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POPULATION DYNAMICS OF TROUT, WITH CRAYFISH AS FOOD, IN THREE POTHOLE LAKES IN MICHIGAN [1]

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ABSTRACT

In the fall of 1965, populations of brook trout (juvenile and adult) were established in three pothole lakes in the Pigeon River area, at densities of 188, 411, and 1,399 fish per hectare. The lakes were closed to fishing; fish removal was limited to monthly samples for study of food consumption and growth. Population estimates were made periodically of surviving trout, and of an abundant species of crayfish.

The trout populations diminished drastically (by 89 to 99%) over a 2-year period, due mostly to natural mortality rather than to our sampling. Heaviest mortality occurred during either the first winter, or the first summer, related to high vs. low density. Growth was related to trout density and to food consumption. Crayfish made up 13% of the trout's diet in one lake, and a high of 71% in the third lake. Trout ate only age-0 crayfish; obviously the older crayfish were too large. Trout consumed as little as 1%, but as much as 43%, of the annual production of age-0 crayfish in the three lakes, but apparently did not "stress" the crayfish population.

During a second 2-year period, rainbow trout and brook trout were compared in two lakes, starting with like stocking rates and size of fish. The rainbow did better in survival and in production (44 kg/ha) than did the brook trout (14 kg/ha). The rainbow fed more on cladocerans; the brook trout more on crayfish.

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Introduction

This study was made on three pothole, limestone sink lakes in the Pigeon River State Forest. These lakes--South Twin, North Twin, and West Lost--contained hatchery brook trout which in 1965 were planted at three densities: low, intermediate, and high. Over a 2-year period, we determined the survival, growth, feeding habits and production of these brook trout, and especially the impact of trout predation on populations of the crayfish *Orconectes virilis* in relation to the three levels of density of trout.

Crayfish commonly comprise a major portion of the macrobenthos of marl lakes in northern Michigan. These lakes, high in transparency and low in organic matter, have a paucity of aquatic vegetation. Benthic algae account for most of the photosynthesis (Hooper and Ball, 1964), whereas phytoplankton production is typically low (Raymond, 1937). Production of insects is limited by lack of aquatic plants (Wohlschlag, 1950; Berg, 1949). In general, rates of production in marl lakes are considered low for all trophic levels (Wetzel, 1970).

In the fall of 1967 the rainbow trout was included in the study. A high standing crop of large adult rainbow trout was planted in North Twin Lake, and a similar stock of brook trout was established in West Lost Lake. Again, we measured the biology of these trout populations during 1968 and 1969, and determined what fraction of crayfish production went into trout production.

Thus, to recapitulate, this study in the initial phase describes changes in brook trout populations of mostly small fish of varying density and their influence on crayfish populations; and in the second phase it deals with dense populations of large rainbow trout and brook trout.

Description of the lakes

South Twin, North Twin and West Lost lakes are shown on the map (Fig. 1) of the Pigeon River fisheries research area in Otsego County. The lakes are similar with respect to morphometry. They are small in area, subcircular in outline, steeply cone-shaped in form, and lack either inlet or outlet. Lake surfaces are 12 to 18 meters below the surrounding terrain, and the basins have very steep slopes. Areas range from 1.4 to 1.9 hectares; mean depths are 7.3 to 8.5 m (Table 1). The shoal areas, defined as water less than 1.2 m in depth, are narrow and comprise only 11.0 to 15.3% of the total bottom. The predominant soil types are sand in the shoal area and outward to a depth of 3 m; organic matter out to 6 m, and pulpy peat in the deeper parts. Logs are abundant in the littoral area; they are marl encrusted in West Lost Lake. The limited submerged aquatic vegetation consists mainly of the yellow water lily, *Nuphar variegatum* Engelm. Most of the emergent aquatic vegetation consists of *Carex aquatilis* var. *substricta*.

The lakes were studied during the period from November 1965 to October 1969. Thermal stratification occurs in these lakes, characteristic of temperate lakes of the second order (Fig. 2). In August 1966, during the summer stagnation period, water temperature was 20 C at the surface, while near the bottom of the hypolimnion it ranged from 7 C (North Twin) to 12 C (South Twin). At this time, oxygen levels > 3.9 ppm extended down into the thermocline to depths varying from 7 m (South Twin) to 9 m (North Twin). North Twin water was the softest and the poorest in conductivity of the three lakes, while West Lost Lake water was the hardest and the most highly conductive (Table 1). Additional limnological information is given by Tanner (1960).

Methods

Estimates of population size of the adult crayfish were made during the spring and summer of 1966, 1967, 1968, and 1969. The common, round, wire minnow trap was used for collecting adults. Traps baited with fish were set for 24 hours, and then lifted and re-baited. The crayfish were marked, measured, and weighed, and then released in the center of the lake. Estimates of young-of-the-year crayfish were made in late summer. The young were those with length of cephalothorax less than 20 mm; these were collected with long-handled dip nets 0.5 m in diameter. Each sampling operation consisted of one trip around the circumference of the lake. Young crayfish were released at random points in shallow water, after being measured and marked. Populations of crayfish were estimated by the Schumacher-Eschmeyer formula as listed by Ricker (1958).

Age composition was analyzed from size frequency graphs, by following the growth of known-age individuals and by use of arithmetic probability paper as described by Hopkins (1966). Because of molting, the growth of crayfish is stepwise. Size frequency polygons apportion the population into natural size groups with distinct, easily followed modes. Carapace length was measured in millimeters with vernier calipers along the dorsal midline from the tip of the rostrum to its posterior end; it is used as the length measurement throughout this paper. Use of the length frequency technique, and its accuracy in aging crayfish, are discussed in Momot (1967a). The population age structure, determined by using the length frequency technique, differed little from that obtained using the arithmetic probability paper method. However, use of these methods with the more rapidly growing southern populations might not prove effective due to the overlapping of growth of the different age groups (W. Schaaf, personal communication).

We converted growth data from units of length to weight, by use of a length-weight relationship computed from empirical data (Momot, 1967a). Crayfish with complete sets of appendages were measured to the nearest millimeter and weighed to the nearest 0.1 g. No statistical difference ($P < 0.01$) in weight for a given length was found between males and females for the size ranges examined (for df = 108, $t_{.05} = 0.558$, Momot, 1967a).

Derivation of instantaneous growth rates (g), instantaneous mortality rates, and of annual mortality rates, followed the procedure and employed the symbols of Ricker (1958); his method was also used to compute production.

During the spring of the year, females with eggs attached to the pleopods were sampled with a small hand net. Direct counts were made of attached eggs.

Populations of trout are maintained in North Twin, South Twin, and West Lost lakes by stocking, as reproduction is non-existent in the first two lakes and nearly so in the third. Prior to 1965, the lakes were generally stocked annually in the fall with brook trout at an average length of about 127 mm, or 5 inches, and at the rate of 250 fish per hectare. In October of 1965, residual populations of brook trout varied from 268 (167.5/ha) in South Twin, to 208 (148.5/ha) in West Lost, to 118 (62.1/ha) in North Twin. These populations were composed of from two to four year classes, the 1964 year class representing not less than 87%, nor more than 97%, of the fish in any one lake. Fish of the 1964 year class were marked by excision of the dorsal and left pelvic (or ventral) fins and are referred to as DLV's.

The rate of stocking in the fall of 1965 (i.e., for the present study) was increased five-fold in West Lost, reduced 50% in North Twin, and left unaltered in South Twin Lake. In early November 1965, 1,750 brook trout of the 1965 year class were stocked in West Lost; 390 were stocked in South Twin, and 240 in North Twin Lake. These fish ranged between 127 and 152 mm, and averaged 142 mm in length. Weight per fish was nearly 29 g. All were marked by removal of the adipose and left pectoral fins for later identification and henceforth are referred to as ALP's.

In the spring and fall of 1966 and again in 1967, estimates of the trout populations were made by the Petersen mark-and-recapture method, generally employing the field procedure recommended by Waters (1960) which involved the capture of fish by one kind of gear for marking, and recapture by a different kind of gear.

Growth, condition, and other parameters of the trout populations were based on monthly samples of ALP fish collected from each lake, mostly by angling and infrequently by electrofishing and gill nets. About 10 trout per month were removed from West Lost and South Twin lakes, and about 5 per month from North Twin Lake. When possible, monthly samples included 5 fish from the 1964 year class (DLV). The occasional older fish (1963, 1962, and 1961 year classes) captured during the sampling period were not released back to the lake. The diet of trout was studied in all fish in the monthly sample.

Items in stomach contents were identified, counted, and volume determined by water displacement. Between December 1965 and October 1967, 152 trout stomachs were collected from North Twin; this number was 42% of the initial, November (1965) population. Similarly, trout sampled for stomach analysis amounted to about 37% of the initial population in South Twin, and 14% in West Lost Lake.

The monthly consumption of crayfish by trout was determined in the following manner. First, the mean daily ration of crayfish was determined from the monthly sample of trout. This ration was then divided by a digestion factor calculated from data given by Hess and Rainwater (1939), and Philips et al. (1960) to correct for differences in digestion rates of crayfish at various lake temperatures. Finally, the figure is multiplied by the mean size of the trout population and the number of days in the month. The monthly mean size of the trout population was determined on the assumption that mortality rates were constant between spring and fall and between fall and spring. The method employed semi-logarithmic paper, with the abscissa as a time scale and the ordinate as population size. Two successive point estimates are plotted and connected by a straight line. At any point in time during this interval, the population size can be read from the line.

In October 1967, the small remnant trout populations in North Twin and South Twin lakes were removed by gill nets. However in West Lost Lake, 209 ALP-marked trout remained. In addition, there were 6 lake-spawned trout. This population was augmented by the stocking of 385 brook trout, marked right pectoral, on December 6, 1967. Altogether the population now consisted of 600 brook trout that ranged in length from 196 to 310 mm and averaged 267 mm. Population density was nearly 429 fish per hectare. Also in December 1967, a rainbow trout population was established in North Twin Lake which duplicated the length-frequency distribution and density of brook trout in West Lost Lake.

Trout populations in West Lost and North Twin were assessed semiannually during 1968 and 1969. To monitor the seasonal diet and consumption of crayfish by trout, a sample of 10 trout was removed monthly from each lake. On June 3, 1969, the population in West Lost Lake was bolstered by the stocking of 200 brook trout that averaged 254 mm in length and 204 g in weight. The study was terminated in the fall of 1969 when gill nets were employed to remove and assess the residual populations.

The condition of trout was originally derived by the English system,

$$C_{TL} = W \times \frac{1}{L^3} \times 10^5$$

where W = weight in pounds

and L = total length in inches

Condition C was converted to the metric system on the basis that

$$K_{TL} = 0.0276\ C.$$

Results

Trout population dynamics and their predation on crayfish are discussed for two periods of approximately 2 years each, namely, fall 1965 to fall 1967, and fall 1967 to fall 1969. The first period concerns the performance of brook trout in three lakes, each initially containing a different density of fish, both subadults and adults, and relates to their predation on crayfish. The second period deals in a similar fashion with adult rainbow trout in one lake and brook trout in another, with comparable population density and size of fish.

Trout populations 1965-1967

Abundance. -- The populations of brook trout, stocked at three different densities in North Twin, South Twin, and West Lost lakes in 1965, were all reduced substantially by the fall of 1967 (Fig. 3). Following are further details on these reductions. The trout in North Twin Lake started at 188.4 fish per hectare, of which about 67% were ALP-marked subadults of the 1965 year class (142 mm mean total length), 32% were DLV-marked adults of the 1964 year class (236 mm mean length), and 1% were other trout. In October 1967, the population was down by 97.2% to 5.3 fish per hectare. South Twin Lake started in the fall of 1965 with 658 trout, or 411.3 fish per hectare; these were 60% ALP-marked subadults (142 mm mean length), 37% DLV-marked adults (221 mm mean length), and 3% other trout. By the fall of 1967, this population was reduced 98.3% to 6.9 fish per hectare. Lastly, West Lost Lake started with 1,398 fish per hectare, of which 89% were ALP-marked fish (142 mm mean length), 9% were DLV-marked fish (231 mm mean length), and 2% were other trout. By October 1967, the population in West Lost was down 89.3% to 149.3 fish per hectare; at this time no DLV trout remained; however, six lake-spawned trout were observed. Initial stock densities for North

Twin, South Twin, and West Lost lakes were in the ratio of 1 to 2.2 to 7.4, respectively; terminal densities were 1 to 1.3 to 28.2.

Mortality.--Among ALP-marked trout, the instantaneous natural mortality rate (q) was generally greater from April to October than from October to April (Table 2). One exception to this occurred in West Lost Lake where the instantaneous natural mortality rate during the first winter was greater than during the following summer. Instantaneous natural mortality rates during winter months differed between years but showed a similar pattern in all lakes, with mortality being greater the second winter. In summer, instantaneous natural mortality rates in West Lost and South Twin lakes also differed between years, and again mortalities from natural causes in the second summer were greater than during the first summer. However, North Twin was an exception in that instantaneous natural mortality was lower the second summer. Differences in total instantaneous natural mortality rates (q) between lakes varied from 1.550 in North Twin, 1.855 in West Lost, to 2.116 in South Twin Lake.

In all lakes the populations of DLV-marked trout were reduced most severely during the first winter; total instantaneous mortality rates (i) amounted to 0.746 in North Twin, 0.949 in South Twin, and 0.994 in West Lost Lake. During this period instantaneous mortality rates from natural causes were relatively high in West Lost ($q = 0.680$) and South Twin ($q = 0.790$); and were comparatively low for fishing (p), amounting to 0.314 and 0.159 for the two lakes, respectively. In North Twin Lake, however, the instantaneous natural mortality rate (q) was comparatively small (0.435) and approximated the instantaneous fishing mortality rate ($p = 0.311$). The instantaneous fishing mortality rate (p) represents the mortality caused by the monthly removal of trout, usually by angling, for stomach and growth analysis. The reduction in population size during this study was, in part, due to our scheduled removal of trout; monthly samples of trout represented 42.4% of the initial stock in North Twin, 37.7% in South Twin, and 14% in West Lost Lake.

Growth.--Growth provides a means for assessing the performance of a species; growth of the individual fish is one aspect of production in a population. Seasonal growth in length of ALP-marked trout in these lakes followed a sigmoid curve (Fig. 4). Typically, growth was most rapid during late spring and summer, diminished during the fall, and was minimal during the winter. Growth was superior in North Twin, intermediate in South Twin, and poorest in West Lost Lake. ALP-marked brook trout in North Twin gained a clear edge in growth over South Twin trout (ALP) by July 1966 at a length of about 214 mm, and maintained this superiority to the end of the study, attaining a length of about 336 mm in October 1967 (Fig. 4). Growth of brook trout (ALP) in West Lost Lake was slow at the outset and remained comparatively slow; the fish reached a length of only 240 mm by October 1967.

Growth in weight of ALP-marked brook trout followed a seasonal pattern similar to growth in length. Between November 1965 and April 1966, increase in weight was comparatively slow. ALP-marked brook trout in North Twin and South Twin lakes gained 26% and 35%, respectively, of their weight at planting, while ALP-trout in West Lost actually showed a net loss of 9% (Fig. 5). Growth was most rapid in all lakes from May through October 1966, particularly in early summer. The instantaneous growth rate of trout in North Twin was 31% faster than in South Twin, and 87% faster than in West Lost Lake. From October 1966 to April 1967, growth was negligible in all lakes. Finally, from April 1967 through October 1967, growth was again rapid in all lakes; instantaneous growth rates (g) varied from 0.779 for West Lost, to 0.959 for South Twin, to 2.000 for North Twin Lake.

For the period November 1965 to October 1966, growth in weight of DLV-marked brook trout followed a seasonal pattern similar to ALP-marked trout. During the winter period, November 1965 to April 1966, growth was negligible in North Twin and South Twin lakes, whereas trout in West Lost Lake actually showed a weight loss as occurred among ALP-marked fish. During the warmer months--May to October 1966--there was a moderate increase in growth rate in North and South Twin lakes, and relatively little in West Lost Lake. The instantaneous growth rate of DLV-marked brook trout was 43% faster in North Twin than in South Twin, and more than twice as fast as in West Lost Lake.

ALP trout in North Twin gained an average of 168 g in the first year and 361 g in the second, or 529 g altogether. ALP trout in South Twin gained 112 and 227 g in the first and second year, respectively. In West Lost Lake ALP trout showed the poorest average weight gain--35 g the first year and 87 g the second year.

For DLV trout, the average gain in weight during the first year was 167 g in North Twin and 97 g in South Twin; however, in West Lost Lake DLV trout had an average loss in weight of 13%. No DLV trout survived beyond the first year (1966) in West Lost Lake, and only a relatively few did so in the other two lakes.

Condition.--Additional evidence of the performance of trout in these lakes was provided by the coefficient of condition (k). In general, the condition of ALP trout in North Twin Lake was highest throughout most of the first 17 months for which consecutive monthly samples are available, and poorest in West Lost Lake (Fig. 6). Condition of brook trout in South Twin was somewhat intermediate. Typically, condition of trout is poorest in March, increases rapidly in May and June, reaches a peak in July and again in September, before dropping to a low in winter.

Standing crop and production

Semiannual estimates of trout, along with seasonal measurement of their weights, provided a basis for determining production. Production is the total weight of trout flesh elaborated during an interval of time and includes both survivals and mortalities. The standing crop of ALP brook trout established at the outset varied from 6.92 kg (3.64 kg/ha) in North Twin, to 11.24 kg (7.02 kg/ha) in South Twin, and to 50.45 kg (36.04 kg/ha) in West Lost (Table 3). In October 1966, after one growing season, the standing crop reached a peak in all lakes. This amounted to 13.39 kg (7.05 kg/ha) in North Twin, 18.45 kg (11.53 kg/ha) in South Twin, and 61.46 kg (43.90 kg/ha) in West Lost Lake. The greatest biomass of DLV trout in all lakes was present at the start of the study; thereafter it diminished.

Trout production was lowest in winter and highest in summer. Production of ALP trout during the first winter was comparatively small--1.58 kg (0.83 kg/ha) in North Twin, 3.42 kg (2.14 kg/ha) in South Twin, and 3.93 kg (2.81 kg/ha) in West Lost Lake (Table 3). Combining the 1964 and 1965 year classes in a lake, trout production was equivalent to about 0.40 kg/mo. in North Twin, 0.62 kg/mo. in South Twin and 1.87 kg/mo. in West Lost Lake. Maximum production of fish flesh was achieved in all lakes during the first summer. Again, when year classes are combined, production during this period was 21.97 kg (11.56 kg/ha) in North Twin, 25.04 kg (15.65 kg/ha) in South Twin, and 41.34 kg (29.53 kg/ha) in West Lost (Table 4). ALP trout constituted 74% of this total production in North Twin, 76% in South Twin, and 98% in West Lost Lake. Production was again minimal during the second winter period, October 1966 to April 1967, followed by an increase during the second summer (April to October 1967).

The production of all trout flesh within each lake during this period of nearly 2 years was estimated to be 32.56 kg or 17.14 kg/ha in North Twin, 34.52 kg or 21.58 kg/ha in South Twin, and 82.85 kg or 59.18 kg/ha in West Lost.

Trout diet

In general, a trout population has its own unique feeding habits which are related to food preference and/or to the relative abundance of different organisms in the lake. Some qualitative measures of the trout diet are examined.

Between November 1965 and October 1967, a total of 152 brook trout were removed from North Twin, 246 from South Twin, and 275 from West Lost Lake for an analysis of the diet (Table 5). Among these totals, trout with empty stomachs were: 9 from North Twin, 12 from West Lost, and 14 from South Twin. The trout examined ranged in length from 130 mm to 370 mm and included all year classes known to be in a lake.

Stomach analyses provide a qualitative assessment of what a trout eats. An evaluation of the relative importance of various food items is based primarily on volume measurement, even though this tends to underestimate soft-bodied organisms and overestimate the presence of those with chitinous covering.

Nine orders of insects were represented in the diet of brook trout from all lakes, seven of which were common in the diet of trout in all lakes (Table 6). Of the crustacea found in the stomachs, only two orders were important: Decapoda and Cladocera. The six most important insect orders included Hemiptera, mostly corixids and some notonectids; Diptera, primarily tendipedid larvae and to a lesser extent *Chaoborus*; Odonata, mainly dragonfly and damselfly larvae in the ratio of about 3 to 1; Coleoptera, largely dytiscid adults and some gyrinids; Ephemeroptera, mostly Baetidae; Trichoptera, primarily limnephilids. The Crustacea referred to here are *Daphnia galeata mendotae* and the decapod, *Orconectes virilis*. If we consider six orders of insects together with the decapods and cladocerans, this assemblage would represent 85 to 94% of the total volume of food found in the stomachs of brook trout sampled in any one lake between December 1965 and October 1967. These food categories are used in the discussion that follows.

The food habits of brook trout are based on our observations made during the 12 months of 1966. We selected this period because it provided the best coverage in terms of consecutive monthly samples and because we had large samples. During 1966, 181 brook trout stomach samples from West Lost Lake were examined; at the rate of about 15 fish per month. In South Twin and North Twin lakes, 161 and 109 brook trout were analyzed, or 13 and 9 fish per month, respectively. Brook trout ranged in length from 127 to 345 mm.

During the spring and early summer, insects were an important component (38-81%) of the diet of brook trout in West Lost Lake, and for the balance of the year they contributed only about 2 to 11% (Table 7). Cladocerans contributed to the diet mostly during the fall and winter (17-30%). Crayfish were an important item in the diet (Fig. 7). In 9 out of 12 months of the year, they were the principal item of food in the stomachs.

Insects were a major food item in the diet of brook trout in North Twin during spring (April-May) and again in early fall (September-October). During the balance of the year, with the exception of March and November, insects made a reasonably stable (40-71%) contribution to the trout diet. Cladocerans were a significant component of the diet in August and again in January and February. Crayfish in the diet varied seasonally, from 0 to 59%; important months were March (57%), June (59%), October (39%), and November (44%).

By far, the major component of the diet of brook trout in South Twin was insects. During 10 of the 12 months, insects made the largest contribution to the total volume of food (Table 7). Cladocerans contributed to the diet mostly in January, February and March (27-97%), and also in May (33%) and October (26%). Crayfish were poorly represented in the diet of brook trout in South Twin; only in February (43%) and June (34%) were they of any significance. In 7 of the 12 months they were not observed in the diet.

At any one instant, large trout (> 228 mm) in each of the three lakes contained a larger volume of food than did small trout (<229 mm); collectively the mean for the former was 0.96, versus 0.27 cc per fish for the latter. In both North Twin and South Twin lakes, large trout contained a larger volume of insects per stomach than did small trout; however, they contributed about equally to the diet of both groups--59-62% for the large trout, and 63-65% for the small trout (Table 8). In West Lost Lake the volumes of insects per stomach of both large and small trout were similar, the former representing about 5% and the latter 20% of the total volume of food of their respective size groups.

Crayfish did not contribute to the diet of small trout in North Twin and South Twin lakes, whereas in West Lost they represented more than 50% of the total volume of food of small trout. The volume of crayfish per stomach of large trout (1.30 cc) in West Lost was greater than for small trout (0.12 cc) in the same lake, and exceeded that for large trout in North Twin (0.29 cc) and South Twin (0.10 cc). Of the three categories of food, crayfish represented 95, 26, and 20% of the total volume in the stomachs of large brook trout in West Lost, North Twin and South Twin lakes, respectively.

There was a greater representation of cladocerans in the stomachs of small trout than in large trout. Cladocerans were not observed in the diet of large trout in West Lost Lake during 1966 (some were observed in 1967), and represented about 15% of the total volume of food of small trout. In South Twin the volume of cladocerans per small fish was 0.08 cc (26%), compared to 0.02 cc (3.2%) for large trout. Small trout in North Twin contained 0.05 cc of cladocerans per stomach, representing 20% of the total volume of food of this size group, whereas for large trout it was 0.04 cc, or only 3% of the total volume of food.

The diet of small trout (< 229 mm) and large trout (> 228 mm) varied somewhat with the seasons. In West Lost Lake small trout tended to utilize insects during the spring and summer, cladocera during the fall and early winter, and crayfish in fall and winter (Table 8). Large trout (> 228 mm) showed a high incidence of crayfish in the diet throughout the year, and of insects in the spring.

Among small trout in North Twin Lake, insects were the predominant group in the diet (Table 8). Beginning about mid-winter (February) and ending in early summer, insects became an increasingly dominant group in the diet of small trout. Cladocerans were important in July and in January and February. Crayfish were not represented in the diet of small trout. Insects were the predominant organisms in the diet of large trout, prevailing in 7 of the 11 months for which there are measurements. Relatively few cladocerans were observed in the diet of large trout. Crayfish appeared in the diet of large trout in all seasons and also were quite variable.

Again, in South Twin Lake as in North Twin, insects were a major component of the diet of small trout, particularly during spring and early summer (Table 8). Cladocerans were observed in trout stomachs mostly during the winter. Crayfish were not part of the diet of small trout. Insects were also the principal food item of large trout, showing no discernible seasonal role. Comparatively few cladocerans were consumed. Crayfish were evident in the diet of large trout; however, they appeared in only five monthly samples.

Trout predation on crayfish

Crayfish are subject to predation by brook trout almost exclusively during the first year of life of the crayfish (Momot, 1965). Young-of-the-year crayfish first become available to trout in July, shortly after being shed by the female, at a carapace length of about 6 mm. In September they have reached a length of approximately 14 mm, and by June of the following year most have attained a length of about 21 mm which approaches the upper size limit of crayfish eaten by brook trout of the size present in these lakes.

In an earlier study (1962-1963) in West Lost Lake, Momot (1967b) indicated that only the larger brook trout consumed crayfish, and consequently he based predation rates on that portion of the trout population > 228 mm in length (T. L.). However, we found that brook trout between 127 and 228 mm preyed heavily upon crayfish, most noticeably in West Lost Lake which had a very high density of small trout. We used two categories of trout for calculation of predation rates, those > 228 mm, and those <229 mm. This facilitated comparisons with the earlier study of Momot (op. cit.). The numbers of trout > 228 mm, and <229 mm, in the population at any one time were based on the length distribution of trout observed in monthly samples of fish taken for stomach analysis and on length measurements of fish sampled in the spring and fall to obtain population estimates.

In the spring of 1966, the estimated populations of adult female crayfish were 5,586 in West Lost Lake, 4,342 in North Twin, and 3,121 in South Twin. Starting with these numbers for brood stock, the number of eggs attached to the pleopods of females was used as a measure of reproductive capacity. Mean number of attached eggs per female (Table 11) times the number of breeding females gave estimates of the stocks of hatchlings. By this method, we estimated the populations of hatchlings in June 1966 to be 345,773 in West Lost Lake, 111,589 in North Twin, and 101,745 in South Twin. These figures converted to standing crops of 16.06 kg/ha in West Lost, 3.82 kg/ha in North Twin, and 4.13 kg/ha in South Twin Lake. By early September the stock in West Lost Lake was reduced to 54,996 crayfish (Table 12), for a total mortality rate (a) of 0.841. In North Twin and South Twin lakes, total mortality rates (a) were 0.597 and 0.611, respectively, resulting in September stocks of 44,959 and 39,586 crayfish.

During the period from June to September, an estimated 37,564 age-0 crayfish were eaten by brook trout in West Lost Lake. The population density of brook trout ranged from 779 fish per hectare at the outset to 719 fish per hectare at the end. On the average about 98% of the trout were <229 mm. Thus, trout predation accounted for 13% of the total loss of young-of-the-year crayfish during the first summer.

In North Twin, from June to September, only 260 young-of-the-year crayfish were consumed by brook trout, and all by trout > 228 mm in length. Trout density ranged from 76 to 56 trout per hectare, and was equally divided between small (<229 mm) and large (> 228 mm) fish. The 260 age-0 crayfish represented less than 1% of the total mortality between July and September as attributable to trout predation. In South Twin Lake, brook trout > 228 mm ate 720 age-0 crayfish during July to September 1966. The trout population ranged from 164 to 126 per hectare, about 44% of which were > 228 mm. About 1% of the total loss of age-0 crayfish was due to trout predation.

Young crayfish in West Lost Lake incurred a total mortality of 0.928, between September 1966 and August 1967, after two summer growing seasons. The crayfish population in August of 1967 consisted of 1,823 males and 2,137 females (Table 13). Comparable mortalities during this same period reduced the crayfish populations to 4,789 in North Twin Lake and 4,069 in South Twin Lake.

Brook trout density in West Lost Lake between September 1966 and June 1967 ranged from 684 trout per hectare at the outset in October 1966 to 282 per hectare in June 1967. About 95% to 84% of these fish were <229 mm. Altogether 34,136 crayfish were cropped primarily by fish <229 mm. Trout predation represented 23% of the total crayfish mortality.

In North Twin Lake brook trout density ranged from about 46 fish per hectare at the outset to 10 per hectare in June, more than 93% of these being > 228 mm. Brook trout consumed an estimated 693 crayfish and thus accounted for about 1% of the total mortality between September 1966 and August 1967.

The population density of brook trout in South Twin ranged from 108 per hectare in October 1966 to 19 per hectare in June 1967; percentage of fish > 228 mm in any one month varied from 62% to 83%. Brook trout consumed 944 young-of-the-year crayfish during this period which represented almost 2% of the total mortality of age-0 crayfish.

Crayfish production of the 1966 year class in West Lost Lake was 131.18 kg after two summer's growth (Table 14). Brook trout consumed 56.49 kg, or 43%, of this production during this period. In North Twin Lake crayfish production was 129.20 kg, quite comparable to that for West Lost Lake. Brook trout predation, however, accounted for only 0.84 kg, a negligible fraction of this production. In the case of South Twin Lake, crayfish production was 141.06 kg, or about 7% larger than West Lost Lake. Brook trout in South Twin, like those in North Twin, cropped only a small fraction of crayfish production--1.61 kg or about 1%.

Trout populations, 1967-1969

Abundance.--Stocks of adult trout established at a density of about 430 fish per hectare in each of two lakes were reduced to 4 and 81 trout per hectare in 22 months, representing losses of 99 and 81%. About 27% of this reduction was attributable to our monthly sampling of trout.

A brook trout population present in West Lost Lake in December 1967 consisted of a residual stock of 209 ALP-marked trout and 6 lake-spawned trout, augmented by a new stocking of 385 fish (right-pectoral clipped), for a total of 600 trout, or 428 trout per hectare. These fish ranged in length (T.L.) from 180 to 310 mm, and averaged 267 mm. After the first 10 months (October 1968), and the removal of 95 trout for stomach analysis, trout density was down to 77 trout per hectare (Fig. 8). After another 8 months, to June 1969, during which time an additional 67 trout were removed for diet studies, the population was down to a small remnant, and it was augmented at that time by another stocking of 200 adult brook trout. By October 1969, after 45 fish from this stocking were sampled for stomach analysis, survival was down to 5%.

In North Twin Lake in December 1967, a rainbow trout population was established with a size structure and mean length nearly identical to brook trout in West Lost. During the first 10 months the population declined from 432 to 171 trout per hectare. At the termination of the study in October 1969, the population was down to 81 trout per hectare (determined by intensive gill netting). The overall mortality was 81%, of which monthly samples of trout for stomach analysis accounted for 27%.

Mortality.--Characteristic of both brook and rainbow trout populations was the similar seasonal pattern of the instantaneous natural mortality rate (q) in 1968 and 1969. This rate was less during winter than during summer (Table 15). Also, for both species, the rate was higher during the first summer than during the second. Both species showed comparable instantaneous natural mortality rates during the first winter, but thereafter it was higher among brook trout in West Lost Lake.

Growth.--Both rainbow and brook trout in their respective lakes grew poorly during the first 5 months. In the ensuing 18 months, rainbows gained and maintained a margin of growth over brook trout. Between December 1967 and April 1968, rainbow and brook trout showed an average loss in weight of about 14% of their initial weight at stocking (Fig. 9). Brook trout failed to recover their initial stocking weight by April 1969. The increase in instantaneous growth rate (g) of brook trout after this date, as shown in Figure 9, represents the performance of fish planted in June 1969. On the other hand, growth (g) of rainbow trout was comparatively slow during the first and second summer.

Standing crop and production

During the nearly 2-year period of study, the identical standing crops of trout in the two lakes decreased, but at different rates. The initial standing crop of trout established in each lake was approximately 95 kg/ha, the maximum for each lake during the study period. Nearly a year later the standing crop of rainbow trout in North Twin was 48 kg/ha, whereas it was 13 kg/ha for brook trout in West Lost Lake (Table 16). At the termination of the study the standing crop of rainbow trout was 31 kg/ha; for brook trout it was less than 1 kg/ha.

As a small standing crop of only 4 kg/ha remained by April 1969, 200 adult brook trout (mean length 254 mm) were stocked in West Lost Lake in early June 1969. The new standing crop of 29 kg/ha was reduced 70% by October 1969; monthly sampling of trout accounted for 30% of the loss.

Production of fish flesh in the two lakes differed both quantitatively and seasonally. In North Twin, rainbow trout production in the summer exceeded production of the preceding winter period (Table 16). Also, production during the first winter (5.4 kg per month) exceeded that generated during the second summer period (2.4 kg per month). A maximum production of 42 kg, or 7.0 kg per month, accrued during the first summer.

For brook trout in West Lost Lake, maximum production was achieved during the first winter period; this amounted to 14 kg, about 41% less than rainbow production for the same period. Only 4 kg were generated during the first summer, and less than 2 kg during the second year. Production of brook trout stocked in June 1969 amounted to less than 1 kg.

Thus for approximately 22 1/2 months rainbow trout production in North Twin amounted to 44.5 kg/ha, while brook trout production in West Lost totaled 14.0 kg/ha, a difference on the order of 3.2 to 1.

Trout diet

Samples of 10 trout per month provided a basis for obtaining a qualitative measure of the diet of trout. For the 22 months of sampling between January 1968 and October 1969, 218 rainbow and 210 brook trout were removed from North Twin and West Lost lakes, respectively, and their stomach contents analyzed (Table 17). These included 3 rainbow and 11 brook trout with empty stomachs. The rainbow trout ranged in length between 221 and 387 mm (T. L.) while brook trout varied from 206 to 340 mm.

Rainbow and brook trout showed a diverse diet, 12 to 13 orders of animals were found in their stomachs (Table 18). However, the mainstay of their diet was Diptera, Odonata, Hemiptera, and Coleoptera along with crayfish and Cladocera. These groups, along with Trichoptera and Ephemeroptera, constituted about 94% of the total volume of food consumed by trout and was the basis for the seasonal analysis of diet. During the first winter and spring, rainbow trout relied heavily upon insects (Table 19 and Fig. 10). The diet then shifted to cladocerans during the summer months and returned to insects again in the fall. Cladocerans were strongly represented in the diet during the second winter. For the spring, summer, and fall of the second year, the seasonal diet of insects and cladocerans was, in general, similar to that of the first year. A seasonal trend of crayfish in the diet was not evident during 1968 and 1969, as their occurrence was very irregular, not exceeding 20% of the total volume in 14 of the 22 months. Ratios (by volume) of crayfish, cladocerans, and insects in the stomachs of rainbow trout were on the order of 1 to 1.6 to 3.1.

The diet of brook trout in West Lost differed markedly from rainbow in North Twin as seen in Figure 10. In West Lost Lake crayfish constituted an overwhelming part of the brook trout diet representing nearly 70% of the total volume sampled during the entire period of study. In 16 of the 22 months they represented more than 50% of the total monthly volume. Important months for insects (> 50%) were September, October, and December 1968 and May 1969. Cladocerans contributed to the diet mostly in July and August 1968 and June (35%) 1969.

Trout predation on crayfish

Brook trout in West Lost Lake at numerical densities two- to seven-fold smaller than rainbow trout in North Twin, cropped roughly 19% more young-of-the-year crayfish from stocks of comparable size.

In June 1968, a breeding stock of 2,227 female crayfish (Table 10) produced an estimated crop of 260,114 young in North Twin Lake or about 136,902 per hectare. By September the population of young decreased to 22,710 (11,953 per hectare), a total mortality rate (a) of 0.913. During this period rainbow trout (> 228 mm T. L.), ranging in density between 236 and 189 fish per hectare, cropped an estimated 4,961 young-of-the-year crayfish. Of the total loss of crayfish during this period about 2% was attributable to trout predation.

Between September 1968 and August 1969, the stock of age-0 crayfish was reduced to an estimated 6,020 yearlings (Table 13), or 3,168 per hectare, a total mortality rate (a) of 0.735. Average density of rainbow trout ranged from 169 to 98 fish per hectare during the period of crayfish cropping. Trout predation accounted for 7,181 young-of-the-year crayfish or about 43% of the total loss that occurred during this period.

An estimated breeding stock of 2,008 females in West Lost Lake brought off an estimated crop of 184,937 young-of-the-year crayfish in June 1968, equivalent to 132,098 per hectare and comparable to that in North Twin Lake. By September, 21,077 young crayfish survived or 15,055 per hectare. This represents a 26% greater density than in North Twin. Brook trout density between October 1968 and June 1969 averaged between 146 and 98 fish per hectare and about 82% were > 228 mm in length. Brook trout consumed an estimated 4,802 age-0 crayfish or about 3% of the total loss for this period.

Between September 1968 and August 1969, the total mortality rate (a) of age-0 crayfish was 0.741; the terminal population was an estimated 5,459 yearling crayfish or 3,899 per hectare. This density of young is about 23% greater than in North Twin. At the outset of this 11-month period brook trout density averaged about 76 fish per hectare and more than 91% of the trout were > 228 mm in total length.

By May, density was only 19 fish per hectare. Stocking in June bolstered the density to 148 fish per hectare. Brook trout consumption of young-of-the-year crayfish during this period was calculated to be 9,675 animals, about 62% of the total mortality of age-0 crayfish for the period.

Predation is best reflected in terms of the weight of crayfish production cropped by trout. Crayfish during their first 14 months of life (1968 year class) in North Twin Lake generated about 82 kg of flesh (Table 20). Rainbow trout utilized about 9 kg during this period or about 11%. During this same year crayfish production in West Lost Lake was nearly 83 kg, almost the same as that for North Twin Lake. However, brook trout in West Lost Lake consumed a larger portion of crayfish production, about 13 kg or 16%.

Discussion

Mortality

Populations of salmonids in lakes are generally maintained by periodic stockings. Comparatively few fish are reported to survive two summers in lakes from stockings of either fall fingerling brook trout or spring yearling rainbow trout at densities ranging from 158 to 741 trout per hectare (Johnson and Hasler, 1954; Johnson, 1955; Latta, 1963). This applied as well to older fall stocked rainbow and brook trout (Alexander and Shetter, 1969). Tuunainen (1970) reported the near disappearance of rainbow trout fry about one and a half years after stocking in a small oligohumous lake in Finland previously treated with rotenone. In other small lakes containing slow growing and lightly exploited populations, he reported that rainbow trout survived for 3-5 growth periods and brown trout for 4-5. According to Tuunainen, in Jamtland, Sweden, rainbow trout disappeared from lakes treated with rotenone generally after 4 years.

Johnson and Hasler (1954) estimated the natural mortality of age-I rainbow trout (152-178 mm) to be 32-60% between mid-April and mid-October in three dystrophic lakes in Wisconsin. Stocking densities ranged from 546-741 rainbow trout per hectare. For age-II rainbow trout, natural mortality was 15-19%. The authors reported that natural mortality was not dependent on density of trout but on abundance of predators present. Mergansers were suspected to be the principal predators.

Johnson (1955) reported that fingerling rainbow trout (149 mm) stocked at a density of 158 fish per hectare in a small northern Minnesota lake in the spring, suffered a total mortality of 88% by fall. Similarly rainbow trout planted at a mean length of 162 mm and at a density of 403 fish per hectare had a total mortality of 98.3% after two summers. For rainbows having a mean length of 102 mm and stocked at the rate of 342 fish per hectare, total mortality was 99.8% after three growing seasons. Fishing pressure was termed moderate.

Latta (1963) showed that fall fingerling brook trout stocked at the rate of 1,250 and 1,427 fish per hectare in two limestone sink lakes had total annual mortalities (a) of 0.87 and 0.80. Also, brook trout fingerlings stocked at 247 fish per hectare annually in each of two lakes, over a 3-year period, had an average total annual mortality (a) of 0.81 and 0.67. Latta indicated that overwinter loss of trout was negligible, and with a diminution in size of spring populations there was a decrease in natural mortality rates (n) during summer.

Alexander and Shetter (1969) made five annual consecutive fall plantings of 300 brook and 300 rainbow trout in a 6.5-hectare lake. Average density was 92 fish per hectare. The matched plantings of trout ranged in length from 216 to 241 mm (T. L.). During the first year brook trout suffered a total loss of 99% on the average of which angling accounted for 39%. Roughly one-third of the brook trout mortalities occurred between mid-October and mid-December, prior to ice cover. On the other hand, nearly 98% of the rainbow trout survived the winter to late April and then about 86% succumbed to angling. The authors suggested that brook trout mortalities were mainly the result of mammalian and avian predation as this species, more than rainbow trout, is littoral oriented.

In the more uniform environments of farm ponds, Eipper (1964) and Saila (1952) reported similar survival rates for different salmonid species. Some trout mortality in ponds was attributed to herons, ducks, and kingfishers. Eipper (1961) found natural mortality of spring fingerling brook, rainbow, and brown x brook hybrid trout of comparable age to be quite variable the first growing season in New York farm ponds. Fall fingerlings gave more reliable results especially in the presence of residual stocks of older trout. Mortality was not related to stocking rates up to 1,977 fingerlings per hectare.

In North Twin, South Twin, and West Lost lakes the relationship between the annual natural mortality rate and density of age-I brook (1965 year class) was anomalous from fall 1965 to fall 1966. In North Twin where density was smallest, diminishing from 188 to 47 fish per hectare, natural mortality rate of age-I trout was greatest, 0.551 (Table 21). And where density was greatest in West Lost, ranging from 1,398 to 693 trout per hectare, natural mortality rate was smallest, 0.401. The unusually small natural mortality rate of trout in West Lost Lake during the first summer accounted for much of this disparity. During this same period natural mortality rates for age-II trout (1964 year class) were in reverse order to age-I trout, North Twin brook trout having a mortality of 0.605, South Twin trout 0.709, and West Lost trout 0.787. All were in excess of mortality rates for age-I trout. On a seasonal basis, however, natural mortality of age-II trout was greater than age-I trout during the first winter in all lakes, and only in West Lost Lake did the natural mortality of age-II trout exceed that of age-I trout in the first summer.

At subsequent lower densities, in the range of 693 to 21 trout per hectare, natural mortality rates for age-II trout (1965 year class) varied directly with density; for North Twin, South Twin, and West Lost, in ascending order of density, natural mortality rates were 0.500, 0.681, and 0.736, respectively.

For two other lakes in this same immediate area, Latta (1963) reported summer mortality rates of 0.72 and 0.80 for age-I brook trout stocked the previous fall at the rate of 1,427 fingerlings per hectare and mortalities of 0.38 and 0.52 for age-II trout the second summer. In our lakes, first summer mortality rates ranged from 0.15 to 0.51 and for age-II trout the second summer they varied from 0.33 to 0.69. Latta found the largest natural loss of fall stocked trout occurred during the first summer after planting as we did for the low and intermediate density lakes. However, at the highest density in West Lost Lake, the largest loss of trout occurred during the first winter after stocking.

For age-II rainbow and brook trout stocked at comparatively high rates, each in one of two lakes, natural mortality of the latter was generally higher. Age-II rainbow trout when stocked in North Twin Lake in late fall at 428 fish per hectare, had a natural mortality rate of 0.523 the first year (Table 22). In West Lost Lake natural mortality rate was 0.749 for brook trout of comparable age, size, and density. Natural mortality in both instances was greater in summer than in winter. Natural mortality rate of age-IV rainbow trout was 0.241 in 1969 and 0.556 for brook trout, the latter having one-third the density of the former.

Smith (1956) increased brook trout survival in a New Brunswick lake through control of predatory fish and birds. There were relatively few observations of fish predators in our lakes. These lakes have steep bottom gradients at the shore and are not readily fished by wading predators. A few hooded mergansers (*Lophodytes cucullatus*) infrequently visit the lakes in spring and fall. We conjecture the main cause of natural mortality to be physiological, stress associated with the attainment of sexual maturity, disease and interspecific competition. While our observation of the greater natural mortality of brook trout over rainbow trout is not directly comparable, it corroborates to some extent the differential mortality of these species in oligotrophic lakes as indicated by Alexander and Shetter (1969).

Growth and production

In the range of 188 to 1,398 brook trout per hectare there was an apparent inverse relationship between density and growth of trout. Johnson and Hasler (1954) noted a similar relationship between standing crop, ranging between 19-103 kg per hectare, and growth of age-I rainbow trout. As reported by Tuunainen (1970), Lundgren suggested that small Swedish lakes reclaimed by rotenone be given introductory densities of 500 fry or 200 one-summer-old brook or rainbow trout per hectare. Given introductory densities of 500-5,000 fry per hectare, one-summer-old fish were 75 and 11 g, respectively. In small Finnish lakes treated with rotenone and stocked at densities of 187-2,500 fry per hectare, one-summer-old brown trout were about 45-9 g and rainbow trout 90-50 g, respectively.

The 1965 year class of brook trout in North Twin Lake showed a 583% increase in weight the first year (1966) when the density range was 188-47 fish per hectare. Similarly in South Twin Lake where the density range was 411-111 fish per hectare, the 1965 year class had a 389% weight gain. In West Lost Lake when the range in density was 1,393-693 fish per hectare, the 1965 year class showed a gain in weight during the first year of only 124%. With a reduction in density the second year, the gain in weight of trout in North Twin and South Twin lakes was about 183 and 161, respectively, and in West Lost 133%. It was evident in West Lost that intense interspecific competition for food and space occurred among brook trout. Another measure that reflected this competition was the relatively poor condition (K) of trout in West Lost Lake compared to both South Twin and North Twin trout. Went and Frost (1942) and Cooper (1953) reported a direct correlation between growth in length and condition.

The 1964 year class in each lake during the first year (1966) did not fare as well as the 1965 year class, the former showing a 115% gain in weight in North Twin, 83% in South Twin, and a 13% loss in West Lost Lake.

At extremely high introductory densities of adult trout, growth was sharply suppressed. Age-III rainbow trout showed an average gain in weight of 27% the first year when the density range was 432-171 fish per hectare. With a diminution in density the second year (171-81 fish per hectare), age-IV trout showed an average gain in weight of 33%.

The average weight of age-III brook trout dropped about 20% after 1 year in West Lost Lake when density ranged from 428 to 77 fish per hectare. This resulted in part because of the greater mortality among the larger right-pectoral-marked trout than among ALP-marked trout which together comprised the initial population. Only a small remnant of the initial population survived to the fall of the second year.

Alexander and Shetter (1969) found the average increment in growth of age-II brook trout to be 414 g per year in a productive lake, roughly 15% greater than age-II brook trout in North Twin Lake. Aside from differences in the productivity of these two lakes, the effects of extremely divergent densities on growth of rainbow trout are quite evident. For age-III rainbow trout in East Fish Lake average growth increment was 885 g during their 4th year of life, when density was generally less than 92 trout per hectare. In North Twin Lake age-III rainbow trout showed an average increment of only 61 g when density ranged from 432 to 171 fish per hectare.

Alexander and Shetter (1969) reported trout production of 16.82 kg per hectare in an oligotrophic lake (6.5 ha) the first year after stocking age-I trout at the rate of 10.06 kg per hectare in the fall. While this stocking represented the combined and equal weight of both brook and rainbow trout, production of the former was 3.74 kg per hectare and the latter 13.08 kg per hectare. In a 38-hectare soft-water lake in Wisconsin, Brynildson and Kempinger (1973) stocked age-0 brown and rainbow trout at the combined rate of 1.84 kg per hectare in June. In the following 11 months, production was 31.64 kg per hectare, about 75% of which represented rainbow trout production. Production in part was influenced by the age composition of these populations as the instantaneous rate of growth diminished with increasing size of fish.

For age-0 brook trout stocked in West Lost in November 1965, production was 31.63 kg per hectare during the following year, nearly the same as reported by Brynildson and Kempinger (1973). However, the stocking rate was nearly 20-fold greater in West Lost Lake than in the lake studied by these authors. At this high density in West Lost Lake competition was apparently intense and, as brook trout showed a high survival rate (0.68-0.80), little more than maintenance occurred as attested by their relatively poor growth and condition. In fact, during the first 6 months of this period the instantaneous growth rate (g) was negative. In effect, production was achieved by a relatively large number of fish each attaining a small increment in weight. In contrast, North Twin with the smallest stock of age-0 brook trout at the outset (3.64 kg per hectare) showed the largest return in production (9.38 kg per hectare) on the initial investment 1 year after stocking. While the initial biomass of age-0 trout in South Twin was 7.02 kg per hectare, almost 2-fold greater than North Twin brook trout, the production of 14.00 kg per hectare represented a 23% smaller increment over the initial stock than in North Twin.

Production the first year was abetted principally by age-II brook trout present in all lakes but comprising a relatively larger portion of the populations in South Twin and North Twin lakes. Thus, with standing crops of age-0 and age-I trout at the outset of 12.86, 29.46, and 55.89 kg per hectare in North Twin, South Twin, and West Lost lakes, production in turn was 12.71, 18.18, and 36.90 kg per hectare during the first year, representing differences in the order of 1 to 1.4 to 2.9. Production of all trout in each lake after 2 years was 17.14 kg per hectare in North Twin, 21.58 in South Twin, and 59.18 in West Lost. Standing crops were generally highest in lakes stocked at the highest rate per hectare.

Again, when the introductory stocking rate was high, 96 kg per hectare as in North Twin and West Lost lakes in December 1967, the instantaneous growth rate (g) was poor or negative. Instantaneous growth was negative for both age-III rainbow trout in North Twin and brook trout in West Lost Lake during the first 5 months after stocking and in the months that followed brook trout never fully recovered (Fig. 26). Rainbow trout, however, recovered during the first summer. Production of rainbow trout the first year was 35.14 kg per hectare and for 2 years, it amounted to 44.55 kg per hectare. In contrast, production of brook trout was only 13.10 kg per hectare the first year and for both years, 14.06 kg per hectare. Brook trout survival was poor in West Lost Lake. In North Twin Lake rainbow trout survival was better; production in this lake reflected a relatively large but slow-growing trout population.

Diet

The food habits of brook trout in each of the three lakes were distinctive. Of the total volume of food consumed by trout sampled in West Lost Lake between December 1965 and October 1967, crayfish comprised 71% and cladocerans 12% (Table 6). No other order of organisms exceeded 3%. In South Twin Lake where the mean volume of food per stomach was 0.52 cc compared to 0.54 cc for West Lost trout, diptera, mostly tendipedid larvae, comprised 37% of the total volume with crayfish ranking second at 13% followed by odonata at 10%. In North Twin Lake where trout growth and condition were superior, the mean volume of food per stomach was 0.99 cc, nearly twice that of South Twin and West Lost trout. For North Twin trout crayfish ranked first at

30%, hemipterans (corixids and notonectids) 22%, and diptera (tendipedids) 16%. In both North Twin and South Twin lakes the trout diet showed a stronger, broader base of food organisms than trout in West Lost Lake.

Looking at seasonal changes during 1966, among the three categories of food organisms observed in trout stomachs, insects made a large contribution during the spring in all lakes; and for 4-6 months of the remainder of the year, insects were more than half of the total food in North Twin and South Twin lakes (Table 7). Cladocera generally entered the diet in the fall and winter. For trout in West Lost Lake, crayfish was the food item of all seasons, whereas in North Twin and South Twin lakes, their use was variable and seasonal.

Small trout (<229 mm) in all lakes relied upon insects throughout the year and upon cladocerans in the fall and winter. Only in West Lost Lake did crayfish contribute to the diet of small trout, primarily in the fall and winter. This is in marked contrast to 1962-1963, when Momot (1967b) noted the absence of crayfish in the diet of small trout in West Lost Lake which had a light density of fish. Among large trout (> 228 mm), insects were eaten most of the year in North Twin and South Twin lakes and to a much lesser extent by West Lost trout. Cladocerans were infrequently found in the stomachs of large trout; in West Lost Lake none were observed. Crayfish appeared irregularly in the diet of large trout during the year in North Twin and South Twin lakes and regularly in West Lost trout.

The diet of brook trout in West Lost Lake during 1968-1969 remained essentially unchanged from 1966-1967. Again crayfish played a dominant role throughout most of the year, representing about 70% of the total volume of food consumed by brook trout sampled between January 1968 and October 1969. The contribution of cladocerans dropped from 12% to 4% during the latter years, which suggested over-grazing by small trout during 1966-1967.

When the food habits of brook trout in North Twin Lake during 1966-1967 are compared with rainbow trout in the same lake during 1968-1969, two principal differences are evident. First, as rainbow trout are planktivorous, cladocerans, among all orders of organisms present, represented the single largest volume of food (27%) in their stomachs, as compared to 12% for brook trout. Secondly, crayfish were the principal food of brook trout, representing 30% of the total volume sampled, whereas for rainbow trout crayfish made up only 17%.

In only 3 out of 22 monthly samples of rainbow trout were cladocerans absent from the diet. Relatively larger contributions of cladocerans occurred during the summer and during November 1968; also during the spring and summer of 1969. The mean volume of cladocera per rainbow stomach remained practically the same for both years, 0.20 cc in 1968 and 0.19 in 1969.

Interactions between trout and crayfish populations

Brook trout appear to be closely associated with the lake bottom, particularly in the littoral zone, in contrast to the pelagic behavior of rainbow trout. Young-of-the-year crayfish first become vulnerable to the larger invertebrates and trout in late June, after being shed by the female. With few exceptions only age-0 crayfish were consumed by trout. Most young-of-the-year crayfish are initially found in the immediate shore area, but as summer progresses their range increases. Generally crayfish vulnerability to trout is least during the period of summer stratification.

In studies conducted during 1962-1963, Momot (1967b) reported that brook trout (mean length, 126 mm), when stocked annually in the fall at the rate of 250 fish per hectare, were ineffective in controlling populations of crayfish in West Lost Lake. Brook trout utilized 2.9% of the total annual production and 4.2% of the annual production of young-of-the-year crayfish. During the present study, much greater utilization of age-0 crayfish occurred in this lake under a higher trout density. From July 1966 through August 1967, when density ranged from 779 to 228 fish per hectare, brook trout predation accounted for 43% of the young crayfish production. As this production period is about 14 months compared to 12 months used by Momot, an adjustment of our data to 1 year would inflate the percent of crayfish cropping. Momot (1967b) reported that few brook trout <229 mm consumed age-0 crayfish, whereas we observed considerable cropping of them by small trout, which comprised about 98-84% of the total trout population. Evidently at this high trout density there was considerable competition for food, and crayfish were an available source of sustenance.

In both North Twin and South Twin lakes, where density of trout was relatively lighter than on West Lost, having a maximum range of 164-10 fish per hectare, trout consumed 1% or less of the production of young crayfish over a 14-month period. Production of crayfish in both of these lakes was equal to, or greater than, that in West Lost Lake. Small trout did not utilize age-0 crayfish in these lakes. Obviously trout in North Twin and South Twin lakes had little impact on populations of young-of-the-year crayfish. Of the total numerical loss of young-of-the-year crayfish during their first year of life, 21% was attributable to trout predation in West Lost, and less than 2% in North Twin and South Twin lakes. Even though larger numbers of crayfish were consumed by trout in West Lost, the size of the population of young after 1 year was comparable to both North Twin and South Twin lakes.

Changing from a low density brook trout population of age-I and age-II fish in North Twin (1966-1967), to a high density population of age-III and age-IV rainbow trout in the same lake (1968-1969), increased the utilization of the available crop of young-of-the-year crayfish from less than 1% for the former to 11% for the latter period.

However, rainbow trout at the high density showed relatively poorer growth than did brook trout at low density.

In West Lost Lake a numerically high density of age-I and age-II brook trout in 1966-1967 was replaced by a greater biomass of larger (older) brook trout in 1968-1969. The younger brook trout cropped a larger portion (43%) of the available production of young-of-the-year crayfish than did the older and larger trout in West Lost Lake (16%). These rates of exploitation of crayfish were achieved at trout densities that resulted in populations of slow-growing fish which had no evident impact on the age-0 crayfish. To achieve acceptable growth of individual trout, stocking rates will be in the lower range as indicated here and by others (Alexander and Shetter, 1969; and Brynildson and Kempinger, 1973).

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Table 1.--Physical and chemical characteristics of three Pigeon River Area lakes (1966)

Lake	Surface area (ha)	Depth (m)		Percent shoal[1]	Average total alkalinity	pH (mean)	Specific resistance (ohms-cm)[2]
		Maximum	Average				
West Lost	1.4	13.1	8.5	11.0	134.4	8.0	4,156
North Twin	1.9	12.5	8.2	13.0	29.2	7.4	20,900
South Twin	1.6	10.1	7.3	15.3	65.2	7.8	8,400

[1] Water less than 1.2 m.

[2] Corrected to 25 C.

Table 2.--Seasonal mortality rates among two groups of brook trout, fin-clipped ALP and DLV, in three Pigeon River Area lakes, between November 1965 and October 1967

Initial densities in number per hectare were: W. Lost, 1250.0 ALP, 129.3 DLV; N. Twin, 126.3 ALP, 60.0 DLV; S. Twin, 243.8 ALP, 151.9 DLV

Lake and date	Instantaneous mortality rates					
	Total i		Fishing p		Natural q	
	ALP	DLV	ALP	DLV	ALP	DLV
W. Lost						
Nov 1965						
	0.383	0.994	0.040	0.314	0.343	0.680
Apr 1966						
	0.226	1.313	0.065	0.482	0.161	0.831
Oct 1966						
	0.494	--	0.082	--	0.412	--
Apr 1967						
	1.022	--	0.083	--	0.939	--
Oct 1967						
N. Twin						
Nov 1965						
	0.272	0.746	0.148	0.311	0.124	0.435
Apr 1966						
	0.989	0.944	0.275	0.486	0.714	0.458
Oct 1966						
	0.887	2.354	0.576	0.000	0.311	2.354
Apr 1967						
	1.030	--	0.629	--	0.401	--
Oct 1967						
S. Twin						
Nov 1965						
	0.276	0.949	0.147	0.159	0.129	0.790
Apr 1966						
	0.816	0.715	0.252	0.388	0.564	0.327
Oct 1966						
	0.924	2.733	0.643	1.208	0.281	1.525
Apr 1967						
	1.754	0.406	0.612	0.406	1.142	0.000
Oct 1967						

Table 3.--Estimated production in kilograms of ALP-marked brook trout in West Lost, North Twin, and South Twin lakes from the stocking date in November 1965 to October 1967

Lake and date	Estimated number	s	i	Standing crop (kg)	W_t/W_o	g	g-i	$\overline{W}$	Production $(g-i)\overline{W}$
W. Lost									
Nov 1965	1750			50.45					
Apr 1966	1193	0.682	0.383	31.18	0.618	-0.481	0.098	40.07	3.93
Oct 1966	952	0.798	0.226	61.46	1.971	0.678	0.904	44.65	40.36
Apr 1967	581	0.610	0.494	40.12	0.653	-0.426	0.068	50.06	3.40
Oct 1967	209	0.360	1.022	31.50	0.785	-0.292	0.780	35.64	27.80
N. Twin									
Nov 1965	240			6.92					
Apr 1966	183	0.762	0.272	6.67	0.964	-0.037	0.235	6.73	1.58
Oct 1966	68	0.372	0.989	13.39	2.007	0.697	1.686	9.64	16.25
Apr 1967	28	0.412	0.887	4.72	0.352	-1.044	0.157	8.31	1.30
Oct 1967	10	0.357	1.030	5.58	1.182	0.167	1.197	5.14	6.14
S. Twin									
Nov 1965	390			11.24					
Apr 1966	296	0.759	0.276	11.56	1.028	-0.028	0.304	11.25	3.42
Oct 1966	131	0.442	0.816	18.45	1.600	0.470	1.286	14.76	18.98
Apr 1967	52	0.397	0.924	7.33	0.397	0.924	0.000	12.04	0.00
Oct 1967	9	0.173	1.754	3.31	0.452	0.794	0.960	5.06	4.86

Table 4.--Estimated standing crop and production in kilograms of all age classes of brook trout in West Lost (5), North Twin (3), and South Twin (5) lakes between November 1965 and October 1967

Lake	Date	Standing crop	Production
W. Lost	Nov 1965	78.24	
	Apr 1966	37.98	10.31
	Oct 1966	63.66	41.34
	Apr 1967	40.12	3.40
	Oct 1967	31.50	27.80
N. Twin	Nov 1965	24.44	
	Apr 1966	14.15	2.18
	Oct 1966	19.97	21.97
	Apr 1967	5.60	2.27
	Oct 1967	5.58	6.14
S. Twin	Nov 1965	47.14	
	Apr 1966	22.96	4.04
	Oct 1966	28.32	25.04
	Apr 1967	7.93	0.21
	Oct 1967	4.02	5.23

Table 5.--Monthly averages of volume (cc) of food observed in brook trout stomachs for the period December 1965 to October 1967

Year and month	West Lost		North Twin		South Twin	
	Number of fish	Volume /fish	Number of fish	Volume /fish	Number of fish	Volume /fish
1965						
Dec	19	0.31	9	1.10	20	0.44
1966						
Jan	16	0.08	11	0.29	16	0.35
Feb	22	1.17	10	0.12	16	0.18
Mar	16	0.51	11	0.48	15	0.20
Apr	16	0.29	15	0.07	16	0.88
May	16	0.18	2	0.48	11	0.26
June	12	0.41	8	1.23	9	0.07
July	13	0.40	10	0.54	17	0.56
Aug	11	0.54	10	0.18	8	0.10
Sep	17	0.71	5	3.85	11	0.38
Oct	17	0.32	10	0.32	16	0.31
Nov	10	0.39	8	1.13	13	0.37
Dec	15	0.79	9	2.22	13	0.47
1967						
Jan	13	1.09	5	0.38	14	0.44
Feb	11	0.27	8	0.55	15	0.24
Mar	10	0.34	5	1.77	5	0.53
Apr	12	0.59	5	0.71	14	2.50
June	10	0.82	--	--	1	1.60
Aug	9	0.23	5	6.39	5	0.78
Oct	10	1.32	6	1.52	11	0.65
Total or mean	275	0.54	152	0.99	246	0.52

Table 6.--Percentage of various orders of organisms found in the stomachs of 275 brook trout from West Lost, 152 from North Twin, and 246 from South Twin lakes sampled between December 1965 and October 1967

Order	Percent of total volume		
	W. Lost	N. Twin	S. Twin
Diptera	2	16	37
Odonata	2	5	10
Hemiptera	3	22	8
Coleoptera	2	9	5
Trichoptera	<1	1	2
Ephemeroptera	<1	1	1
Homoptera	--	--	<1
Hymenoptera	1	<1	<1
Lepidoptera	<1	<1	--
Decapoda	71	30	13
Cladocera	12	4	9
Amphipoda	<1	--	1
Copepoda	--	--	<1
Ostracoda	1	<1	--
Annelida	2	4	2
Salientia	--	--	1
Caudata	--	<1	--
Hydracarina	<1	--	<1
Fish eggs	1	<1	2
Unidentified	1	5	8

Table 7.--The occurrence of crayfish, insects, and cladocerans in the stomachs of brook trout from three Pigeon River Area lakes during 1966, analyzed by month

Lake and month	Number of fish	Total volume of food (cc)	Percent of volume in		
			Crayfish	Insects	Cladocerans
W. Lost					
Jan	16	1.35	59	11	30
Feb	22	25.70	98	1	--
Mar	16	8.10	96	4	--
Apr	16	4.60	59	40	--
May	16	2.90	17	81	2
June	12	4.95	24	37	--
July	13	5.25	80	8	11
Aug	11	5.90	47	10	--
Sep	17	12.05	87	11	--
Oct	17	5.50	67	6	24
Nov	10	3.90	19	--	27
Dec	15	11.90	80	3	17
N. Twin					
Jan	11	3.15	--	51	46
Feb	10	1.25	--	60	40
Mar	11	5.25	57	6	--
Apr	15	1.05	--	100	--
May	2	0.95	--	79	--
June	8	9.85	59	39	2
July	10	5.40	18	56	--
Aug	10	1.75	11	37	40
Sep	5	19.25	--	94	--
Oct	10	3.25	38	62	--
Nov	8	9.05	44	23	8
Dec	9	19.95	14	71	6
S. Twin					
Jan	16	5.55	--	67	27
Feb	16	2.80	43	14	43
Mar	15	3.05	--	3	97
Apr	16	14.05	--	77	--
May	11	2.85	--	63	33
June	9	0.65	--	77	--
July	17	9.50	34	43	5
Aug	8	0.80	--	100	--
Sep	11	4.20	17	80	1
Oct	16	5.05	--	34	26
Nov	13	4.80	2	16	11
Dec	13	6.15	8	90	1

Table 8.--The occurrence of crayfish, insects, and cladocerans in the stomachs of small trout, less than 229 mm, and large trout, more than 228 mm in total length, in West Lost, North Twin, and South Twin lakes

Lake, and length of fish (mm)	Number of fish	Total volume (cc)	Volume per fish	Volume per stomach		
				Crayfish	Insects	Cladocerans
West Lost						
< 229	144	35.90	0.25	0.12	0.05	0.04
> 228	37	54.20	1.47	1.40	0.07	--
North Twin						
< 229	47	12.40	0.26	--	0.17	0.05
> 228	62	67.75	1.09	0.29	0.65	0.04
South Twin						
< 229	103	30.90	0.30	--	0.19	0.08
> 228	58	28.55	0.49	0.10	0.30	0.02

Table 9.--The occurrence of crayfish (A), insects (B), and cladocerans (C) in the stomachs of small trout (< 229 mm) and large trout (>228 mm) in the Pigeon River Area lakes during 1966 analyzed by month

Lake and month	Trout <229 mm total length					Trout >228 mm total length				
	Number of fish	Total volume of food	Percent of total volume in			Number of fish	Total volume of food	Percent of total volume in		
			A	B	C			A	B	C
W. Lost										
Jan	12	0.90	44	11	44	4	0.45	89	11	--
Feb	13	2.10	81	19	--	9	23.60	100	--	--
Mar	11	0.15	--	100	--	5	7.95	98	2	--
Apr	14	1.95	36	62	--	2	2.65	76	25	--
May	11	1.25	--	96	4	5	1.65	30	70	--
June	12	4.95	24	37	--					
July	10	0.80	--	18	75	3	4.45	94	6	--
Aug	9	2.95	--	15	--	2	2.95	95	5	--
Sep	16	9.35	83	14	--	1	2.70	100	--	--
Oct	15	3.95	56	6	33	2	1.55	97	3	--
Nov	10	3.90	20	--	27					
Dec	11	5.65	58	5	36	4	6.25	99	1	--
N. Twin										
Jan	6	1.45	--	--	100	5	1.70	--	100	--
Feb	6	0.80	--	38	62	4	0.45	--	100	--
Mar	7	0.45	--	44	--	4	4.80	62	2	--
Apr	12	0.20	--	50	--	3	0.85	--	100	--
May	2	0.95	--	79	--					
June	6	3.85	--	95	5	2	6.00	97	3	--
July	4	4.10	--	66	--	6	1.30	77	23	--
Aug	3	0.50	--	40	60	7	1.25	16	36	32
Sep						5	19.25	--	94	--
Oct						10	3.25	38	62	--
Nov						8	9.05	45	23	6
Dec	1	0.10	--	100	--	8	19.85	14	71	6
S. Twin										
Jan	14	3.80	--	51	40	2	1.75	--	100	--
Feb	11	1.20	--	--	100	5	1.60	75	25	--
Mar	14	3.05	--	3	97	1				
Apr	13	11.10	--	100	--	3	2.95	--	100	--
May	11	2.85	--	67	33					
June	5	0.30	--	100	--	4	0.35	--	57	--
July	11	2.65	--	57	17	6	6.85	47	39	--
Aug	3					5	0.80	--	100	--
Sep	3	1.20	--	100	--	8	3.00	24	72	2
Oct	12	3.45	--	25	29	4	1.60	--	56	19
Nov	3	1.15	--	30	--	10	3.65	3	11	15
Dec	3	0.15	--	67	33	10	6.00	8	91	--

Table 10.--Spring estimates of adult female crayfish in the three lakes

Lake and year	Age II	Age III	Total
W. Lost			
1966	5,289	297	5,586
1967	3,230	791	4,021
1968	1,903	105	2,008
1969	2,754	243	2,997
N. Twin			
1966	4,157	185	4,342
1967	2,021	577	2,598
1968	2,094	133	2,227
1969	1,432	199	1,632
S. Twin			
1966	3,092	29	3,121
1967	1,576	364	1,940
1968	1,701	41	1,742
1969	2,802	185	2,987

Table 11.--Counts of attached eggs on *Orconectes virilis* in three Pigeon River Area lakes

Lake and year	Female crayfish examined		Egg counts	
	Number	Size range (mm)	Mean number	S.E. (±)
W. Lost				
1966	73	20-34	61.9	3.8
1967	42	21-32	64.8	5.6
1968	43	24-31	92.1	5.3
1969	52	22-34	78.4	5.5
N. Twin				
1966	78	20-36	25.7	3.3
1967	54	21-32	68.0	5.0
1968	33	24-32	116.8	6.6
1969	37	22-35	82.1	8.3
S. Twin				
1966	64	22-29	32.6	3.1
1967	47	24-33	105.9	5.1
1968	45	26-34	149.1	5.7
1969	59	20-33	78.8	5.1

Table 12.--Population estimates of young-of-the-year crayfish in the lakes during the summers of 1966, 1967, 1968, and 1969

Year and lake	Sampling			Population estimates	
	Number of days	Number marked	Recapture rate(%)	Number	95% confidence limits
1966					
W. Lost	8	14,158	20	54,996	52,702- 57,498
N. Twin	11	1,323	3	44,959	26,378-160,666
S. Twin	13	1,379	2	39,586	30,030- 59,880
1967					
W. Lost	20	2,904	6	46,996	40,485- 54,054
N. Twin	19	995	3	37,243	25,773- 39,370
S. Twin	27	1,240	4	36,245	20,883-142,857
1968					
W. Lost	13	3,832	24	21,077	19,305- 23,255
N. Twin	26	3,777	15	22,710	20,242- 25,906
1969					
W. Lost	13	3,467	6	64,154	57,471- 65,359
N. Twin	15	1,097	10	47,194	28,011- 38,023
S. Twin	17	1,439	6	32,096	34,246- 78,125

Table 13.--Summer population estimates of crayfish in the three lakes

Lake	Sex	Year	Age group 0	I	II	III	Total
W. Lost	♂	1966	24,809	12,022	13,150	521	50,502
		1967	18,584	1,823	3,009	70	23,486
		1968	8,641	2,887	1,799	47	13,374
		1969	32,077	3,350	2,109	33	37,569
	♀	1966	30,187	6,713	3,758	34	40,692
		1967	28,412	2,137	1,453	113	32,115
		1968	12,436	2,545	1,313	28	16,322
		1969	32,077	2,109	2,178	34	36,398
		1962	13,163	3,753	1,073	248	18,017
		1963	7,128	4,940	1,073	124	13,265
N. Twin	♂	1966	20,874	10,279	2,447	60	33,660
		1967	17,091	2,379	1,592	110	21,172
		1968	9,992	6,177	1,104	73	17,346
		1969	23,597	3,570	1,491	47	28,705
	♀	1966	24,085	5,853	4,057	60	34,125
		1967	20,152	2,410	1,895	110	24,518
		1968	12,718	3,442	984	45	17,189
		1969	23,597	2,450	1,425	84	27,556
S. Twin	♂	1966	19,290	6,606	5,314	---	31,210
		1967	15,905	2,324	1,670	91	19,990
		1968	9,936	15,893	1,270	---	27,099
		1969	16,048	3,329	1,692	16	21,085
	♀	1966	20,296	3,119	1,621	---	25,036
		1967	20,340	1,745	1,448	32	23,565
		1968	24,824	6,852	1,454	50	33,180
		1969	16,048	1,797	1,301	---	19,076

Table 14.--Production of crayfish during their first two growing seasons, from June 1966 to August 1967, and their consumption by brook trout in West Lost, North Twin, and South Twin lakes

Lake, date and sex	Estimated number of crayfish	i	Standing crop (kg)	Wo/ W_t	g	g-i	$\overline{W}$	Production (kg) $(g-i)\overline{W}$	Brook trout consumption
W. Lost									
June 1966									
♂	172,886		11.24						
♀	172,887		11.24						
Sep 1966									
♂	24,809	1.945	14.88	1.324	0.281	2.226	12.95	28.83	
♀	30,187	1.743	18.11	1.611	0.476	2.219	14.43	32.02	
♂ + ♀								60.85	27.92
Aug 1967									
♂	1,823	2.617	14.18	0.953	-0.048	2.569	14.56	37.40	
♀	2,137	2.659	11.84	0.654	-0.425	2.234	14.74	32.93	
♂ + ♀								70.43	28.57
N. Twin									
June 1966									
♂	55,794		3.62						
♀	55,795		3.63						
Sep 1966									
♂	20,874	0.983	20.66	5.707	1.741	2.724	9.79	26.67	
♀	24,085	0.839	19.50	5.372	1.681	2.520	9.44	23.79	
♂ + ♀								50.46	0.16
Aug 1967									
♂	2,379	2.171	21.84	1.057	0.055	2.226	21.42	47.68	
♀	2,410	2.302	13.30	0.682	-0.383	1.919	16.19	31.06	
♂ + ♀								78.74	0.68
S. Twin									
June 1966									
♂	50,872		3.30						
♀	50,873		3.31						
Sep 1966									
♂	19,290	0.970	25.07	7.600	2.028	2.998	10.74	32.20	
♀	20,296	0.919	23.34	7.051	1.953	2.872	10.26	29.47	
♂ + ♀								61.67	0.55
Aug 1967									
♂	2,324	2.120	21.98	0.877	-0.131	1.989	23.54	46.82	
♀	1,745	2.453	12.83	0.549	-0.599	1.854	17.57	32.57	
♂ + ♀								79.39	1.06

Table 15.--Instantaneous rates of total mortality (i), sampling mortality (p), and natural mortality (g) for brook trout in West Lost Lake and rainbow trout in North Twin Lake

Lake and date	Instantaneous mortality rates		
	Total	Sampling	Natural
W. Lost			
Dec 1967			
	0.305	0.075	0.230
Apr 1968			
	1.410	0.237	1.173
Oct 1968			
	1.184	0.900	0.284
Apr 1969			
	1.884	1.227	0.607
Oct 1969			
N. Twin			
Dec 1967			
	0.294	0.056	0.238
Apr 1968			
	0.637	0.135	0.502
Oct 1968			
	0.473	0.229	0.244
Apr 1969			
	0.272	0.272	0.000
Oct 1969			

Table 16.--Estimated standing crop and production in kilograms of brook trout in West Lost Lake and rainbow trout in North Twin Lake from stocking in December 1967 to October 1969

Lake and date	Estimated number	s	i	Standing crop (kg)	W_o/W_t	g	g-i	$\overline{W}$	Production $(g-i)\overline{W}$
W. Lost									
Dec 1967	600			133.04					
Apr 1968	442	0.737	0.305	85.81	0.645	-0.438	0.133	107.83	14.34
Oct 1968	108	0.244	1.410	19.14	0.223	-1.500	0.090	44.45	4.00
Apr 1969	33	0.306	1.184	5.84	0.305	-1.187	0.003	11.21	0.03
Oct 1969	5	0.152	1.884	1.36	0.233	-1.457	0.427	3.07	1.31
N. Twin									
Dec 1967	821			182.37					
Apr 1968	612	0.745	0.294	114.98	0.630	-0.462	0.168	146.05	24.54
Oct 1968	324	0.529	0.637	91.79	0.798	-0.226	0.411	102.77	42.23
Apr 1969	202	0.623	0.473	59.70	0.650	-0.431	0.042	74.54	3.13
Oct 1969	154	0.762	0.272	58.21	0.975	-0.025	0.247	59.68	14.74

Table 17.--Average volume of food per fish based on monthly samples of brook trout in West Lost Lake and rainbow trout in North Twin Lake between January 1968 and October 1969

Year and month	Brook trout in West Lost Lake		Rainbow trout in North Twin Lake	
	Number of fish	Volume /fish	Number of fish	Volume /fish
1968				
Jan	9	0.29	10	1.64
Feb	10	0.92	10	0.35
Mar	9	1.92	10	0.08
Apr	10	0.98	10	1.25
May	10	0.98	10	0.99
June	9	1.46	10	0.74
July	10	0.96	10	0.69
Aug	10	0.42	10	0.17
Sep	10	0.72	10	0.69
Oct	8	0.74	11	0.85
Nov	8	2.41	10	0.72
Dec	9	1.19	10	0.61
1969				
Jan	10	2.52	10	0.27
Feb	10	3.35	10	0.38
Mar	10	2.08	10	1.04
Apr	10	2.45	9	1.20
May	10	2.43	10	2.32
June	10	0.86	10	1.17
July	9	1.88	10	0.28
Aug	10	2.27	10	0.22
Sep	9	1.08	8	0.17
Oct	10	1.72	10	0.18
Total or mean	210	1.54	218	0.73

Table 18.--Percentage of various orders of organisms found in the stomachs of 210 brook trout from West Lost Lake and 218 rainbow trout from North Twin Lake sampled between January 1968 and October 1969

Order	Percent of total volume	
	W. Lost	N. Twin
Diptera	7	21
Odonata	4	8
Hemiptera	4	5
Coleoptera	5	11
Trichoptera	<1	2
Ephemeroptera	1	3
Hymenoptera	--	<1
Lepidoptera	<1	--
Megaloptera	<1	<1
Decapoda	70	17
Cladocera	4	27
Annelida	--	1
Salientia	<1	--
Caudata	--	> 1
Hydracarina	<1	--
Pelecypoda	--	> 1
Fish eggs	3	1
Algae	2	--
Unidentified	<1	2

Table 19.--The occurrence of crayfish, insects, and cladocerans in the stomachs of brook trout from West Lost Lake and rainbow trout from North Twin Lake based on monthly sampling between January 1968 and October 1969

Year and month	Brook trout in West Lost Lake: Number of fish	Total volume of food	Percent of total volume in: Crayfish	Insects	Cladocerans	Rainbow trout in North Twin Lake: Number of fish	Total volume of food	Percent of total volume in: Crayfish	Insects	Cladocerans
1968										
Jan	9	2.65	30	55	15	10	16.35	--	98	2
Feb	10	9.25	99	1	--	10	3.50	23	69	6
Mar	9	17.30	97	--	3	10	0.85	--	100	--
Apr	10	9.80	76	22	2	10	12.50	28	56	--
May	10	9.80	89	8	1	10	9.90	--	91	9
June	9	13.15	92	6	2	10	7.40	--	--	100
July	10	9.65	56	20	23	10	6.90	35	8	57
Aug	10	4.15	75	--	25	10	1.70	17	21	62
Sep	10	7.25	37	63	--	10	6.90	2	91	7
Oct	8	5.95	35	59	--	11	9.35	11	55	21
Nov	8	19.30	62	27	2	10	7.25	--	3	97
Dec	9	10.70	32	47	13	10	6.10	29	50	21
1969										
Jan	10	25.20	68	29	2	10	2.70	13	33	50
Feb	10	33.50	79	2	--	10	3.80	16	13	41
Mar	10	20.75	78	13	4	10	10.35	54	17	17
Apr	10	24.50	86	10	3	9	10.85	16	46	30
May	10	24.30	33	67	--	10	23.15	3	73	17
June	10	8.65	51	13	35	10	11.70	54	16	30
July	9	16.95	90	2	8	10	2.75	--	--	100
Aug	10	22.70	83	--	3	10	2.15	47	30	23
Sep	9	9.75	58	42	--	8	1.35	22	67	11
Oct	10	17.15	47	23	1	10	1.85	--	73	--

Table 20.--Production of crayfish during their first two growing seasons, from June 1968 to August 1969, and their consumption by brook trout in West Lost Lake and rainbow trout in North Twin Lake

Lake, date and sex	Estimated number of crayfish	i	Standing crop (kg)	W_o/W_t	g	g-i	$\overline{W}$	Production (kg) $(g-i)\overline{W}$	Trout predation loss (kg)
W. Lost									
June 1968									
♂	92,468		6.01						
♀	92,469		6.01						
Sep 1968									
♂	8,641	2.375	6.05	1.007	0.006	2.381	7.01	16.69	
♀	12,436	2.009	7.46	1.241	0.215	2.224	6.74	14.99	
♂ + ♀								31.68	2.50
Aug 1969									
♂	3,350	0.947	25.33	4.187	1.431	2.378	13.47	32.03	
♀	2,109	1.772	10.57	1.417	0.348	2.120	8.94	18.95	
♂ + ♀								50.98	10.94
N. Twin									
June 1968									
♂	130,057		8.45						
♀	130,057		8.45						
Sep 1968									
♂	9,992	2.564	6.79	0.804	-0.218	2.346	7.60	17.83	
♀	12,718	2.323	7.63	0.903	-0.102	2.221	8.04	17.86	
♂ + ♀								35.69	4.60
Aug 1969									
♂	3,570	1.030	21.53	3.171	1.154	2.189	12.77	27.89	
♀	2,450	1.645	10.88	1.426	0.354	1.999	9.18	18.35	
♂ + ♀								46.24	4.51

Table 21.--Annual rates of natural mortality (n) for brook trout of the 1964 and 1965 year classes in three Pigeon River Area lakes, 1966-1967

Year class	Year and lake					
	1966			1967		
	West Lost	North Twin	South Twin	West Lost	North Twin	South Twin
1964	0.787	0.605	0.709			
1965	0.401	0.551	0.486	0.736	0.500	0.681

Table 22.--Annual rates of natural mortality for the 1965 brook and rainbow trout year classes in West Lost and North Twin lakes, respectively, in 1968 and 1969

Year class and species	Year and lake			
	1968		1969	
	West Lost	North Twin	West Lost	North Twin
1965				
Brook trout	0.749		0.556	
Rainbow trout		0.523		0.241

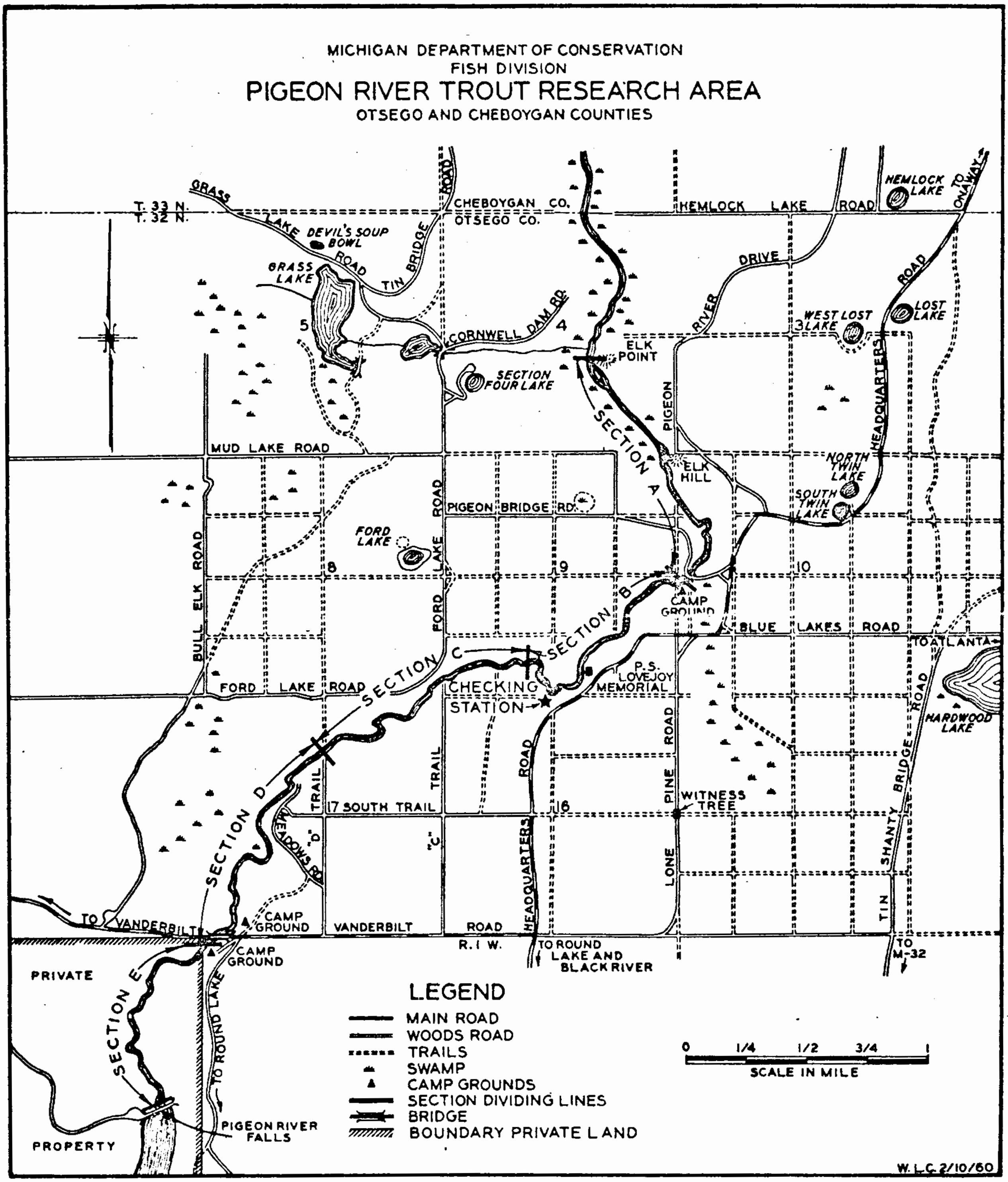

Figure 1.--Map showing location of study lakes.

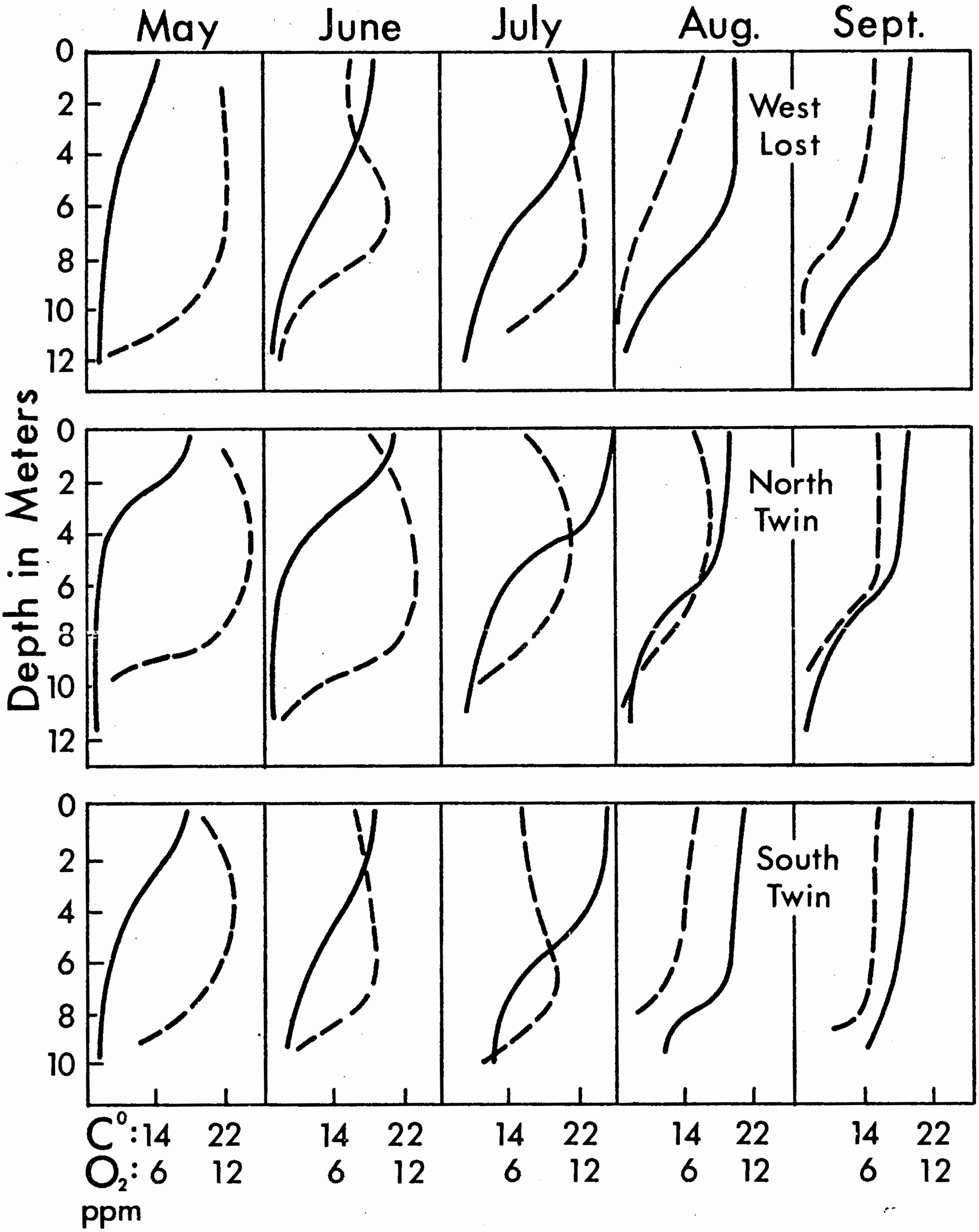

Figure 2.--Monthly profiles of water temperature in degrees Centigrade (solid line) and dissolved oxygen (dashed line) in three Pigeon River Area lakes, May to September, 1966.

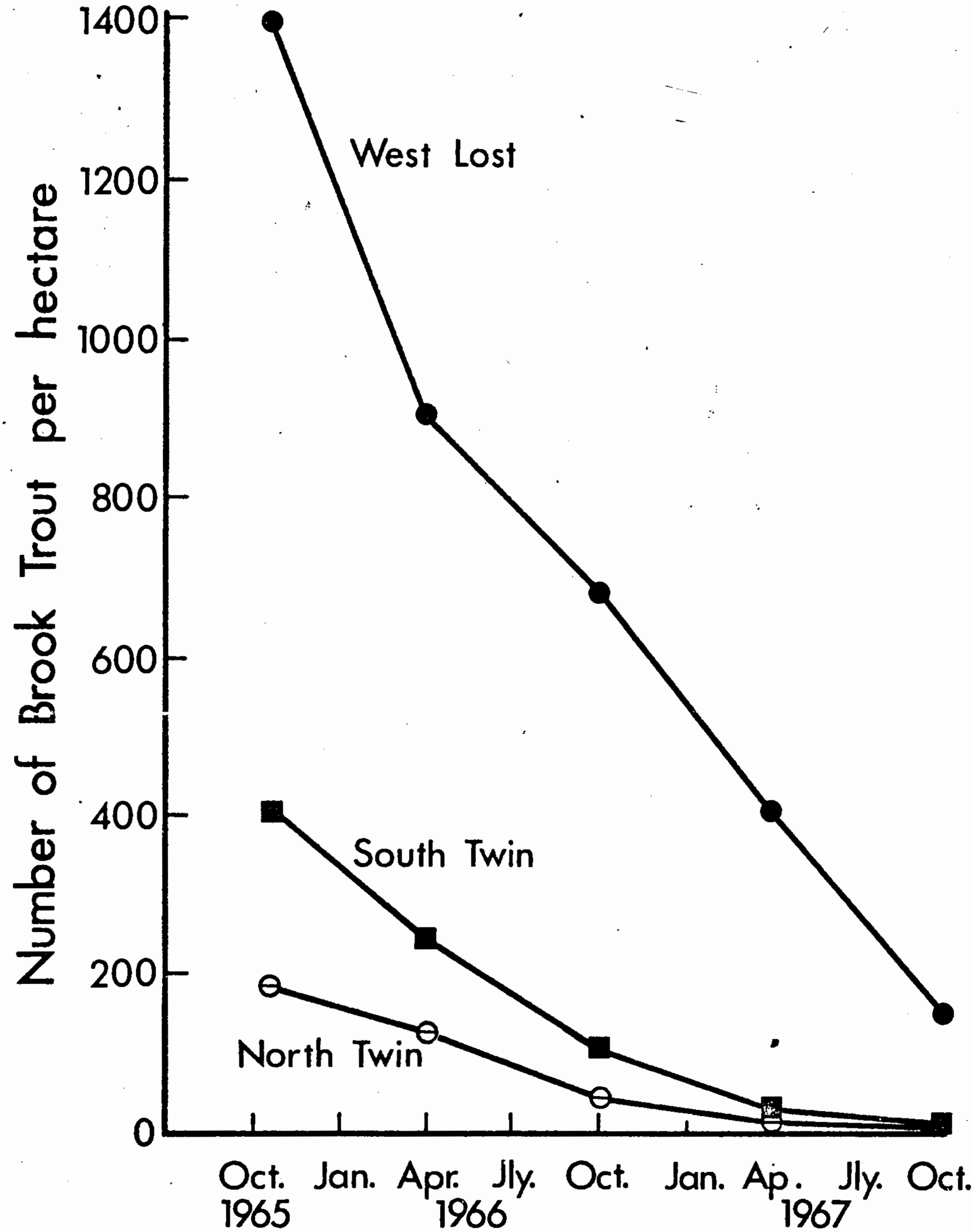

Figure 3.--Decline of brook trout populations in West Lost, North Twin, and South Twin lakes from the fall 1965 to fall 1967.

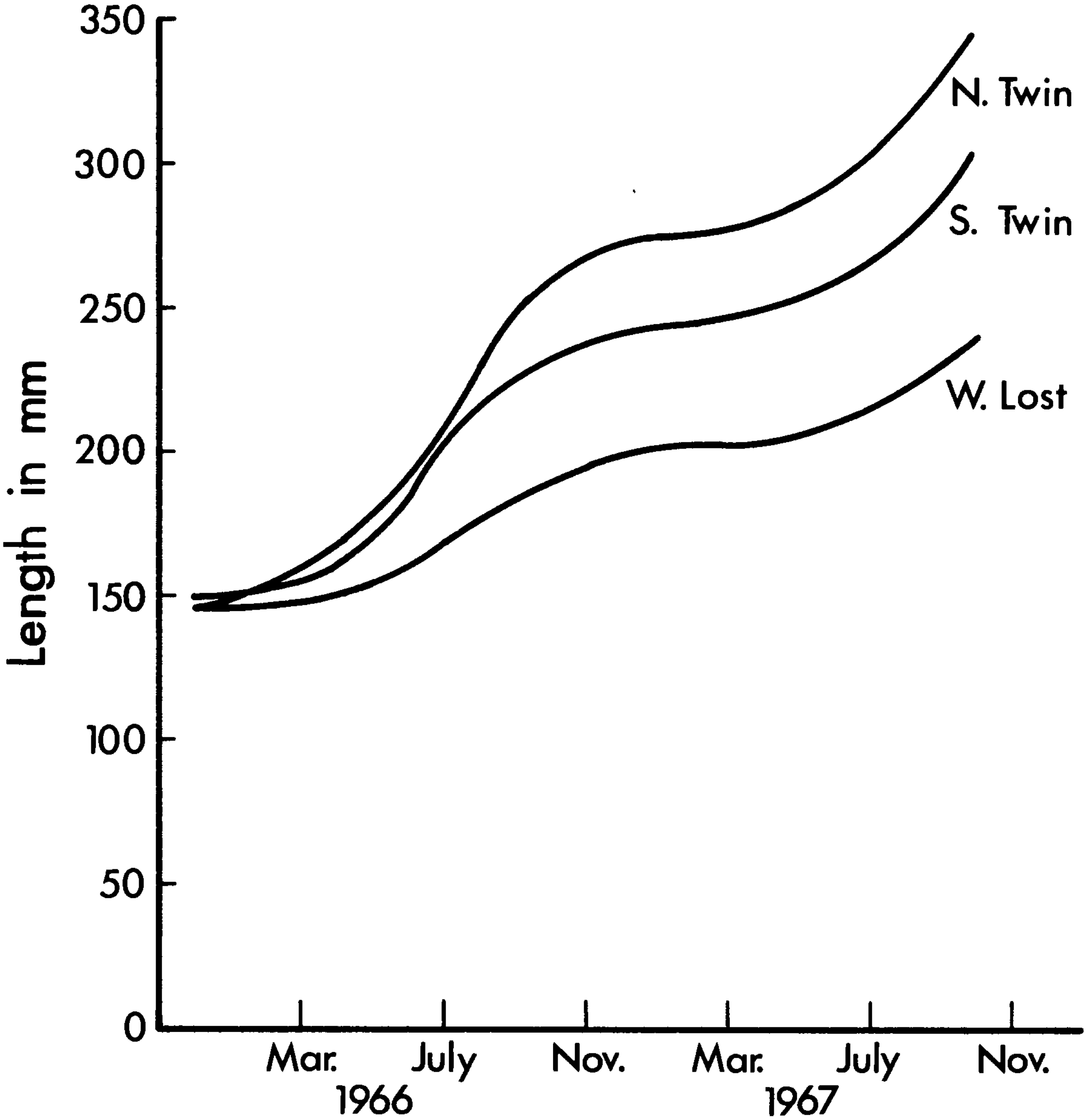

Figure 4.--Growth rates of ALP-marked brook trout in West Lost, North Twin, and South Twin lakes; initial densities of 1250.0, 126.3, and 243.8 fish per hectare, respectively.

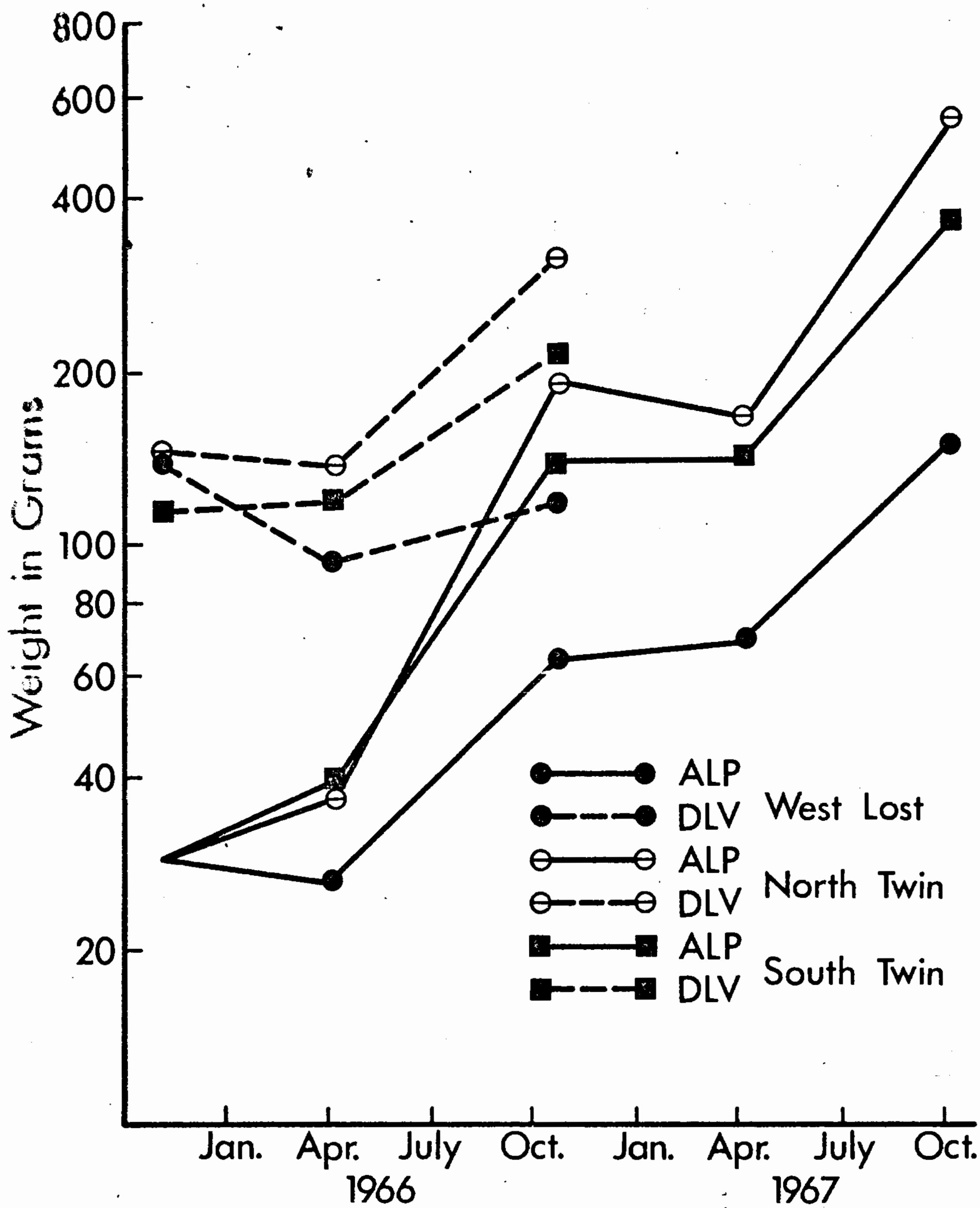

Figure 5.--Seasonal instantaneous growth rates (g) of ALP- and DLV-marked brook trout in West Lost, North Twin, and South Twin lakes during 1966 and 1967 plotted on semi-log scale.

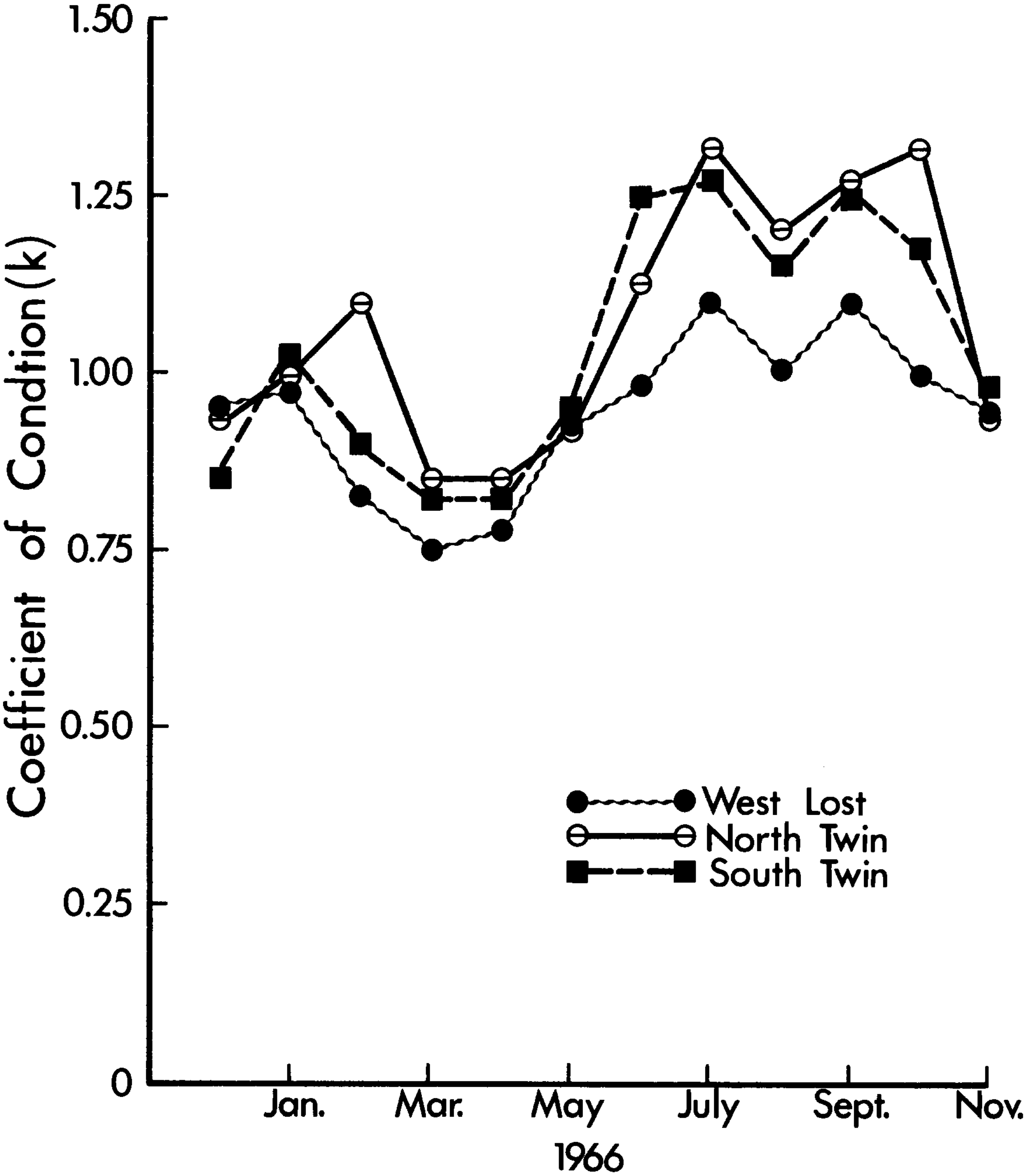

Figure 6.--Seasonal trend in coefficient of condition (K) of ALP-marked brook trout in West Lost, North Twin, and South Twin lakes during 1966.

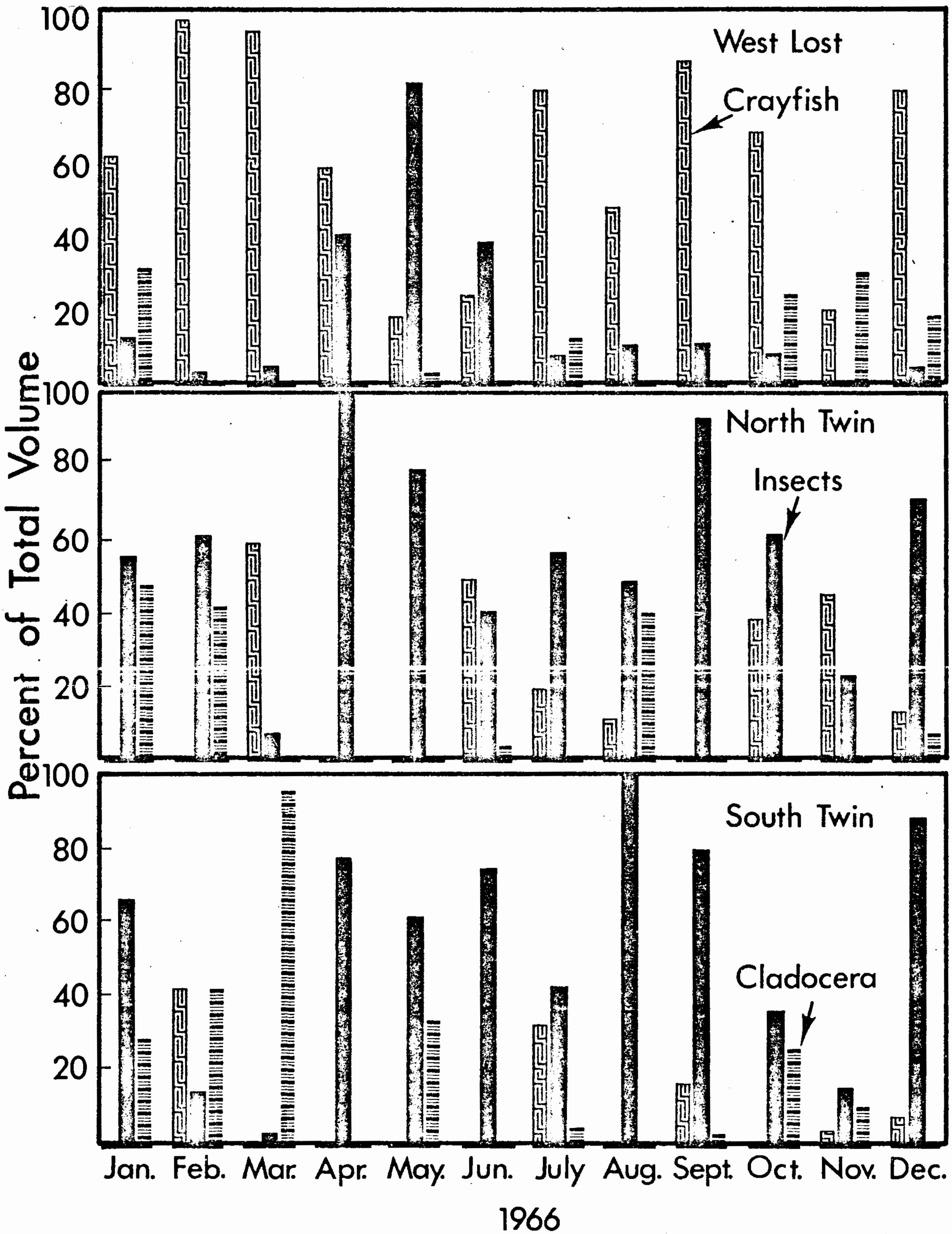

Figure 7.--Percentage by volume of three major food organisms (crayfish, insects and cladocerans) in the stomachs of brook trout in West Lost, North Twin, and South Twin lakes during 1966. (Cross hatch = crayfish; solid bar = insects; stippled bar = cladocerans)

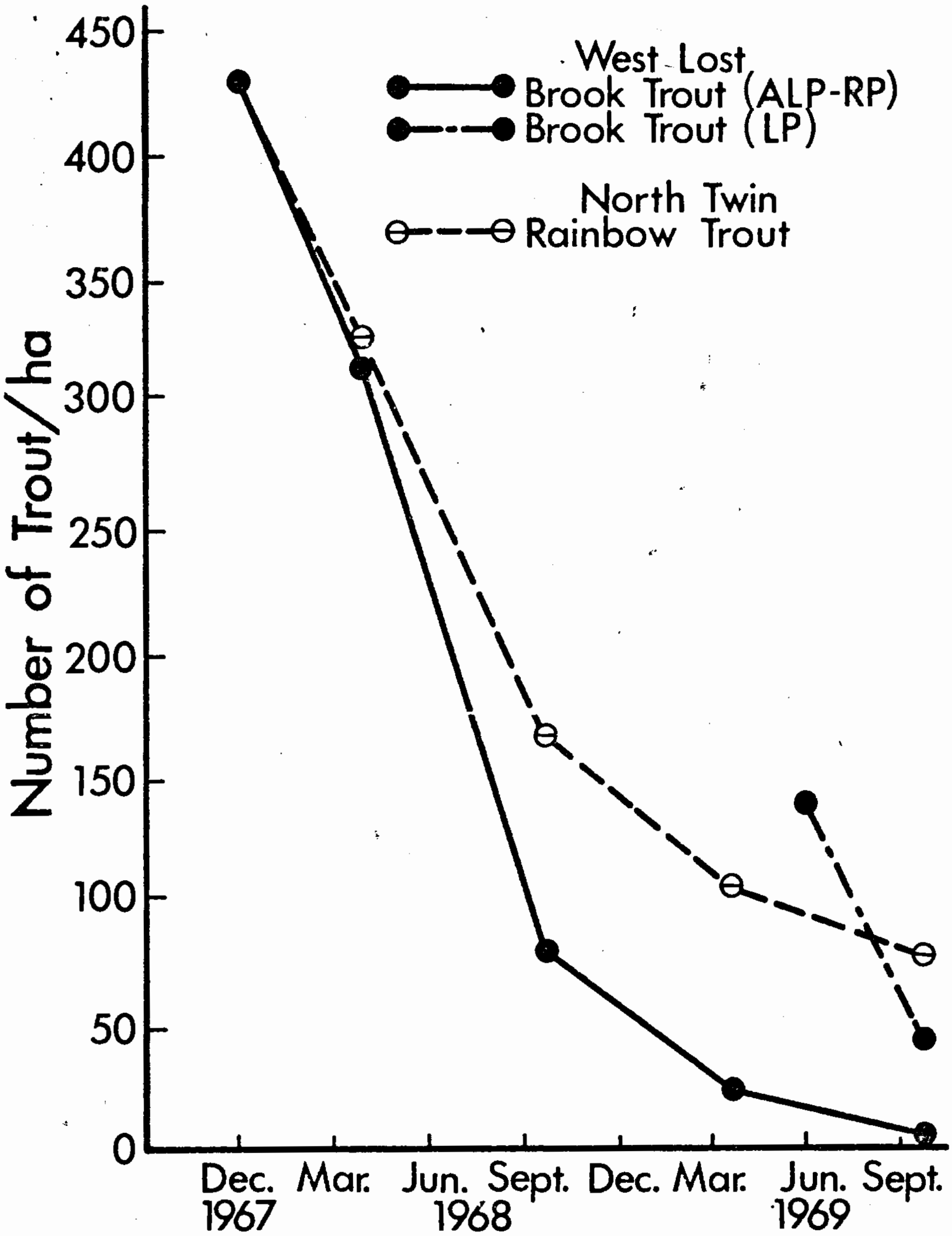

Figure 8.--The decline of adult stocks of brook trout planted in West Lost Lake (428 fish/ha) and rainbow trout in North Twin Lake (432 fish/ha) from December 1967 to October 1969. West Lost Lake planted with 200 brook trout, 143 fish per hectare, in June 1969.

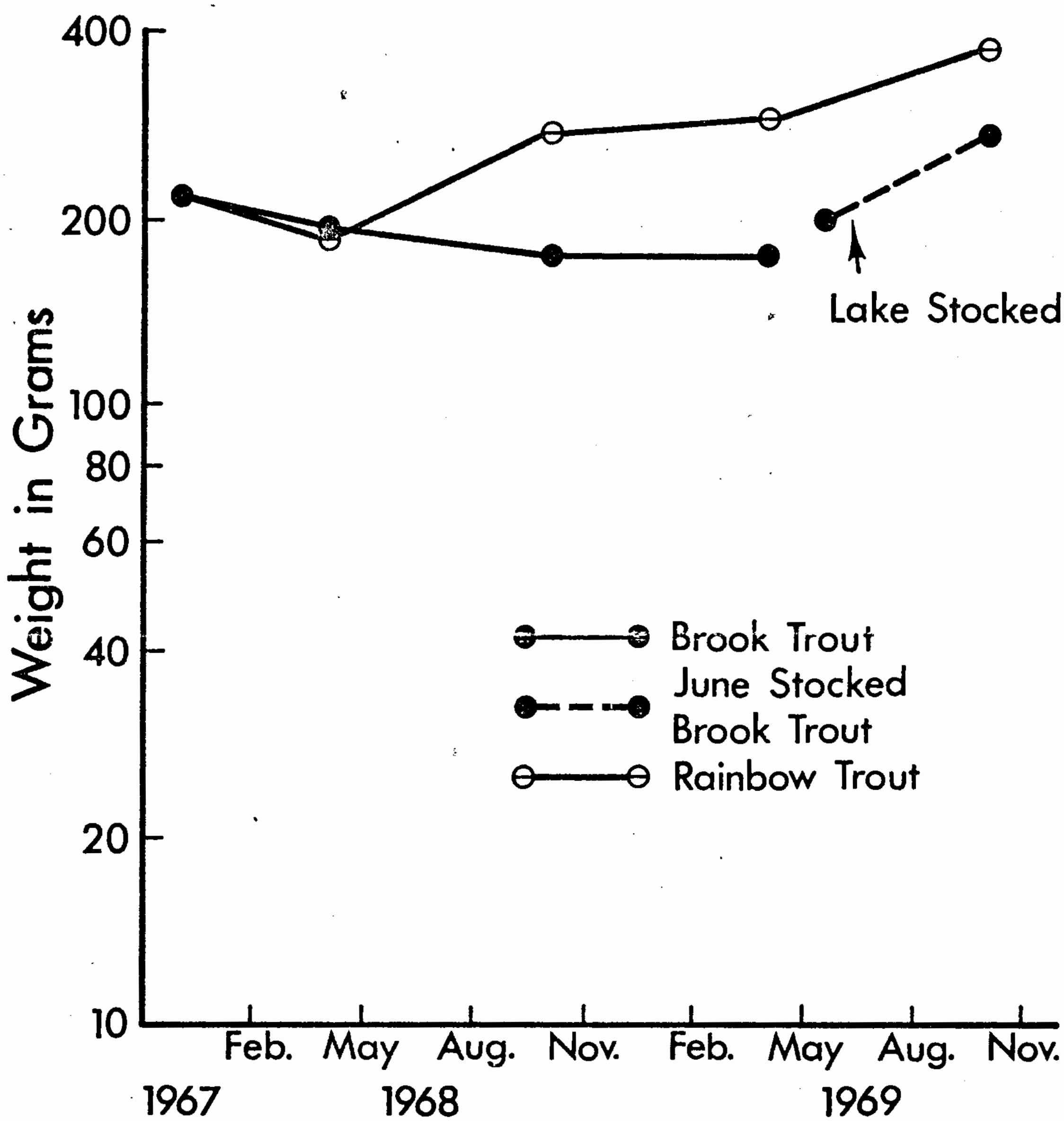

Figure 9.--Seasonal instantaneous growth rates (g) of brook trout in West Lost Lake and rainbow trout in North Twin Lake during 1968 and 1969 plotted on semi-log scale.

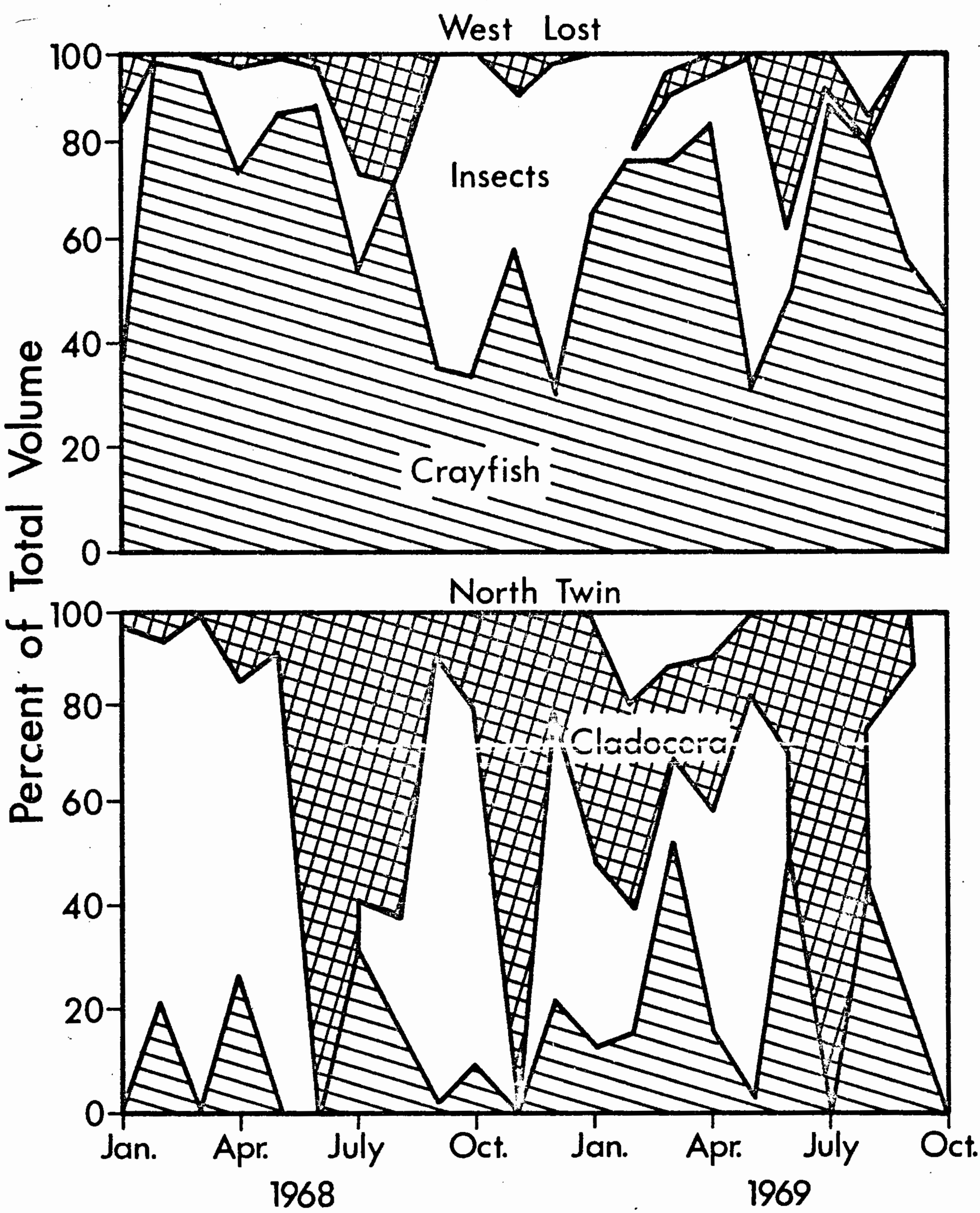

Figure 10.--Percentage by volume of three primary food organisms comprising the stomach contents of 210 brook trout (206-340 mm, total length) from West Lost Lake and 218 rainbow trout (221-389 mm, total length) from North Twin Lake. About 10 trout per month were sampled, from January 1968 to October, 1969.

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