25	33	15	10
June	11	43.1	3.8	12	35	34	10	9
July	10	50.4	10.5	7	25	41	12	15
Aug	8	48.0	9.7	11	21	48	11	10
Sept	10	52.8	6.7	2	9	58	19	12
Oct	10	72.9	6.0	31	10	38	14	8
Nov	9	83.3	8.9	38	16	29	9	8
Dec	10	86.0	7.5	22	25	38	10	6
West Lost								
Jan	10	12.3	1.6	56	43	1	0	0
Feb	9	11.8	2.9	36	52	3	0	8
Mar	10	16.1	2.1	10	83	7	0	1
Apr	10	21.4	2.0	9	29	46	14	2
May	10	25.9	2.8	36	17	28	11	7
June	10	34.0	5.0	13	31	28	16	11
July	10	51.4	7.1	4	14	59	15	8
Aug	6	66.3	7.3	6	17	60	9	9
Sept	10	53.2	3.7	1	13	49	22	15
Oct	10	64.1	8.0	37	4	35	17	7
Nov	10	84.4	8.6	31	21	28	15	5
Dec	11	117.7	11.9	38	21	30	10	1
South Twin								
Jan	7	1.8	1.6	61	33	6	0	0
Feb	10	3.3	0.3	76	12	6	3	3
Mar	10	4.8	1.1	52	40	8	0	0
Apr	10	5.8	0.7	50	29	14	5	2
May	10	10.5	1.0	18	42	34	6	0
June	10	24.2	1.6	17	33	34	12	4
July	10	35.5	5.8	38	18	27	12	4
Aug	8	52.6	10.0	6	22	48	13	11
Sept	10	27.5	6.0	1	11	60	15	13
Oct	10	46.3	5.0	30	2	42	17	8
Nov	9	84.9	12.7	41	20	21	14	4
Dec	10	98.2	17.9	27	33	27	8	4

Table 4.--concluded

Month	Number of trout	Mean number gill lice per trout		Percentage in each stage of development				
		Mean	Std. error	Very young	Immature	Early mature	Late mature	Senescent
Hemlock								
Jan	10	2.8	1.2	75	7	4	0	14
Feb	10	5.4	1.0	59	24	7	2	7
Mar	10	3.9	1.0	51	36	10	0	3
Apr	10	6.5	0.5	32	52	11	5	0
May	10	7.7	1.7	55	16	18	8	4
June	17	9.3	1.4	25	39	18	9	10
July	12	17.8	1.8	25	13	37	15	10
Aug	9	34.8	6.3	49	12	25	10	3
Sept	10	38.2	6.2	9	15	45	21	11
Oct	10	43.3	5.0	15	7	45	26	6
Nov	9	51.1	13.2	31	12	40	11	7
Dec	10	56.8	9.4	27	19	36	15	4
Lost								
Jan	11	3.5	0.6	77	14	9	0	0
Feb	10	2.6	0.7	35	58	8	0	0
Mar	10	4.0	0.7	20	65	15	0	0
Apr	10	1.8	0.6	11	56	17	0	17
May	10	4.3	0.8	44	12	30	9	5
June	9	2.8	0.4	14	21	36	21	7
July	16	3.1	0.8	13	23	32	13	19
Aug	8	3.6	1.0	34	11	34	17	3
Sept	10	1.5	0.5	33	13	33	13	7
Oct	10	5.7	1.3	63	5	21	5	5
Nov	9	14.1	2.4	58	23	13	5	0
Dec	10	10.7	1.6	48	22	19	9	2
Ford								
Jan	10	0.7	0.1	57	14	14	0	14
Feb	10	0.8	0.3	50	50	0	0	0
Mar	10	1.0	0.3	30	50	10	10	0
Apr	10	1.4	0.5	29	21	43	7	0
May	10	4.0	0.6	58	20	12	5	5
June	10	6.0	1.2	5	35	30	13	17
July	10	4.5	0.9	0	84	0	0	16
Aug	8	0.0	-	0	0	0	0	0
Sept	10	0.0	-	0	0	0	0	0
Oct	10	0.0	-	0	0	0	0	0
Nov	8	0.0	-	0	0	0	0	0
Dec	9	0.0	-	0	0	0	0	0

Table 5.--Mean number (and standard error) of gill lice per trout of the 1962 and 1961 year classes for each month January-April, 1964, in six lakes (number of fish in parentheses)

Month and year class		Lake					
		North Twin	West Lost	South Twin	Hem-lock	Lost	Ford
Jan	1962	88.7± 8.5 (13)	49.8± 9.8 (6)	37.0± 12.2 (4)	49.0± 6.3 (6)	10.6± 2.0 (10)	7.2± 2.2 (4)
	1961	175.5± 50.5 (2)	58.0± 14.5 (3)	58.7± 11.2 (3)	14.0 (1)	-	7.5± 6.5 (2)
Feb	1962	63.0± 25.7 (3)	52.0± 6.5 (4)	31.5± 5.5 (4)	38.0± 9.9 (5)	8.2± 2.1 (5)	4.7± 1.2 (3)
	1961	127.5± 28.5 (2)	63.0 (1)	39.0 (1)	-	-	10.0± 6.0 (2)
Mar	1962	62.0± 3.3 (4)	48.2± 9.3 (4)	18.0± 6.7 (3)	32.8± 11.4 (4)	10.0± 2.3 (4)	3.7± 1.4 (3)
	1961	154.0 (1)	37.0 (1)	20.0± 13.0 (3)	127.0 (1)	27.0 (1)	38.0 (1)
Apr	1962	147.5± 46.5 (2)	51.6± 10.4 (5)	26.8± 5.5 (4)	31.0± 13.0 (5)	9.8± 1.4 (5)	4.4± 2.0 (5)
	1961	137.5± 21.5 (2)	-	44.0 (1)	-	-	-

Table 6.--Percentage in each stage of development of mean number of gill lice per trout for the 1962 year class, January-April, 1964, in six lakes

Month	Number of trout	Stage of development				
		Very young	Imma-ture	Early mature	Late mature	Senes-cent
North Twin						
Jan	13	2	29	49	18	2
Feb	3	4	21	50	18	7
Mar	4	4	19	46	21	10
Apr	2	2	12	53	30	3
West Lost						
Jan	6	2	48	35	9	6
Feb	4	2	25	43	19	11
Mar	4	0	19	54	20	7
Apr	5	3	12	54	27	3
South Twin						
Jan	4	1	16	76	2	5
Feb	4	3	15	45	19	17
Mar	3	6	18	52	15	9
Apr	4	3	10	55	22	9
Hemlock						
Jan	6	1	17	49	22	11
Feb	5	8	7	48	25	12
Mar	4	8	14	54	21	4
Apr	5	5	17	52	25	1
Lost						
Jan	10	22	34	30	11	3
Feb	5	12	34	41	10	2
Mar	4	2	50	30	12	5
Apr	5	2	35	39	18	6
Ford						
Jan	4	17	17	25	7	35
Feb	3	21	28	36	15	0
Mar	3	8	27	19	8	35
Apr	5	14	23	23	27	14

Table 7.--Characteristics of gill louse infestation for 1963, and 1962 and older, year classes of trout in six lakes in 1964

Lake	1963 year class			1962 and older year classes
	Annual mean number of gill lice per trout [1]	Log intercept of gill lice infestation [2] a	Rate of increase of gill lice infestation [3] b	Estimated number of gill lice per lake, fall, 1963 ($x 10^3$)
North Twin	46.8	1.216	0.062	21.6
West Lost	46.6	0.937	0.098	8.6
South Twin	33.0	0.236	0.155	6.7
Hemlock	23.1	0.328	0.128	5.7
Lost	4.8	-	-	1.4
Ford	1.5	-	-	2.4

[1] All means are significantly different at the 95% level except North Twin and West Lost. Lost and Ford lakes were not included in the analysis.

[2] All intercepts are significantly different at the 95% level.

[3] All slopes are significantly different at the 95% level except South Twin and Hemlock.

Table 8.--Number of cubic feet of water per trout for the total volume and the thermocline-oxygen stratum in six lakes

Lake	Total lake volume per trout, Nov 1963 (feet^3 x 10^3)	Thermocline-oxygen strata volume per trout, June-Sept. 1964 (feet^3 x 10^3)
North Twin	5.0	7.7
West Lost	5.1	6.9
South Twin	5.1	7.1
Hemlock	7.1	15.6
Lost	6.2	16.8
Ford	1.1	8.1

Table 9.--Monthly and annual mean coefficient of condition, C, for trout of the 1963 year class in six lakes, 1964 [a]

Month	Lake					
	North Twin	West Lost	South Twin	Hem-lock	Lost	Ford
January	34.8	35.0	30.6	31.9	31.2	32.9
February	33.6	33.6	29.6	34.0	30.5	32.8
March	34.0	31.9	31.3	32.7	29.4	31.3
April	31.0	31.8	31.0	34.3	29.7	32.0
May	40.4	38.0	43.3	36.5	31.3	37.0
June	39.5	44.4	46.7	37.0	38.8	39.8
July	44.9	42.2	44.2	39.8	34.4	42.3
August	41.0	41.6	45.2	40.7	35.2	42.8
September	42.5	45.0	43.9	40.3	37.6	40.9
October	37.7	42.8	38.5	37.6	33.5	41.1
November	32.8	36.3	37.0	36.0	31.4	38.0
December	37.4	35.5	37.2	35.1	32.3	35.8
Annual mean	37.5	38.2	38.2	36.3	32.9	37.2

[a] Number of fish in each monthly sample is given in Table 4.

Table 10.--Correlation coefficients, r, for number of gill lice and coefficients of condition, C, for trout of the 1963 and 1962 year classes in six lakes, December and January, 1964

	Lake					
	North Twin	West Lost	South Twin	Hem-lock	Lost	Ford
1963 year class, December 1964						
Mean number gill lice per trout	86.0	117.7	98.2	56.8	10.7	0.0
Mean condition factor C	37.4	35.5	37.2	35.1	32.3	35.8
Number of trout	10	11	10	10	10	9
Correlation coefficient r	+0.01	-0.27	-0.41	-0.51	+0.09	-
1962 year class, January 1964						
Mean number gill lice per trout	88.7	49.8	37.0	48.8	10.6	7.2
Mean condition factor C	34.1	36.3	31.1	37.5	31.7	40.8
Number of trout	13	6	4	6	10	4
Correlation coefficient r	-0.42	+0.21	-0.54	-0.58	-0.52	-0.84 [a]

[a] Not significant $P<0.10$.

Table 11.--Mortality rates for brook trout of the 1963, and 1962 and older, year classes in six lakes, 1964

Lake	1963 year class		1962 and older year classes		
	Total mortality *i*	Natural mortality *q*	Mean number of gill lice per trout Jan 1964	Total mortality *i*	Natural mortality *q*
North Twin	1.27	0.71	100.3 ± 11.9	2.30	0.94
West Lost	1.17	0.36	52.6 ± 7.7	2.04	0.71
South Twin	1.61	0.77	46.3 ± 8.9	1.24	0.45
Hemlock	1.20	0.44	44.0 ± 7.3	3.00	1.80
Lost	1.27	0.84	10.6 ± 2.0	2.81	1.15
Ford	2.12	1.76	7.3 ± 2.2	2.66	1.38

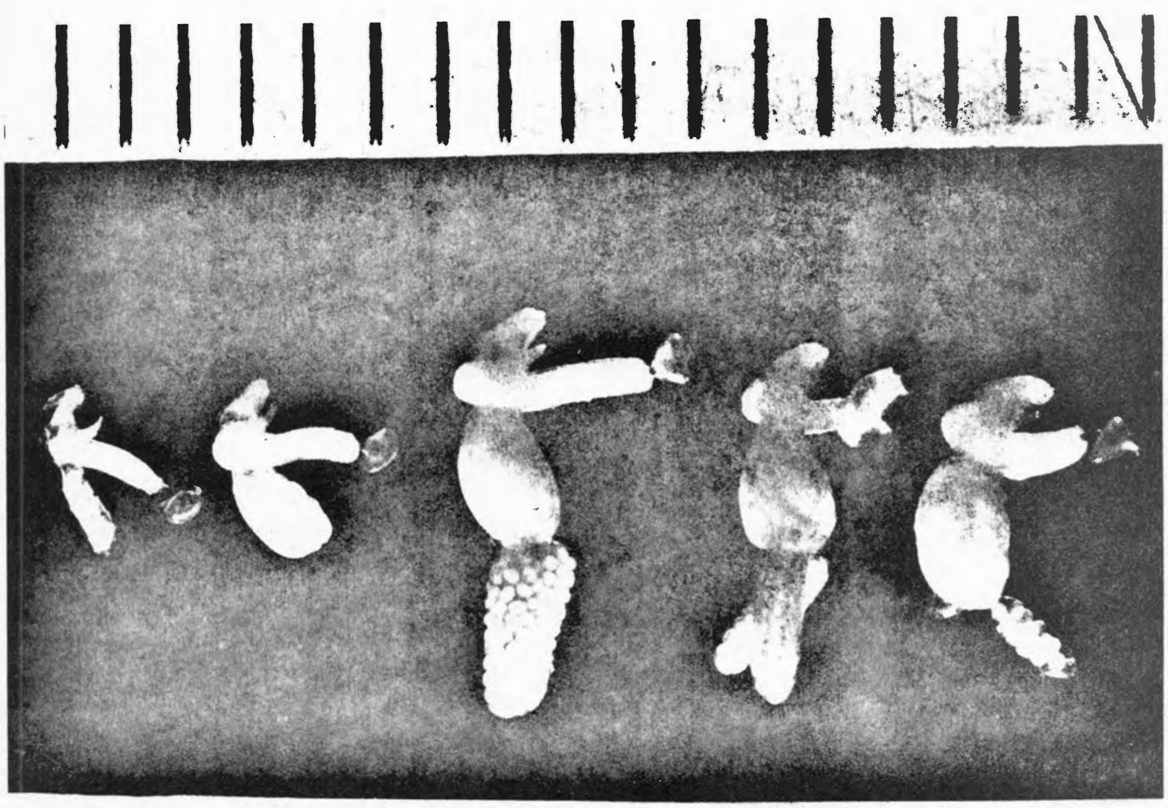

Figure 1.--Stages of development of the gill louse. From left to right the classification is as follows: very young, immature, early mature, late mature and senescent. Scale in millimeters.

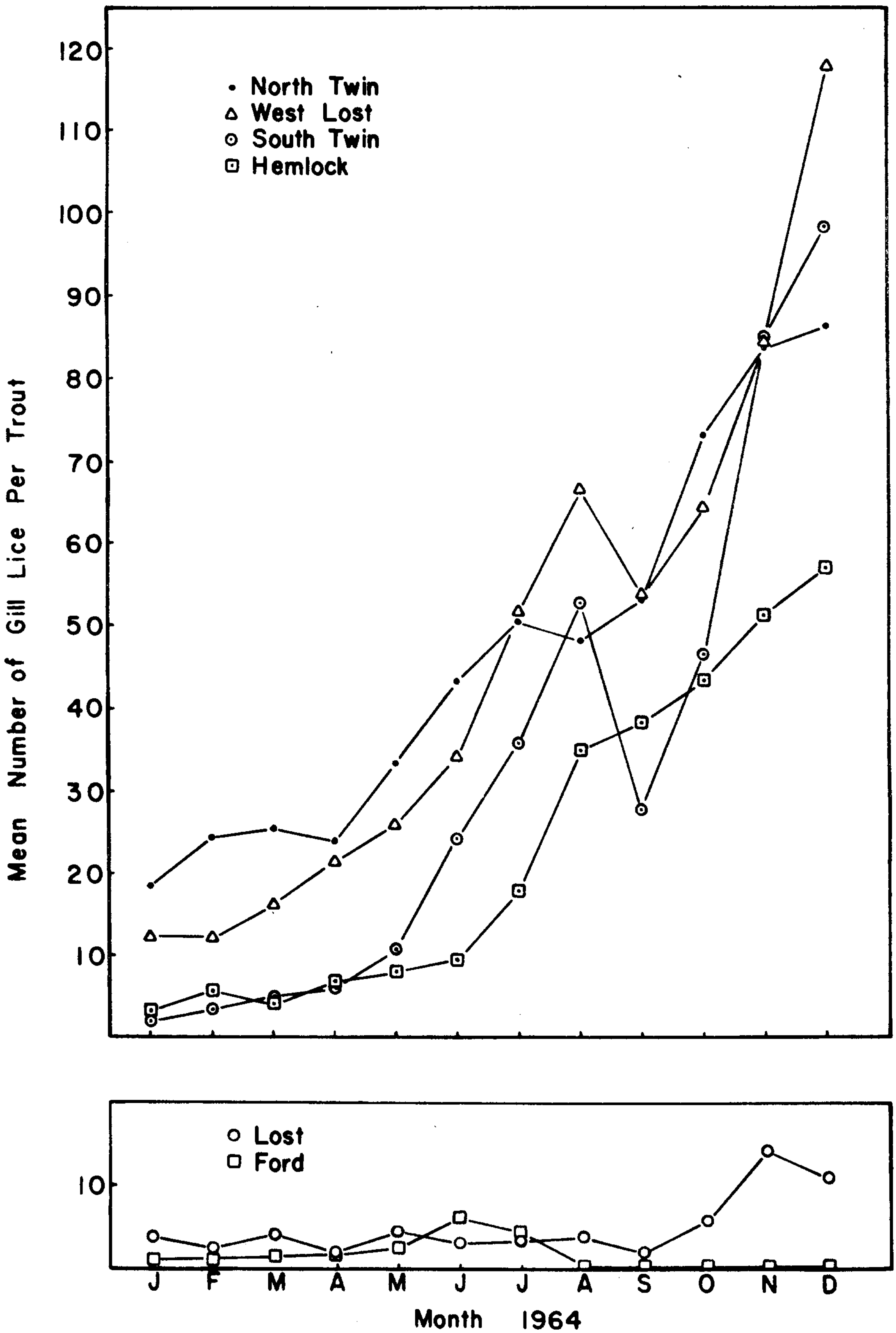

Figure 2.--Mean number of gill lice per trout of the 1963 year class for each month in 1964 in six lakes.