POPULATION DYNAMICS OF THE CRAYFISH, *ORCONECTES VIRILIS*

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1964

I. F. R. Report No. 1687

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

by

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A dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor of
Philosophy in the University of Michigan
1964

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ACKNOWLEDGMENTS

I am grateful to many persons and agencies for help in this study. Included among them are: Professors Karl F. Lagler, John E. Bardach, and Francis C. Evans of the University; Drs. Gerald P. Cooper, Frank F. Hooper, James T. McFadden, and W. Carl Latta and Messrs. Paul M. Earl, Robert C. Barber and Harry Westers all of the Institute for Fisheries Research, Michigan Department of Conservation.

Financial support for the study was provided by the Institute for Fisheries Research and particularly extensive use was made of the facilities of its Pigeon River Trout Experiment Station.

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I. INTRODUCTION

A quantitative study of the production of a macroscopic benthic invertebrate that serves as a major food item for game and/or predaceous fishes contributes to the knowledge necessary for answering basic questions on fish production and yield to fishermen. The present study is also important in adding new information on food-chain relationships in marl lakes. The invertebrate studied is one of the common crayfishes of Michigan, Orconectes virilis (Hagen).

This report deals with the mortality, seasonal production, and rate of population turnover of this species.

Heretofore some studies of crayfish life history and estimates of standing crops have been made in shallow ponds, often artificially enriched by man (e.g., Tack, 1941, Goellner, 1943). However, few published data are available on the quantitative aspects of crayfish productivity and resilience to predation in natural lentic environments. This study aims at presenting an accurate description of the various characteristics of a crayfish population in a natural lake in northern Michigan and prey-predator relationships between crayfish and the brook trout, Salvelinus fontinalis.

II. SUMMARY OF THE LIFE HISTORY OF O. virilis

Orconectes virilis was placed in the genus Faxonius by Creaser (1933) and earlier by many others in the genus Cambarus. It is an abundant species in the streams and lakes of Michigan and is often found in association with O. propinquus. These two species are most populous in well-oxygenated, clear, cool water streams with rocky substrates but may also be quite abundant in clean lakes and ponds. Two other crayfishes encountered in lakes in Michigan are *O. immunis*, inhabiting stagnant ponds with soft mud bottoms, and *Cambarus diogenes*, dwelling in lakes during the breeding season but usually occurring in burrows, sometimes at a considerable distance from the open water.

Only *O. propinquus* and *O. virilis*, are important faunal components of the great majority of fish producing habitats since they do not burrow or leave the open water. The life histories of these two species have many similar features (Table 1).

Despite the several casual references in the literature, no detailed account of the life history of *O. virilis* has been published. The account by Steele (1902) is said to be that of *O. nais* and not *O. virilis* (Creaser 1933). The life cycle of *O. virilis* in northern Michigan may be summarized as follows:

Breeding takes place from July to October but the fertilized eggs are not laid until the next spring from late April to early May. Eggs are carried by the female on her pleopods for six to eight weeks before hatching. The young hatch in June and have a carapace length of from 4.5 to 5.1 mm. They leave the pleopods of the female after about a week at a length of approximately 6 mm. They undergo several molts during the summer and by the end of October they are mostly between 15 and 20 mm. in carapace length. Sexual maturity is attained in the month of July of the second grow-

TABLE 1

Comparative summary of selected features of the life history of two species of crayfish of the genus *Orconectes* (= *Faxonius*)

Feature	*propinquus*	*virilis*
1. Eggs laid	October to November	April to May
2. Number of young per female	5 to 250	1 to 220, averaging 83 at age 2, 107 at age 3
3. Hatching date	April to May	June
4. Broods per lifetime per female	Usually one, certain individuals may have two	Usually one, about 15 per cent of these survive to produce a second brood
5. Life span	Maximum is two years, two seasons of growth for maturity	Maximum is three years, two seasons of growth are needed for maturity.
6. Growth rate per year in mm. (carapace length)	0 1 Max.(Mich.) 9-24 20-30 35	0 1 2 3 Max. ♂ 15-20 28 35 38 45 ♀ 15-19 26 32 35 38
7. Size at maturity	17 mm.	25 mm.
8. Active period	Daytime	Nighttime
9. Adult molts	Two for males, one for females	Two for males, one for females
10. Mating period	July to October	July to October
11. Principal food	Aquatic vegetation	Aquatic vegetation, algae, marl (value as food uncertain)
12. Largest individuals	Females	Males

Authority Creaser, 1933 - 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12 Momot - 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12

Creaser, 1931 - 1

ing season, at which time females are about 26 mm. and males about 29 mm. Adult males molt twice in their second growing season, once in early June and once again a month later in July when the males' copulatory appendages acquire reproductive form. Breeding follows this molt which coincides with the molt to sexual maturity of yearlings. Adult females as either two or three-year-olds undergo a single molt about two weeks after the young are shed, sometime in early July. Most two-year-old females produce a single brood of young. After this event about 85 per cent die; the survivors produce a second brood the next spring when they are three years old. Mortality is greater in two-year-old adult females than in males of the same age and maturity so that the majority of the three-year-olds are males. There is a difference in growth rate between the sexes; males reach a maximum size of 45 mm. and females 38 mm. The life span is about three years.

III. AREA OF STUDY

The field work was conducted during the summers of 1962 and 1963 at West Lost Lake, Otsego County, Michigan. This lake is part of an experimental area designated as the Pigeon River Trout Research Area which is under the administration of the Institute for Fisheries Research of the Michigan Department of Conservation.

West Lost Lake has a surface area of 3.7 acres, a maximum depth of 44 ft., and an average depth of 28 ft. The water is hard, its prevalent methyl orange alkalinity is 138 p.p.m. Aquatic vegetation is scarce. The bottom soil is amorphous marl and sand in the shoal and sub-littoral regions with pulpy peat in the depths. Encrustation marl is present on all of the numerous logs and on the stems and petioles of the sparse plants of the yellow water lily (Nuphar). The shoal area (water less than 4 ft. deep at the drop-off) is only 11 per cent of the total bottom area. The lake is symmetrical in outline with steep slopes. The lake basin is thought to have originated as a limestone sink. This lake was chosen for study because it is small in area, lacks both inlet and outlet, is entirely State property, and has a substantial crayfish population consisting of only one species, Orconectes virilis. A detailed description of its limnological characteristics can be found in Tanner (1952) from which most of the foregoing descriptive data were selected.

The only fish species present in West Lost Lake is the brook trout, stocked annually at a length of 5 inches and a rate of 100 per acre of surface water; it has no natural reproduction in the lake. An intensive creel census of all fishermen on the lake by Institute staff members has provided data on the harvest of the fish in the lake. Reliable estimates of the trout population are made annually in the fall and the age and growth of the trout are also known.

IV. METHODS

In assessing population size, individual growth, mortality, reproduction, and age composition of the crayfish, it was necessary to adapt old techniques and to develop certain new ones.

A. Population and age estimates

Population estimates of the crayfish were made in the summer of 1962 and the spring and summer of 1963. Because of the small narrow shoal area, steep slopes and the many logs scattered about the shoal individuals were sampled with rectangular wire mesh traps baited with fish remains. The traps sampled all age groups of crayfish for study except the young which were taken instead with a small minnow seine of $\frac{1}{4}$ inch x 6 ft. x 4 ft. mesh along the shore after dark.

A collection of young-of-the-year consisted of hauls made once around the circumference of the lake. The traps were made of $\frac{1}{4}$ inch galvanized mesh screen stapled on to a welded iron rod frame 24 inch x 12 inch x 12 inch with a funnel of the same size mesh at each end. The funnel at one end was hinged along one edge so that all the captured animals could be removed. Also used were round wire "minnow" traps such as can be purchased in many hardware or sporting goods stores. Both round and rectangular traps proved equally effective in sampling crayfish larger than 24 mm. in cephalothorax length. Such traps were fished for 24-hour periods, lifted and rebaited. All trapped crayfish were released in the center of the lake after processing.

Estimates of population numbers were made using the Schumacher (1943) mark and recapture method. It was chosen over the Schnabel (1938) method because it does not require iterative procedures for estimation, it reduces errors due to lack of random sampling by weighting each sample by sample size rather than by proportion marked (DeLury 1958, Ricker 1958a). The formula used for calculation is:

$$p = \sum_t x_t X_t / {}_t n_t X_t^2$$

where $p = 1/N$; N = estimate of population size,

x_t = number of animals in the sample,

X_t = total number of animals previously marked,

n_t = number of marked animals in the sample, and

t = time interval

To establish the validity of my actual techniques experiments were conducted which compared the Schumacher and the Schnabel methods of estimation and appraised the differences between the two types of gear used in sampling a given population. These experiments were carried out in ponds of the U.S. Fish and Wildlife Service, at Northville, Michigan, and in ponds at Hastings Fisheries Research Station of the Institute for Fisheries Research at Hastings, Michigan. Results of the tests (Table 2) indicate that estimates obtained with a 50 ft. bag seine did not differ substantially from those obtained with baited wire traps. Schumacher type estimates were slightly higher than Schnabel estimates but gave much narrower confidence intervals. There was no significant difference in the mean size of crayfish sampled by either type of gear ($t=1.395$, $\alpha=.01$, $n=530$). A 0.25 recapture rate proved sufficient to give consistent estimates of population size.

A marking technique for crayfish developed and described

TABLE 2

Summary of experiments to validate methods for estimating population size in crayfishes

A. Comparison of estimates of a known population of 284 crayfish in a pond by the Schumacher and Schnabel methods

Collection number	Date 1962	Percentage recaptures	Schumacher estimate	95% confidence limits	Schnabel estimate	95% confidence limits
1	7/10	--	--		--	
2	7/11	.18	185		167	
3	7/12	.25	293		274	
4	7/13	.33	330		300	
5	7/14	.59	221	203-240	201	158-736

B. Comparison of estimates of a population of unknown size using 2 collection techniques at Northville, ponds

	Seine	Confidence limits 99%	Percentage of Recapture	Trap	Confidence limits 99%	Percentage of Recapture
Schnabel method	860	667-1210	.637	721	631-1683	.667
Schumacher method	881	851-913	.637	842	751- 958	.667

Number of trials = 20 total marked = 586 by Goellner (1943), which involves clipping pleura with a fine-pointed scissors, proved to be an effective although laborious field method for marking large numbers of crayfish. Injection of ink beneath the abdomen with a hypodermic syringe was also successful, but it was difficult to use in the field. Crayfish kept in my laboratory aquaria and marked by clipping retained the scar of a clipped pleuron for three molts following the excision. In the field, adults marked by such a clip were recognizable for the duration of the study ($1\frac{1}{2}$ years). Immature animals thus marked in September of 1962 could still be identified in May of 1963. Pleural clipping did not disturb the ecdysis and apparently had little effect upon general health of the crayfish even though regeneration of the excision produces a deformed pleuron.

The technique of pleural clipping seemed to meet many assumptions of the mark and recapture method of numerical population estimations.

1) Marked crayfish are easily recognized on recapture.
2) Marks are not lost.
3) Marked and unmarked animals are equally susceptible to capture.
4) Recruitment, by growth of the next younger age group into the age group being estimated, or of the members of the age group being estimated, could distort estimates of the rate of recapture; this is eliminated by marking only during the intermolt period when no growth occurs.
5) Marked and unmarked individuals have the same rate of mortality.
6) Marked animals disperse themselves randomly in the sampling area.

If the sample of any one age group was too small to give reliable estimates of the population size for that age group, then samples of adjacent age groups were combined. Estimates of the numbers of individuals in the component age groups in such a combined sample were obtained by dividing the estimate for the combined sample by the percentages of the component age groups represented in the cumulative catch during the sampling period.

Estimates of age composition were made by analysis of size-frequency graphs utilizing probability paper and by following the size ranges of groups of known age individuals that had been marked previously (1962) and recaptured in 1963. Because of molting, growth in crayfish is stepwise. Thus a size-frequency polygon using the length of the cephalothorax plotted in millimeter intervals as the abscissa and numbers of individuals as the ordinate breaks up the population sample into natural size groups with distinct easily followed modes (Van Deventer 1937). Young-of-the-year and yearlings form the most distinct group, the size-frequency graph becomes polymodal for older age groups but the number of molts per season are reduced and the shift in mode of any age group after a molt can be easily followed throughout the growing season. Thus a series of size-frequency graphs at various times during the growing season permits a reasonable estimate of the rate of growth.

Crayfish belonging to a certain age group can be identified by marking them within the estimated size range for that age group. This size range is established from the size-frequency graph. Although the flanks of two adjacent size groups overlap, the percentage of the population of one age group included in the size range of the next adjacent one is about the same for the two overlapping groups. About 80 per cent of the population of two and three-year-old crayfish fall within the modal range that excludes the components of overlapping flanks (Fig. 1).

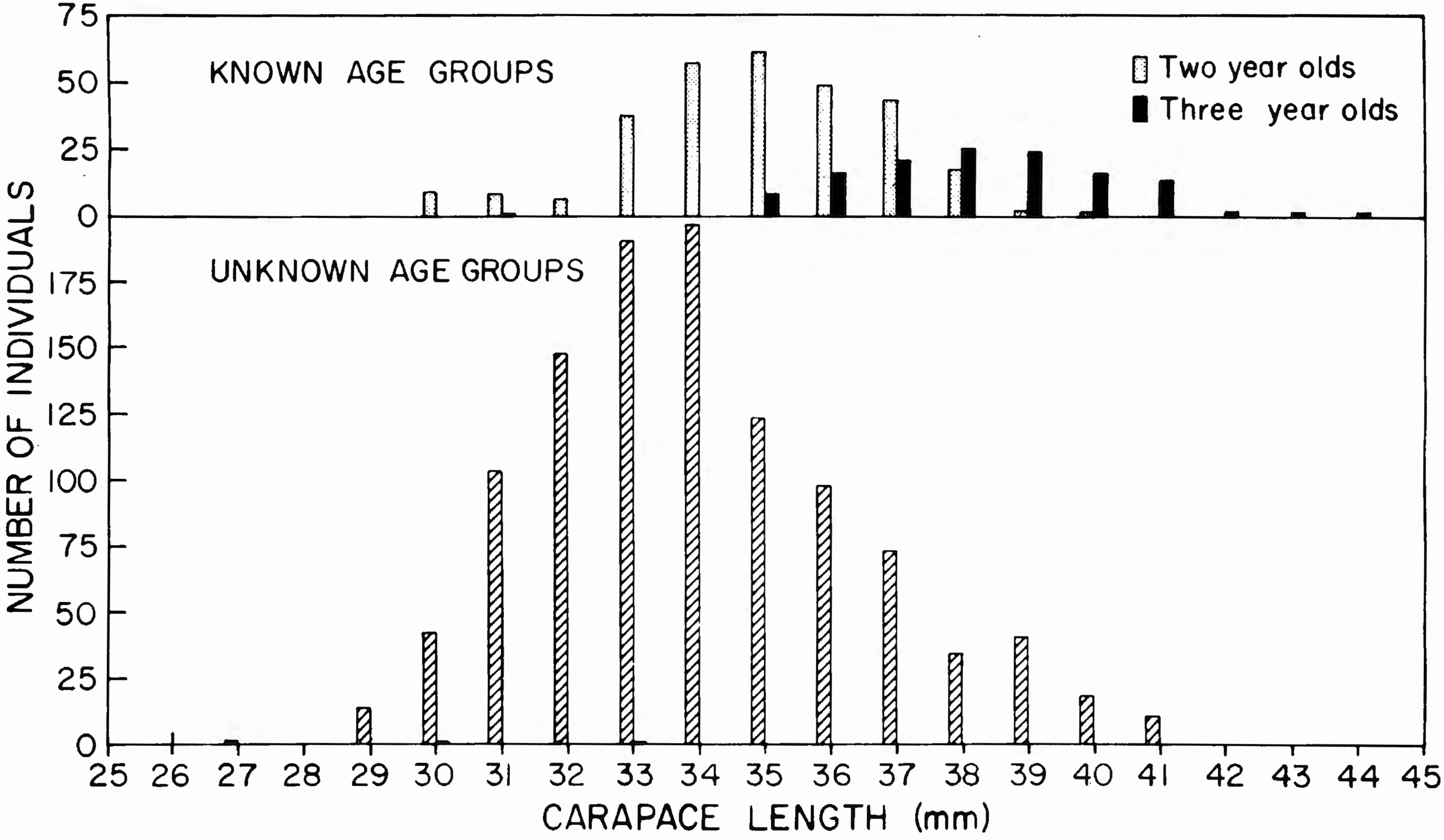
B. Growth

Because flexibility of the abdomen makes total length difficult to measure, all of the lengths used in this study are of the carapace from the tip of the rostrum to its posterior extremity at the abdomen. All measurements were made with vernier calipers to the nearest 0.1 mm.

Each of the serial population samples yielded plots of length frequency using one-millimeter groupings as the ordinate, these plots are the basis for analysis of seasonal growth (Fig. 2). Fractional measurements are reduced to one-millimeter size classes, e.g., those from 18.6 through but not beyond 19.5 are counted as 19.0 mm. The total catch in each interval of time was charted separately for growth analysis. In each of the periodic samples, recaptures (previously marked specimens) were excluded. Estimates of growth rate were calculated from length measurements of unmarked individuals encountered during the population estimates. A test of propriety showed that I could have used the data for marked individuals as well; large sample sizes would have obliterated the effects of repeated recapture on growth.

Figure 1

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



75
50
25
0
175
150
125
100
75
50
25
0
NUMBER OF INDIVIDUALS
KNOWN AGE GROUPS
UNKNOWN AGE GROUPS
Two year olds
Three year olds
25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45
CARAPACE LENGTH (mm)

Figure 1

Figure 2

Actual average and projected growth of *O. virilis* in West Lost Lake

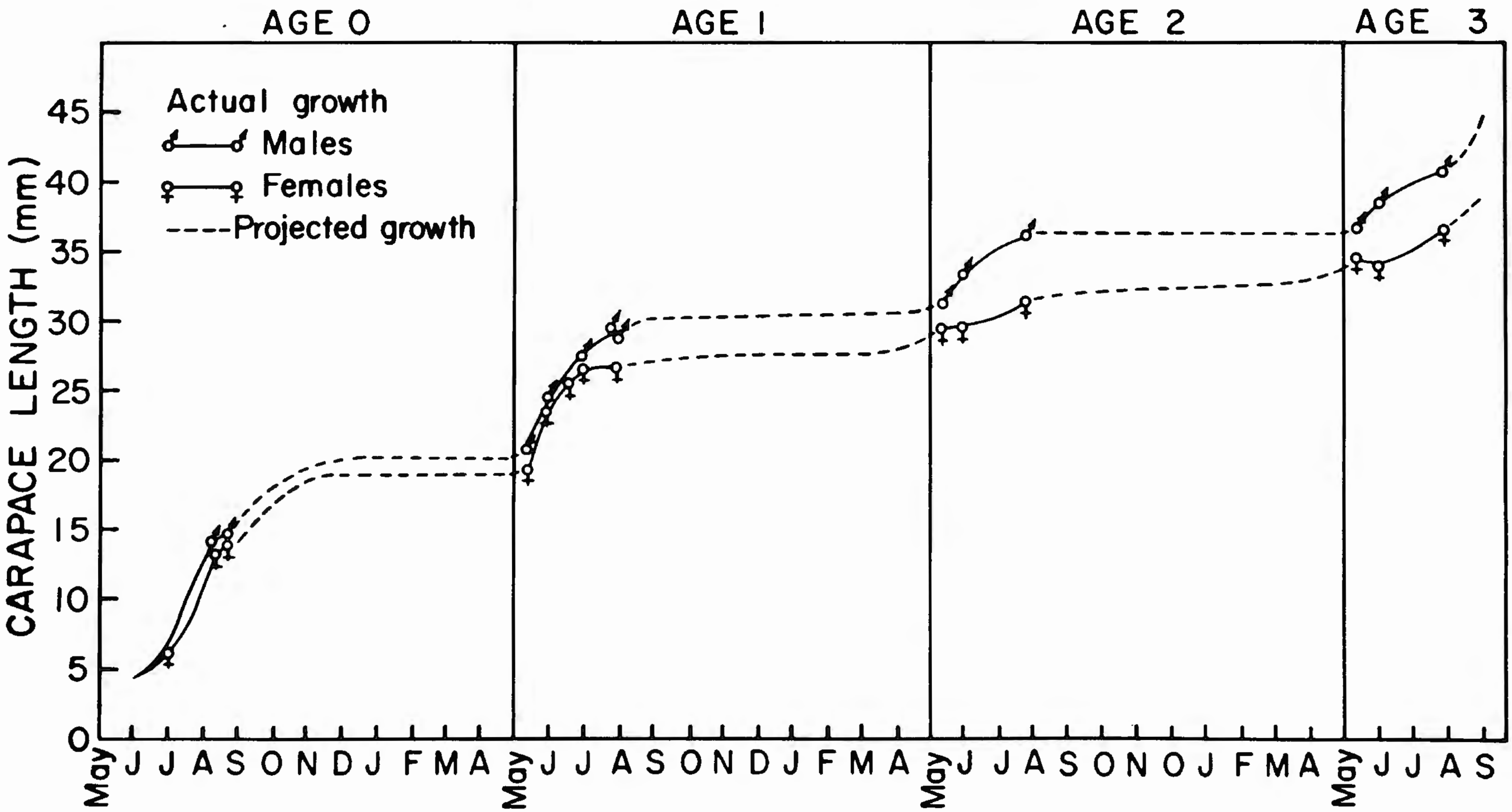

AGE 0
AGE 1
AGE 2
AGE 3
Actual growth
♂——♂ Males
♀——♀ Females
----Projected growth
CARAPACE LENGTH (mm)
0
5
10
15
20
25
30
35
40
45
May J J A S O N D J F M A
May J J A S O N D J F M A
May J J A S O N O J F M A
May J J A S

Figure 2

Growth of yearlings and young-of-the-year was easy to follow since there was no overlap with other age groups. As seen in Figure 1, age groups two and three have overlapping size ranges. The point of division for assessing ages to unknown age groups was determined from the shape of the size frequency curve. Thus in Figure 1, 37 mm. is selected as the point of division between the size ranges of recently molted three-year-old and two-year-old males collected between June 1 and June 30. No overlap was assumed between the two- and three-year-olds.

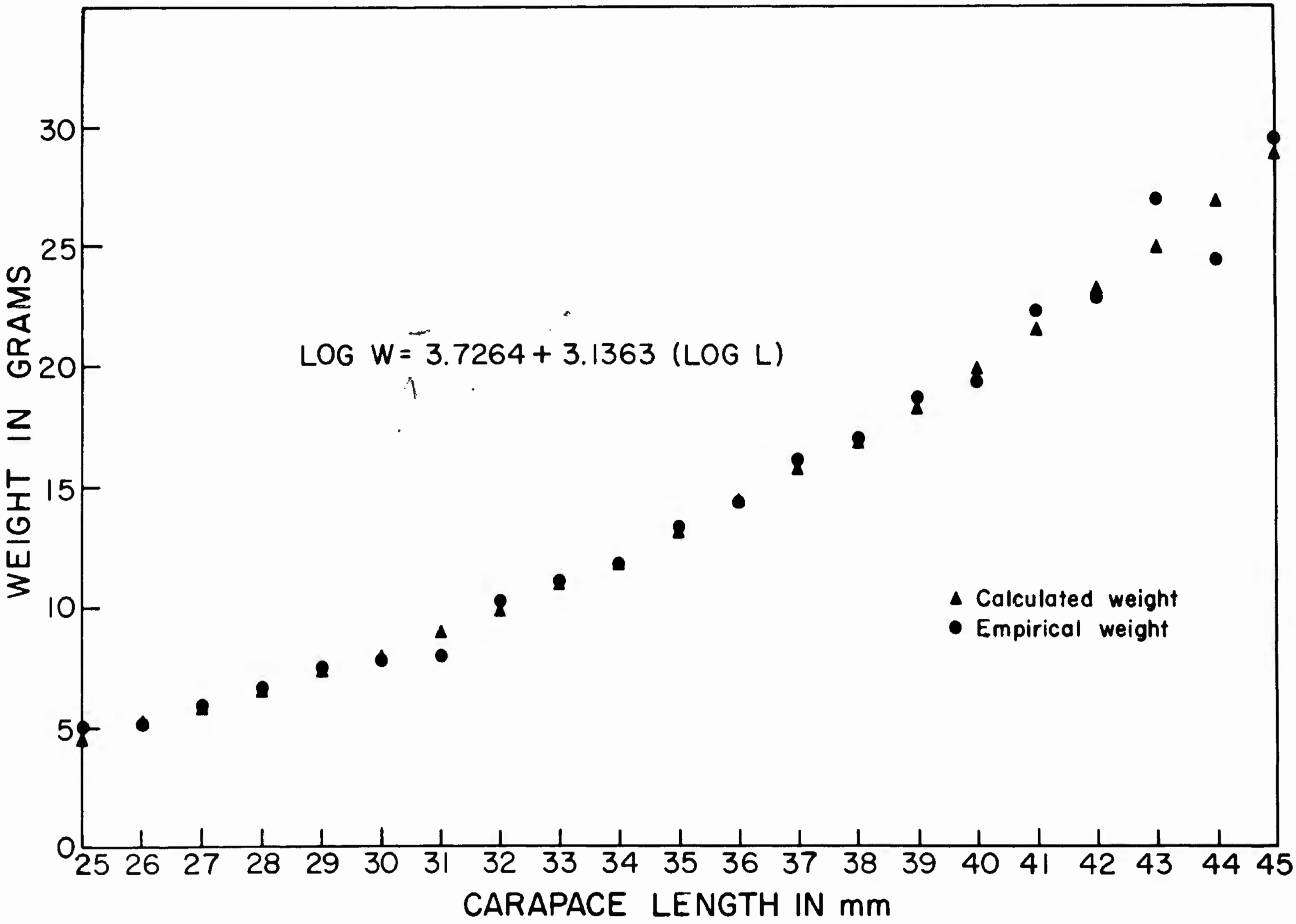
Examination of known-age material disclosed that the size range of an age group determined in the foregoing manner includes 80 per cent of the population making up this age group. The other 20 per cent overlaps with the adjacent age group. This percentage of overlap from each population was the same for both age-two and age-three groups. It was obtained by dividing the number of known age animals occurring within the size range determined from the size frequency graph of unknown age groups divided by the total number of known age animals.

Growth in length was converted to weight units by use of a length-weight relationship computed from empirical data (Fig. 3). No statistical difference in weight between males and females was found for the size ranges examined ($t = .558$, $\alpha = .05$, $n = 108$). Crayfish used to compute this curve had complete sets of appendages and had been measured to the nearest millimeter interval ±0.1 mm. and were weighed to the nearest 0.1 gram.

Instantaneous growth rates were calculated by converting to the natural logarithm the rate of growth using the average weight of a crayfish of a given length at successive

Figure 3

Length-weight relationship for adult *Orconectes virilis* in West Lost Lake



30
25
20
15
10
5
0
WEIGHT IN GRAMS
LOG W= 3.7264 + 3.1363 (LOG L)
▲ Calculated weight
● Empirical weight
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
CARAPACE LENGTH IN mm

Figure 3

ages, and using the formula of Ricker (1958a):

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

where

g=instantaneous growth rate,
e=base of natural logarithm,
W_t=weight at the end of time t, and
W_o=initial weight

C. Reproduction

Reproductive potential is customarily measured by egg counts. In crayfish, production of fertilized eggs may be estimated by counts of eggs carried on the pleopods of females. Direct ovarian egg counts were made of mature females collected in August. Counts of eggs attached to the pleopods of the females were made on series of live animals captured during marking experiments and on a sample of females collected by seining at night in May. Eggs were removed from live animals only when necessary to facilitate counting. The females were then marked before being returned to the lake so as not to be used for egg counts more than once. Females collected by seining were preserved in alcohol and the eggs subsequently enumerated.

D. Predation

Stomachs of the brook trout were studied in order to determine the extent to which crayfish are utilized as a food by the trout. Stomachs were saved from all trout caught by anglers from West Lost Lake during August and September of 1962 and from April to September 1963. These samples were augmented by others of at least 15 fish, each collected at intervals of about two months during the spring, and winter periods that were closed to angling. The identity, weight in grams, volume in cubic centimeters by displacement of water and frequency of occurrence of the items found in the trout stomachs were determined. The effect of trout predation on the crayfish population involved calculations made from empirical observations of the rate of consumption of crayfish. This was then related to the size of the stock, and the numbers and sizes of the predators. The equilibrium yield for a given rate of predation was calculated for the population by a method developed by Ricker (1958a) substituting theoretical rates of predation for fishing mortality. This allows us to theorize about the effect of virtual differences in predation rates on yield of crayfish.

V. CHARACTERISTICS OF THE CRAYFISH POPULATION

A. Size

Variation from year to year in the size of the population is governed by two factors: (1) the amount of recruitment to the population in the spring and (2) differential mortality of component age groups of both sexes. The best estimate of the 1962 summer population is 1.4 times greater than that for the summer of 1963 (Table 3). The difference is due chiefly to a considerable decrease in the number of young-of-the-year crayfish rather than changes in the population of older crayfish. The population of the young-of-

TABLE 3

Seasonal change in the population of two sexes of the crayfish of West Lost Lake

Age group and sex	Summer 1962	Spring 1963	Summer 1963
0 Males	11,808	94,765	5,772
Females	13,163	94,765	7,128
1 Males	4,073	8,870*	5,933
Females	3,753	9,051*	4,940
2 Males	3,321	2,804	2,678
Females	853	2,121	1,073
3 Males	458	1,726	362
Females	248	132	124
Totals:			
Males	19,660	108,165	14,745
Females	18,017	105,839	13,267
Grand Total	37,677	214,004	28,010

* Derived as the average of 1962 age 0 and 1963 age 1

the-year for the spring of 1963 was estimated by multiplying the average pleopod egg count per adult female by the number of mature females in the population during the spawning season. All other estimates are from the mark and recapture procedure described previously. When mark and recapture data for age groups were combined (due to lack or smallness of samples), the resulting estimate was higher than for separate age groups (as demonstrated for comparable treatment of fish by size groups in Cooper and Lagler 1956) (Table 4) Thus, for age 0 crayfish in 1962, the combined estimate for the two sexes was 25,233, whereas for males alone it was 11,808, and for females 13,163 for a total of only 24,971.

The marking period for some estimates in 1962 was longer than in 1963, a fact reflected in the high recapture rates recorded for 1962. In general, the marking was prolonged in 1962 until a recapture rate of at least 25 per cent was achieved for a period of a few days. These rates were lower than 25 per cent in 6 of 15 estimates, especially for the young-of-the-year of the large 1962 year class.

In the spring, marking terminated when the age group being estimated began its molt. Recently molted crayfish did not enter traps with the same efficiency as individuals in the intermolt stage; as a result, population estimates with long intervals during which marking was carried out would be biased. Because yearlings had to be 25 mm. long before they could be sampled effectively, they had a rather long marking period in the spring estimate for 1963. This intensive sampling provided at least one trap for every

TABLE 4

Summary of the periodic estimates of the crayfish population in West Lost Lake

Age groups and sex	Termination date of estimate	Length of marking period in days	N	95 percent confidence limit	Percentage of recaptures	Number Marked
0 males	8/27/63	13	5772	4819-7220	.294	1432
0 females	8/27/63	13	7128	5900-9050	.221	1539
0 males	9/11-62	12	11808	8473-19470	.049	1560
0 females	9/11/62	12	13163	10005-19124	.101	1786
1 males	7/25/63	36	5933	5595-6357	.325	2031
1 females	8/5/63	36	4940	4653-5288	.178	1194
1 males	9/10/62	40	4073	3768-4436	.695	2508
2 males	6/1/63	14	2804	1988-4784	.186	725*
2 males	8/6/63	19	2678	2386-3058	.440	1412
2&3 males	9/10/62	40	3379	3359-3400	.793	2743
3 males	6/1/63	15	1726	1565-1926	.383	714**
3 males	8/6/63	18	362	254-769	.500	199
1,2&3 females	9/10/62	32	4854	4780-4931	.296	1332
2&3 females	7/7/63	18	2352	2208-2518	.555	956
2&3 females	8/12/63	19	1197	1124-1207	.181	299

*, ** = numbers marked at time of last estimate.

0.185 acres of surface area, collecting a total of 21,535 in 1963, as compared to 14,839 individuals in 1962; in these figures recaptures of marked individuals are counted a second time.

Considerable seasonal variation occurred in age composition and bathymetric distribution of the population complicates calculations of population size. Extrinsic factors such as molting, weather conditions, and quality of bait added to the problem of estimation. Hence the population obviously cannot be characterized accurately by taking a few samples at one period of time.

B. Mortality

The population estimates provided data for the estimates of mortality or of its reciprocal, survival. For comparison, recapture data on previously marked animals were also used to give mortality analysis by another method as follows (Ricker, 1958a):

$$N_{\underline{t}}/N_o = \underline{e}^{-\underline{it}}$$

where

$N_{\underline{t}}$ = the number of animals surviving to time t,

N_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

$\underline{e}$ = base of natural logarithms.

Based on recaptures in one year of animals marked in the previous year, which gives a Peterson-type population estimate (Ricker 1958a), the estimate of survival of male 2-year-olds from the summer of 1962 to the summer of 1963 was .38. (The survival estimate based on Schumacher population size data was .65.) For three-year-olds the recapture data gave a survival estimate of 0.23, whereas the Schumacher population estimates gave a survival rate of .30. The lower survival rate for the recapture data is due in part to sampling errors which are larger in Peterson population estimates than in those using the Schumacher method,(a variation in susceptibility to recapture of the previously marked (in 1962) animals after July 30). This was perhaps due to loss of identification after so long a period since marking, and/or to changes in behavior due to onset of the mating season.

The basic statistics derived from the data for population estimates were a, s, and i, respectively, the total animals dying from all causes, the number surviving, and the instantaneous rate of mortality. The instantaneous rate of mortality (i) is an average rate since the mortality rate is not constant over the period involved. In fact, this mortality is associated with molting periods in older age groups. Both rates of mortality and survival were calculated for all of the age groups in the summer of 1962, and in the spring and summer of 1963. These were based on seasonal point estimates of age groups. The calculations represent natural mortality (predation, physiological aging, etc.), since there is no complicating human exploitation of the crayfish. Of the agencies of natural mortality, however, only predation was subjected to special investigation. I tried to estimate that proportion of the total natural mortality rate which might be due to predation by the brook trout, the principal aquatic predator. The results are reported in a later section.

Over winter mortality for all age groups and both sexes of the crayfish is quite severe. However, after the first summer of life, the survival rate of males is greater than that of females. When compared with males, a striking change in rate of survival is seen in two-year-old females; after carrying their first brood of young, their survival from the spring to the summer is only one half that of males of this age. For three-year-olds, the survival from spring to summer is also less in females. Over winter survival following age three is negligible. A very few males, but no females, survive the fourth winter.

Although the sex ratio at hatching may be assumed to be one to one, females outnumber males at the end of the first growing season; in subsequent seasons, however, males are always more abundant. In adults the bulk of mortality occurs in the middle of the second year for females and the middle of the third year for males. This apparent change in survival rate between the sexes is first reflected in the winter mortality of the young-of-the-year and is therefore not associated with the onset of maturity. (Table 5, Figure 4)

Differential mortality favoring the male sex is not reported in other species of crayfishes. Tack (1941), Chidester (1912), Ortmann (1906), Van Deventer (1937),

TABLE 5

Total rate of survival (s) and rate of mortality (a) of *Orconectes virilis* in West Lost Lake

	s		a	
Age group	males	females	males	females
0 spring 63 to 0 summer 63	.0608	.0705	.9392	.9250
0 summer 62 to 1 summer 63	.5016	.3791	.4984	.6269
1 summer 62 to 2 spring 63	.6907	.1557	.3093	.3874
to 2 summer 63	.9512	.9418	.0488	.4934
2 summer 62 to 3 spring 63	.5220	.6126	.4780	.8443
to 3 summer 63	.6005	.5066	.3995	.0562

Figure 4

Survivorship of the two sexes of *O. virilis* in West Lost Lake

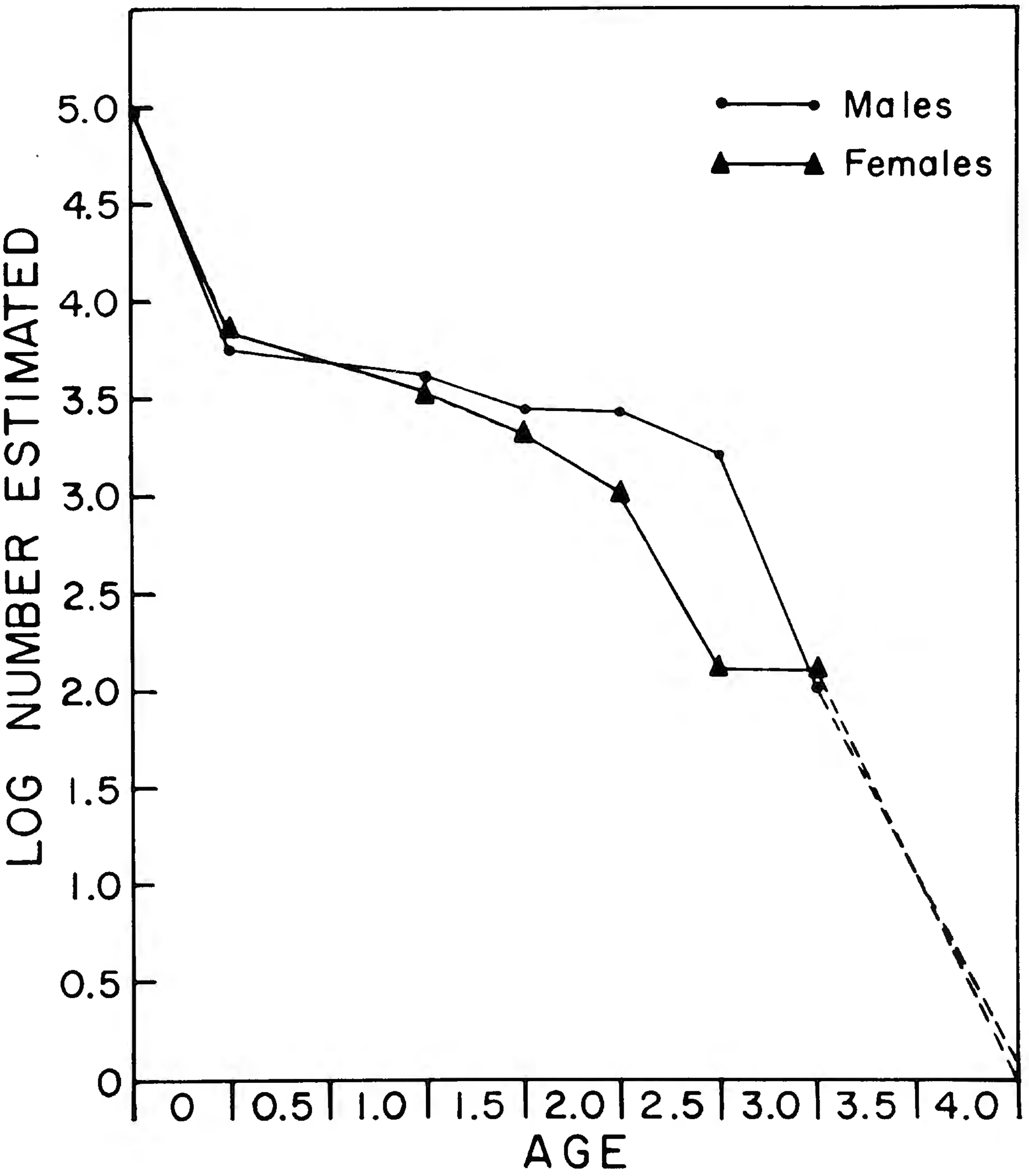

Males
Females
LOG NUMBER ESTIMATED
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
AGE

Figure 4

Creaser (1933), and Andrews (1904) found mass mortality occurring among males in various species of crayfish. Such a phenomenon during the molting period is widely reported among the foregoing references and elsewhere in the literature. All the authors conclude that this mortality is due to internal physiological causes rather than to external causes such as predation, disease or starvation. Van Deventer (1937) summarized the evidence cited in other literature and noted that the occurrence of a wave of natural deaths is coincident with attainment of maturity and ordinary maximum size range. Because no catastrophe was evident in my population and because the mortality affected only certain year classes, Van Deventer's conclusion seems applicable.

O. virilis, although it has a longer life span than O. immunis, has the same general pattern of periodic mortality in certain age groups. This pattern is reflected both in my data on recovery of previously marked animals and in periodic estimates of population size. Despite equal trapping effort, a very striking decrease occurred in the rate of recapture of two-and three-year-old males in the period June 21 to July 10 compared to the period June 1 to 20. During the interval from July 10 to 30 the rate of recapture again dropped severely for the three-year-olds but not for two-year-olds. This is the period during which 90 per cent of the adult males molted.

Year class fluctuation for the population of O. virilis is clearly indicated. In West Lost Lake, the 1962 year class was approximately twice as large as that of 1963. Regrettably, the factors affecting the survival of the young-of-the-year were not identified; they may, of course, be quite different from those affecting yearling adults. Although no spring estimates are available for the female population in 1962, the summer populations of 1962 and 1963 are not very different, 853 vs. 1073. Assuming that female mortality was not different in 1962 from 1963, then the brood stock was about the same. Therefore survival differences between the two years may not be due to differences in stock of adults but to some other factor.

Annual variation in survival makes it impossible to estimate survival rates by using the ratio of various age groups composing samples taken in various years.

C. Growth

Growth of crayfishes in length is stepwise rather than continuous, since it is directly related to the number of molts that the animal undergoes in a growing season. Newly hatched young-of-the-year are about 4.5 mm. in length. In West Lost Lake when they leave the female in the spring they are 6 mm. long and by September males reach an average length of 15.2 mm. and females averaged 14.1 mm. By late October and early November, males are 20.8 and females 19.2 mm. long. Two-year-old males reach an average length of 31.2 and three-year-olds, average 36.5 mm. in length. A few males which may be four-year-olds reach an average size of 40.8 mm. Two-year-old females are 29.5 mm. and three-year-olds are 36.4 mm. in average length. The maximum size for males was 45 mm., and for females, 38 mm. (Table 6).

TABLE 6

Carapace length (mm.) of various age groups of crayfish
in West Lost Lake
Data taken from length frequency analysis (see text)

A. Males

Year	Age group	Date	Mean $\bar{X}$	Standard deviation	Number
1962	0	9/1 - 9/9	15.25	2.65	44
	1	8/1 - 9/9	30.94	1.58	1,641
	2	8/1 - 9/9	36.78	1.61	1,872
	3	8/1 - 9/9	40.96	1.14	566
1963	0	8/28	14.60	1.70	87
	1	8/1 - 8/14	28.69	1.85	321
	2	7/19- 8/6	36.23	0.68	1,118
	3	7/10- 8/6	40.80	0.88	84

B. Females

1962	0	9/1 - 9/9	14.17	2.10	29
	1	8/1 - 9/9	28.04	1.17	284
	2	8/1 - 9/9	31.54	1.43	551
	3	8/1 - 9/9	36.96	1.33	29
1963	0	8/28	13.78	1.63	74
	1	8/1 - 8/14	26.76	1.73	267
	2	7/25- 8/12	31.41	1.07	289
	3	7/25- 8/12	36.44	1.22	9

Great variation in the growth rate of crayfishes appears in the first growing season. Yearling males collected in May had a size range of 16 to 25 mm., and females ranged from 14 to 24 mm. By August males varied from 24 to 33 mm., and females from 20 to 30 mm. There was also an observable difference between sexes in the mean length at the end of the first growing season. This difference between the sexes increased with time because adult females molted only once whereas the males molted twice during a single growing season.

The reproductive appendages of males have three morphological forms which are easily recognized as follows: (1) a juvenile form present before sexual maturity; (2) a non-breeding adult form, termed second form which appears first in adult males during their first molt of the new growing season in the spring of the year; and (3) a final form characteristic of breeding adults which first appears at sexual maturity and also appears in adult males after the second molt of the growing season in the summer as the breeding season is approached. Thus in sexually mature, male adults you have typically two forms of the reproductive appendages: the non-reproductive second form followed by the reproductive first form. Mating follows the appearance of first form males. After the yearling males become mature during the second summer of life, the sequence of molts in males is always the same; thus they go from reproductive to non-reproductive form in the spring and from non-reproductive to reproductive form in the summer.

In 1963 the spring molt of two-year-old males in West Lost Lake occurred between June 1 and July 4. However 90 per cent of males had molted within two weeks (i.e. by June 14). Three-year-old males began their spring molt a week later on June 8. The process lasted until July 16, but 90 per cent of the individuals had molted by July 4. The summer molt to reproductive form for both two- and three-year-olds began on July 5th. It lasted until August 6 for the three-year-olds (though 90 per cent had molted within a period of 17 days) and until August 9 for the two-year-olds (though 90 per cent had molted within a period of 20 days). The molting period was prolonged because a few individuals molted earlier, and others later, than the bulk of the population.

If for convenience we call the molt "complete" when 90 per cent of the individuals of an age group in a sample are recently molted crayfish, we can say that in the spring age-two crayfish molt a week before age-three animals and that the molting period is twice as long in three-year-olds. The summer molt comes three weeks after two-year-olds complete their spring molt whereas in three-year-olds, it follows almost immediately. Thus, the two molting periods of the three-year-olds overlap considerably. The molt is completed in both age groups at about the same time, so that the reproductive season for both two- and three-year-old male adults begins in early August. Yearling male crayfish begin and complete their molt to reproductive form from July 8 to July 27, a period of 19 days. However, they undergo three to four molts prior to their molt to reproductive form when they become mature.

There is a difference in the growth rates between the sexes of age groups within any one year, and from one year to the next. A comparison of the growth rate of both sexes of the age-one year groups showed that they differed significantly for the two years 1962 and 1963. The 1963 age-one year groups were smaller in mean length than the age-one year groups for 1962 (for females, $t=10.60, \alpha=.05$, $n=551$; for males $t=29.86$; $\alpha=.05$, $n=1960$). Since the 1962 year class was larger than the 1963 year class it may be that changes in density caused the difference in growth.

Stunting in crayfish has been described (Svärdson, 1948). Food is a factor often suggested as affecting the growth of crayfish. Kurata (1962) found that starvation markedly affected the growth increments at molting, as well as the interval between molts. Poor food conditions usually lengthen the intermolt period and simple quantitative correspondence is suggested between the degree of food shortage and of its lengthening effect on the intermolt intervals.

In West Lost Lake, adult females began their sole molt of the year on July 7, 1963, about the same time that the adult males began their molt to reproductive form. This came two weeks after the young had hatched and left their parent females. Yearling females began their molt to maturity on June 17, 1963; it lasted until July 8, a period of 21 days.

Along with a lowering of water temperatures, growth and molting ceases; low temperature presumably reduces physiological processes to a basic maintenance level, as reflected by a reduction in the movements of crayfish. This is indicated by comparing my spring trap catches with ones made when the water temperature had risen (Fig. 7). At a temperature of 55°F crayfish are very sluggish and can be easily picked up with the bare hand. Molting did not occur while the lake was ice covered. Absence of molting during the winter was indicated by the dark coloration and dryness to the touch of the exoskeleton in the early spring. In contrast newly molted animals in the spring and summer are lighter colored and slippery to the touch.

Geographical differences in growth rate and time of maturity have been recorded for Orconectes propinquus (Van Deventer 1937), and similar variations probably exist for O. virilis, although they have not been reported.

The instantaneous growth rate (g) declines with age though seasonal variations occur (Table 7). Instantaneous growth rate was derived from the length-weight relationship calculated from empirical data (Fig. 3).

D. Reproduction

Sexual maturity is attained by both males and females during the second growing season. In yearling males maturity is indicated by a change of the copulatory appendages to re-

TABLE 7

Instantaneous rates of growth (g), instantaneous rates of mortality (i) and instantaneous rates of increase in biomass (k) for various age groups of crayfish in West Lost Lake

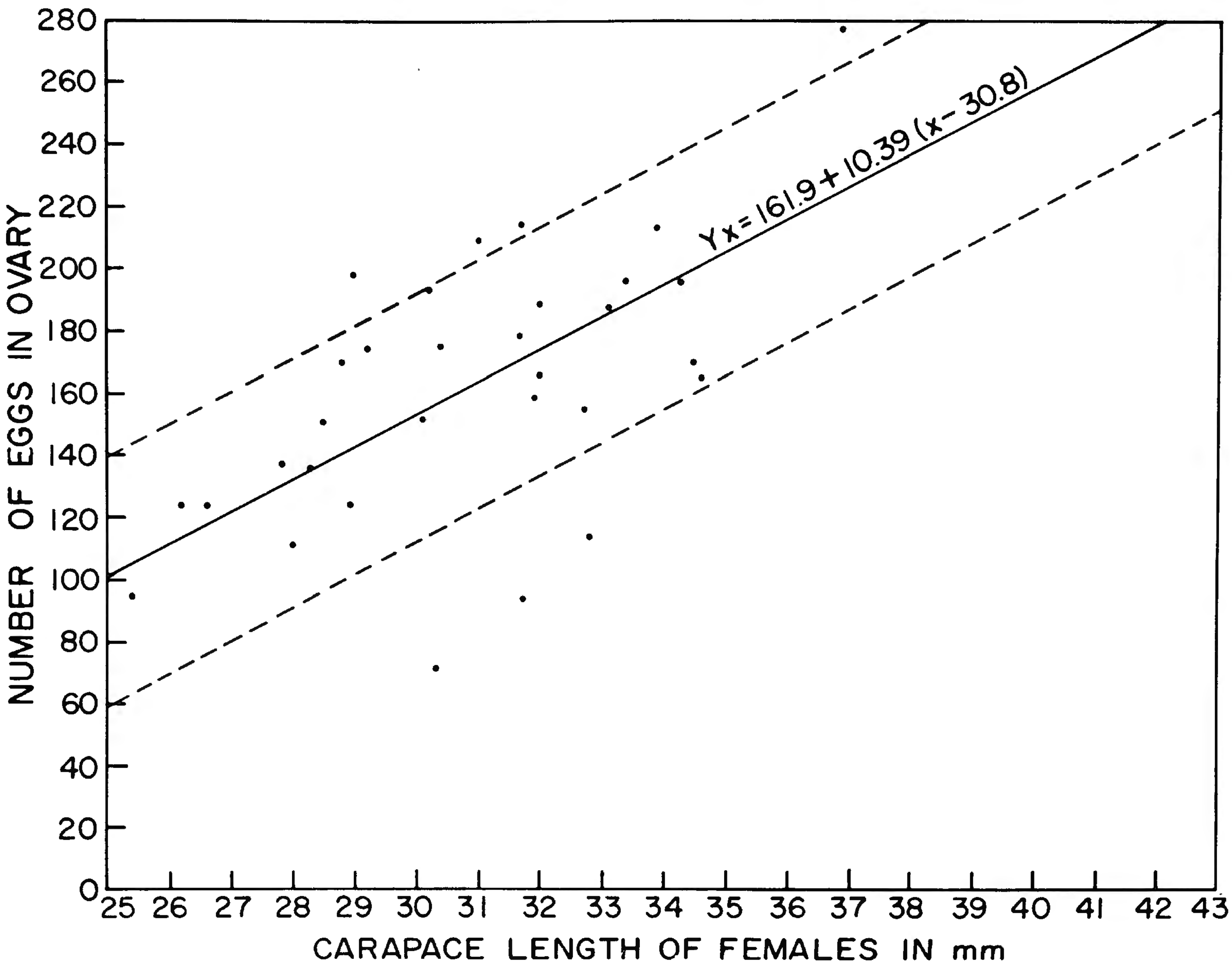
Season and age group	g		i		k	
	Males	Females	Males	Females	Males	Females
Summer 0	4.7185	4.7185	2.7985	2.5881	1.9197	2.1304
Summer 1	2.20387	2.03732	0.6880	0.9754	1.5158	1.0619
Spring 2	0.26236	0.30748	0.3739	0.4869	-0.1116	-0.1795
Summer 2	0.46373	0.19062	0.0465	0.6836	0.4172	-0.4930
Spring 3	0.01980	0.29267	0.6574	1.8658	-0.6376	-0.5731
Summer 3	0.35767	0.18232	0.5130	0.0626	-0.1554	0.1197

productive form. In West Lost Lake, this occurred between July 8 and July 27 in 1963. In the same year the yearling females reached the minimum size at maturity of 25 mm. between June 17 and July 8. Adult males two-year-olds and older must molt to reproductive form before they can mate; this molt occurred between July 5 and August 9. The mating season began soon thereafter and crayfish were observed copulating during the remainder of August and in September. In Wisconsin, two annual periods of mating have been reported, one in the fall and one in early spring (Threinen 1958), but I did not observe mating in the early spring because the lake was ice covered until near the end of April. Females with eggs were first observed in the sample I took on May 11. Creaser (1931) reported that eggs are laid before the last of April.

Ovarian eggs averaged 161.9 per female O. virilis in West Lost Lake. This is a measure of reproductive capacity. The regression of the number of eggs in the ovary against length of the carapace was linear (Fig. 5). However, the relationship for the number of eggs attached to the pleopods versus carapace length was not linear. The mean number of eggs per female attached to the pleopods was 94.02 in 1963. This is 58 per cent of the average ovarian egg count and is then the percentage of reproductive potential utilized. Thus 42 per cent of the ovarian eggs are lost, perhaps because of failure in attachment of eggs to pleopods or failure to extrude the full complement (Figure 6).

Figure 5

Relationship of female length to ovarian egg count of O. virilis in West Lost Lake

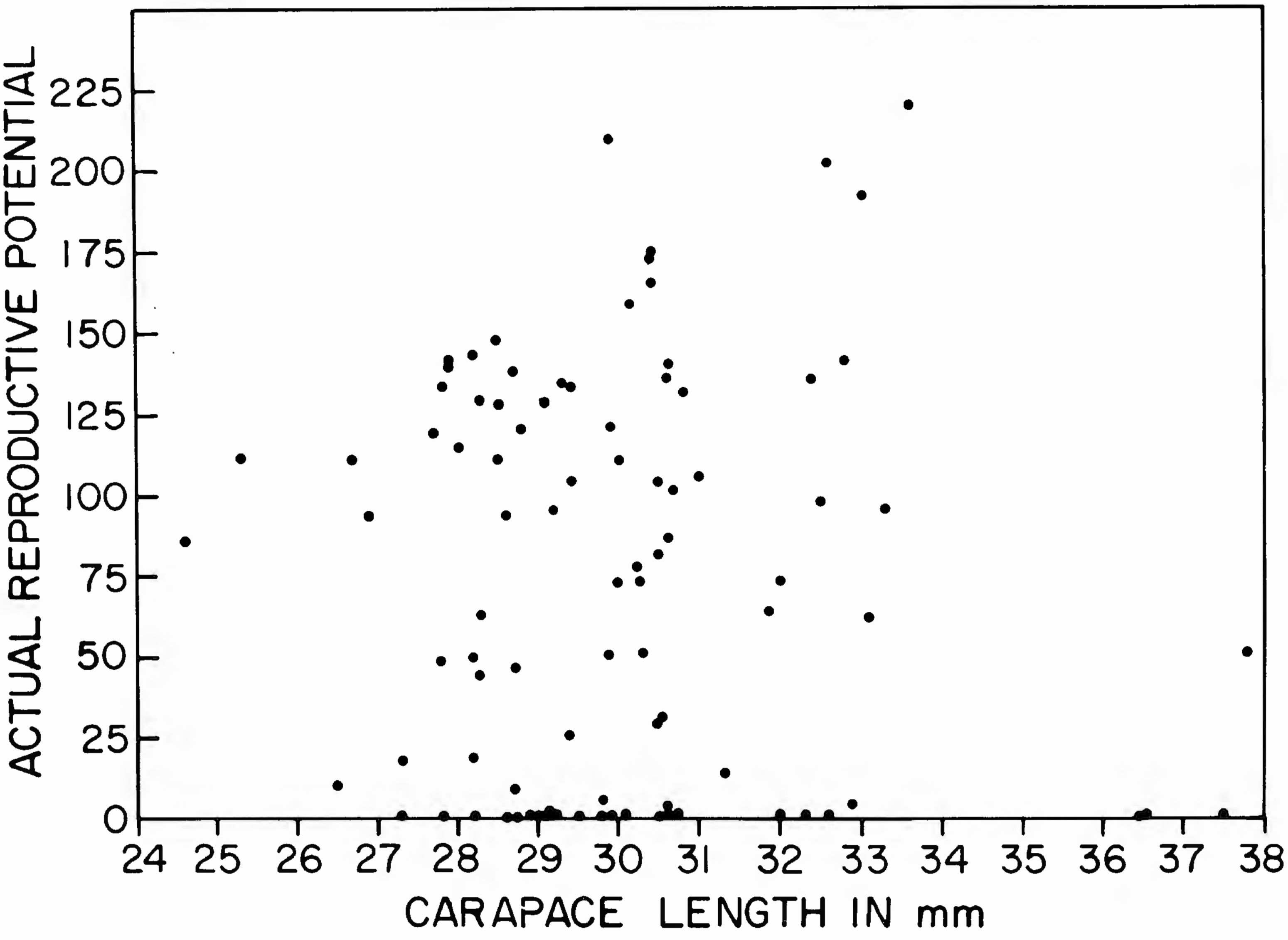


NUMBER OF EGGS IN OVARY
0
20
40
60
80
100
120
140
160
180
200
220
240
260
280
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
CARAPACE LENGTH OF FEMALES IN mm
$Y_x = 161.9 + 10.39 (x - 30.8)$

Figure 6

Relationship of female length to number of eggs carried on
pleopods (actual reproductive potential)
of O. virilis in West Lost Lake

Figure 6


ACTUAL REPRODUCTIVE POTENTIAL
0
25
50
75
100
125
150
175
200
225
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
CARAPACE LENGTH IN mm

Two-year-old females accounted for the bulk (92.5 per cent) of the young produced in 1963. The smallest egg-bearing female (24.6 mm. in carapace length) had 87 eggs on its pleopods; the largest was 37.8 mm. and had 53 eggs. The greatest number of eggs (220) was found on a female 33.6 mm. long. Age-two females carried an average of 82.7 eggs and age-three females, 107.0. Failure of attachment of all of the eggs produced in the ovaries is about the same for two- and three-year-olds, an exception being the very largest females. This may be due to physiological problems associated with aging and/or with accelerated activity in the largest females which may cause eggs to be dislodged from the pleopods. Females continue to feed when carrying the eggs; 21 out of 26 egg-bearing females examined on May 20, 1963, contained materials in their stomachs consisting of algae and "aufwuchs" found on the encrustation marl, and on plant material. Crayfishes in West Lost Lake are predominantly herbivorous, as is true in the literature for most species. However, they are also known to be scavengers on animal carcasses. This is clearly indicated by the attraction of crayfish to the dead fish used to bait traps.

E. Age Composition

The age composition of the population differs from year to year and changes seasonally a year. The latter was shown by the striking shift in age structure from spring to summer (Table 8).

In the spring of 1963, young-of-the-year, comprised nearly 90 per cent of the total number of individuals in the

TABLE 8

Seasonal and annual variation in the age group composition expressed as percentage of the estimated standing crops of the crayfish population by sexes in West Lost Lake

Age group	Spring 1963		Summer 1963		Summer 1962	
	Males	Females	Males	Females	Males	Females
0	87.6	89.3	39.1	53.7	60.0	72.6
1	8.2	8.5	40.2	37.6	20.7	20.8
2	2.6	2.0	18.1	8.1	16.8	4.7
3	1.6	0.2	2.6	0.6	2.5	1.9

population, but by mid summer the young made up only 40 per cent of the male population and 50 per cent of the female population. By contrast, in the summer of 1962, 60 per cent of the crayfish were young-of-the-year males and 70 per cent of the females were young-of-the-year. Comparison of these for the two years, shows that the 1962 year class was twice as large as that of 1963. Consequently in the summer of 1963 there were more yearling males than young-of-the-year males in the population. Contrastingly, in 1962, male yearlings were one-fourth as numerous as the-young-of-the-year males. Differences also existed in this regard for the females in these two years.

F. Seasonal Bathymetric Distribution

O. virilis changes it's depth distribution seasonally with size. From May through August, 1963 catch was recorded daily on the basis of age groups, sexes, and depth of capture and cumulated every 20 days. The last period had only 13 days but the data were extrapolated to 20 days. Due to catch fluctuations the data could not be utilized in obtaining population estimates by the DeLury method as outlined in Ricker (1958a).

The catch of *O. virilis* in West Lost Lake was dependent upon both the size of the population and the amount of movement during the trapping period. The largest catch per unit of effort came between July 31 and August 12, 1963; the catch consisted of about 80 per cent males, and was equally divided between yearlings and adults. The total catch per 20-day period increased steadily from May to August (Fig. 7).

Figure 7

Seasonal variation of catch per unit effort for crayfish in West Lost Lake, 1963

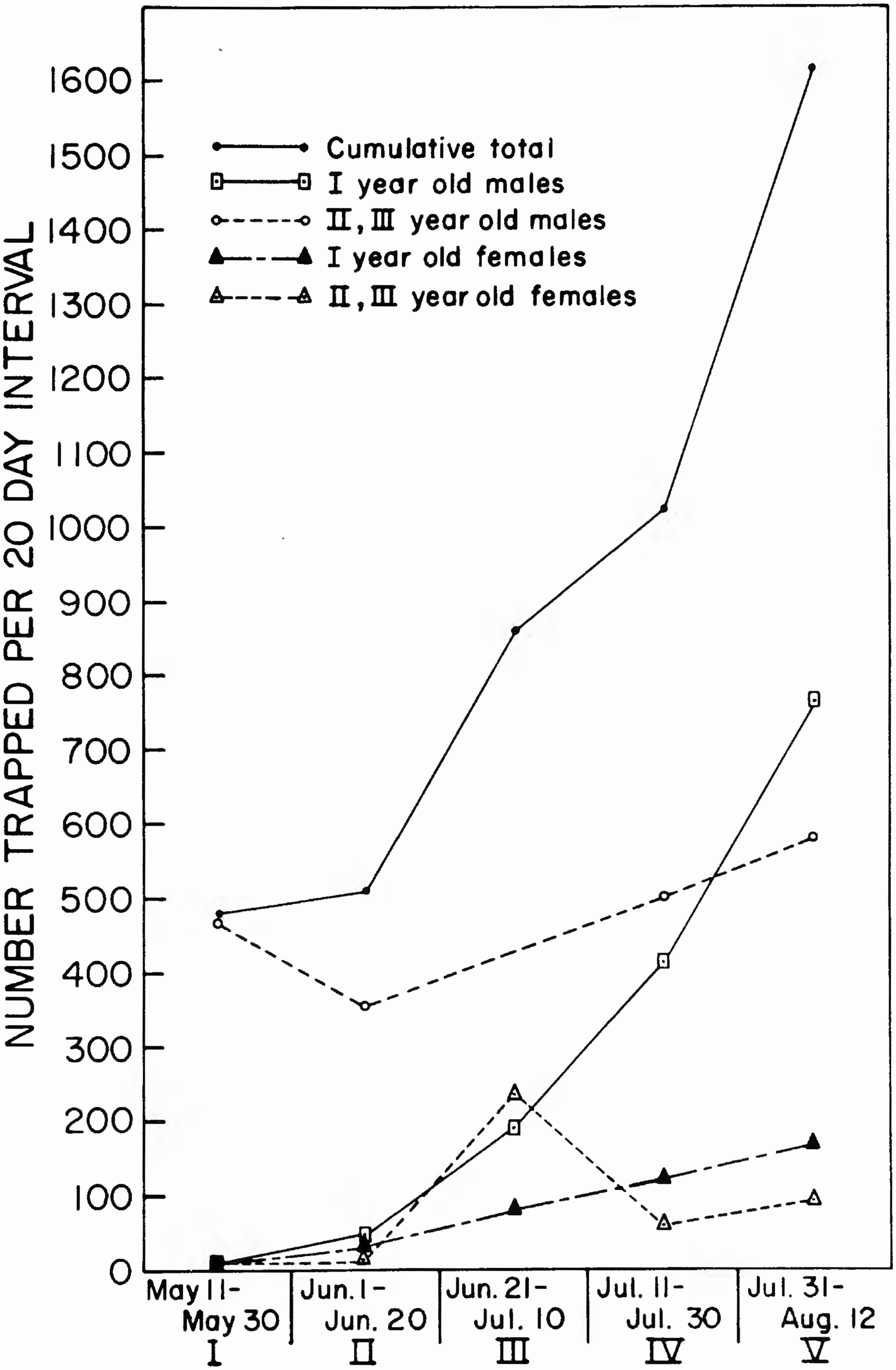

NUMBER TRAPPED PER 20 DAY INTERVAL
0
100
200
300
400
500
600
700
800
900
1000
1100
1200
1300
1400
1500
1600
Cumulative total
I year old males
II, III year old males
I year old females
II, III year old females
May 11- May 30
I
Jun. 1- Jun. 20
II
Jun. 21- Jul. 10
III
Jul. 11- Jul. 30
IV
Jul. 31- Aug. 12
V

Figure 7

Yearlings of both sexes formed a larger proportion of the catch as the season progressed. Females reached a peak in the catch per unit of effort and in percentage of the total catch in the period from June 11 to July 10 which followed hatching of the young. Thereafter the female catch declined. Thus males were most active in mid summer while females moved most in early summer.

Catch per unit of effort at any depth was assumed to reflect population density there. In May and June crayfish were found mostly in depths of less than 10 feet (Figs. 8, 9 and 10). At these months both females with eggs on their pleopods and yearlings of both sexes were found largely in the shoal zone. Older males occurred between 5 and 20 feet with no distinct preference. Yearlings stayed in this shallow water until the middle of July and then gradually moved into deep water. Migration started earlier for adult females; by August they were concentrated at 25 feet with the adult males, at 20 feet. In comparison, by this time 65 per cent of the yearlings were at depths between 10 and 20 feet with 35 per cent of them below 20 feet. This compared with the presence of about 70 per cent of the adult females at this depth. Obviously a major summer shift in bathymetric distribution occurred in August.

There are several possible explanations of the summer shift in depth distribution of Orconectes virilis. This crayfish is quite sensitive to light; Roberts (1944) concluded that within normal fluctuations of temperature, oxygen

Figure 8

Seasonal shift in bathymetric distribution of crayfish of all ages in West Lost Lake, 1963

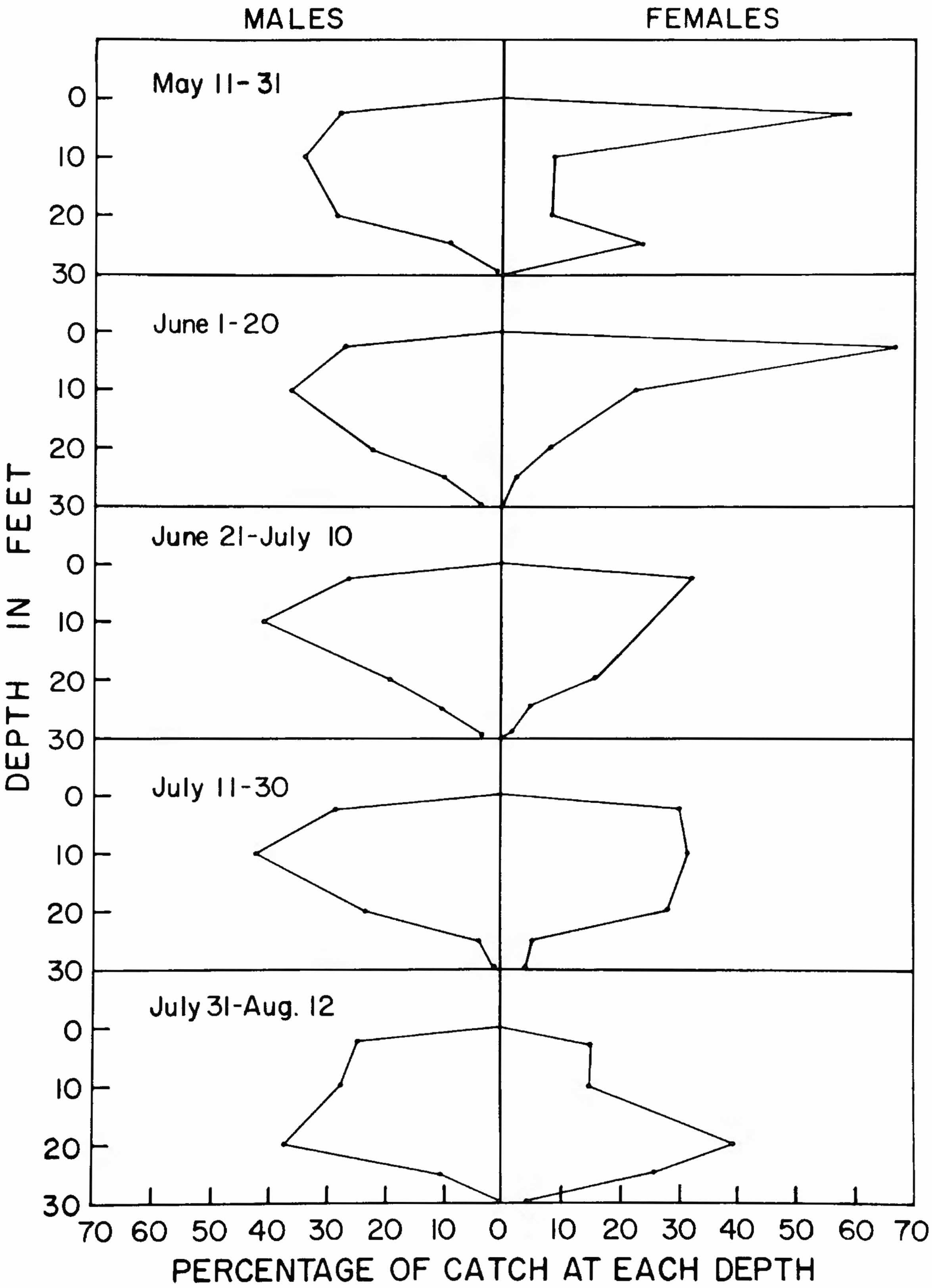

MALES
FEMALES
May 11-31
June 1-20
June 21-July 10
July 11-30
July 31-Aug. 12
DEPTH IN FEET
0
10
20
30
70 60 50 40 30 20 10 0 10 20 30 40 50 60 70
PERCENTAGE OF CATCH AT EACH DEPTH

Figure 8

Figure 9

Seasonal shift in bathymetric distribution of yearling crayfish in West Lost Lake, 1963

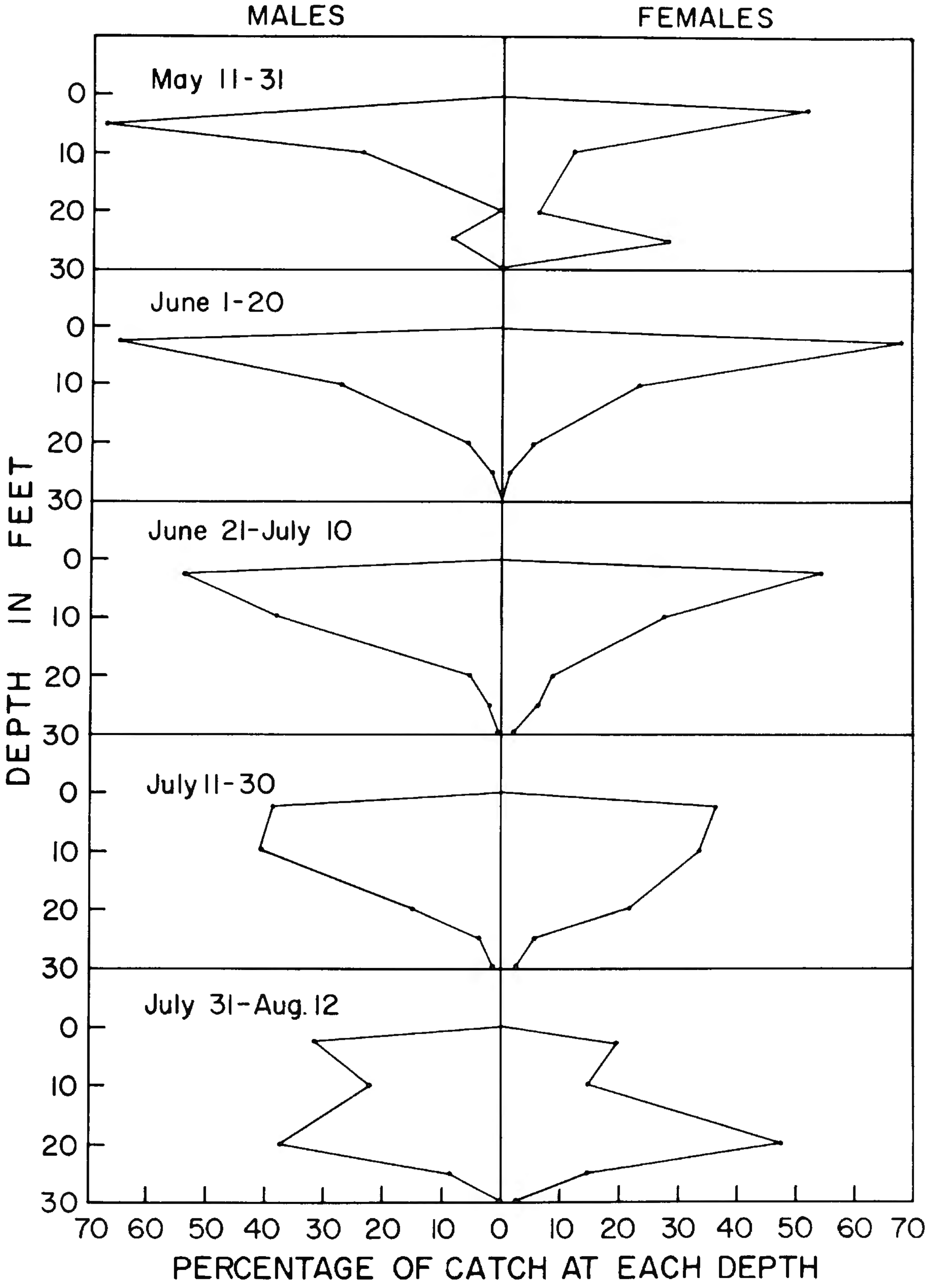

MALES
FEMALES
May 11-31
June 1-20
June 21-July 10
July 11-30
July 31-Aug. 12
DEPTH IN FEET
0
10
20
30
70 60 50 40 30 20 10 0 10 20 30 40 50 60 70
PERCENTAGE OF CATCH AT EACH DEPTH

Figure 9

Figure 10

Seasonal shift in bathymetric distribution of two-and-three year old crayfish in West Lost Lake, 1963

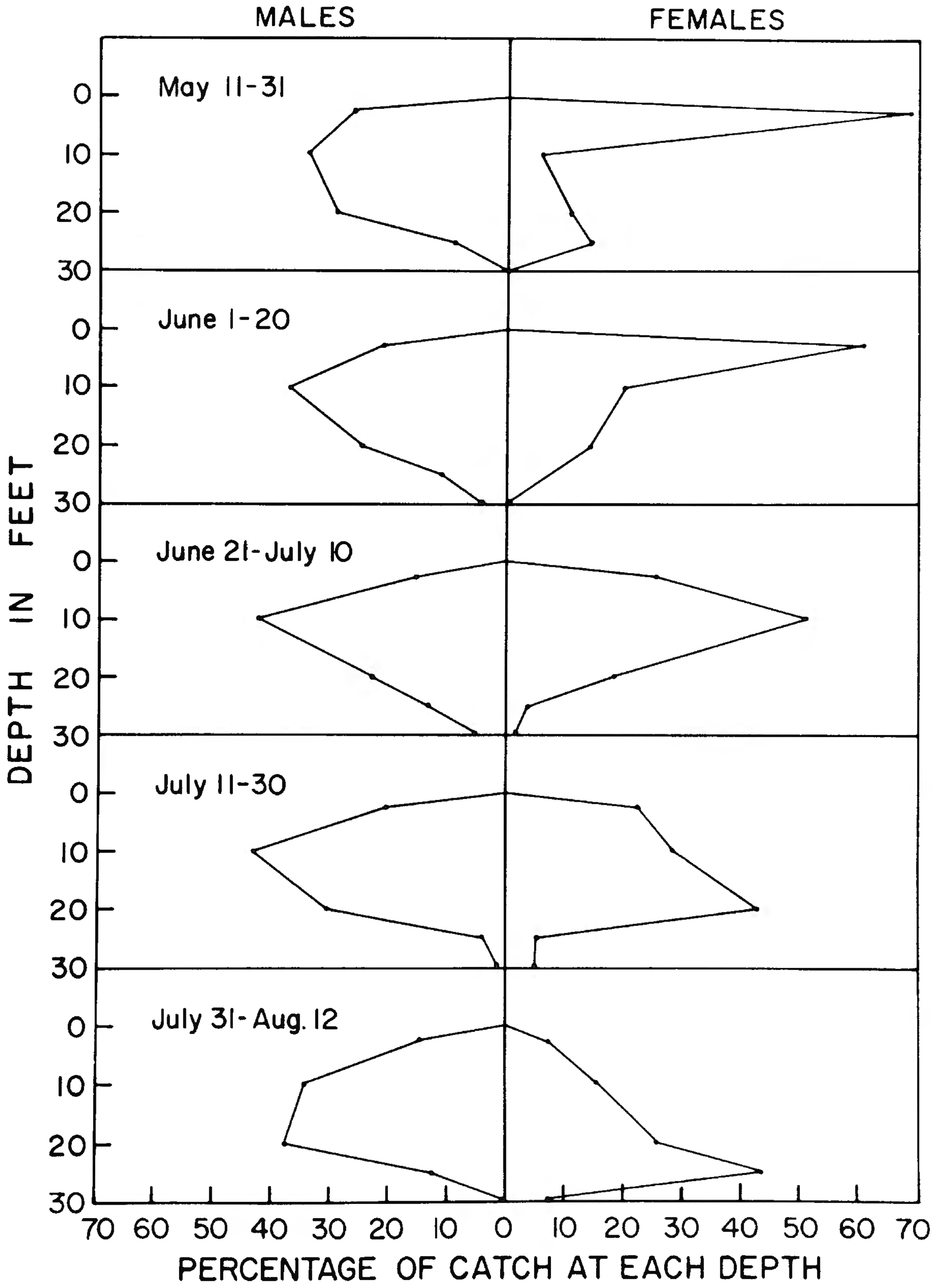

MALES
FEMALES
May 11-31
June 1-20
June 21-July 10
July 11-30
July 31-Aug. 12
0
10
20
30
DEPTH IN FEET
70 60 50 40 30 20 10 0 10 20 30 40 50 60 70
PERCENTAGE OF CATCH AT EACH DEPTH

Figure 10

concentration, and pH, light is the one environmental factor capable of regulating the movement of <u>O. virilis</u>. In the summer of 1963 the West Lost Lake population was concentrated in the middle of the thermocline. At this time the thermocline extended from 20 to 35 feet; and the temperature at 35 feet was 64°F. During the same time in 1962 most crayfish concentrated at the bottom of the thermocline at a temperature of 56.6°F. Roberts held that locomotor intensity is independent of the temperature between 32° and 78.8°F. Since migration in West Lost Lake follows the molt to maturity in yearlings and adults of both sexes, it may have been associated with the maturation of the gonads which could be related to the reduction in light intensity at these depths. Stephens (1952) found that length of photoperiod is involved in the reproductive cycle of <u>O. virilis</u> as for many other animals studied in this regard.

VI. DYNAMIC ASPECTS OF THE POPULATION

A. Seasonal Production

The tendency for the weight of a year class to be diminished by natural mortality is counterbalanced by the growth in size of its individual members. Thus the biomass of a year class of crayfish may increase, decrease, or remain static while the numbers of its members decrease.

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,

g = the instantaneous rate of growth, and

i = the instantaneous rate of mortality

Ways of determining g and i have been discussed previously. The values of g and i used to calculate the seasonal change in biomass per kilogram of recruits are given in Table 6.

Mortality was the most salient factor in determining trends in biomass for three-year-old males in the spring and for two-year-old females in the summer while growth was the most important when the animals were younger than these ages.

The two sexes reached their respective maximum at different times; for males, the maximum came in the summer of the third and for females, in the summer of the second growing season. The difference was a result of the greater mortality rate for two- and three-year-old females as compared to males of the same age (Fig.11). In the spring of the third growing season, female mortality was about ten times as great as that of males; in the fourth it was twice as great.

Although total production, in terms of weight for the sexes combined, was greatest in the summer of the second growing season, males reached their maximum weight in the summer of their third growing season. Variations in growth rate affected the accuracy of the calculated instantaneous growth rates. From a total weight at hatching of about 2 kilograms the year class reached a maximum of 55.5 kilograms by the end of the second summer (Table 9). Some decline in

Figure 11

Standing crop of crayfish in West Lost Lake

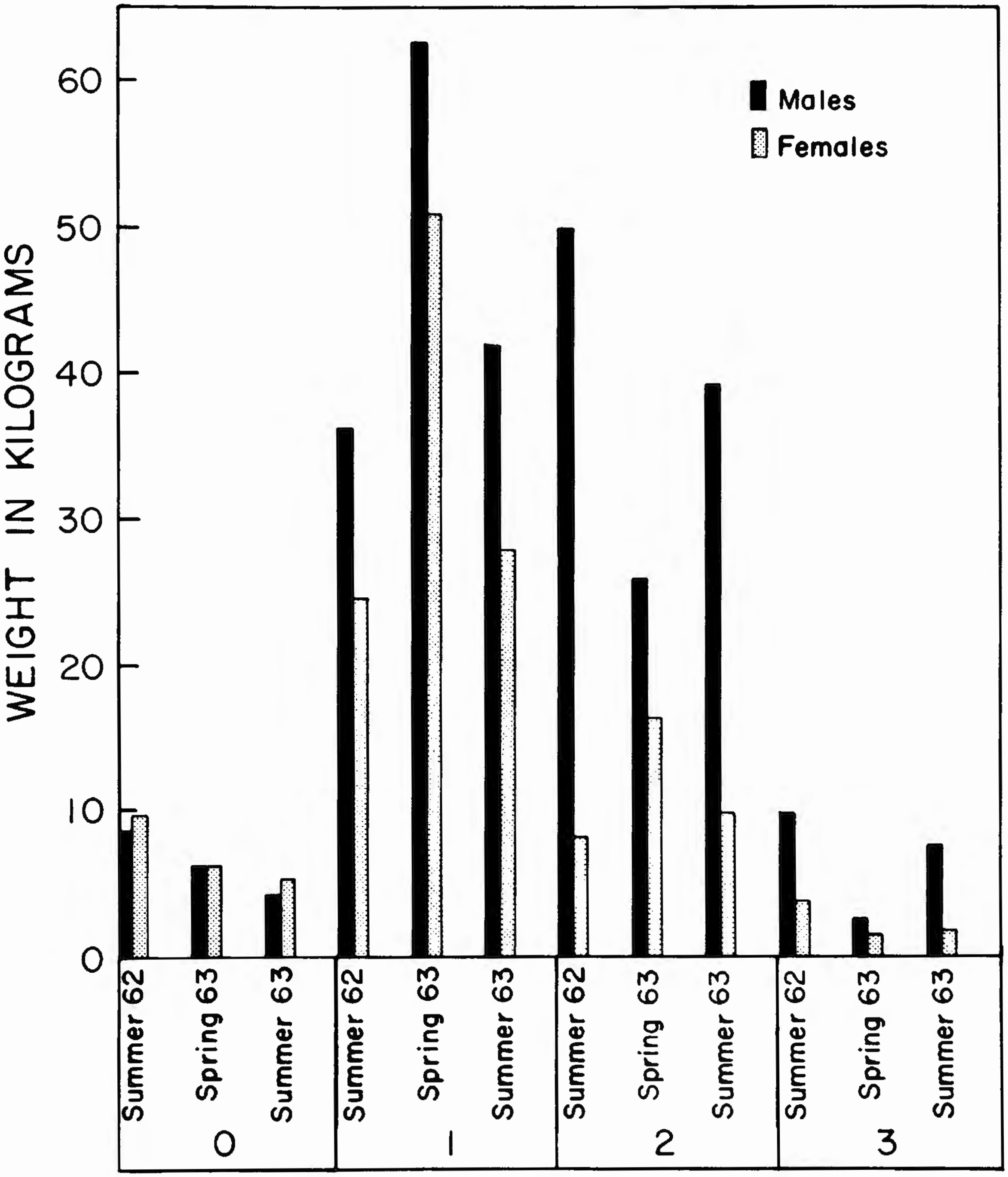

WEIGHT IN KILOGRAMS
0
10
20
30
40
50
60
Males
Females
Summer 62
Spring 63
Summer 63
0
Summer 62
Spring 63
Summer 63
1
Summer 62
Spring 63
Summer 63
2
Summer 62
Spring 63
Summer 63
3

Figure 11

TABLE 9

Theoretical changes in biomass for one kilogram of crayfish recruits at age-0 in West Lost Lake using the rates of growth and mortality from Table 6

Age and season	Males	Females	Total Kgs.
Spring 0	1.000	1.000	2.000
Summer 0	6.821	8.415	15.236
Summer 1	31.186	24.289	55.475
Spring 2	27.936	20.288	48.224
Summer 2	42.518	12.428	54.946
Spring 3	22.419	7.028	29.447
Summer 3	3.535	7.824	11.459

biomass occurred in the spring of the second year due to mortality of females, but the rapid growth of males produced a second peak, of 55 kilograms, about equal to that of the first peak, by the third summer. From then on biomass declined through the third year of life. Thus the biomass in the second year of life was nearly the same as in the first but the year class in the second year was mainly made up of male crayfish, both in numbers and weight. In the spring of 1963 about 70 per cent of the total weight of crayfish consisted of yearlings (Fig. 11) but by summer, although yearlings were still the largest age group present, their margin had declined to little over 50 per cent of the total weight. Most of this decline was due to mortality of females. Meanwhile, the other age groups increased in their bulk (Figure 12).

Over winter in 1962-63 only yearlings increased in total biomass in West Lost Lake. Two-year-olds declined slightly and three-year-olds severely, from the 57.7 kgs. estimated in late summer of 1962 to 4.19 kgs. in the spring of 1963.

The entire standing crops for 1962 and 1963 respectively were 150.2 kgs. and 137.6 kgs. showing a decline of 12.6 kgs. and corresponding to a drop in value from 40.6 kgs. per hectare to 37.2 kgs. per hectare. The age-0 year group was about one-half as large in 1963 as 1962 (18.3 kg / ha. to 9.5 kg / ha.). The crop of yearlings in 1963 was 9.0 kgs. per hectare greater. This partly compensated for the smaller crop of 0. year crayfish. While two- and three-year-olds declined, on a per hectare basis the spring crop did not vary greatly from the summer one. Thus the total weight went from

Figure 12

Seasonal change in biomass of a year class of *O. virilis* in West Lost Lake

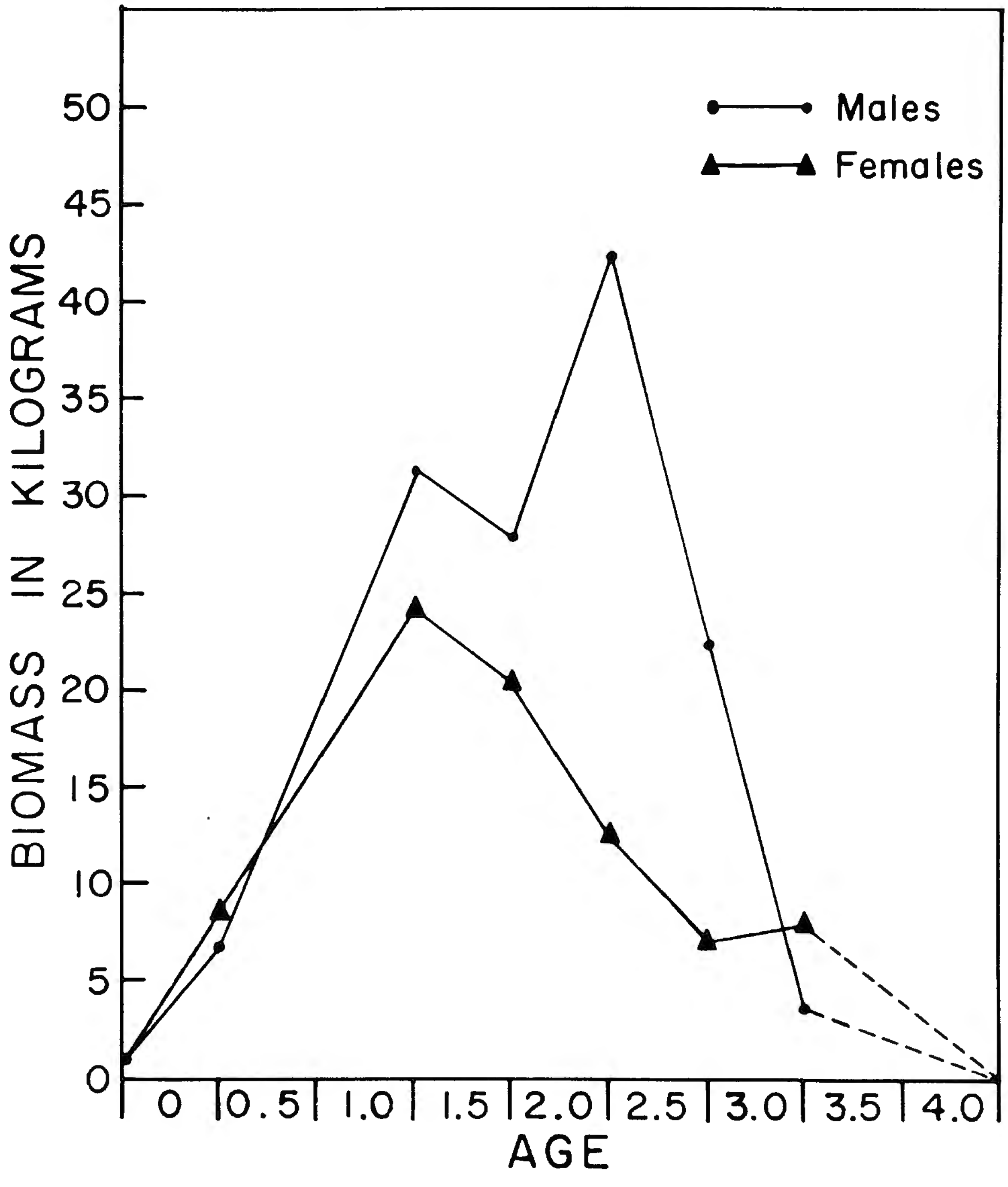

Males
Females
BIOMASS IN KILOGRAMS
50
45
40
35
30
25
20
15
10
5
0
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
AGE

Figure 12

100.3 ~~40.6~~ kgs. per hectare in the summer of 1962 to 119.5 ~~46.23~~ kgs. per hectare in the spring of 1963 to 91.8 ~~37.2~~ kgs. per hectare in the summer of 1963. Evidently the total standing crop remains rather constant despite changes in age group composition (Table 10).

The total standing crop reached a peak in the spring. Within it, the value for the yearling crop in the spring was estimated very carefully by taking the average of the age-0 group in 1962 and the age-one group in the summer of 1963.

Life-table data show a reproductive rate per generation, $R_0 = .777$ (Table 11) and indicate that the population was declining from its present level. However, since the 1963 year class was only one-half as large as that of 1962, this value must be accepted with caution. The 1963 year class could have been unusually small or that of 1962 unusually large.

Lack of suitable data prevents the establishment of the relationship between egg production and progeny. In 1963 the 2,253 female adults produced an estimated crop of 189,530 young. If the survival between spring and summer was the same in both 1962 and 1963, there were about 1,953 females at the time of egg production in 1962 (Table 3). At the average rate of egg production per female, the yield in 1962 and 1963 were in the same general magnitude, the number of progeny was estimated to be twice as large in 1962 as in 1963. This suggests that the difference in numbers of young produced was not primarily due to difference in the numbers

TABLE 10

Successive estimates of standing crop in kilograms of the crayfish in West Lost Lake

Age group and sex	Summer 1962	Total Males & Females	Spring 1963	Total Males & Females	Summer 1963	Total Males & Females
0 males	8.66		6.197		4.23	
0 females	9.66	18.32	6.197	13.39	5.23	9.46
1 males	36.16		68.53		41.87	
1 females	24.46	60.62	50.96	119.49	27.81	69.68
2 males	49.68		25.70		39.01	
2 females	8.04	57.72	16.28	41.98	9.98	48.99
3 males	9.80		2.55		7.65	
3 females	3.78	13.58	1.64	4.19	1.83	9.48
Total	150.24	100.27 ~~40.60~~ kg./ha.	179.05	119.49 ~~46.23~~ kg./ha.	137.61	91.83 ~~37.19~~ kg./ha.

TABLE 11

Life table for *Orconectes virilis* in West Lost Lake

x	l_x	m_x	$l_x m_x$
0	1.000	.000	0.0
0.5	.075	.000	0.0
1.5	.028	.000	0.0
2.0	.017	41.35	0.70295
2.5	.0088	0.000	0.0
3.0	.0014	53.5	.07490
3.5	.0013		0.0

$R_o = \sum l_x m_x = \sum 0.77785$

x = time in years

l_x = number of survivors out of 1000 during the interval x.

m_x = number of females produced by a female during the interval x.

R_o = reproductive rate per generation.

of the adult stock in the two years. The year 1963 was noticeably warmer and drier than 1962. The lake level in 1962 was so high that the shoal area was extended by flooding, and vegetation normally on dry land was immersed.

It is difficult to compare published estimates of crayfish production with those from West Lost Lake because most of them are from shallow ponds. *Orconectes immunis*, well adapted to life in stagnant shallow warmwater ponds, yielded between 46 3/8 and 255 ¼ lbs. per acre (Tack 1941). Tack's highest standing crop was attained in a pond fertilized at two-week intervals with hay and cottonseed meal and the lowest was in a pond also fertilized at two-week intervals with hay, but this pond contained another decapod, the freshwater shrimp, *Palaemonetes exilipes*. Tack quotes Lydell (1938) as giving standing crop estimates of 689 to 811 lbs. per acre for *O. immunis* in a 4.35-acre pond. Goellner (1943) had values of 50 to 1200 lbs. per acre for *O. immunis* in ponds. Wickliff (1940) gave estimates of the standing crop of "stream crayfish" to be between 26.9 and 651.8 lbs. per acre. The species was not indicated.

Although West Lost Lake is a coolwater, sand-bottomed, marl lake its standing crop of crayfish is greater than that in ~~six~~ FIVE of the ten mud bottomed, productive ponds discussed by Tack (*op. cit.*).

The highest standing crop estimate from West Lost Lake was 101.7 lbs. per acre in the spring of 1963, declining to 81.8 lbs. per acre in the summer. These values can be compared to the trout harvest for 1962 which was 23.7 lbs. per acre and a standing crop estimate for bottom invertebrates in 1948 of ~~3.05~~ 5.75 lbs. per acre (Tanner, 1952).

The food habits of the crayfish demonstrate its role as a primary consumer in this marl lake. Contents of 31 crayfish stomachs collected on September 10, 1962, and of 26 taken on May 20, 1963, were composed of the green algae from the marl incrustations on rocks and other fixed objects in the water. Also found was the "aufwuchs" associated with the surface of these incrustations as well as remains of higher plants which were of common occurrence. No seasonal difference in stomach contents was noted. In addition, crayfish acted as scavengers on animal remains when present. Thus they may be classed principally as herbivores and fortuitously as scavengers.

Higher aquatic plants are usually scarce in marl lakes, a factor that probably limits the production of many bottom invertebrates other than crayfish. The ability of crayfish to use marl producing algae and associated "aufwuchs" as a source of food places them in a unique position in the trophic structure of marl lake ecosystems. This may be a factor why annual crayfish net production in West Lost Lake ~~nearly equals~~ IS 8.9X that of all the other bottom invertebrates combined. The net production of crayfish between the summers of 1962 and 1963 was ~~173.2~~ 310.8 kgs. This production is equal to the total number of animals dying during the entire yearly life cycle multiplied by their weights at the time of mortality. Net production in crayfish is ~~1.26~~ 2.33 times the summer standing crop and is the turnover rate of biomass in the population. This rate of turnover is ~~almost~~ 2.33

greater than ~~exactly the same as~~ the value of 1.25 estimated by Borutsky (1939) for all of the bottom invertebrates in Lake Beloie. He also gave turnover rates for the following invertebrates: *Tanypus* sp. .75, *Corethra* sp. 2.5, Oligochaeta 1.27. For *Tanytarsus jucundus*, the reported net production for a Southern Michigan lake is 67 lbs/acre and the turnover rate, 3.6 (Anderson and Hooper, 1956). The turnover rate for the total bottom fauna of one lake has been given as 3.5 (Gerking, 1962).

Taking the standing crop of bottom invertebrates other than crayfish in West Lost Lake in 1948 of 5.7 lbs. / acre (Tanner 1952) as a representative value and a reasonable estimate of maximum turnover rate to be 3.6, the net production might be 20.7 lbs./acre. If this is so the net production of 18.4 lbs./acre I calculated for the crayfish population very nearly 8.9 X ~~equals~~ that of all the other bottom invertebrates together.

A comparison of the percentage daily numerical turnover rate of crayfish with two other aquatic invertebrate crustaceans reveals that crayfish have the lowest rate, as follows: *O. virilis*, 2.0; *Hyallela azteca*, 2.5 (Cooper 1964); and *Daphnia*, 25.0 (Hall 1962). Since both *Daphnia*, a cladoceran, and *Hyallela*, an amphipod, have a much shorter life cycle than *Orconectes*, the difference may not be unexpected. Quite possibly if converted to weight units the difference among the foregoing may not be so great. Also predation is very effective on the later life history stages of these animals as compared to its effect on only the early life history stages in this crayfish. The rate of removal by predation may help maintain the high turnover rates for the cladoceran and the amphipod.

B. Comparative Effects Of Predation By The Brook Trout

Predation by the brook trout not only affects the dynamics of the crayfish population *per se* but it may interact with other factors that regulate abundance of the crayfish.

Analysis of the seasonal food habits of the brook trout in West Lost Lake showed that only fish 8.6 inches or longer were important as predators of the crayfish. The smallest fish that had eaten a crayfish was 7.7 inches long and only 4 of the 29 fish that contained crayfish were less than 9.1 inches long. Hence monthly predation rates were determined from stomach content analysis of trout of a mean length of 8.6 inches and above.

Predation rates were assessed as follows. At monthly intervals the numbers of fish greater than a mean length of 9.0 inches were estimated by the staff of the Pigeon River Trout Research Station in the autumns of 1962 and 1963 and in the spring of 1963 using the Petersen mark and recapture method. From these estimates the total instantaneous mortality rate (*i*) was obtained for the period October 1962 to October 1963 by the method of Ricker (1958a). The instantaneous fishing mortality rate (*p*), known from creel census records, was subtracted from the total instantaneous mortality rate (*i*) to give the natural instantaneous mortality rate (*q*) for the brook trout population. The percentage of each of the year classes present in the lake that was 8.6

inches in length or longer was determined by a graphical method (Fig. 13) given by Allen (1954). This method provides estimates of the proportion of a year class that is legal-sized for any given mean length and size limit. In Figure 13, the mean length corresponding to that of the fish under consideration is found on the right hand vertical scale, and the diagonal line followed to the left of the point of intersection with the horizontal line associated with the 9-inch limit (left hand vertical scale). From this point of intersection, the vertical line is followed downward to the percentage value of the year class which is of "legal" size, i.e., 9 inches or longer. The relative deviation used in calculating the values in the graph is 0.111 and was taken from a brook trout population study in Wisconsin (McFadden, 1961) since large enough samples were not available from the West Lost Lake trout population for this purpose. The numbers of trout longer than, or equal to 8.6 inches present in the lake at monthly intervals was then multiplied by the average number of crayfish eaten in one day by a 9-inch or longer trout. This gave the number of crayfish eaten by the population of 9-inch or longer trout in one day which was then multiplied by a correction factor for the daily rate of passage of food through the fish stomach. The correction factor was constructed arbitrarily from data given by Hess and Rainwater (1939) and Phillips et al. (1960). The mortality due to trout predation and the contribution of a year class of crayfish to the food of the trout could then be estimated for the entire year (Table 12).

TABLE 12

Number of crayfish eaten monthly by nine-to-twelve inch trout in West Lost Lake, Michigan

Month	Numbers of 9 to 12 inch trout present	Average Numbers of Crayfish Eaten/day	*Digestion Rate Factor	Number of Days	Total Crayfish consumed
Aug.	122	46.0	1	31	1,426
Sept.	108	51.7	1	30	1,551
Oct.	108	0.0	2	30	0
Nov.-Dec.	129	28.4	2	61	866
Jan.-Feb.	94	81.7	4	59	1,204
Mar.	86	172.0	4	31	1,333
Apr.	64	37.1	2	30	555
May-June	79	0.0	2	30	0
July	110	60.5	1	31	1,875
Aug.	116	20.9	1	31	648
Sept.	109	50.1	1	30	1,503
Oct.-Nov.	104	0.0	2	31	0

*Estimated from data by Phillips, A. M. et. al. (1960) and Hess and Rainwater (1949), 1 = 24 hrs., 2 = 48 hrs., 4 = 96 hrs.

Figure 13

Relationship of mean length of a year class to percentage of fish of legal size under various minimum size limits based on a relative deviation of 0.111

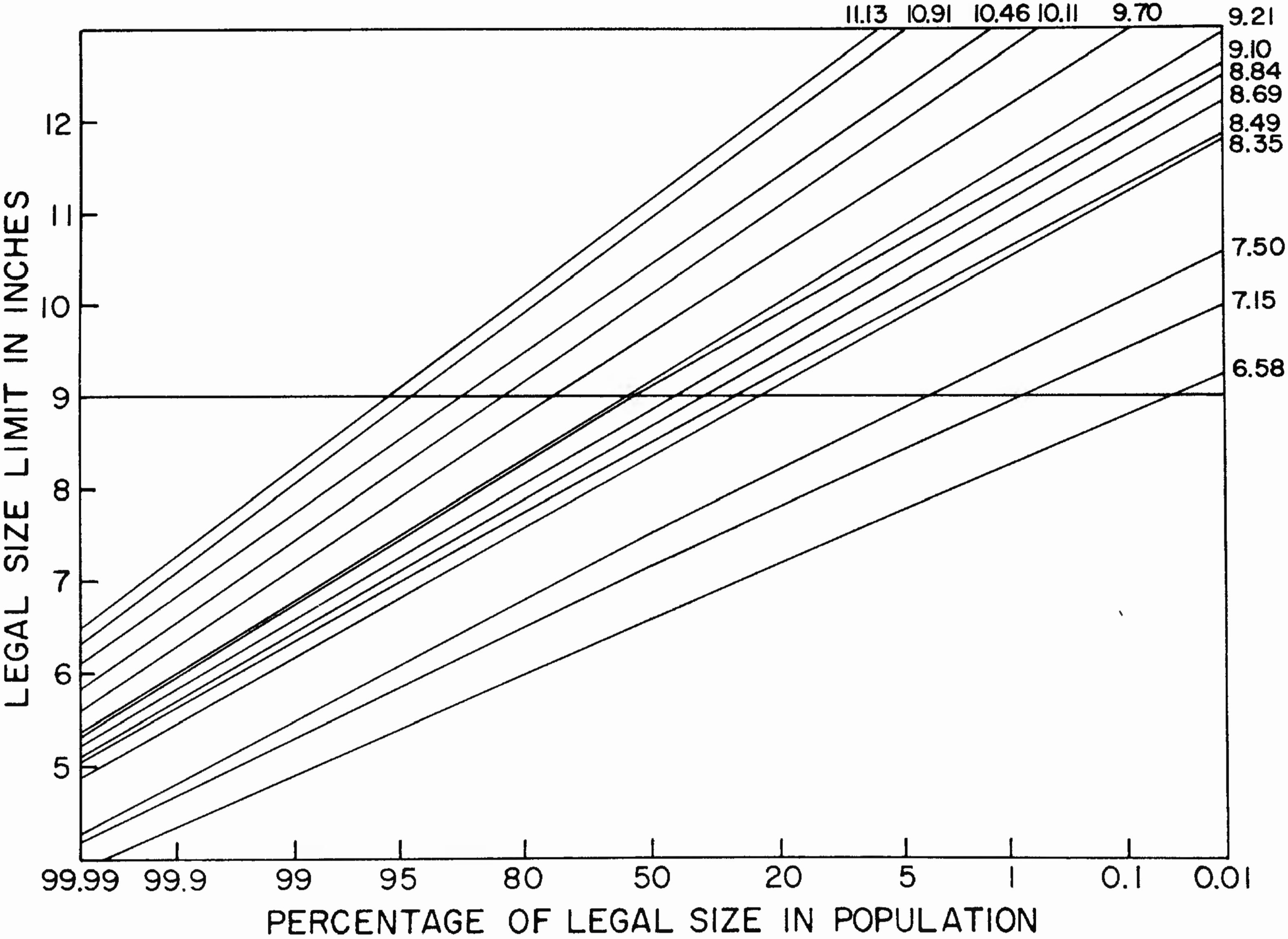

11.13
10.91
10.46
10.11
9.70
9.21
9.10
8.84
8.69
8.49
8.35
7.50
7.15
6.58
LEGAL SIZE LIMIT IN INCHES
12
11
10
9
8
7
6
5
99.99
99.9
99
95
80
50
20
5
1
0.1
0.01
PERCENTAGE OF LEGAL SIZE IN POPULATION

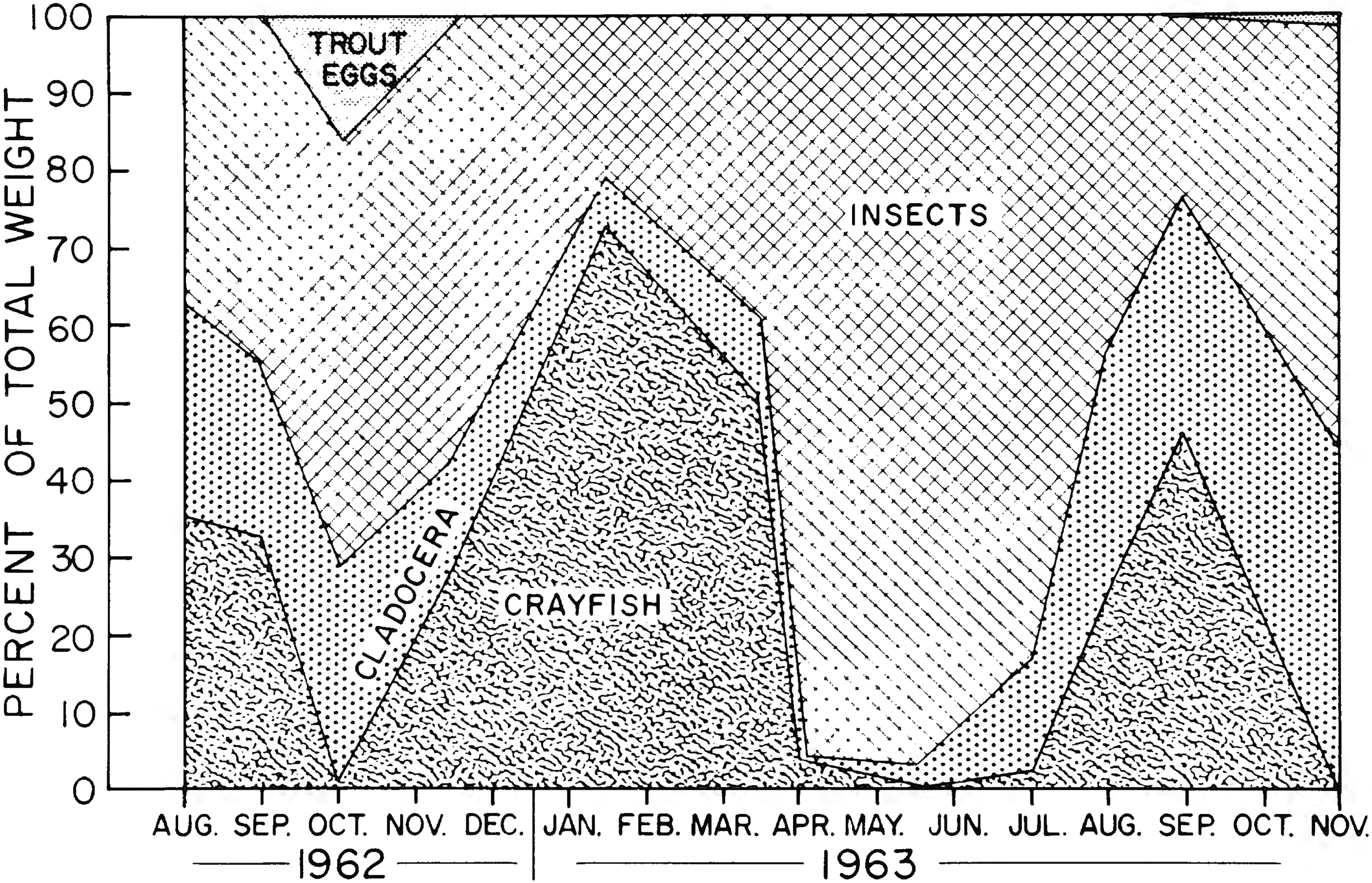
Figure 13

The brook trout in West Lost Lake fed exclusively on young-of-the-year crayfish in all seasons; at least no adults were found in the 273 stomachs examined. The contribution of a year class as a food item for the trout can be derived from the estimate of the young-of-the-year crayfish consumed in a time interval divided by the estimated number present at the beginning and end of that interval. On this basis, brook trout predation accounted for 2.8 per cent of the total mortality rate of young-of-the-year crayfish between July and October, while from October to June 56.0 percent of the total mortality rate was due to predation of the trout. The trout was therefore an effective predator on crayfish between one half and one years old. No predation occurs after the crayfish are one year old because they become too large to serve as trout food.

During the winter months some of the increased predation on crayfish in the second half of their first year of life probably occurs because of the lack of emerging insects which form so very large a part of the trout's diet in the early summer (Fig. 14). The trout effectively use crayfish as food during the winter also because crayfish increase in weight substantially during the second half of the first growing season; the average weight at hatching being 0.06 gms. vs. 0.73 gms. at the end of summer. The utilization of crayfish declines abruptly in April, by June it is nil, but it begins to rise again in July. One apparent reason for the decline in June is that most yearling crayfish are larger than 21 mm., which is the upper limit of size eaten by the brook trout;

Figure 14

Monthly summaries of the stomach contents of 239 specimens of the brook trout 5 to 14 inches long from West Lost Lake expressed as percentage of the total weight of the food



100
90
80
70
60
50
40
30
20
10
0
PERCENT OF TOTAL WEIGHT
TROUT EGGS
INSECTS
CLADOCERA
CRAYFISH
AUG.
SEP.
OCT.
NOV.
DEC.
JAN.
FEB.
MAR.
APR.
MAY.
JUN.
JUL.
AUG.
SEP.
OCT.
NOV.
1962
1963

Figure 14

meanwhile, the young-of-the-year have not yet hatched to provide an understory of animals of suitable size for consumption. From July to November, a second period of intensive utilization occurs but it was not as great in terms of weight as that of the winter period. In July, an average of 60 crayfish a day were eaten which averaged 11 mm. in length compared to 43 mm. in March; in terms of weight, the consumption per day amounted to 30.0 gms. in March vs. 0.4 gm. in April. From October through November no crayfish occurred in the stomachs examined, but trout eggs appeared. This interval is the spawning season for the brook trout. Since suitable spawning grounds with flowing water are not available, the eggs are simply dropped on the bottom. Seasonally these eggs may buffer predation on crayfish young by the trout.

In summary, the maximum periods of utilization of crayfish by the brook trout are in midwinter and late summer, and only young-of-the-year crayfish are consumed. Periods of little use of crayfish by trout are in early spring and late fall. One must note, though, in comparing the standing crop of crayfish available for food of trout that only the young-of-the-year can be used correctly for comparison with other items. Thus, out of a total standing crop of 150.2 kgs. for the summer of 1962 only 18.3 kgs. were available as trout food, for the spring of 1963, 13.3 kgs. out of a total of 179.0 kgs. and for the summer of 1963, 9.4 kgs. out of 137.6. The drop of almost 50 per cent from the summer of 1962 to that of 1963 is notable.

Predation by the brook trout has its most evident effect on the age distribution of the crayfish population. The population responds by adjusting the survivorship distribution rather than by a change in fecundity values because adult crayfish are not subject to intense predation. To confirm that the crayfish population was large enough to withstand the predation to which it was subjected and also to predict the effects of an increase in predation on the population, pertinent experiments could not be conducted in the allotted time, especially not with necessary replications. Nevertheless, some of the theoretical effects of various rates of predation can be examined by using Ricker's formula for estimation of equilibrium yield at different rates of fishing predation (Ricker, 1958a). The population growth and mortality are broken into short enough time intervals so that neither growth rate nor mortality are too rapid within any period. Then if growth rate balances death rate in such a short period one can compute the net change in bulk of a year class. In order to test the resiliency of the crayfish population to trout predation, I have used Ricker's equilibrium yield equation and have substituted the predation rate of trout for the fishing mortality term (which is predation by man) to give the equilibrium yield of crayfish for varying rates of trout predation (Table 13). Only the yield of young-of-the-year females per unit weight of female recruits need be calculated since it alone determines the increases, decreases, and stability of the population. The growth rate and the total instantaneous mortality for the young-of-the-

TABLE 13

Equilibrium yield of female young-of-the-year crayfish at varying rates of predation by brook trout 8.6 inches or more in length, in West Lost Lake, Michigan

Rate of Predation	Yield in Kgs. per Kg. of Female Recruits	Density of Predator Population
1/2 p	03.86	50
p	07.94	100
2p	10.95	200
3p	18.92	300
4p	12.27	400
5p	14.32	500
6.0p	12.85	600
7p	11.52	700
8p	9.65	800
10 p	5.16	1000

p is the instantaneous rate of mortality due to the predation of brook trout; p for the 0 to 0.5 age group is 0.059; p for the 0.5 to 1.0 age group is 0.469.

year gave the net change in bulk for the period for which the equilibrium yields per kg. of recruits were determined. The young-of-the-year were divided into two age groups, those less than a half year old and those between a half and one year of age, because natural mortality and predation rates varied considerably for these two age intervals. More than 50 per cent of the total mortality rate of young-of-the-year female crayfish was due to predation during the second half of their first year of life as compared to less than 7 per cent in the first half.

To determine the effect of predation, the predation rates or multiples thereof were added to the instantaneous mortality rate to give the effect of the difference in the weight change factor on yield of young-of-the-year crayfish (Table 13). On this basis the yield per kg. of recruits would reach its replacement value at a predation rate about six times the present rate. This points out the resiliency of the crayfish population to predation by trout. If we assume that predation rate is proportional to the population density of trout larger than or equal to 9 inches, the maximum density of these trout (predators) which the crayfish population (prey) can support is about 600 fish. A threefold increase from the present average of about 100 fish to 300 fish INCREASES ~~reduces~~ yield about one third, from 8 to 12 kgs., and when raised to 500 fish yield is reduced to 14.3 kgs. At 800 fish the crayfish population is not able to withstand predation and would decline to about one FIFTH its previous YIELD ~~abundance~~.

This estimate involved several assumptions: (1) the growth of the crayfish and that of the fish not are not dependent on population density; (2) crayfish reproduction rates are not substantially altered by changes in density; (3) predation remains proportional to density of predators; and (4) increase in the rate of predation does not alter mortality due to other causes, i.e., mortality due to other factors remains constant.

Even though some of the assumptions are not strictly met, the results confirm the suspicion that the crayfish population could easily withstand an increase in the predation rate by trout beyond that at present because trout predation is not the main source of mortality. It appears to be of real importance as source of mortality only in the winter months.

What then may be the other sources of major mortality for the crayfish population? Trout predation does not account for a large part of the losses of young-of-the-year crayfish in the first full year of growth.

Predators, e.g., dragonfly nymphs, small frogs, aquatic snakes, turtles, etc. which are relatively harmless to large crayfish, may contribute to the mortality of the young. Few large potential predators are found in West Lost Lake. Though abundant, the painted turtle, Chrysemys picta marginata is not known to be an extensive predator of crayfish (Lagler, 1944). Only two adult crayfish were found in the stomachs of a collection of 33 green frogs, Rana clamitans. Birds (e.g., mergansers, herons, etc.) are not abundant in this area in the summer, and the ice cover prevents predation in the winter by either birds or mammals (e.g., the otter). Though they can be of importance in streams, the lack of an extensive shoal area eliminates mammals and birds as important in West Lost Lake. The flatness of the survivorship curve after the first year of life indicates good survival up to the end of the life span when suddenly there is a large rise in mortality that is due ostensibly to old age.

In aquaria, crayfish display very aggressive behavior and dominance by the largest and strongest individuals over the weakest and smallest ones. This dominance often results, through cannibalism, in the survival of only one crayfish of several originally placed in an aquarium. Periods of molting are especially dangerous and often the newly molted individual is eaten by the others if some sort of shelter is not available to it. Newly molted animals are characterized by erratic and sensitive behavior; they are very active and violent when disturbed. Therefore one of the causal factors of mortality probably includes the physiological stresses of molting individuals. These conditions occur much more frequently in young than in adults. Soft-shelled newly molted young individuals are susceptible to predation by trout and to cannibalism by other crayfish.

Molting is a vulnerable time for crayfish not only because for 24 to 36 hours after the molt, the newly molted crayfish has a very soft exoskeleton, but the withdrawal from the old exoskeleton, if mechanically impaired, results in death. In nature male adult crayfish molt in the spring before females. Males are thus the first to have a hardened exoskeleton and move and feed actively; meanwhile, females are in seclusion till the young leave them. Males do undergo a second molt in the summer slightly after the females begin their only molt of the season. Another source of increased mortality for females is the possibility that their resistance may be somewhat lowered from carrying the young. Overall physiological condition at the time of the molt apparently can be a significant factor in determining survival. Availability of food is not considered to be a factor of prime import in their survival since it seems that herbivorous invertebrates seldom lack food in an aquatic environment.

In summary, predation is not here considered to be as important a factor in limiting population size as the behavior of the animals, combined with the physiological and mechanical problems associated with molting. In West Lost Lake predation has its main impact on the overwinter survival of the young-of-the-year and, although it removes about 37 per cent of these individuals, more than enough are left to restock the population.

For the brook trout in West Lost Lake efficiency of crayfish utilization could be improved by stocking fish at a larger length than the present 5 inches. Such larger fish would quickly reach effective predator length of nine inches or more. One could also introduce another species of crayfish, O. propinquus. This species might be a more suitable forage than O. virilis because it attains a much smaller size, and has about the same reproductive potential. However, it might be a little less resilient to predation since it has only one brood per generation. If the effect of heavy predation on young-of-the-year of *O. virilis* comes while natural mortality is still in the compensatory stage, it is equivalent to a reduction of the spawning stock which produced the brood in question. Theoretically, such a reduction in spawning stock will at first increase net production of recruits which in turn produces an increased number of eggs and a large increase in numbers of young-of-the-year in future years. This would hold only if *O. virilis* is one of the species for which numbers of recruits begin to decrease after the stock reaches some large magnitude. The stock would continue to increase until a level is reached that produces maximum recruits (Ricker, 1954). For *O. virilis* all of this would depend on whether or not it has a density dependent type of mortality. At present there is a lack of data necessary to contrast the reproductive potential of adults with the density of stock that produced them.

VII. SUMMARY

This study of the role of a large aquatic invertebrate in the trophic dynamic aspect of marl lakes suggests that crayfish make efficient use of the energy not available to most of the other aquatic invertebrates in such ecosystems. It also contributes much to the understanding of predator-prey relationship between fish and crayfish by measuring the effect of trout predation on the population dynamics of crayfish.

Density and age structure of the crayfish stock in West Lost Lake, Michigan as determined from systematic estimates of the population size, showed that year class fluctuation was a feature of the age structure of the crayfish population. The 1963 year class was twice as large as that of 1962. A typical year class of the crayfish began with the production of some 180,000 eggs in the spring. From these about 13,000 to 25,000 young-of-the-year survived till September. By the next spring, overwinter mortality reduced this to 18,000 individuals. By the end of that summer 8,000 to 11,000 yearlings were left. Overwinter mortality reduced this number to 5,000 from which about 4,000 were left at the end of the third growing season. Only 500 to 700 survived the third winter. The maximum age is therefore at three years.

At the start of the first summer of growth females outnumbered males, the annual mortality rate for males was 0.94 compared to 0.925 for females. After the first summer's growth, male survivorship exceeded that of females. After the first year, the death rate for females was highest in the second year, a natural annual rate of 0.49 compared to 0.05 for males. For males, greatest death rate occurred in the third year of life, a rate of 0.40 compared to 0.06 for females. The overwinter mortality rate was severe for both sexes. For males, at age 0 it was 0.38, at age one it was 0.61, at age two it was 0.15. For females it was 0.63 at age 0, 0.39 at age one and 0.84 at age two. Mechanical and physiological problems associated with molting probably accounted for much of the severe mortality that always occurred during a molting period. Survival of young-of-the-year did not appear to be caused by differences in numerical size of adult stock. Though the adult female stock was the same in both years, in 1963 the age 0 population estimate was 12,900 whereas in 1962, it was 24,971. Other than predation by the brook trout, factors contributing to mortality in the first year were not identified.

Because adult males molted twice, whereas females molted only once they were larger than females of corresponding age. This difference in rate of growth between sexes could be also detected in the 0-age group with males larger than females. Maturity for both sexes occurred in the second growing season (age one), and mating took place from July until October. Males were larger at maturity than females, an average respectively of 29.4 mm. versus 26.7 mm. The age structure of the population varied considerably throughout the growing season because of differential survival of year classes at different ages. In the two years under study a wide range of sizes was attained by the 0-age groups which persisted throughout the growth histories of the two groups. The average carapace lengths for males in September was 15.2 mm. at age 0, 30.9 mm. for age one, 36.8 mm. for age two, and 40.9 mm. for age three. For females the corresponding average lengths were 14.6 mm. for 0, 28.0 mm. for age one, 31.5 mm. for age two, and 36.9 mm. for age three.

Productive capacity determined from counts of attached eggs was 58 per cent of the potential obtained from counts of ovarian eggs. Age three females averaged 107 eggs per individual; age two females, 83 per individual. Maturity occurred during the second growing season (age one) but the eggs were laid first the next spring. The percentage of ovarian eggs not found attached to the pleopods was about the same for all but the largest females which were more active than the smaller ones and less able to find places of refuge. The two-year-old females in the population produced most of the season's eggs (92.5 per cent).

After the young-of-the-year leave the female, they remained along the shore at depths of less than 5 ft. The adult females molted shortly thereafter, and migrated to a depth of 25 ft. where they concentrated throughout the summer. The adult males also migrated but concentration in the deep water was less pronounced than that of the females. This female migration may be associated with the reproductive cycle of the female since the migration follows the molt which precedes the breeding season.

A year class made its greatest contribution to total biomass in the summer of the second growing season at age one. The increase in male biomass from 31 kg. to 42.5 kg., produced another peak in the third growing season at age two even though the female biomass at age two declined from 24 kg. to 12 kg. The maximum peak of biomass of 179 kg. occurred in the spring. Only a slight difference in standing crop existed between two successive summers; in 1962, it was 150.2 kgs., and in 1963, 137.6 kgs. A decline in young-of-the-year from 18.2 in 1962 to 9.5 in 1963 kgs., was offset by an increase in age one crayfish from 60.6 in 1962 to 69.7 in 1963.

The effect of year class fluctuation on age structure and production was evident. The low reproductive rate per generation of 0.78 includes the small 1963 year class. Compared to other estimates of standing crop for crayfish, 82 lbs./acre in the summer of 1963 was nearly the lowest among several previously cited, but most of the values reported were for shallow, warm water, fish cultural ponds.

The total net production of crayfish in West Lost Lake between the summers of 1962 and 1963 was 173 kgs. with a turnover rate of 1.3, which compares favorably with that of estimates for other bottom invertebrates. With 3.6 as a reasonable estimate for the maximum rate of turnover of the other bottom fauna in West Lost Lake, annual net production is 20.7 lbs./acre. This value is MUCH LESS THAN THE 184.8 ~~nearly the same as the 10.3~~ lbs./acre for the crayfish population. The ability of the crayfish to utilize the part of the energy in a marl lake ecosystem not available to most of the other bottom invertebrates accounts for this high level of net production.

Predation on the crayfish by the trout was almost entirely confined to fish greater than 9.0 inches in length. During the winter months it accounted for about 37 per cent of the natural mortality of the young-of-the-year. In contrast, during the summer and fall it accounted for less than 7 per cent of the mortality of the young-of-the-year. Crayfish older than one year, after they had reached a carapace length of 21 mm. ap~~x~~pro. , were not eaten by trout. Trout predation on crayfish reached two seasonal peaks, midwinter and late summer whereas intervening periods of reduced predation were in the spring and late fall. The increased predation in midwinter occurred perhaps because of a lack of emerging insects. The weight of crayfish eaten by trout was greatest in winter, when young-of-the-year crayfish were individually at maximum weight. In comparing crayfish to other trout food such as insects and cladocerans, only the age-0 component of its standing crop can be used. Thus out of a standing crop of 150.2 kgs. present in the summer of 1962, only 18.3 kgs. (the 0-age group) was available as food to the trout. Since trout predation involves the age-0 year class it does not affect fecundity values, but only the age distribution within the population.

To test the effect of increased trout predation on crayfish, I used Ricker's equilibrium yield equation and have substituted rates of trout predation for fishing mortality term. This disclosed that crayfish could even withstand predation by trout at a theoretical maximum density of 600 fish, about six times the present predator population density. Predation was not as likely a factor in limiting population size of the crayfish as the aggressive behavior of the crayfish (indicated by observations in laboratory aquaria) combined with the physiological and mechanical problems associated with molting. Thus though trout predation removed some [illegible] per cent of the young-of-the-year during the winter months more than enough survived to restock the population.

Increased yield to the trout from the crayfish population could be improved by stocking larger fish than those presently stocked or perhaps by introducing another species of crayfish such as *Orconectes propinquus*, which grows to a smaller average maximum size than *O. virilis* yet has about the same reproductive protential.

The present rate of removal of young-of-the-year crayfish by the trout is equivalent to a reduction in the spawning stock which produced the brood in question. If the reproduction in *O. virilis* decreases after the stock reaches some large magnitude (i.e., density dependence) then the net increase in reproduction of recruits resulting from a reduction of adult stock by increased fish predation would increase the number of eggs. This would permit a large increase in young-of-the-year in future years, thus increasing the yield to trout.

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