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THE POPULATION DYNAMICS OF THE CRAYFISH, *ORCONECTES VIRILIS* IN RELATION TO PREDATION BY THE BROOK TROUT, *SALVELINUS FONTINALIS* [1]

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INTRODUCTION

Results of studies of the quantitative aspects of trophic ecology are expressed in terms of the productivity of the component food groups involved. Important in the trophic dynamics of any ecosystem are the myriad of organisms, mainly invertebrates, that contribute to the secondary level of production. These are the primary consumers in the food chain dependent on the primary producers for energy and in turn serve as food organisms for higher levels in the chain.

Arthropods are one of the principal components of the secondary level of productivity in aquatic ecosystems. Previous work on the productivity of arthropod populations in natural freshwater ecosystems has in general neglected the crustaceans, e. g., Borutsky (1939), Anderson and Hooper (1956), Miller (1941) and Lundbeck (1926). Recently studies of secondary productivity among crustacea have been made on cladocerans (Hall, 1964) and amphipods (Cooper, 1964). These crustacea are relatively short-lived, small organisms.

Among the freshwater crustacea of North America crayfish are a somewhat specialized type of consumer, i. e., they are larger and have a longer life span than other members of the class. Consideration of the comparative population dynamics of members of this taxonomic class raises questions such as: (1) how does size and length of life span influence the rate of energy flow and the rate of turnover, (2) are population regulating mechanisms similar in the small, short-lived forms, and in larger long-lived crayfish?

Crayfish are certainly among the most conspicuous and abundant invertebrates of the marl lakes of northern Michigan. Typically marl lakes are lakes of high transparency, have little or no higher aquatic vegetation and have light colored sediments that are low in organic matter but contain a high percentage of marl (Hale, 1903). Marl incrustations produced by algae usually cover rocks and other fixed objects within the epilimnion. Benthic algae probably account for a major portion of the energy fixed by photosynthesis within these lakes (Hooper and Ball, 1964), and in lakes of this type production by phytoplankton is low compared to non-marl lakes (Raymond, 1937). Production of invertebrate bottom fauna other than crayfish in marl lakes is also low and is probably in part limited by the sparsity of aquatic plants (Wohlschlag, 1950). Since crayfish frequently abound in these waters and seemingly far exceed other bottom fauna in terms of standing crop, it is of considerable ecological interest to examine their production rates and their trophic position.

Earlier studies of North American crayfish have dealt chiefly with life histories or have provided estimates of the standing crops in shallow artificial ponds (e.g., Tack, 1941; Goellner, 1943; Van Deventer, 1937). None of these studies have focused attention upon productivity and the resilience to predation of a natural population within a lake. The objective of this study, viz. to define the role of the crayfish as a consumer in the trophic dynamics of a marl lake ecosystem, required detailed knowledge of the growth, reproduction, mortality, and density of the crayfish population of this habitat. To meet the above objective it was also necessary to measure the annual net production of this crustacean, to establish some insight into the factors controlling its production, and to compare its production with that of other members of the benthos.

The principal mortality factor examined was the effect of trout predation upon the crayfish population. This predation study made possible measurement of the efficiency of energy transfer from one trophic level to another and the assessment of the relative importance of this interspecies interaction. Only when the pattern of population interaction is understood can populations be manipulated so as to produce an increase in efficiency of energy transfer from one trophic unit to another. By means of such studies the efficiency, with which an economically important predator utilizes the net annual production of its prey, can be increased. The ecological relationship between trout and crayfish presented in this paper can serve as an example of this avenue of approach; an approach that can be used to direct and to channelize the potential productivity of an aquatic ecosystem for maximum human benefit.

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AREA OF STUDY

The field work was conducted from August 1962 to November 1963 on West Lost Lake, Otsego County, Michigan. This lake is one of a series of small lakes within the Pigeon River Trout Research Area, an area administered by the Institute for Fisheries Research of the Michigan Department of Conservation.

Tanner (1952) has described the limnological features of West Lost Lake. The lake has a surface area of 1.5 hectares, a maximum depth of 13.4 m, and an average depth of 8.5 m. The shoal area (water less than 1.2 m) is only 11% of the total bottom. The basin is symmetrical in outline with steep slopes and is believed to have originated as a limestone sink.

Logs are abundant in the littoral area and are covered with thick incrustation of marl. Stems and petioles of the yellow water lily are also heavily incrusted. The water is hard, the methyl orange alkalinity is 138 ppm. Aquatic vegetation is acarce. Bottom soils are marl and sand.

Brook trout is the only species of fish present in West Lost Lake but there is no natural reproduction. Fish averaging 126 mm in length are planted annually at a rate of 300 per surface hectare. The catch of all fishermen is examined by the staff of the Pigeon River Research Station. This census has provided data on the yield, age and growth, and food habits of the trout. Estimates of trout population density are made each fall. Estimates were also made in the spring of 1962 and 1963.

METHODS

Population and age estimates

Estimates of the size of the crayfish population were made during the summer of 1962 and during the spring and summer of 1963. The narrow, steep littoral zone, which in many areas was covered with logs and branches, was difficult to seine. Rectangular wire traps baited with fish remains proved to be the most satisfactory collecting device. These traps sampled crayfish larger than 24 mm in cephalothorax length. Traps were constructed by stapling 0.635 cm mesh galvanized screen to a welded iron frame having the dimensions 61 cm x 30.5 cm x 30.5 cm. A funnel at one end of the trap was hinged to permit removal of trapped animals. Round wire minnow traps of the type available at sporting goods stores also were used. Round and rectangular traps proved equally effective. Traps were fished for 24 hours and were then lifted and re-baited. After being processed (marked, measured, weighed, etc.) crayfish were released in the center of the lake.

Young crayfish (less than 24 mm in length) were collected by seining along the shore after dark with a minnow seine of 0.635 cm mesh. Each collection of young crayfish consisted of a series of seine hauls which extended around the entire circumference of the lake.

The Schumacher method (Schumacher, 1943) was chosen over the Schnabel method (Schnabel, 1938) for making population estimates because it does not require iterative procedures and because it reduces errors due to non-random sampling by weighting each sample by sample size rather than by the proportion marked (DeLury, 1958; Ricker, 1958). The formula used for calculation is:

$$\underline{p} = \Sigma_{\underline{t}}\ x_{\underline{t}} X_{\underline{t}} \ / \ \Sigma_{\underline{t}}\ n_{\underline{t}}\ X_{\underline{t}}^2$$

where $\underline{p} = 1/N$; N = estimate of population size,

$x_{\underline{t}}$ = number of animals in the sample,

$X_{\underline{t}}$ = total number of animals previously marked,

$n_{\underline{t}}$ = number of marked animals in the sample, and

$\underline{t}$ = time interval.

To establish the validity of my procedures I conducted experiments to compare the Schumacher and the Schnabel methods of estimation. Also I attempted to find out whether or not the two types of collecting gear that were used gave different population estimates. These experiments were carried out in ponds of the U. S. Fish and Wildlife Service at Northville, Michigan, and in ponds at the Hastings Fisheries Research Station of the Institute for Fisheries Research at Hastings, Michigan. Results indicated that estimates obtained with a 15.25 m bag seine did not differ substantially from those obtained with baited wire traps (Table 1). Schumacher type estimates were slightly higher than Schnabel estimates but gave narrower confidence intervals. There was no significant difference in the mean size of crayfish sampled by either type of gear ($t_{.01} = 1.395$, $n = 530$). A 0.25 recapture rate gave consistent estimates of population size.

Goellner (1943) developed and described a marking technique for crayfish in which the pleura are clipped with fine-pointed scissors. This proved to be effective but was quite laborious if large numbers of crayfish were marked. Injection of ink beneath the abdomen with a hypodermic syringe was also successful, but was difficult to use in the field. Crayfish marked by clipping the pleuron and kept in aquaria, retained the scar for three molts following the excision. Adult crayfish marked in West Lost Lake retained the clipping mark for the duration of the study (1 1/2 years). Immature animals marked in September of 1962 could be identified in May of 1963. Regeneration of the excision produces a deformed pleuron but clipping the pleura did not disturb ecdysis and apparently had little effect upon general health of crayfish.

The technique of pleural clipping satisfied many of the assumptions.

(1) Marked crayfish were easily recognized on recapture.

(2) Marks were not lost.

(3) There was no evidence to indicate that marked and unmarked animals were not equally susceptible to capture.

(4) Growth of the age group being estimated and growth of the next younger age group could distort estimates of the rate of recapture; this source of error was eliminated by marking only during the intermolt period when no growth occurs.

(5) There was no evidence to indicate that marked and unmarked individuals did not have the same rate of mortality.

(6) After processing, marked animals dispersed themselves at random within the sampling area.

If the sample of a given age group was too small to give a reliable estimate of the population of that group (e. g., age-I), it was combined with samples of adjacent age-groups (e. g., age-0 and age-II). An estimate was then made of the combined sample (e. g., age-0, age-I, age-II). Population estimates of each component were obtained by multiplying the combined estimate by the percentage of each of the component age groups in the cumulative catch during the sampling period.

Age composition was analyzed from size-frequency graphs, and by the following of the growth of groups of known-age individuals. Because of molting, the growth of crayfish is stepwise. Size-frequency polygons using length of the cephalothorax plotted in millimeter intervals as the abscissa and number of individuals as the ordinate, break up the population into natural size groups with distinct, easily followed modes (Van Deventer, 1937). Young-of-the-year and yearlings form the most distinct groups.

Size-frequency graphs become polymodal for older age groups. However, the number of molts per season is reduced and the shift in mode of an age group after a molt can be recognized throughout the growing season. Thus a series of size-frequency graphs plotted at intervals during the growing season permit a reasonable estimate of the rate of growth.

Age assessments for yearlings and young-of-the-year were easily made since there was no overlap with other age groups (Fig. 1). Age groups II and III have overlapping size ranges. Arbitrary length intervals for these two age groups were decided upon by inspecting the length-frequency curve. The percentage of 2- and 3-year-olds within these intervals among known-age crayfish was then assigned to all unknowns falling within these length limits. For example when the interval 29 to 37 mm was used for 2-year-old males (cf. Fig. 1) it was found that this interval included 80% of the known-age 2-year-olds and 20% of the known-age 3-year-olds.

Growth

Total length is difficult to measure because the abdomen of crayfish is flexible. For this reason the carapace lengths were used. Measurements were made with vernier calipers to 0.1 mm along the dorsal surface from the tip of the rostrum to the abdomen.

The length frequency plots from each series of samples used for population estimates were used for analysis of seasonal growth. The plotted points are the means of the length-frequency distributions (Fig. 2). Fractional measurements were reduced to 1 mm size classes, e.g., those from 18.6 through but not beyond 19.5 are counted as 19.0 mm. Estimates of growth rate were calculated from length measurements of only the unmarked individuals encountered during the population estimates. A test of propriety showed that data from marked individuals could have been used as well since the large sample sizes obliterated the effect of repeated recapture upon growth.

I converted growth in length to weight units by use of a length-weight relationship computed from empirical data (Fig. 3). To compute this curve crayfish with complete sets of appendages were measured to the nearest millimeter and were weighed to the nearest 0.1 gm. No statistical difference in weight was found between males and females for the size ranges examined ($t_{.05} = 0.558$, $n = 108$).

The average weight of crayfish of a given length at successive ages was used to calculate instantaneous growth rates. The formula used in this calculation is as follows (cf. Ricker, 1958):

$$g = \log_e (W_t / W_o);$$

where g = instantaneous growth rate,

e = base of natural logarithm,

W_t = weight at the end of time t, and

W_o = initial weight.

Reproduction

Reproductive potential is customarily measured by egg counts. Ovarian egg counts were made from mature females collected in August. The production of fertilized eggs by crayfish may be estimated from counts of eggs carried on the pleopods of females. A series of live females captured during marking experiments and females collected by seining were used for these counts. Eggs of crayfish used in marking tests were counted in the field and the crayfish returned to the water after making counts. In counting I avoided removing eggs from these specimens. The sample collected by seining was preserved in alcohol and counted in the laboratory.

Predation

Brook trout stomachs were examined in order to determine the extent to which crayfish are utilized as food. Stomachs were removed from all fish caught by anglers during August and September of 1962, and from April to September in 1963. During the remainder of the year when West Lost Lake was closed to fishing, fish were collected with an a-c electrofishing device or by hook and line. Collections were made at intervals not greater than two months. Each food item was identified, weighed, and its volume in ml determined by water displacement. In the analysis of trout predation it was necessary to make calculations of the rate of consumption of crayfish from empirical observations. This rate was then related to the size of the stock of crayfish, and the numbers and sizes of the predators. The equilibrium yield was calculated for females of the population, under various rates of predation, by substituting predation rates for fishing mortality in the equation for yield given by Ricker (1958).

The expression used for calculating the equilibrium yield is:

$$Y_E = \Sigma_{T = T_R}^{T = T_\lambda} \quad \underline{p}_T \overline{W}_T$$

where T = successive intervals or periods in the life of the crayfish,

T_R = the first period under consideration,

T_λ = the last period under consideration,

$\underline{p}$ = instantaneous rate of fishing mortality, and

$\overline{W}$ = average weight of the stock

Y_E = equilibrium yield

RESULTS

Population fluctuations

Population estimates of the young-of-the-year crayfish for the spring of 1963 were made by multiplying the average pleopod egg count for adult females by the estimated number of females present during the spawning season. It is assumed that all attached eggs are fertilized and hatch. All other population estimates (Table 2) were obtained by using the mark-and-recapture procedure mentioned above. The combined estimates were not significantly higher than the sum of estimates for separate groups. Thus for age-0 crayfish in 1962, the combined estimate for the two sexes was 25, 233, whereas the estimate for males was 11, 808 and for females 13, 163 giving a total of 24, 971.

The marking period used for some groups was longer in 1962 than in 1963. This gave higher recapture rates in 1962 (Table 2). Recaptures were 25% or more in 1962. Most of the estimates based on rates less than 25% were for young-of-the-year. Recently molted crayfish did not enter traps with the same frequency as crayfish in the intermolt condition. To avoid bias marking was discontinued in the spring when molting began.

Both seasonal and year-to-year fluctuation in the population are apparent (Table 3). The summer population was 1.4 times greater in 1962 than in 1963. This difference was due to a better survival of age-0 crayfish in 1962 than in 1963. Differences between 1962 and 1963 in the summer populations of older crayfish were less than the differences between these 2 years in recently hatched animals and in most instances the confidence limits of the former estimates overlapped broadly.

Considerable seasonal variation occurred in age composition and bathymetric distribution of the population. Such variations together with factors such as molting, weather conditions, and quality of bait complicated calculation of population size. Hence the population size could not be accurately estimated without sampling for an extended period.

Mortality

Population estimates provided data for calculating estimates of mortality and its reciprocal, survival. Estimates of mortality rates were made from successive population estimates and also, for comparison, from recapture data on previously marked animals (cf. Ricker, 1958). The expression used for calculating the instantaneous rate of mortality is:

$$\underline{N}_{\underline{t}} / \underline{N}_{\underline{o}} = e^{-\underline{it}}$$

where $\underline{N}_{\underline{t}}$ = the number of animals surviving to time t,

$\underline{N}_{\underline{o}}$ = the number of animals present at the beginning of the time interval,

$\underline{t}$ = the length of the time interval,

$\underline{i}$ = the instantaneous rate of mortality for the time period and age group in question, and e = base of natural logarithms.

Recapture in one year of animals marked the previous year (using a Petersen-type population estimate, Ricker, 1958) gave estimates of survival of 0.38 for 2-year-old males from the summer of 1962 to the summer of 1963. A comparable survival estimate based on population size data using Schumacher estimates was 0.65. For 3-year-olds the recapture data gave a survival estimate of 0.23, whereas the Schumacher population estimates gave a survival rate of 0.30. The lower survival rate obtained from recapture data is perhaps caused by a loss of identification during a prolonged marking period.

Loss of identification marks would have a much greater effect upon the Petersen type estimate than upon the Schumacher estimate since the time period between marking and recapture was longer (9 months) in the case of the Petersen estimate. The Schumacher estimate was obtained from two separate estimates which spanned much shorter periods. One extended from the summer of 1962 to the spring of 1963, the other from the spring of 1963 to the summer of 1963. Changes in behavior with the onset of the mating season might also have caused discrepancies. The basic statistics derived from the data for population estimates were: the total number of animals dying from all causes (a), the number surviving (s), and the instantaneous rate of mortality (i). The instantaneous mortality rate is an average rate since mortality is not constant over a given time period.

Mortality was calculated for all of the age groups present during the summer of 1962, and for those present during the spring and summer of 1963 (Table 4). This was based on seasonal population estimates of age groups given above (Table 2). Mortality data represent all forms of natural mortality (predation, physiological aging, etc.). Predation by trout was the only type of natural mortality studied. Estimates of the proportion of the total natural mortality rate caused by predation of the brook trout are reported in a later section.

The sex ratio at hatching has been assumed to be one to one. Females outnumbered males at the end of the first growing season; in subsequent seasons, however, males were always more abundant (Fig. 4). After the first summer of life, the mortality rate was greater for females than for males (Table 4). The shift in mortality rates resulting in greater mortality of females took place during the first winter of life, and preceded the onset of sexual maturity.

The greatest percentage of adult mortality occurred in the middle of the second year for females and the middle of the third year for males. The rate of mortality from spring to summer of 2-year-old females after shedding their first brood of young was ten times that of 2-year-old males for the same period. However, mortality from spring to summer of 3-year-old females was about one eighth that of males. Overwinter mortality of crayfish of all ages and of both sexes was quite severe. A very few males, but no females, lived through the fourth winter.

Differential mortality favoring the male sex has not been reported in other species of crayfish. Tack (1941), Chidester (1912), Ortmann (1906), Van Deventer (1937), Creaser (1933), and Andrews (1904) all noted a mass mortality among males rather than females of the species they studied. High mortalities during molting periods are widely reported in the literature. Most authors conclude that these deaths are due to internal physiological changes rather than to external causes such as predation, disease or starvation. Van Deventer (1937) noted that a wave of natural deaths occurred with attainment of sexual maturity. No catastrophes were evident in the West Lost Lake population, but differences in mortality rates did appear among year classes. Van Deventer's observation on natural deaths occurring with attainment of sexual maturity in *Orconectes propinquus* is more applicable to the West Lost Lake population of *O. virilis* than to those of the other authors. Although *O. virilis* has a longer life span than *O. propinquus*, the two species show the same pattern of mortality among age groups. This pattern for *O. virilis* is evident from data based upon recovery of previously marked animals and from periodic estimates of population size. The rate of recapture of 2- and 3-year-old males was much lower between June 21 and July 10 as compared to the period from June 1 to 20. Trapping effort was the same during these periods. Between July 10 and 30 the rate of recapture again dropped for the 3-year-olds but not for 2-year-olds. This is the period during which 90% of the adult males molted. Hence molting may be responsible for periodic mortality patterns.

Year class fluctuations were noted in the population of *O. virilis*. The 1962 year class was approximately twice as large as that of 1963. The summer population of adult females was 853 in 1962 and 1,073 in 1963. Presumably the spring breeding populations in 1962 and 1963 were about the same size. Thus it seems that the 1962 and 1963 year classes arose from brood stocks of about the same size and that the larger, 1962 year class was the result of better survival.

Growth

Growth of crayfishes is directly related to the number of molts that the animals undergo during a growing season, hence it is stepwise rather than continuous. In West Lost Lake newly hatched young-of-the-year are about 4.5 mm long. When they leave the female in the spring the young are 6 mm long and by September males have an average length of 15.2 mm and females 14.1 mm. By late October and early November, males are 20.8 mm and females 19.2 mm. Yearling males have an average length of 31.2 and age-II males average 36.5 mm in length. A few males were collected which appeared to be age-III; they had an average length of 40.8 mm. Yearling females are 29.5 mm and age-II females are 36.4 mm in average length. The maximum size for males was 45 mm, and for females, 38 mm. Geographical differences in growth rate and time of maturity have been reported for *Orconectes propinquus* (Van Deventer, 1937) and probably occur in *O. virilis.*

Instantaneous growth rates declined with age although considerable seasonal variation is apparent (Table 5). A wide variation in growth rate was noted during the first growing season. Yearling males collected in May ranged from 16 to 25 mm, and females from 14 to 24 mm. By August males ranged from 24 to 33 mm, and females from 20 to 30 mm. At the end of the first growing season there was a significant difference between sexes in mean length (Table 6). This difference increased with time. It is probably associated with molting, since adult females molt only once per year whereas males molt twice each year.

There were also year-to-year differences in the growth rates of age groups (Table 6). The growth rates of both sexes of 1-year-olds differed significantly for the two years 1962 and 1963. Age-I crayfish were smaller in 1963 than in 1962 (for females, $t_{.05} = 10.6$, $n = 551$; for males $t_{.05} = 29.85$, $n = 1,960$). This difference in the growth rate of 1-year-olds between 1962 and 1963 is probably related to population density. Stunting in crayfish has been described (Svardson, 1948) and probably takes place at high density levels. Kurata (1962) found that starvation markedly affected the growth increments at molting, as well as the time interval between molts. The more severe the food shortage the longer the intermolt period.

Molting

The reproductive appendages of males have three morphological forms: (1) a juvenile form present before sexual maturity; (2) a non-breeding adult form, termed second form, which appears each spring after the first molt of a new growing season; and (3) a form characteristic of breeding adults, termed first form, which first appears at sexual maturity and is the second molt of the growing season usually occurring during the summer. After yearling males become mature during the second summer of life, the sequence of molts is always the same; they change from reproductive to non-reproductive form in the spring and from non-reproductive to reproductive form in the summer.

In 1963 the spring molting period of 2-year-old males extended from June 1 to July 4. However, 19% of these males had completed their molt by June 14. Aiken (1965) reported that in New Hampshire the spring molt occurs in the final week of June. He reported that O. virilis began its molt on June 19 and completed it by July 7, which approximates what I found in Michigan. However, he also stated that only 61% of the male adult crayfish had molted for which I have no explanation. Three-year-old males in Michigan began their spring molt a week later (June 8) than 2-year-olds. Molting continued until July 16, but 90% of the individuals had molted by July 4. The summer molt to reproductive form of both 2- and 3-year-olds began on July 5. It continued until August 6 (32 days) for 3-year-olds (90% molted within 17 days) and until August 9 (35 days) for 2-year-olds (90% molted within 20 days). Aiken (1965) found that in New Hampshire the summer molt took place in the last week of August. This molt lasted about a week and is a little later than noted in West Lost Lake. Regional differences in the occurrence of these events can therefore be expected. The period during which 90% of the crayfish undergo the spring molt in Michigan is about twice as long for 3-year-olds as for 2-year-olds, and in the case of 3-year-olds the spring and summer molts overlapped broadly in time, i.e., late molting individuals were undergoing their spring molt while early molting individuals were undergoing their summer molt. However, the spring and summer molts were separated in the case of 2-year-olds. Aiken (1965) did not separate his crayfish into age groups but reported no overlap in the molting cycles of adult males. In West Lost Lake all individuals were in reproductive form when breeding began in early August. Juvenile (yearling) male crayfish molted three to four times in the spring prior to their molt to reproductive form. Yearling females began their molt to maturity on June 17, 1963; it continued until July 8, a period of 21 days.

Molting ceased with the onset of low temperature, and concurrently there was a reduction in the movements of crayfish. This was indicated by the greater trap catches at higher water temperature (Fig. 5). At a temperature of 13 C crayfish were very sluggish and could be picked up by hand. The dark coloration and dryness of the exoskeleton observed in the spring indicated that crayfish had not molted during the winter. Newly molted animals were lighter colored and were slippery to the touch.

Reproduction

From middle August through September pairs of crayfish were observed copulating. In Wisconsin, two periods of mating have been reported, one in the fall and one in early spring (Threinen, 1958). Mating was not observed when West Lost Lake became free from ice in late April. Females with eggs were first observed in the sample collected on May 11. Creaser (1931) reported that eggs of *O. virilis* in Michigan are laid before the last of April.

The number of ovarian eggs of females is a measure of reproductive capacity. The average number of eggs in the ovary was 162. The mean number of eggs attached to the abdomen of females in 1963 was 94. This is 58% of the ovarian egg count taken the preceding fall. Thus 42% of the ovarian eggs were lost. Such a loss could arise from failure to extrude the full complement or from failure in the attachment of eggs to the pleopods.

The number of ovarian eggs increased with size of the parent and the regression of number of ovarian eggs against size is linear (Fig. 6). The regression of number of attached eggs against length of carapace is not linear. The smallest egg-bearing female (24.6 mm in carapace length) carried 87 eggs; the largest (37.8 mm) carried 53 eggs. The greatest number of eggs was carried by a female 33.6 mm long. Age-II females carried an average of 83 eggs and age-III females, 107. However, because of their greater numbers, 2-year-old females accounted for the bulk (92.5%) of the young produced in 1963. The percentage of ovarian eggs found attached to the pleopods was about the same for 2- and 3-year-olds. Exceptions were the largest 3-year-old females. The lower percentage noted in these females suggested either poor attachment associated with physiological aging or greater activity causing eggs to be dislodged. Females continue to feed while carrying eggs; 21 out of 26 egg-bearing females examined on May 20, 1963, had food in their stomachs. The food was algae of the "aufwuchs" found on marl incrustations and other plant material.

Age composition

The age composition of the population changed from year to year and seasonally within a year. A striking seasonal shift in age structure occurred from spring to summer (Table 7). In the spring of 1963, young-of-the-year comprised nearly 90% of the entire population. By contrast, in the summer of 1962, young-of-the-year comprised 60% of the male and 70% of the female population. Because of the large 1962 year class, there were more yearling than young-of-the-year males in the population during the summer of 1963. In 1962, yearling males were one-fourth as numerous as the young-of-the-year males. In the case of females there were fewer yearlings than young in 1963, however the percentage of yearlings was much higher than in 1962.

Seasonal and bathymetric distribution
of catch

The depth distribution of O. virilis changed seasonally and was not the same for all size groups. From May through August 1963, catch was recorded daily on the basis of age group, sex, and depth of capture. Catch records were grouped into 20-day periods. The last period covered only 13 days but the data were extrapolated to 20 days. Population estimates by the DeLury method were not attempted because of large fluctuations in catch. Traps remained stationary during the period and an equal number (4) were set at the surface, 3 meter, 6 meter, 7.6 meter and 9.1 meter intervals. The circular contours of the lake allowed the traps to be set in a radial pattern forming concentric circles at the different depth contours like the spokes of a wheel.

Catch depended upon population density and the amount of movement during the trapping period. The total catch per 20-day period increased steadily from May to August (Fig. 5). The largest total catch per unit of effort came between July 31 and August 12, 1963. During this period 80%

of the catch consisted of males with almost equal numbers of yearlings and adults. The proportion of yearlings of both sexes in the catch increased as the season progressed. The catch per unit of effort of females reached a peak from June 11 to July 10. This peak followed the hatching of the young. After July 10, the catch of females declined. Hence the catch per unit of effort was greatest in early summer for females and in mid-summer for males.

In May and June most of the crayfish were found at depths of less than 3 m (Figs. 7, 8). At this time females with eggs on their pleopods and yearlings of both sexes occurred in shallowest water (0-1.5 m). Older males occurred between 1.5 and 3.0 m with no distinct concentration zone. Yearlings stayed in shallow water until the middle of July and then gradually moved deeper. Migration to deeper water started earliest for adult females; by August, 70% of the females were below the 6.1 m contour with a concentration at the 7.6 m depth. By contrast, 65% of the yearlings were between the 3.0 and 6.1 m contour and only 35% were below 6.1 m. Clearly a major shift in bathymetric distribution occurred in August.

There are a number of environmental factors that could bring about the summer shift in depth distribution of <u>Orconectes virilis.</u> This species is sensitive to light; Roberts (1944) concluded that within normal fluctuations of temperature, oxygen concentration, and pH, light is the one environmental factor capable of regulating movement. In the summer of 1963 the female population was concentrated in the middle of the thermocline at a depth of about 7.6 m. At this time the thermocline extended from 6 to 10.7 m and the temperature at 7.6 m was 18 C.

During the same period in 1962 an estimated 66% of the female crayfish were at the lower limit of the thermocline at a depth of 9.1 m and a temperature of 14 C. The thermocline in 1962 extended from 6.7 to 9.8 m. The concentration of crayfish therefore seems somewhat independent of water temperature. This is in agreement with the findings of Roberts who showed that locomotor intensity was independent of temperature between 0 and 26 C. In West Lost Lake migration to deeper water followed the molt to maturity in yearlings and the molt to sexual form of adult males. It may, therefore, have been associated with maturation of the gonads which in turn could be related to light penetration rather than water temperature. Stephens (1952) found that length of photoperiod was related to the reproductive cycle of *O. virilis*.

Of 1,479 crayfish collected by Aiken (1965) in Lake Winnepesaukee, New Hampshire, only 7 were females. In a statewide collection of this species he found a sex ratio of 389 males to 100 females. He did not give the dates the collections were made but stated that traps were only occasionally set beyond depths of 6 m. The preponderance of males noted by Aiken could have been due to the small amount of trapping effort allotted to deeper water. Differential seasonal migration such as noted in West Lost Lake may have affected the sex ratio of the New Hampshire collections. If so, it would appear that differential seasonal migration is a widespread rather than a local phenomenon for *O. virilis*.

POPULATION DYNAMICS

Changes in biomass

The tendency for the weight of a year class to be diminshed by natural mortality is counterbalanced by growth. Thus the biomass of a year class may increase, decrease, or remain constant during a period when the number of individuals is decreasing.

The rate of biomass change is given by the formula:

$$\underline{k} = \underline{g} - \underline{i}$$

where

$\underline{k}$ = the instantaneous rate of increase in biomass,

$\underline{g}$ = the instantaneous rate of growth, and

$\underline{i}$ = the instantaneous rate of mortality.

Methods used to determine $\underline{g}$ and $\underline{i}$ have been discussed above. Values of $\underline{g}$ and $\underline{i}$ used to calculate the seasonal change in biomass per kilogram of recruits are given in Table 6.

In general, mortality exceeded growth for males 3 years old and older during the spring, and was greater than growth for females 2 years old and older during the summer. Growth exceeded mortality in younger crayfish. A maximum biomass of males was present during the summer of the second growing season. This difference in time of maximum biomass for individuals of the same age arose from the high mortality rates of 2- and 3-year-old females. Mortality of 2-year-old females was about ten times as great as that of males; for 3-year-old females mortality was twice as great as that of males.

The total biomass of a typical year class (sexes combined) is greatest during the summer of the second growing season (1-year-old crayfish). From a weight at hatching of about 2 kilograms, a year class reaches a maximum of 55.4 kilograms by the end of the second summer (Table 7). Biomass is lower the following spring because of overwinter mortality. It reaches a second peak of 54.9 kg during the third summer. Thereafter the biomass of a year class declines. Thus during the third year of life biomass appears to nearly equal that of the second year but consists of a higher percentage of male crayfish.

The weight of the yearling crop in the spring of 1963 was estimated by taking the average of the age-0 group in 1962 and the age-I group in the summer of 1963. In the spring of 1963 about 80% of the biomass of the entire crayfish population consisted of yearlings (Table 8). By summer, although yearlings were still the largest age group present, they made up only a little over 50% of the biomass. This change was due in large part to mortality of females and to an increase in weight of the other age groups. During the winter of 1962-63 only yearlings increased in biomass. The biomass of 2-year-olds declined slightly but the weight of 3-year-olds fell sharply, from the 57.7 kg in late summer of 1962 to 4.2 kg in the spring of 1963 (Table 9).

The crop of age-0 crayfish in 1963 was about one-half as large as 1962 (9.5 kg/ha vs. 18.3 kg/ha) (Fig. 9). The biomass of yearlings in 1963 was 9.0 kg/ha greater than in 1962. This partly compensated for the smaller crop of age-0 crayfish. Despite the sharp decrease in biomass of 2- and 3-year-olds from spring to summer, the total crop changed very little during this period. Total weight changed from 100.27 kg/ha in the summer of 1962 to 119.49 kg/ha in the spring of 1963 and to 91.83 kg/ha during the summer of 1963. Hence although the total standing crop reaches a peak in the spring, seasonal fluctuations are small due to compensatory changes among age groups (Table 9).

Life table

In the summer of 1963 an estimated 12,900 young crayfish survived from the progeny produced by 2,353 adult females. Data on the number of adult females present at breeding in 1962 are not available, however, an estimate of this number can be calculated from the summer population in 1962 and the survival rates of adult females encountered during the same season in 1963. Use of the 1962 survival rate of adult females is permissible since considerable stability of adult survival rates is indicated by the small differences in number of crayfish from one year to the next among the older age groups. If the 1963 rate is used, an estimate of 1,953 adult females for the spring of 1962 is obtained. This is only slightly below the population of breeding females in 1963. From this female population, 23,971 progeny were estimated to be present in the summer of 1962. This is nearly twice the progeny that survived in 1963. The year 1963 was warmer and drier than 1962 and lake levels were lower. This eliminated much of the submerged vegetation on the shoals and may have reduced survival.

A life table based upon data from a single year must be viewed with caution. Calculation of the reproduction rate per generation (R_o)

based upon the 1963 information gave a value of 0.778 (Table 10). This indicates the population was declining. The low value may merely be a reflection of the small 1963 year class. Subsequent observation of the lake has not indicated a decreasing trend in the population.

Production

No estimates of crayfish production are available from the literature, but there are records of the standing crop present in a number of habitats. Most of the information is from ponds. Tack (1941) found crops of *Orconectes immunis*, a species well adapted to shallow ponds, ranging between 51.5 and 385.8 kg/ha. Highest crops were in ponds fertilized at 2-week intervals with hay and cottonseed meal. The lowest value was in a pond containing the freshwater shrimp *Palaemonetes exilipes*. Lydell (1938) reports crop estimates of *O. immunis* for a 1.66-hectare pond ranging between 772 and 909 kg/ha. Goellner (1943) gives values of 56 to 1,345 kg/ha for *O. immunis* in ponds. Wickliff (1940) estimated the standing crop of an unidentified species in a stream to be between 30.3 and 730.6 kg/ha.

West Lost Lake is a cool marl lake of relatively low productivity, however, its standing crop of crayfish per acre was greater than five of the ten productive ponds studied by Tack (op. cit.). In the spring of 1963, the crop in West Lost Lake was estimated to be 119.5 kg/ha. It fell to 91.8 kg/ha in the summer. The later value can be compared with a trout harvest of 26.6 kg/ha in 1962 and an estimate of 6.4 kg/ha for the standing crop of bottom invertebrates other than crayfish in 1948 (Tanner, 1952).

Net production of crayfish between the summer of 1962 and 1963 was 310.8 kg. This figure is the sum of the weights at the time of mortality of all animals dying during the year. The ratio of net production to the summer standing crop (turnover rate of biomass) was 2.33. This rate of turnover is nearly twice the value reported by Borutsky (1939) for all of the bottom invertebrates in Lake Beloie (1.25). Borutsky also gives turnover rates for other invertebrates: *Tanypus* sp. 0.75, *Corethra* sp. 2.5, and Oligochaeta 1.27. The net production of the midge *Tanytarsus jucundus* in a southern Michigan lake was 75.1 kg/ha (Anderson and Hooper, 1956), giving a turnover rate of 3.6. The estimated turnover rate for the entire bottom fauna of an Indiana lake was 3.5 (Gerking, 1962).

Using Tanner's estimate of 6.4 kg/ha for the summer crop of bottom invertebrates and 3.6 as a reasonable estimate of turnover rate, the net production of invertebrates other than crayfish is 34.8 kg. Thus the net production of crayfish (310.8 kg) appears to be nearly 10 times as great as that of all other bottom invertebrates.

Percentage daily numerical turnover rates of crayfish are low when compared with two other aquatic crustaceans. The value for *O. virilis* is 2.0 compared to 2.5 for *Hyallela azteca* (Cooper, 1964) and 25.0 for *Daphnia galeata mendotae* (Hall, 1962). Since both *Daphnia*, a cladoceran, and *Hyallela*, an amphipod, have a much shorter life span than *Orconectes*, such a difference is to be expected. The above rate of turnover for *Daphnia* is for the summer season only, and Hall concluded that predation was an important factor during this period. Converted to weight units, the difference between these three species would not be as great.

Predation severely affects the later life history stages of Daphnia and Hyallela but is significant only during the early life history stages of Orconectes. Higher rates of removal by predation may maintain higher turnover rates for the cladoceran and the amphipod.

Trophic relationships

The contents of 31 crayfish stomachs collected on September 10, 1962, and of 26 taken on May 20, 1963, were examined. Green algae from the marl incrustations on rocks and other substrates in the water were the principal food items. Included were animals of the "aufwuchs" associated with these incrustations and also the remains of higher aquatic plants. There appeared to be few if any qualitative differences between contents of stomachs collected in the spring and those collected in the fall.

The above observations suggest that the West Lost Lake crayfish are primarily herbivorous although they may at times be facultative scavengers. Higher aquatic plants are ordinarily scarce or absent in Michigan marl lakes, and there are few primary consumers other than crayfish within the bottom fauna. Most species of benthic invertebrates are either ooze browsers (midges) or predators. The ability of crayfish, to utilize marl producing algae and associated aufwuchs as food, places them near the base of the food pyramid and in a food niche of key importance in the trophic structure of marl lake ecosystems.

Effects of predation by brook trout

An analysis of the seasonal food habits of the brook trout in West Lost Lake indicated that only the larger fish preyed upon crayfish. The smallest trout containing a crayfish was 196 mm long and only 4 of 29 fish that contained crayfish were less than 229 mm long. Accordingly trout used in the calculation of monthly predation rates had a minimum length arbitrarily set at 229 mm.

Predation rates were assessed in the following manner: Estimates of the number of fish having a length greater than 229 mm were made in the autumns of 1962 and 1963 and in the spring of 1963 by the staff of the Pigeon River Trout Research Station. The Petersen mark-and-recapture method was employed. From these estimates the total instantaneous mortality rate (i) was obtained for the period from October 1962 to October 1963 using the method given by Ricker (1958). The instantaneous fishing mortality rate (p), which was known from creel census records, was subtracted from the total instantaneous mortality rate (i) to give the natural instantaneous mortality rate (q). The percentage of each year class present in the lake, 229 mm in length or longer, was determined by a graphical method given by Allen (1954). This method provides estimates of the proportion of a year class that is legal-sized for any given length and size limit. It was constructed by plotting the size-frequency distribution of fish of the same age on normal probability paper (Fig. 10). If the distribution is assumed to be a normal distribution such a plot is a straight line. For this nomagraph one also needs to know the relative deviation of the size distribution of fish of a given age. A relative deviation of 0.111 was used in calculating values in the nomagraph. This deviation was taken from a brook trout population study in Wisconsin (McFadden, 1961). Most natural salmonid populations have been shown to have a relative deviation around 0.10 when size-frequency plots are constructed (McFadden, personal communication). In the actual construction of this nomagraph one plots the mean of the size-frequency distribution on the 50% frequency ordinate of normal probability paper and the product of the mean and the relative deviation on the 15.9% frequency ordinate. These points are then connected with a straight line.

In using Figure 10 the mean length of the sample of the fish population is located on the right hand vertical scale. The corresponding diagonal line is followed to the left to the point of intersection with the horizontal line corresponding to a given size limit on the left hand vertical scale (in this case 229 mm). By following a vertical line downward from this point of intersection to the lower horizontal scale one obtains the percentage of the population which is of legal size. This method permitted calculation of the number of trout in the lake longer than 229 mm at any given time.

The number of crayfish eaten each day by trout of a given size was determined empirically from the examination of fish stomachs sampled throughout the year. From August, 1962 to September, 1963, 273 stomachs were examined. Since the population during this sampling period did not exceed 600 fish, this sample represents a major portion of the fish in the lake. Further details of this study and the methods used are available in an earlier paper (Momot, 1965).

Monthly estimates of the number of trout in the lake that were 229 mm long or longer were multiplied by the average number of crayfish eaten in one day by trout 229 mm or longer (Table 11) to give the total number of crayfish eaten each day by trout of the above size range. This figure was divided by a digestion factor calculated from data given by Hess and Rainwater (1939) and Phillips et al. (1960). This factor corrects for differences in digestion rates at various lake temperatures. From these data mortality due to trout predation and the contribution of a given year class of crayfish to the food of the trout were estimated for each month of the year (Table 11).

Only young-of-the-year crayfish were eaten by the brook trout. Trout were effective predators on the 1/2- to 1-year-old crayfish. Apparently crayfish more than a year old were larger than the size of food selected by the trout. The seasonal pattern of predation by the trout reflects this selection.

During the winter months the lack of emerging insects, which are of major importance in the trout's diet during early summer (Fig. 11), intensifies predation upon the crayfish. At this time the young-of-the-year crayfish were at the optimum size for trout. The average weight was 0.73 g. Consumption of crayfish declined abruptly in April; by June most of the yearlings were larger than 21 mm, which is the upper size limit of crayfish eaten by brook trout.

In June, young-of-the-present-year had not yet hatched and were unavailable to trout. From July to November, although many crayfish were eaten, the weight consumed did not equal that of the winter period. In July, an average of 60 crayfish averaging 11 mm in total length were eaten each day compared to 43 per day with an average total length of 43 mm in March. In terms of weight, the consumption dropped from a peak of 30 g per day in March to 0.4 g per day in April. From October through November there were no crayfish in the stomachs examined, but trout eggs appeared. Eggs may buffer predation during this period.

To summarize, periods of maximum utilization of crayfish by the brook trout were in midwinter and late summer. Periods of little or no consumption were early spring and late fall. Only the young were eaten.

The fraction of a year class of crayfish utilized as food by trout was obtained by dividing estimated number of young-of-the-year crayfish consumed during a given time interval by the difference between the number of crayfish present at the beginning and at the end of the interval. For example, there were an estimated 189,530 young-of-the-year crayfish produced in the spring of 1963. By the end of that summer, this number declined to an estimated 12,900 individuals (Table 3). This represents a total mortality from July to September of 176,630. Of this number 4,026 were estimated to have been eaten by the trout (Table 11). These calculations give a figure of 2.3% for the fraction of total mortality of young-of-the-year crayfish accounted for by trout predation between July and October. Similarly 56% of the total mortality of young-of-the-year crayfish between October and June was due to trout predation. Out of a total standing crop of 150.0 kg present in the summer of 1962, 18.3 kg were available as trout food. In the spring of 1963, 13.3 kg out of a total crop of 179.0 kg was available and in the summer of 1963, only 9.4 kg out of 137.6 was of proper size. Hence almost 50% more crayfish were available as trout food in the summer of 1962 than in the summer of 1963 (Fig. 9). In the summer of 1963 less than 0.9 kg of the 9.4 kg available was actually consumed by trout. Even though winter predation accounted for 56% of the total mortality from October to June, this amounted to only 16% of the total available population. The trout is therefore an inefficient predator and should be considered a minor factor in controlling population size of crayfish in this lake.

If trout were stocked at a size greater than the present 126 mm length, utilization of the crayfish would be increased since trout would reach a length at which they utilize crayfish (229 mm) earlier. Orconectes propinquus, a smaller species of crayfish (17 mm at maturity vs 25 mm for O. virilis) might be introduced and would provide food of the proper size for its entire life span. However, this species might be less resilient to predation than O. virilis because only one brood per generation is produced (Van Deventer, 1937).

Equilibrium yield

Predation by brook trout had an important influence upon the age distribution of the population. Since juveniles rather than adults were eaten by trout, the crayfish population responded by adjusting its survivorship distribution rather than through a change in fecundity. To study the resiliency of the crayfish population to trout predation, calculations of equilibrium yield were made for a series of theoretical predation rates. Ricker's formula for estimation of equilibrium yield at different rates of fishing (predation rates) was used (Ricker, 1958). This formula is applicable when growth and mortality rates are reasonably constant during a given time period. It was necessary to break the population down into time intervals meeting this requirement. Calculations of yields were made for only age-0 (young-of-the-year) females since this was the only age group eaten by trout and because only the number of surviving females has a significant influence upon population stability. Since mortality rates were higher during the second half of the first year, young-of-the-year females were divided into two age groups, viz. those less than 6 months old and those more than 6 months old. In these calculations various multiples of the empirically determined predation rate were added to the instantaneous mortality rates of each of these two groups (cf. Ricker, 1958, p. 211). This gave a series of weight change factors which could be used to calculate yields from each kilogram of recruits at age-II (Table 12).

These calculations indicate that a predation rate five times the present rate would result in the maximum equilibrium yield of female crayfish to the trout population. A fivefold increase in predation would nearly double the yield under the observed conditions. Only minor variations in yield occur between a density level of 200 and 600 fish. The yield per individual, if we assume it to be equally divided among all the 299 mm or larger fish present in the population, declines from 79 g per individual at present rates of predation to 55 g per individual at the 200 fish level. At a density of 50 fish, one half the present population, the yield per individual is 77 g. Under the observed predation pattern the yield per trout is about at the maximum level but total yield could be greatly increased by increasing the predator population.

The above estimates require the following assumptions: (1) growth of the crayfish and trout are not dependent upon their respective population densities; (2) crayfish reproduction rates are not substantially altered by changes in crayfish population density; (3) predation remains proportional to density of predators; and (4) changes in rate of predation do not influence mortality from other causes. Even though some of the above assumptions may not be strictly met, the probable error from them is small compared to the large differences between the present yield and equilibrium yield. These calculations therefore suggest that the population could withstand much more trout predation than it receives at present.

DISCUSSION

The principal objective of this study was to define the role of the crayfish in the trophic dynamics of a marl lake. The crayfish occupies a food niche of key importance in the trophic structure of marl lake ecosystems. They are primarily herbivores and thus they occupy a position close to the base of the food pyramid. Secondarily they act as scavengers. In marl lakes much of the primary production is in the form of marl incrustations. These lakes are lacking in aquatic macrophytes and phytoplankton production is below that of other types of lakes (Raymond, 1937). The lack of larger aquatics in turn limits the abundance of the insect fauna since many insects are dependent upon aquatic plants (Berg, 1949).

The importance of crayfish in marl lakes perhaps has been overlooked because they are seldom captured by dredge hauls. The estimated net production of 310.8 kg was nearly tenfold (34.8 kg) the estimated net production of benthic invertebrates taken by dredging (Tanner, 1952). It is hypothesized that this large production is due to the crayfish's ability to utilize marl producing algae and associated organisms as a food source and that this food source is not exploited to a great extent by other benthic invertebrates.

The importance of crayfish in the food pyramid makes it desirable to delimit some of the factors controlling population size and productivity. Since trout predation accounts for only a small fraction of the mortality of crayfish in these lakes, other possible sources should be considered. Possible predators, such as dragonfly nymphs, small frogs and water snakes do not eat large crayfish but may prey upon the young; however none of these forms were very abundant and probably would not limit the size of the crayfish population. The painted turtle, <u>Chrysemys picta marginata</u> is abundant but is not considered an important predator on crayfish (Lagler, 1944). Two adult crayfish were found in a collection of 33 large green frogs, <u>Rana clamitans</u>, from West Lost Lake. This is the only abundant large frog in the lake. Fish-eating birds (e.g., mergansers, herons, etc.) are never abundant during the summer and the narrow shoal area probably limits predation by mammals and birds during the open water season. Ice cover prevents predation by birds and mammals during the winter. In general, population size does not appear to be regulated by predators.

Observations made on West Lost Lake and in the laboratory indicate that molting has an important influence upon mortality rates. Sudden decreases in the abundance of certain age groups followed molting. Crayfish have a very soft exoskeleton for 24 to 36 hours after they molt and are susceptible to predation and cannibalism during this period. In aquaria larger, older crayfish displayed an aggressive behavior toward smaller weaker individuals. This often resulted in cannibalism. Crayfish with hard exoskeletons assumed a menacing position when approached, rearing up and raising their pincers. A change in behavior took place at the time of molting. When approached, newly molted animals, even those which had previously been very aggressive, became very excited and thrashed about the aquarium in an attempt to escape and seek shelter. The aggressive behavior pattern returned when their exoskeletons hardened.

The greater survivorship of older males compared to females in West Lost Lake may have been the result of cannibalism. Since most males completed their molt before the female molt began, an opportunity for cannibalism exists. Although males may very likely eat females that are molting, there is little likelihood that females prey on males because females have started their migration to deep water by the time the male molt is underway. Earlier in the spring when males are undergoing their first molt of the year, females are carrying their young, are very secretive and avoid contact with other crayfish.

The occurrence of natural mortality in the field following molting is widespread in the literature (Tack, 1941; Van Deventer, 1937). Physiological and mechanical problems associated with molting may be important mortality factors. Crayfish die if they are unable to completely withdraw from the old exoskeleton. Crayfish, which had only partially extricated themselves from their old exoskeletons were found dead in aquaria and in the lake. Unmutilated molted individuals were found dead in both the lake and in aquaria. The overall physiological condition at the time of the molt may also be very important in survival. Recently molted females that had been carrying young seemed especially sluggish when handled, compared to recently molted males.

Thus predation does not appear to be as important in regulating population size as behavior at the time of molting together with certain physiological and mechanical problems associated with molting.

The crayfish biomass in West Lost Lake was probably near the carrying capacity of the environment. This was indicated by the small change in biomass between 1962 and 1963. Much of the energy flowing into the crayfish population is returned to the lake by decomposition or is used by the population itself (cannibalism) and is not being passed on to a higher trophic level (trout).

Studies of the population dynamics of major food organisms of game and food fishes offer many possibilities for improving the yield and production of fish populations. Most of the present attempts to manage the production of aquatic communities such as fish ponds and channel the results for human benefit are based on empirical methods (Swingle and Smith, 1941). Such efforts even when beneficial can rarely be explained or understood. A knowledge of the effects of predation upon the vital characteristics of the prey populations offers an analytical approach to the task of harnessing productivity for man's benefit. This type of information can be used to increase the efficiency of predator-prey relationships in aquatic ecosystems.

In terms of reproductive capacity of the crayfish population the effect of a trout eating six young-of-the-year is equivalent to its eating one adult female.[1] In terms of energy flow to the trout the results are not equivalent. One adult female weighs 9.3 g but the six young weigh only 4.2 g. This difference of 5.1 g could be utilized if a species of fish were introduced that preyed on adults. Also trout probably expend more energy in searching for six young than one adult female, hence cropping young is less efficient.

Since there is a surplus of old males and since 3-year-old females contribute only 7.5% of the total egg production in one season, increased predation on adults would probably increase average egg production. Among older age groups males weigh more than females hence greater yield is achieved by predation on males.

Studies of the comparative population dynamics of closely related species of benthic invertebrates can be used to disclose those species of benthic invertebrates having population characteristics which make them valuable as food organisms for fish. The substitution of <u>Orconectes propinquus</u> for <u>O. virilis</u>, as proposed in this study, is a good example. Other possibilities exist not only for crayfish but other aquatic invertebrates.

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[1] 94 young/avg. female x 0.93 (the mortality rate of young from hatching until late summer when they become vulnerable to the trout) = 6 survivors x 0.7 g (the weight of the young by the end of the summer) = 4.2 g (the weight of young produced by one adult female).

SUMMARY

The population dynamics of the crayfish, Orconectes virilis, was studied to define the role of the crayfish as a consumer in a marl lake ecosystem. Insight was gained into the factors controlling its production and an assessment was made of the relative importance of trout predation upon this population.

Estimates of population density revealed year-class fluctuation to be a feature of the age structure of the crayfish population.

There was a difference between sexes in growth rates with males of a given age reaching a larger size than females. After age-I, mortality rates for females were greater than for males.

After a molt in July maturity was attained by both sexes; at age-I mating followed and eggs were laid the following spring. Reproductive capacity, based on counts of eggs attached externally to females, was 58% of the capacity as determined by ovarian egg counts of mature females. Two-year-old females produced most of the eggs (92.5%). The maximum life span for both sexes was three years. The reproductive rate was low (0.78 per generation) due to poor survival of the 1963 year class.

After the newly hatched young left the females, they remained in shallow water. The adult females then molted and migrated to a depth of 7.6 m where most of them remained all summer. A migration of males to deep water followed that of the females.

Trout fed only on crayfish until the crayfish were about one year old. The only trout that fed extensively on crayfish were those over 229 m in

length. Predation by trout accounted for the removal of less than 3% of the population of age-0.0 to 0.5 crayfish during the period from June to January, and 16% of the population of age-0.5 to 1.0 crayfish from January to May. Crayfish appeared in large numbers in the trout diet in midwinter and in late summer. Age-0 crayfish were much larger in midwinter than in summer and made a greater percentage of the fish diet in midwinter than in summer.

By substituting the trout predation rate for fishing mortality in Ricker's equilibrium yield equation, it was found that a maximum yield of crayfish would be attained at five times the current rate of trout predation. It was hypothesized that the yield of crayfish to the trout might be increased by the introduction of another crayfish, O. propinquus, which is smaller in size but has the same reproductive potential as O. virilis.

O. virilis is primary consumer in marl lakes. Though it can be an adventitious scavenger on animal materials, O. virilis is essentially a herbivore in marl lakes, feeding chiefly on the algae and the "aufwuchs" associated with marl incrustations.

The peak standing crop of crayfish (119.49 kg/ha) occurred in the spring of 1963. There was a slight difference in biomass between the summers of 1962 and 1963. The annual net production of crayfish was 205.3 kg/ha. This was 8.9 times greater than an estimate of the production of all other bottom invertebrates in West Lost Lake (23.0 kg/ha). The total net production for the entire lake between the summers of 1962 and 1963 was estimated to be 310.8 kg. This is about 2.33 times the average standing crop during the summer of 1963. Comparing numerical turnover rates per day, crayfish had a lower rate (2.0) than an amphipod, *Hyallela* (2.5) and a cladoceran, *Daphnia* (25.0).

Population size is probably regulated by cannibalism at molting and by physiological and mechanical problems associated with molting. Natural mortality of adults following molting was frequently observed. Predation was not an important population control mechanism.

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Table 1. --Summary of experiments to validate methods for estimating population size in crayfish.

A. Comparison of Schumacher and Schnabel estimates of a pond population of 284 crayfish.

Collection number	Date 1962	Recapture rate	Schumacher estimate	95% confidence limits	Schnabel estimate	95% confidence limits
1	7/11	.18	185	-	167	-
2	7/12	.25	293	-	274	-
3	7/13	.33	330	-	300	-
4	7/14	.59	221	203-240	201	158-736

B. Comparison of estimates of a pond population of unknown size using two collecting techniques. A total of 586 crayfish were marked over a period of 20 days.

Method	Collecting methods					
	Seine			Traps		
	Estimated number	99% confidence limits	Recapture rate	Estimated number	99% confidence limits	Recapture rate
Schnabel	860	667-1210	.637	721	631-1683	.667
Schumacher	881	851- 913	.637	842	751- 958	.667

Table 2. --Summary of population estimates of crayfish in West Lost Lake 1962-1963.

Age group	Sex	Dates of estimates	Number marked	Recapture rate	Estimated population	95% confidence limits
0	Males	8/14-8/27/63	1,432	0.294	5,772	4,819- 7,220
0	Females	8/14-8/27/63	1,539	0.221	7,128	5,900- 9,050
0	Males	8/31-9/11/62	1,560	0.049	11,808	8,473-19,470
0	Females	8/31-9/11/62	1,786	0.101	13,163	10,005-19,124
I	Males	6/20-7/25/63	2,031	0.325	5,933	5,595- 6,357
I	Males	8/2 -9/10/62	2,508	0.695	4,073	3,768- 4,436
I	Females	7/1 -8/5/63	1,194	0.178	4,940	4,653- 5,288
II	Males	5/19-6/1/63	725	0.186	2,804	1,988- 4,784
II	Males	7/18-8/6/63	1,412	0.440	2,678	2,386- 3,058
II, III	Males	8/2 -9/10/62	2,743	0.793	3,379	3,359- 3,400
III	Males	5/19-6/1/63	714	0.383	1,726	1,565- 1,926
III	Males	7/17-8/6/63	199	0.500	362	254- 769
I, II, III	Females	8/9 -9/10/62	1,332	0.296	4,854	4,780- 4,931
II, III	Females	6/19-7/7/63	956	0.555	2,352	2,208- 2,518
II, III	Females	7/24-8/12/63	299	0.181	1,197	1,124- 1,207

Table 3. --Seasonal change in the population of two sexes of crayfish of West Lost Lake.

Age group	Sex	Summer 1962	Spring 1963	Summer 1963
0	Male	11,808	94,765	5,772
	Female	12,163	94,765	7,128
I	Male	4,073	8,870*	5,933
	Female	3,753	9,051*	4,940
II	Male	3,321	2,804	2,678
	Female	853	2,121	1,073
III	Male	458	1,726	362
	Female	248	132	124
Totals	Male	19,660	108,165	14,745
	Female	18,017	105,839	13,265
Grand Total		37,677	214,004	28,010

* Calculated from the average of 1962 age 0 and 1963 age I.

Table 4.--Total rate of mortality (_a_) of _Orconectes virilis_ in West Lost Lake.

Age group	Time interval	Rate of mortality	
		Males	Females
0	Spring 1963 to Summer 1963	.9392	.9250
0-I	Summer 1962 to Summer 1963	.4984	.6309
I-II	Summer 1962 to Spring 1963	.3093	.3874
II	Spring 1963 to Summer 1963	.0488	.4934
II-III	Summer 1962 to Spring 1963	.4780	.8443
III	Spring 1963 to Summer 1963	.3995	.0582

Table 5.--Instantaneous rates of growth (g), mortality (i) and increase in biomass (k) for various age groups of crayfish.

Season	Age group	g		i		k	
		Males	Females	Males	Females	Males	Females
Summer	0	4.7185	4.7185	2.7985	2.5881	1.9197	2.1304
Summer	I	2.20387	2.03732	0.6880	0.9754	1.5158	1.0619
Spring	II	0.26236	0.30748	0.3739	0.4869	-0.1116	-0.1795
Summer	II	0.46373	0.19062	0.0465	0.6836	0.4172	-0.4930
Spring	III	0.01980	0.29267	0.6574	1.8658	-0.6376	-0.5731
Summer	III	0.35767	0.18232	0.5130	0.0626	-0.1554	0.1197

Table 6. --Carapace length of crayfish from West Lost Lake. Age groups determined from a length-frequency analysis (see text).

Year	Age group	Date collected	Number examined	Mean length	± SE
			MALES		
1962	0	9/1-9/9	44	15.25	± .16
	I	8/1-9/9	1,641	30.94	± .06
	II	8/1-9/9	1,872	36.78	± .06
	III	8/1-9/9	566	40.96	± .05
1963	0	8/28	87	14.60	± .31
	I	8/1-8/14	321	28.69	± .19
	II	7/19-8/6	1,118	36.23	± .01
	III	7/10-8/6	84	40.80	± .08
			FEMALES		
1962	0	9/1-9/9	29	14.17	± .82
	I	8/1-9/9	284	28.04	± .08
	II	8/1-9/9	551	31.54	± .09
	III	8/1-9/9	29	36.96	± .33
	0	8/28	74	13.78	± .31
	I	8/1-8/14	267	26.76	± .18
	II	7/25-8/12	289	31.41	± .07
	III	7/25-8/12	9	36.44	± .49

Table 7. --Theoretical seasonal changes in biomass of one kilogram of crayfish recruits from age-0 to age-III. Rates of growth and mortality based on data from Table 5.

Season	Age	Males	Females	Total
Spring	0	1.000	1.000	2.000
Summer	0	6.821	8.415	15.236
Summer	I	31.186	24.289	55.475
Spring	II	27.936	20.288	48.224
Summer	II	42.518	12.428	54.946
Spring	III	22.419	7.028	29.447
Summer	III	3.535	7.824	11.459

Table 8.--Percentage of the estimated standing crop represented by various age groups in 1962 and 1963.

Age group	Summer 1962		Spring 1963		Summer 1963	
	Males	Females	Males	Females	Males	Females
0	60.0	72.6	87.6	89.3	39.1	53.7
I	20.7	20.8	8.2	8.5	40.2	37.6
II	16.8	4.7	2.6	2.0	18.1	8.1
III	2.5	1.9	1.6	0.2	2.6	0.6

Table 9. --Successive estimates of the standing crop of crayfish.

Age group	Sex	Summer 1962	Total males and females	Spring 1963	Total males and females	Summer 1963	Total males and females
0	Males	8.66		6.197		4.23	
0	Females	9.66	18.32	6.197	13.39	5.23	9.46
I	Males	36.16		68.53		41.87	
I	Females	24.46	60.62	50.96	119.49	27.81	69.68
II	Males	49.68		25.70		39.01	
II	Females	8.04	57.72	16.28	41.98	9.98	48.99
III	Males	9.80		2.55		7.65	
III	Females	3.78	13.58	1.64	4.19	1.83	9.48
Total		150.24 kg (100.27 kg/ha)		179.05 kg (119.49 kg/ha)		137.61 kg (91.83 kg/ha)	

Table 10.--Life table of *Orconectes virilis* in West Lost Lake.

Time interval in years (x)	Fraction surviving during interval (l_x)	Number of females produced by a female during that interval (m_x)	$l_x m_x$
0	1.000	0.00	0.0
0.5	.075	0.00	0.0
1.5	.028	0.00	0.0
2.0	.017	41.35	0.7029
2.5	.0088	0.00	0.0
3.0	.0014	53.50	0.0749
3.5	.0013		0.0
			0.778 [1]

[1] Reproductive rate per generation, $R_O = \Sigma l_x m_x = 0.778$.

Table 11. --Estimates of the number of crayfish consumed each month by trout larger than 229 mm.

Month	Number of trout larger than 229 mm	Average numbers of crayfish consumed per day	Digestion rate factor*	Number of days	Total crayfish consumed
August	122	46.0	1	31	1,426
September	108	51.7	1	30	1,551
October	108	0.0	2	30	0
Nov-Dec	129	28.4	2	61	866
Jan-Feb	94	81.7	3	59	1,204
March	86	172.0	3	31	1,333
April	64	37.1	2	30	555
May-June	79	0.0	2	30	0
July	110	60.5	1	31	1,875
August	116	20.9	1	31	648
September	109	50.1	1	30	1,503
Oct-Nov	104	0.0	2	31	0

*Estimated number of days required to digest one crayfish at the temperature of the environment during the month indicated. This factor obtained from the percentage of a natural food items remaining in the stomachs of trout held at various temperatures as determined by Hess and Rainwater (1939) and from the rate of passage of food through the trout intestine as observed by Phillips, et al. (1960).

Table 12. --Equilibrium yield of female crayfish at varying rates of predation by brook trout 229 mm or more in length.

Rate of predation (p)*	Yield of females in kilograms per kilogram female recruits at age-II	Density of predator population	Yield in grams per individual predator
0.5p	3.86	50	77
p	7.94	100	79
2p	10.95	200	55
3p	11.92	300	40
4p	12.27	400	31
5p	14.32	500	29
6p	12.85	600	21
7p	11.52	700	16
8p	9.65	800	12
10p	5.16	1000	5

* p is the instantaneous rate of mortality due to predation of brook trout. A value of p of 0.059 was used for the 0 to 0.5 age group and value of 0.469 was used for the 0.5 to 1.0 age group. The instantaneous mortality rate (p) was calculated from the data of Table 5.

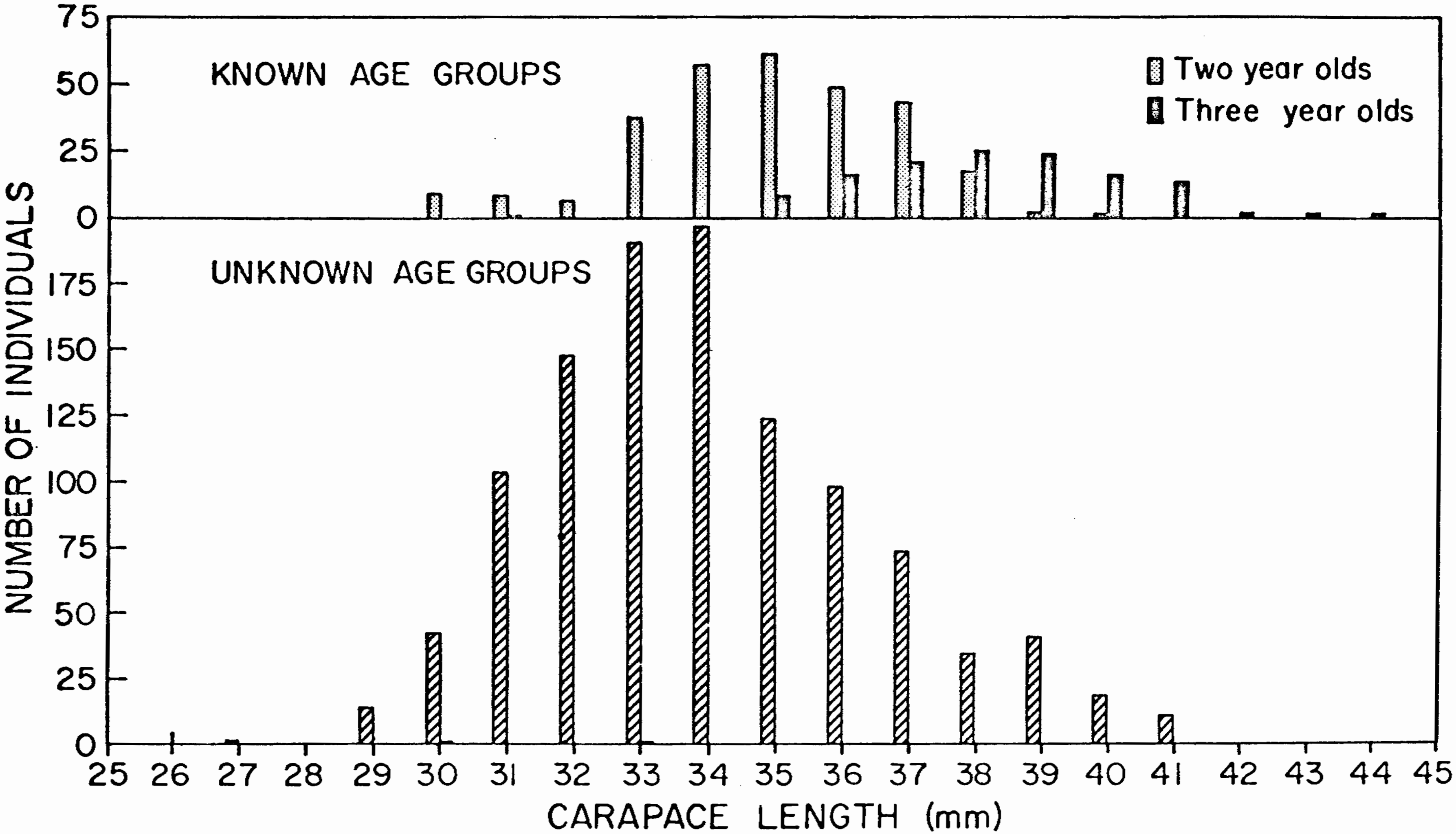

Figure 1. --Size-frequency distribution of the adult male Orconectes virilis in West Lost Lake after the spring molt, June 1-30.

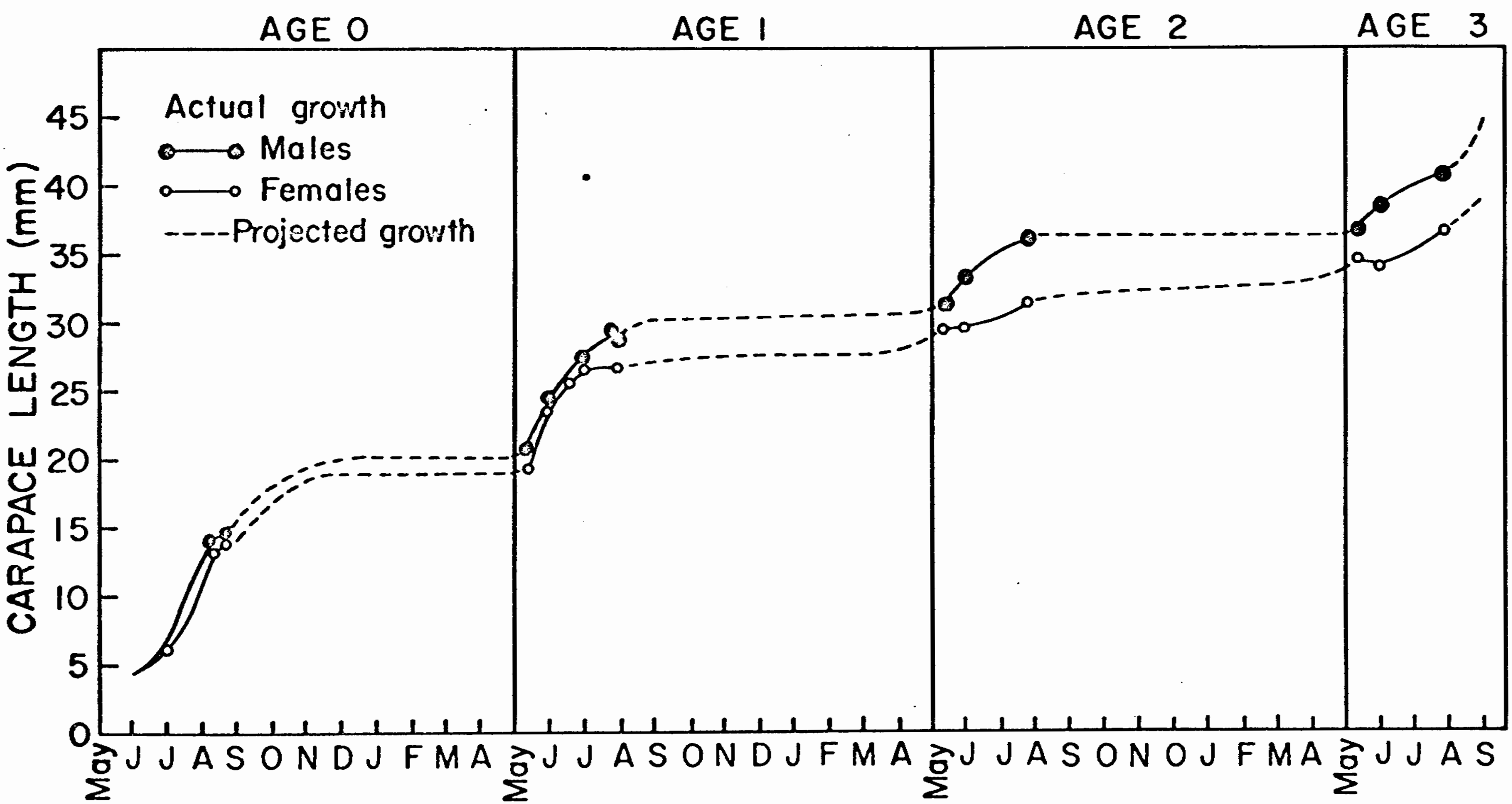

Figure 2. --Growth of Orconectes virilis in West Lost Lake. Symbols indicate average size of individuals captured in 1962.

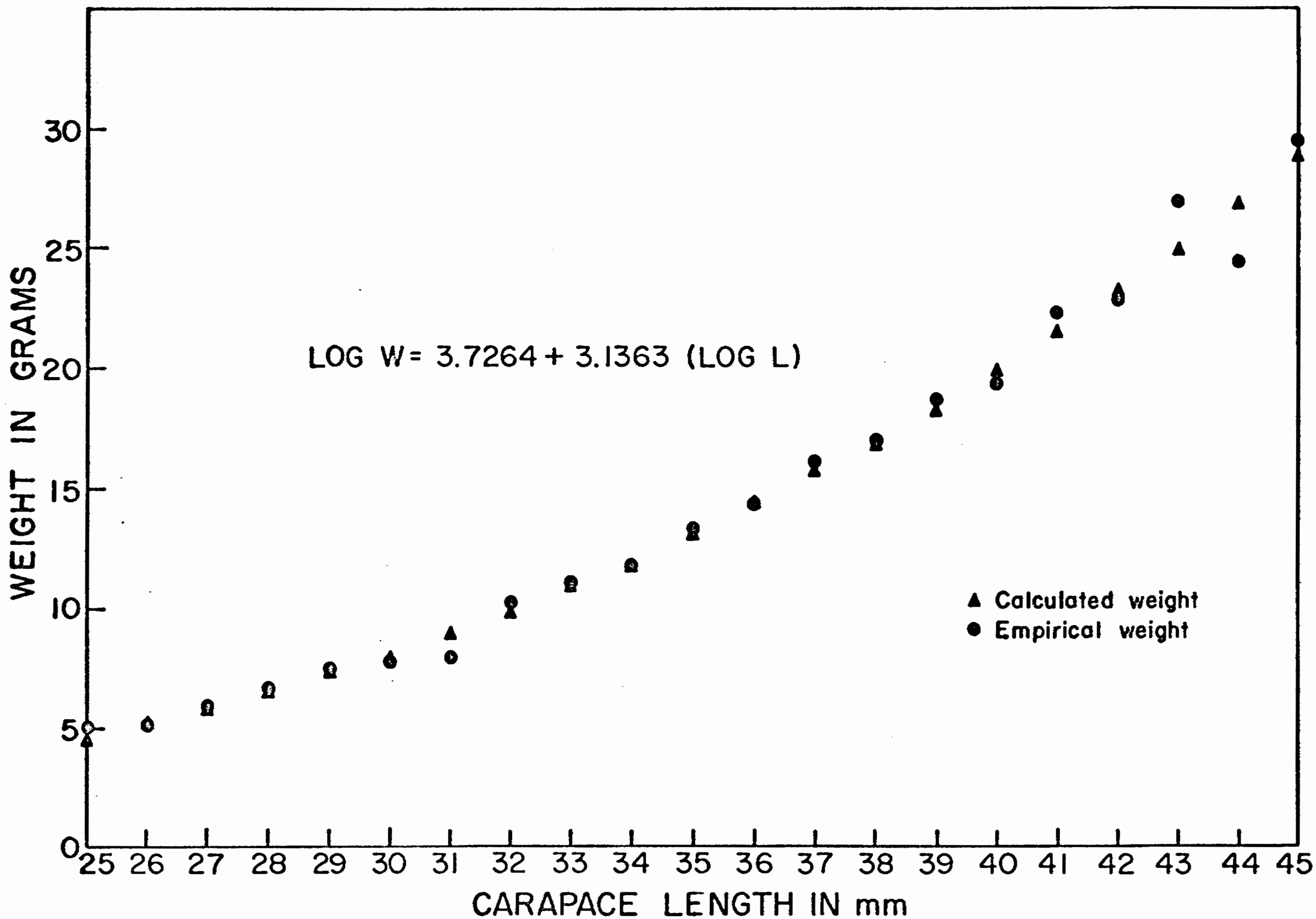

Figure 3. --Length-weight relationship for adult Orconectes virilis captured in West Lost Lake in August 1962.

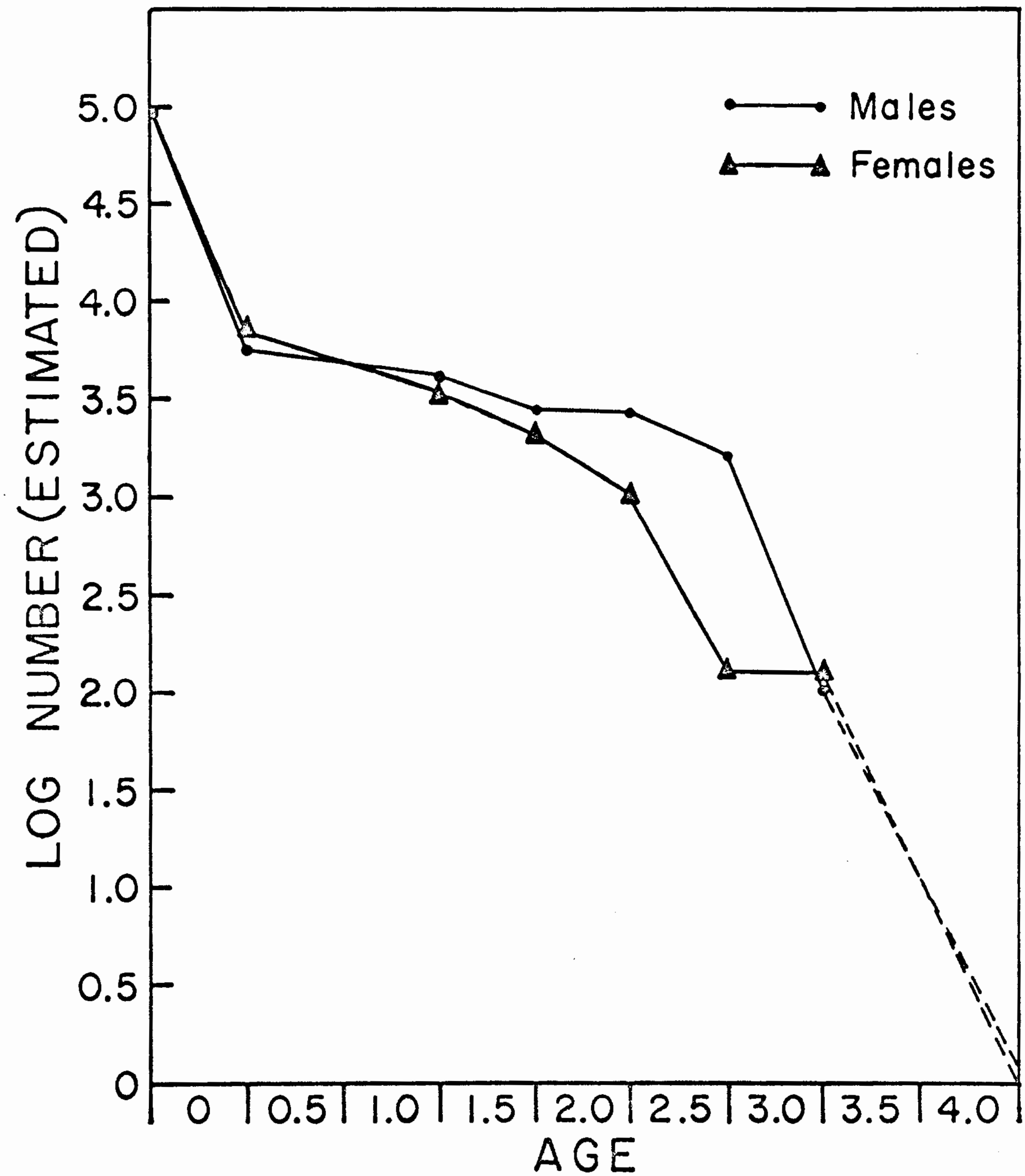

Figure 4. --Survivorships of Orconectes virilis in West Lost Lake.

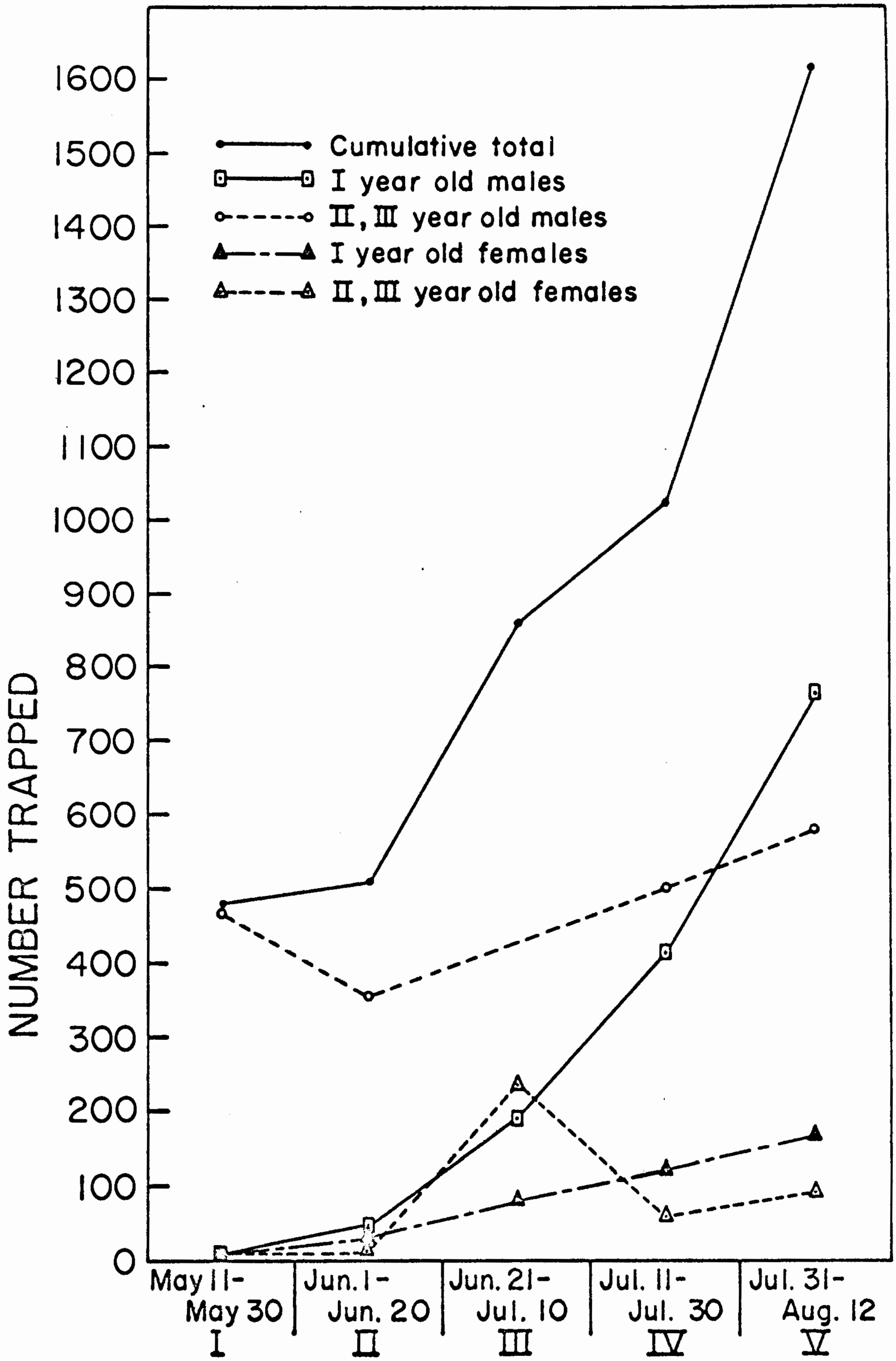

Figure 5. --Catch per unit effort and cumulative catch of crayfish in 1963. Catch per unit effort is given for 20-day periods, cumulative catch is the total number trapped.

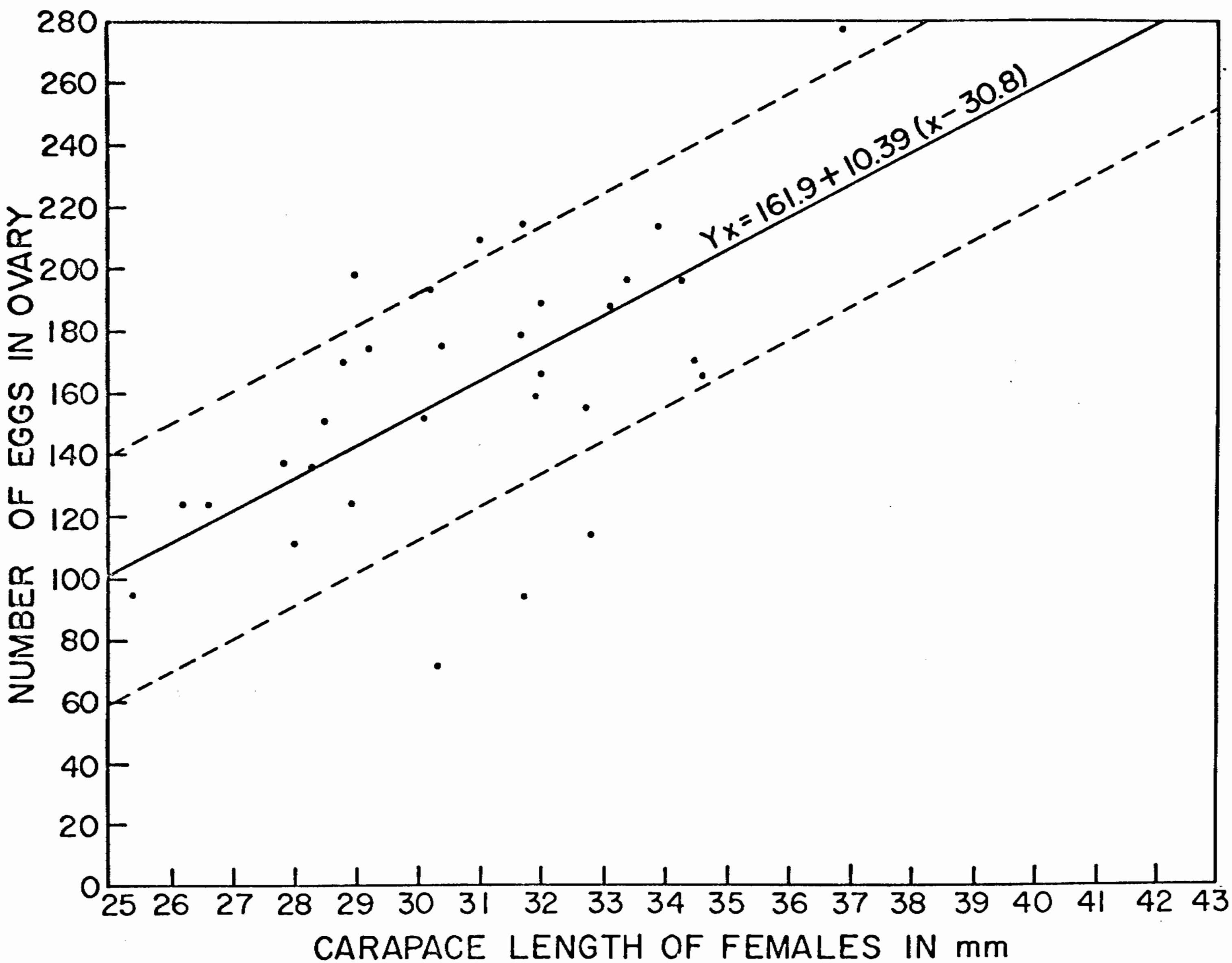

Figure 6.--Relationship of carapace length to ovarian egg count of <u>Orconectes virilis.</u> Dotted lines delimit 2 standard errors of estimate for the dependent variable.

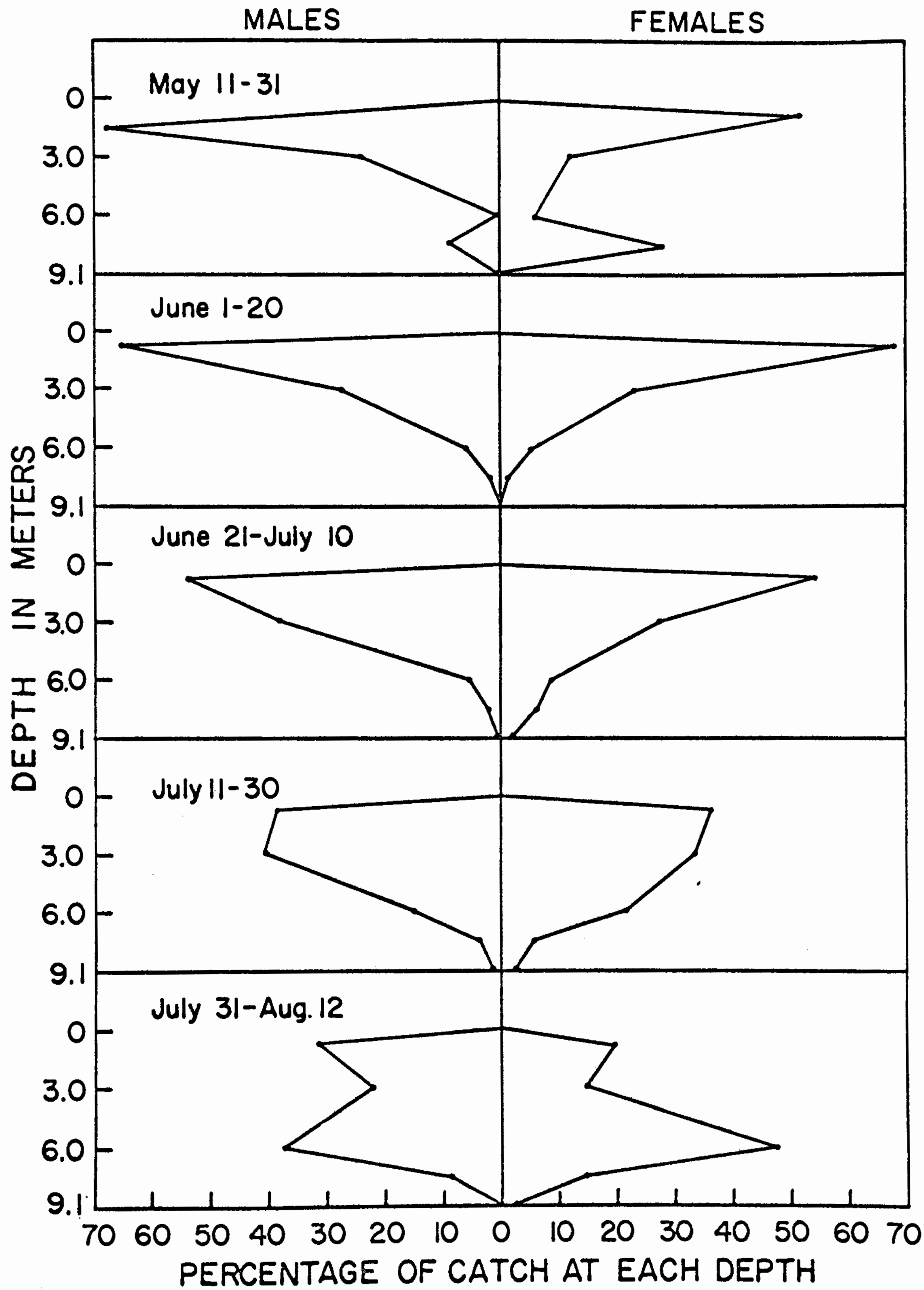

Figure 7.--Bathymetric distribution of yearling crayfish in West Lost Lake, 1963.

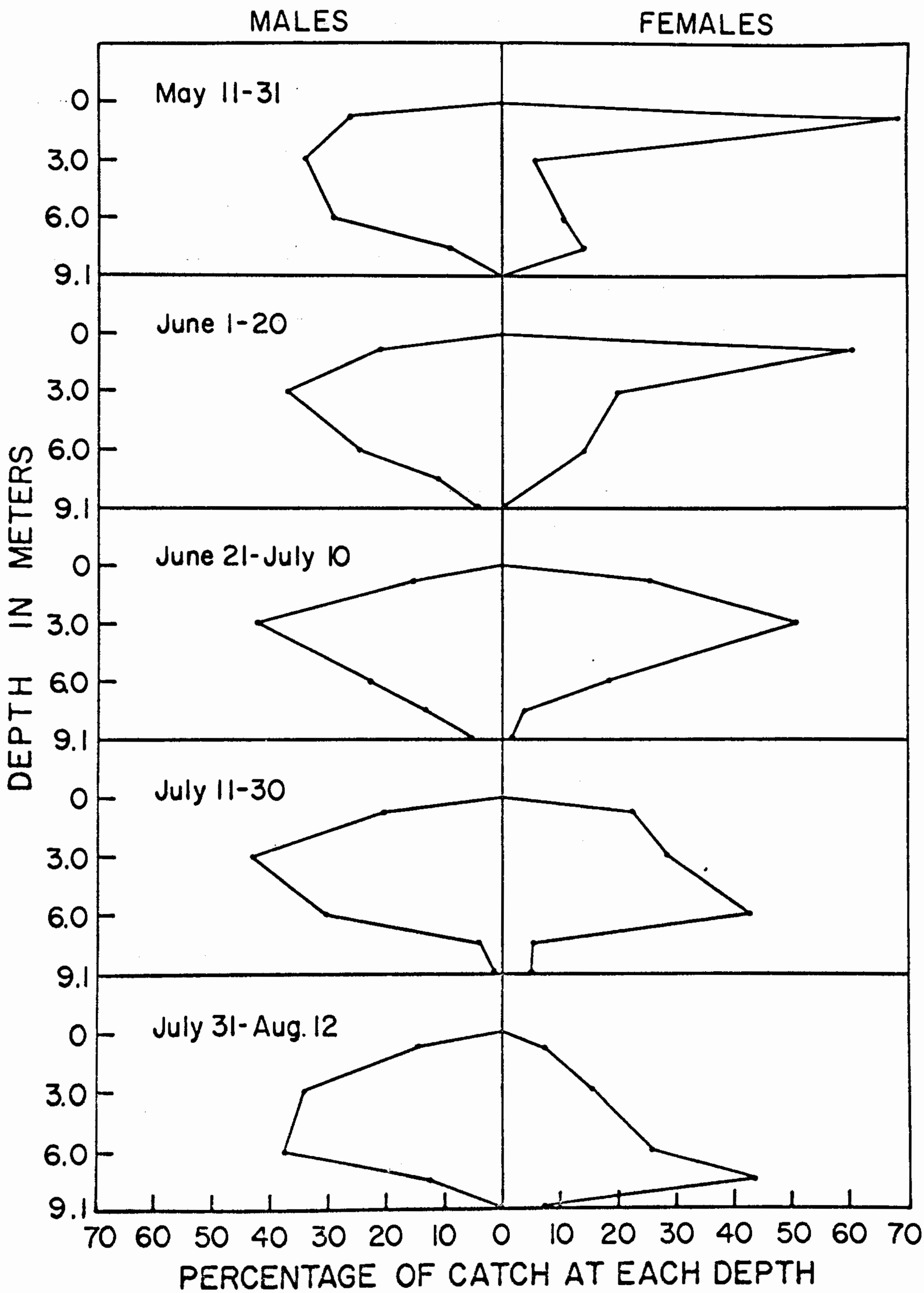

Figure 8.--Bathymetric distribution of 2- and 3-year-old crayfish in West Lost Lake, 1963.

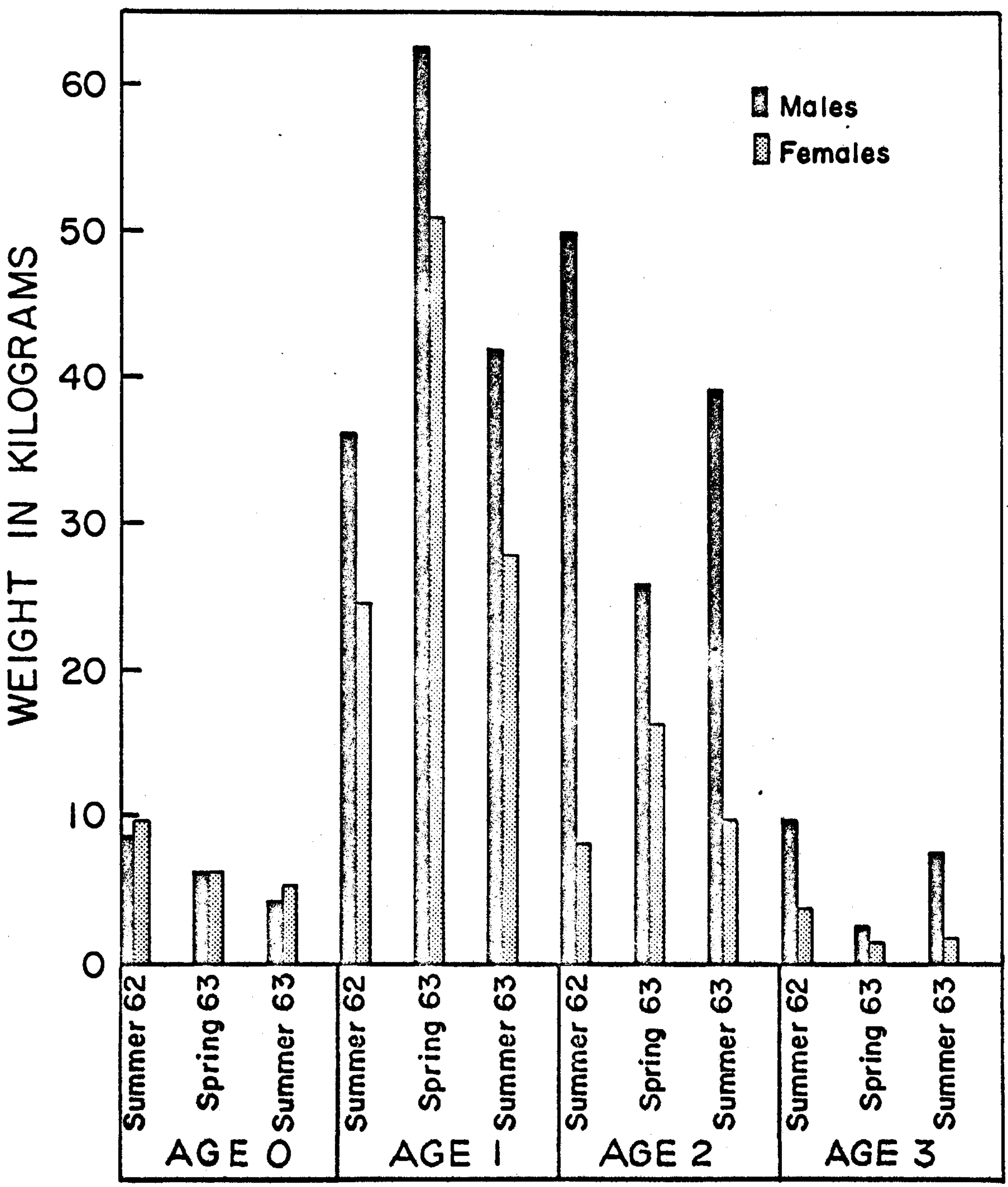

Figure 9.--Weight of crayfish of various age groups in 1962 and 1963.

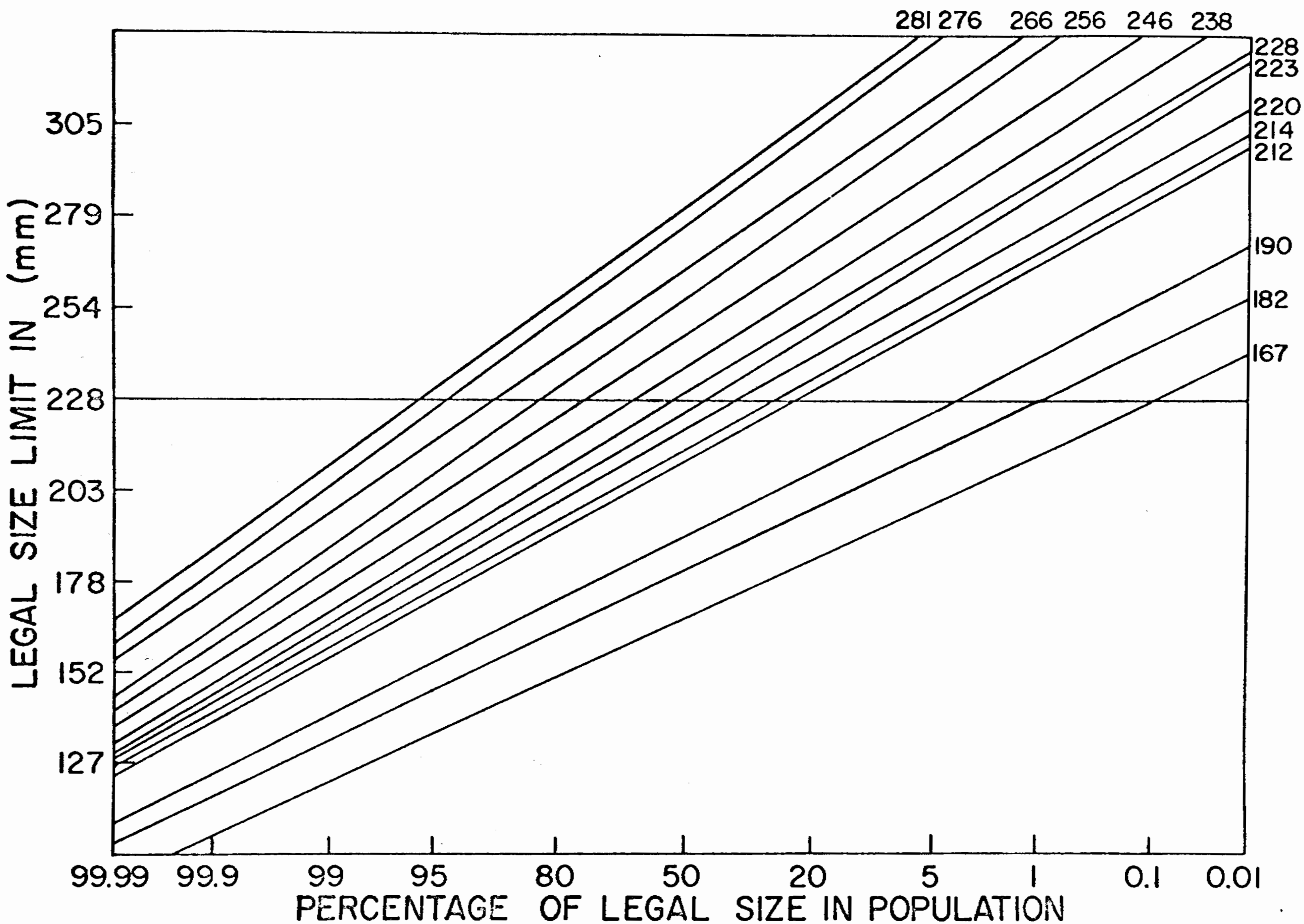

Figure 10. --Relationship of mean length of a year class to the percentage of fish over 9 inches in length. Based on a relative deviation of 0.111. Right hand vertical scale gives the mean length of the fish population sample.

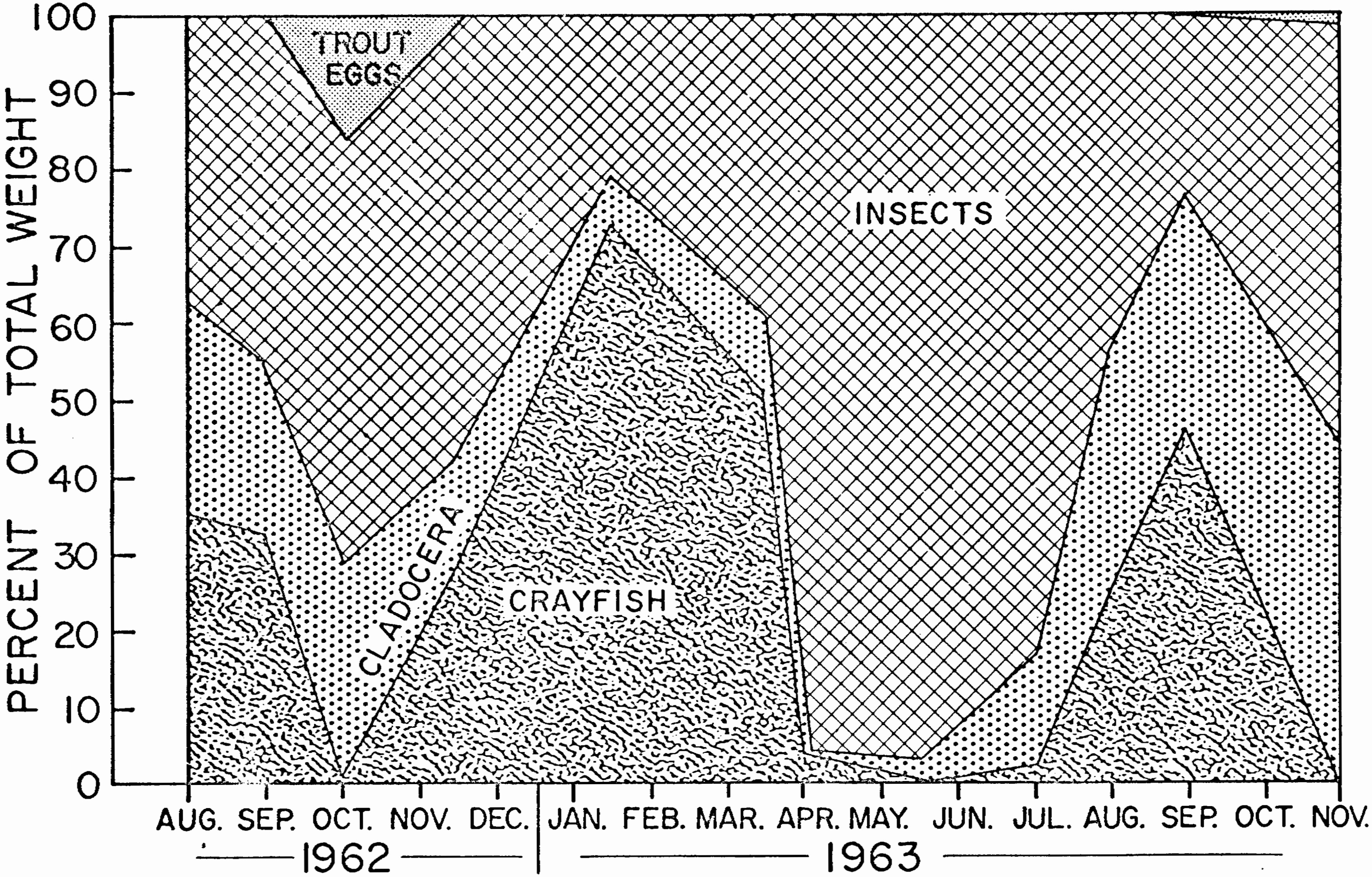

Figure 11. --Percentage of various food items (by weight) making up the stomach contents of brook trout 5 to 14 inches long. Data summarized at monthly intervals 1962-1963. A total of 239 stomachs were examined.