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THE POPULATION DYNAMICS AND FOOD HABITS OF
THE CRAYFISH ORCONECTES PROPINQUUS (GIRARD)
IN NORTHERN MICHIGAN STREAMS

presented by

Robert Scott Stelzer

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of the requirements for

M.S. degree in Zoology

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THE POPULATION DYNAMICS AND FOOD HABITS OF
THE CRAYFISH ORCONECTES PROPINQUUS (GIRARD)
IN NORTHERN MICHIGAN STREAMS

By

Robert Scott Stelzer

A THESIS

Submitted to
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ABSTRACT

THE POPULATION DYNAMICS AND FOOD HABITS OF THE CRAYFISH ORCONECTES PROPINQUUS (GIRARD) IN NORTHERN MICHIGAN STREAMS

By

Robert Scott Stelzer

Two populations of O. propinquus were studied from the Ford River (hard water) and Baraga Creek (soft water) in northern Michigan. Mean crayfish abundance and total net production were greater in the Ford River (9.3 one year old individuals/m² vs 3.0 one year old individuals/m² in 1989, 8.9 g/m² vs. 5.8 g/m² during 7/14/89-7/14/90). Individual growth was greater in Baraga Creek. Early instar Ford River crayfish experienced considerable mortality from the pleopod egg stage through their first three weeks of independence. Some early instar crayfish appeared to change the kind of microhabitat they used as they matured. Diet studies revealed Ford River Orconectes propinquus ate predominantly diatoms, filamentous green algae, and insects, with insects more abundant in juveniles. The diatoms Navicula and Gomphonema achieved different relative abundances when each genus was compared between juvenile and adult crayfish. Some evidence suggests that O. propinquus was selecting Chironomidae from the environment.

This Master's Thesis is dedicated to my parents
Robert William Stelzer and Dolores Jane Stelzer,
whose love and nurturing has allowed me to
pursue a career in biology.

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There are several people that helped with this work. I especially thank Dr. Thomas Burton, Michigan State University, for his guidance, helpful criticism, and general willingness to discuss the progress of my research at any time. He also introduced me to the streams of northern Michigan and first suggested a hard water/soft water comparison study. Dr. Darrell King and Dr. Donald Hall, both of Michigan State University, provided helpful insight at several key junctures during the study. Dr. Hall was the impetus for my study of early instar O. propinquus. Ms. Susan Eggert, Ms. Deborah Repert, and Ms. Melissa Trembl provided much appreciated assistance in the field. Dennis Mullen allowed me the use of his block nets for the duration of my research. I kindly thank Dr. Horton H. Hobbs Jr., Smithsonian Institution, for help with species identification. Mrs. Jennifer Molloy, Michigan State University, contributed helpful guidance with regard to diatom identification. Lastly, Dr. Charles Cress, Michigan State University, provided useful suggestions regarding statistical analysis.

PREFACE

Due to the strong differences among the kind of questions asked and addressed in this study, the thesis was divided into two chapters: 1) Population studies of O. propinquus in two northern Michigan streams. 2) Diet Analysis of O. propinquus in a northern Michigan stream. These two chapters each have separate introductions and were attempted to be made self-sufficient. Themes from each chapter are addressed in a common conclusion at the end of this report.

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Chapter 1: Population studies of O. propinquus
in two northern Michigan streams

INTRODUCTION

Crayfish are often very numerous in freshwater ecosystems and can dominate the invertebrate biomass of lakes (Momot et al 1978) and streams (Webster and Patten 1979, Huryn and Wallace 1987). Total net production of crayfish in streams however, is often less than that of insects (Huryn and Wallace 1987), which usually have faster turnover times. Nevertheless, crayfish often play important roles in communities. They occupy multiple trophic levels feeding as primary consumers, secondary consumers, and detritivores (Vannote 1963, Momot et al 1978). Their role as detritivores in streams often involves the breakdown of allochthonous material, such as leaves, which contributes to nutrient cycling (Momot et al 1978, Webster and Patten 1979, Huryn and Wallace 1987). Crayfish are significant prey items for fish in some locations, in some cases representing the dominant item in their diet (Vannote 1963, Fedoruk 1966, Stein 1977). Several comparison studies have been done examining crayfish growth and other population factors between contiguous lakes (Goldman and Rundquist 1977, Momot and Gowing 1977a, Momot and Gowing 1977b, Jones and Momot 1981, Momot and Gowing 1983, France 1983). Although Corey (1988) compared the growth of two O. propinquus populations from different rivers, I am not aware of any study comparing growth, abundance and production between crayfish populations from different streams. Numerous life history and growth studies

however, have been conducted on Orconectes propinquus (Creaser 1934a, Van Deventer 1937, Bovbjerg 1952, Vannote 1963, Fielder 1972, Capelli 1975, Lodge et al 1986, Corey 1987a, Corey 1987b, Corey 1988).

Calcium is a large component of crayfish exoskeletons and is important in their metabolism and physiology (Robertson 1941). Growth of crayfish increased when individuals were reared in experimental ponds with increased calcium (de la Bretonne et al 1969). Although Capelli (1975) failed to find a statistically significant correlation ($r = .450$) between calcium concentration and crayfish abundance in Wisconsin lakes with crayfish, low calcium concentrations may have restricted crayfish from certain lakes. Albeit improbable, the potential may exist for calcium to influence both the growth and abundance of crayfish in streams.

An important dimension of a crayfish population is the young-of-the-year (YOY) cohort. Mortality is often quite high in this stage of a crayfish's life. The survivorship of the YOY cohort can contribute to the increase or demise of an entire crayfish population. Besides Capelli's (1975) work, data on the survivorship of early crayfish instars is lacking and no researcher to my knowledge has attempted a detailed analysis of this sort for a crayfish population. In addition to learning about the survival of early crayfish instars, it is also important to determine how they use the habitat available to them and if their use of microhabitats changes as they grow. Besides Rabeni (1985) no investigator to my knowledge has performed a detailed habitat analysis of early instar crayfish.

The objectives of this work were:

- (i) to compare the growth, abundance, and net production of O. propinquus in the hard water Ford River and the soft water Baraga Creek in order to determine if these factors are correlated with water hardness within the two systems. Growth, abundance, and net production of O. propinquus was hypothesized to be greater in the Ford River owing to its higher water hardness.
- (ii) to determine the stability of the Ford River population over the course of two summers using life table analysis and year to year comparisons of growth and abundance.
- (iii) to measure the survivorship of the YOY instars of O. propinquus in a detailed manner during their first month of independence from the mother.
- (iv) to analyze the habitat of O. propinquus early instars and to determine if their habitat preference changes during their first month of growth, to gain further insight into the general ecology of crayfish at this life stage.

STUDY SITES

The streams studied were in the Lake Michigan drainage of the upper peninsula of Michigan. One study site each was chosen on the Ford River and Baraga Creek. The 800 m site on the Ford River was located in Dickinson County (Sec 18, T. 43 N., R. 29 W.). The stream averaged 5.3 m in width and 17.5 cm in depth at this location. Speckled alder (Alnus rugosa), balsam poplar (Populus balsamifera) and quaking aspen

(Populus tremuloides) dominated the riparian vegetation, and the stream catchment was largely early successional hardwood forest (Burton 1991). The site's substrate was predominantly cobble. The site on Baraga Creek was also ~ 800 m long and was located in Marquette County (Sec 15, T. 49 N., R. 30 W). The streams average width (7.4 m) and depth (17.8 cm) were similar to the Ford River's. Baraga Creek drained a small lake, and was bordered by dense stands of shrubs, largely Alnus rugosa. The site was less shaded than the Ford River site however, as most of the taller trees were set back 4-6 m from the stream bed. The Baraga stream catchment, like the Ford's, was also mainly forested but was made up of a larger percentage of conifers. Cobble was also the dominant substrate in Baraga Creek. Both sites were virtually void of aquatic macrophytes but did contain an abundance of periphyton. Baraga Creek had water that was much darker in color than the Ford River, suggesting that organic acids were more abundant in Baraga Creek (Burton 1991). The chemical and physical characteristics of the two streams were quite similar (Table 1). The streams differed considerably however, in total water hardness (and conductivity). The Ford River had a mean water hardness of 207 ppm compared to 25 ppm CaCO_3 in Baraga Creek. The two sites will be referred to as the Ford River or Baraga Creek for the rest of this paper unless otherwise stated, with the understanding that any conclusions drawn from this study are based on information collected at the individual sites and cannot necessarily be extrapolated to other areas of each stream.

Table 1. Summer and fall 1989 chemical and physical data for matched sites. Values are means \pm S.E. Sample number is given in parentheses.

Site	Hardness (ppm CaCO_3)	pH	Conductivity ($\mu\text{mho/cm}$)	H ₂ O temp. ($^{\circ}\text{C}$)	Diss. O ₂ (mg/L)	Discharge (m^3/sec)
Ford	207 \pm 10 (6)	8.3 \pm 0.1 (6)	302 \pm 18 (6)	18.8 \pm 2.1 (6)	8.9 \pm 0.3 (6)	0.208 \pm 0.076 (4)
Baraga	25 \pm 1 (6)	7.2 \pm 0.1 (6)	29 \pm 1 (6)	19.0 \pm 2.2 (6)	8.0 \pm 0.3 (4)	0.273 \pm 0.068 (5)

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THE STUDY ORGANISM

O. propinquus is a member of the subfamily Cambarinae in the family Astacidae. It is relatively small compared to most North American crayfish. Its range extends west and south into northwest Missouri and southern Illinois, east into New York, and north into much of Ontario (Crocker and Barr 1968). O. propinquus is clearly the dominant crayfish species in Baraga Creek and the Ford River. Although O. virilis is also present, less than 10 individuals were encountered in both streams during the two year study. References in this report to crayfish in the Ford River and Baraga Creek imply O. propinquus exclusively.

METHODS

Population sampling

Populations of O. propinquus were sampled at two week intervals throughout the summer beginning in June 1989 for both Ford and Baraga populations. After fall and spring sampling trips, sampling was terminated in June 1990 in Baraga Creek and continued through August 1990 in the Ford River. A trip was cancelled in December 1989 due to ice cover on both streams. Five different subsites were utilized per sampling period at each stream, and to avoid harvesting from recently disturbed habitat, no subsite was sampled twice within a six month period. Subsites were marked with dated

flags to indicate that sampling had occurred recently. At both the Ford River and Baraga Creek, crayfish ≥ 7 mm in carapace length were collected by two persons kick seining abreast into a downstream block net (0.25 cm² mesh size). The area sampled per subsite ranged from 2 to 13 m². Larger areas were chosen at Baraga Creek in order to harvest a statistically sufficient number of individuals for mean size determination. A removal collection method (Zippen 1958) was used which involved making three kicking passes at each subsite and collecting crayfish from the block net between trials. Assuming that the number of individuals captured on any given pass was a linear inverse function of the cumulative total, the X-intercept gave the estimated total number of crayfish. I will from here on refer to this X-intercept total as the depletion total (or depletion density when the area sampled is considered). Carapace length of individual crayfish (the distance from the tip of the rostrum to the posterior edge of the carapace along the dorsal midline) was measured to the nearest millimeter using vernier calipers (Total length, which is approximately twice carapace length, is occasionally used in this report). The total number of individuals captured per kick seining trial was noted as well as any evidence of recent molting and the sex of each individual. Male and female crayfish were readily distinguishable. The first and second pleopods are modified as intromittent organs in males, while these pleopods in females are much like the third, fourth, and fifth pairs of pleopods. Females also possess a prominent annulus ventralis, or seminal receptacle, on their ventral

surface between their fourth and fifth periopods. In addition, males typically have larger chelae and a narrower abdomen than females. Year classes were distinguished by applying Harding's (1949) graphical method to length frequency histograms constructed for each sampling date. The cohorts appeared to meet the method's assumptions of normal distribution. Separate histograms were made for male and females as the size range of a given year class was sometimes different for each sex.

Early instar O. propinquus (< 7 mm carapace length) were sampled in the Ford River in 1990 from the time they were recruited into the population (late June) until they could be sampled with the adults using the block net method described (late July). Early instar crayfish were sampled twice a week at twenty-five randomly chosen subsites, each with a 0.5 m² area, using hand held kick seines made with window screen (0.023 cm² mesh size). No subsite was sampled twice during the entire early instar sampling period. Three kicking passes were made at each of the 25 subsites as part of Zippen's (1958) removal collection method. Early instar crayfish were collected from the kick screen between kicking passes using fine forceps. Early instar density was determined using Zippen's (1958) method in the manner applied to adult crayfish. The rationale for using kick screens instead of attempting to sample these early instars with the block net was that the kick screen's smaller mesh size prevented escape and this method reduced the amount of area required to be sorted for early instars. The following

information was recorded at each subsite: (1) number of crayfish obtained in each kicking pass, (2) individual carapace length (some individuals were alternatively measured in the laboratory), (3) stream depth, (4) current velocity at $0.6 \times$ depth, using a Gurley Pygmy meter, (5) latitudinal position of the stream (side or middle; the center $3/5$ stream area was designated as middle, and the $1/5$ area adjacent to each bank, side), and (6) longitudinal position (riffle, run-T, or run-H). Riffles were defined as those areas of the stream where surface turbulence was visible. Areas between adjacent riffles were designated as runs. Runs were subdivided into upper and lower sections as follows. The area zero to five meters immediately downstream from a riffle was considered the head portion of the run (designated as run-H). The portion of the run greater than five meters downstream from a riffle was regarded as the tail portion (run-T). Runs were subdivided on the basis that an unusually high concentration of early instar crayfish were collected in areas immediately downstream from riffles (zero to five meters) early in the sampling regime. The average depth and velocity of these habitats during the early instar sampling period is given in Table 2.

Density

The mean density of individuals in the 800 m study reach of each stream, large enough to be sampled by the block net method, was obtained as follows: the total number of O. propinquus was estimated from each subsite using the

Table 2. Mean depth and velocity of latitudinal habitats from the Ford River during early summer 1990. Standard errors are given in parentheses.

Habitat	Depth (cm)	Velocity (m/s)
riffle	12.0 (0.5)	0.305 (0.022)
run-H	18.6 (1.0)	0.163 (0.013)
run-T	21.1 (1.1)	0.112 (0.009)

removal collection method (Zippen 1958). The densities were then partitioned into year class densities based on the numerical ratio of individuals of different year classes at each subsite. The average of the five subsite partitioned densities for each year class was used in equations 2 and 3. These are the densities used throughout this paper unless otherwise stated. The overall density of early instar YOY individuals sampled with kick screens was determined by weighting the mean densities from the longitudinal habitats based on the relative abundance of those habitats over the entire Ford River site.

Growth and Production

In order to calculate growth and production, carapace length was converted to dry weight using length-weight regressions for each sex. Dry weights were obtained by weighing individuals after oven drying them for 24 hours at 60 C. Growth in each cohort was measured using the instantaneous growth equation (Ricker 1958):

$$G = \frac{\ln \bar{w}_2 - \ln \bar{w}_1}{t} \quad (\text{eq 1})$$

where G = instantaneous growth rate per day

\bar{w}_2 = average dry weight of an individual from a given cohort at time 2.

\bar{w}_1 = average dry weight of an individual from a given cohort at time 1.

t = number of days between time 1 & 2.

Net production of each cohort was obtained using the following equations based on Ricker (1946) and Allen's (1949) work. For the rest of this paper net production will be referred to simply as production.

$$B_1 = D_1 * \bar{w}_1 \quad (\text{eq 2})$$

$$B_2 = D_2 * \bar{w}_2 \quad (\text{eq 3})$$

$$\bar{B} = \frac{B_1 + B_2}{2} \quad (\text{eq 4})$$

$$P = G * \bar{B} * t \quad (\text{eq 5})$$

where B_1 = Grams of dry crayfish biomass per square meter for each cohort at time 1.

B_2 = Grams of dry crayfish biomass per square meter for each cohort at time 2.

D_1 = number of individuals per cohort/m² at time 1.

D_2 = number of individuals per cohort/m² at time 2.

\bar{B} = mean grams of dry crayfish biomass per square meter for each cohort between sampling dates.

P = production of each cohort between sampling dates
in grams/m².

The production/biomass or the P/B ratio, an approximation of the biomass turnover rate (Waters 1969), was calculated by dividing total annual production by the grand mean of weighted mean biomasses determined throughout the year.

RESULTS

Length-weight regressions

Length-weight regressions constructed separately for male and female O. propinquus in the Ford River and Baraga Creek are given in Figures 1-2. A logarithmic function described the relationship between carapace length and dry weight in each of the crayfish subgroups considered. Ford regressions ($R^2 > 0.98$) fit the empirical data slightly better than the Baraga regressions ($R^2 > 0.96$). Male crayfish tended to have a slightly larger dry weight than female crayfish of the same 20 mm carapace length (Figures 1-2). In addition, Ford O. propinquus weighed more than Baraga individuals of the same sex at 20 mm (Figures 1-2).

Size-frequency histograms

Representative length-frequency histograms for male O. propinquus in June and July 1990 are given in Figure 3. The YOY size class, first appearing in the block net on

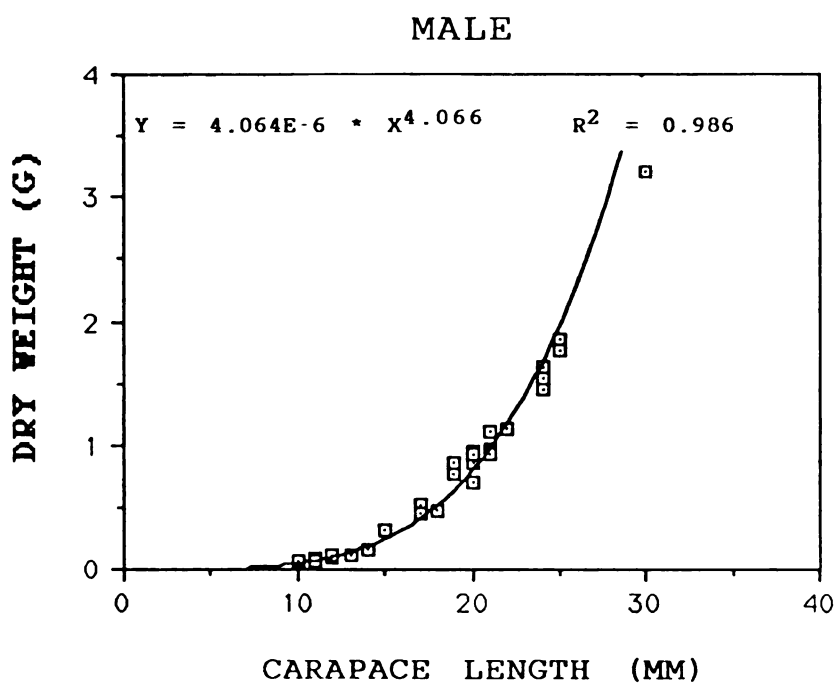
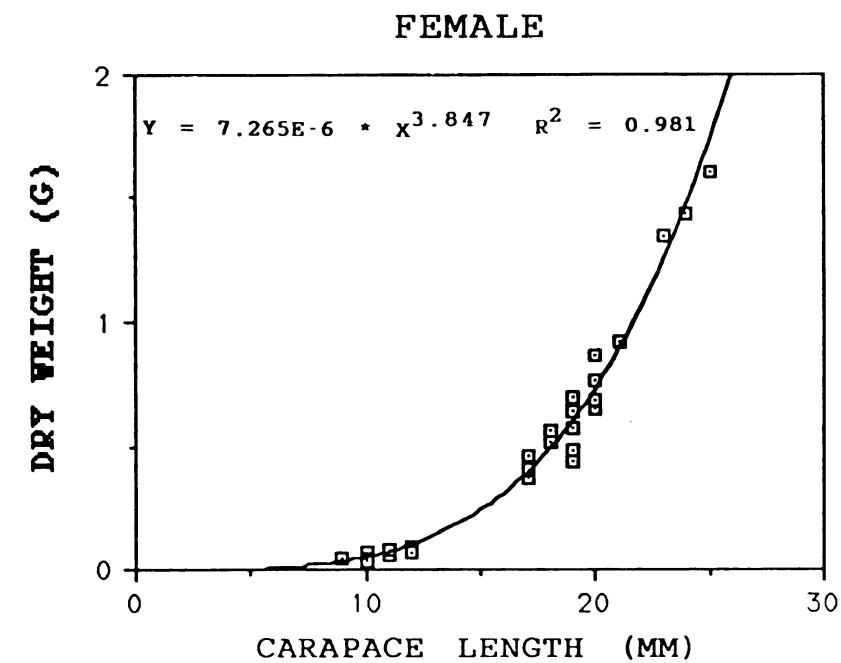


Figure 1. Carapace length-dry weight regressions of female & male *Q. propinquus* from the Ford River. 20 mm carapace length female = 0.734 g; 20 mm c.l. male = 0.793 g.

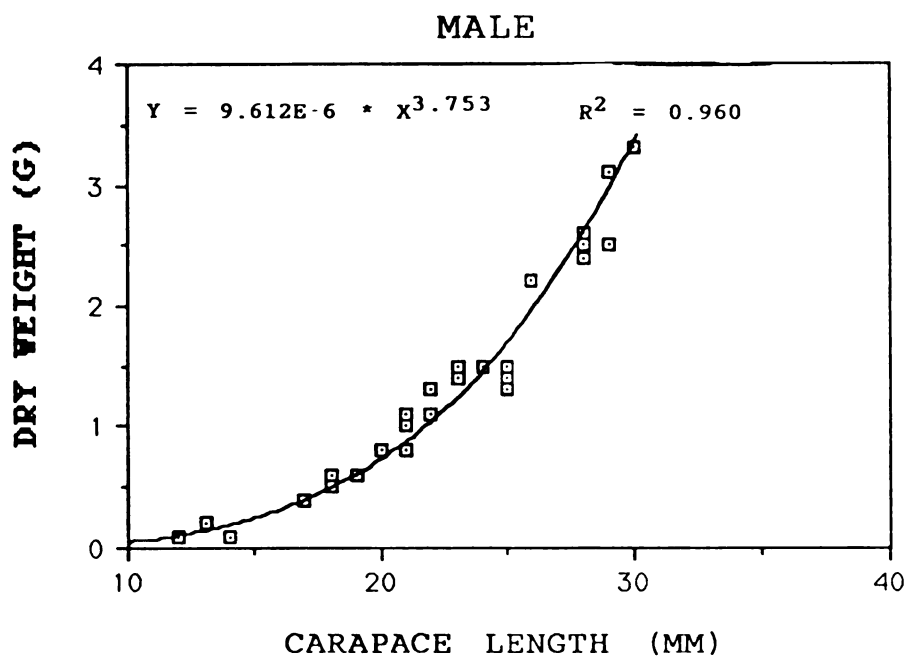
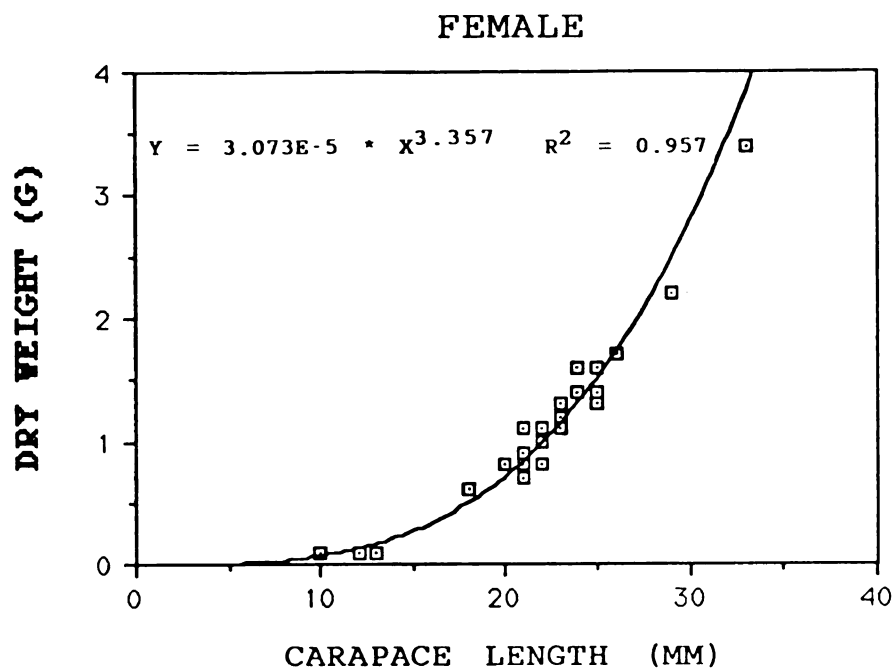


Figure 2. Carapace length-dry weight regressions of female and male *O. propinquus* from Baraga Creek. 20 mm c.l. female = 0.716 g; 20 mm c.l. male = 0.734 g.

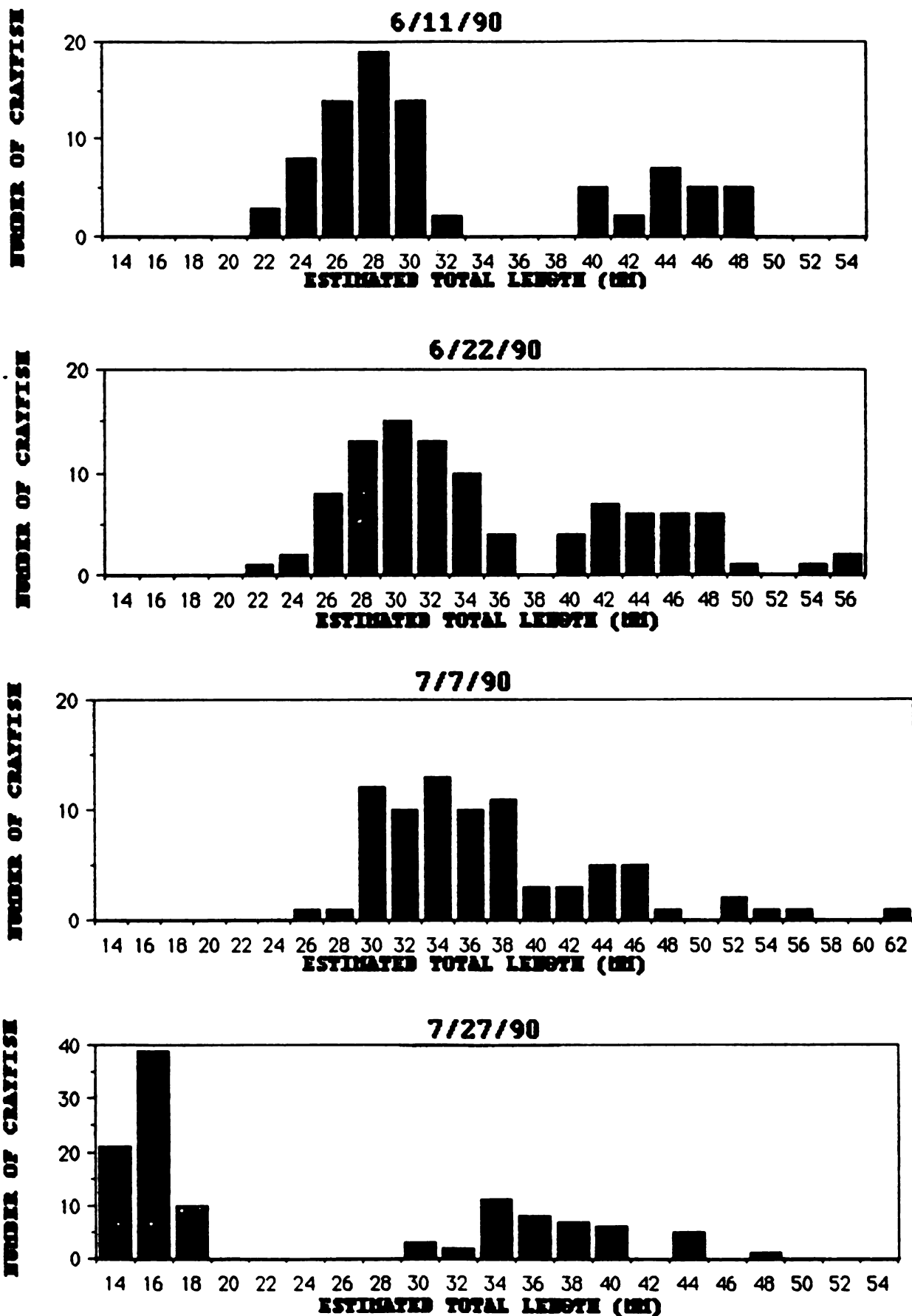


Figure 3. Length-frequency histograms of male *Q. propinquus* from the Ford River showing y1, y2, and YOY size classes.

7/27/90, was easily recognized as they were clearly smaller than year 1 (y1) individuals. The separation of y1 and year 2 (y2) individuals was usually not clearly demarcated. In some cases however, Harding's (1949) method enabled y1 and y2 size classes to be distinguished (Figure 4). Still, because the age of larger relatively rare individuals was not known with certainty, estimation of the abundance of the y2 class was not considered definitive.

Age estimation

The mean age of a year class at a given time of the year was determined based on the assumptions that the members of each cohort hatched from eggs synchronously on a mean date of June 17, and that this date was stable from year to year. June 17 was set as an approximate hatching date based on the fact that ovigerous females from the Ford River were carrying exclusively unhatched eggs on 6/11/90 while the majority of ovigerous females were carrying hatched young on 6/22/90.

Abundance

Some variation in density of y1 and y2 O. propinquus from the Ford River between 1989 and 1990 was suggested ($10.7/\text{m}^2$ vs $7.3/\text{m}^2$) although a t-test showed densities were not significantly different between the two years ($P = 0.10$). Young-of-the-year densities from the Ford River were more similar between 1989 and 1990 ($10.8/\text{m}^2$ vs $10.4/\text{m}^2$, t-test $P = 0.88$) than y1 and y2 densities between the two years

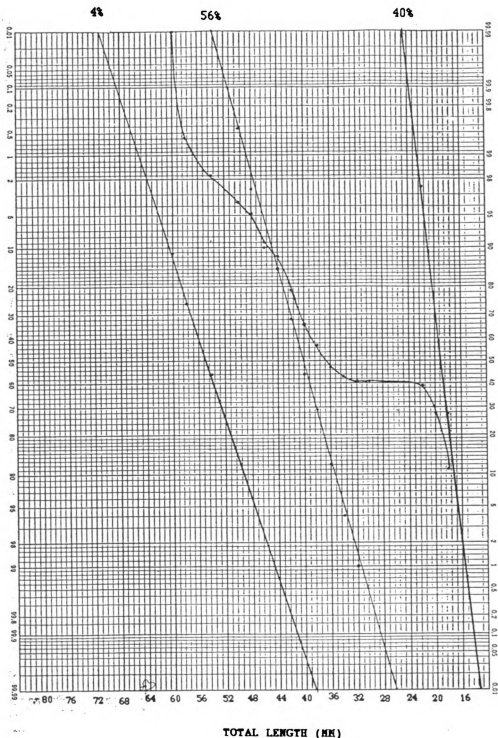


Figure 4. An example of Harding's graphical method used to separate cohorts in a size frequency histogram. The graph shows the separation of YOY (40% of total), Y1 (56%), and Y2 (4%) size classes of male Q. propinquus from the Ford River on 8/4/89. The inflection points on the nonlinear cumulative frequency graph for all size classes indicates the separation points between individual size classes.

(Figures 5-6). In 1989, density of Ford y1's showed a continuous and rapid decline from the beginning of July through October, with an average density of $9.3/\text{m}^2$ during the period (Figure 5). In 1990, Ford y1 densities remained relatively stable from the beginning of May through August. Densities of crayfish 1.15-1.2 years old from each year were similar, with overlapping mean \pm SE intervals. When compared over the same age span, the Ford YOY densities from each year showed a comparable pattern of variation, although the sizable standard errors particularly in 1990 should be noted (Figure 6). Densities of O. propinquus from Baraga Creek during 1989 were considerably lower than Ford values from either year when like size classes were compared (t-tests $P < 0.02$, Figures 5-6). The average y1 density was $3.0/\text{m}^2$ and mean YOY density $1.2/\text{m}^2$. The exceptionally low density of $0.1 \text{ YOY}/\text{m}^2$ on 7/30/90 (Table 3) was not included in the summer average, as this was the first time YOY appeared in the block net at Baraga Creek and a considerable number of individuals may have been overlooked.

Crayfish large enough to be collected in the block net (≥ 7 mm carapace length) were generally homogenously distributed in each stream. Although the standard errors in Figures 5-6 suggest a sometimes clumped distribution, O. propinquus greater than 7 mm in carapace length did not seem to prefer particular areas within the study stretches. Densities of both YOY individuals, and y1s and y2s pooled together were not significantly different between runs and riffles in each stream (t-tests, $P > 0.436$).

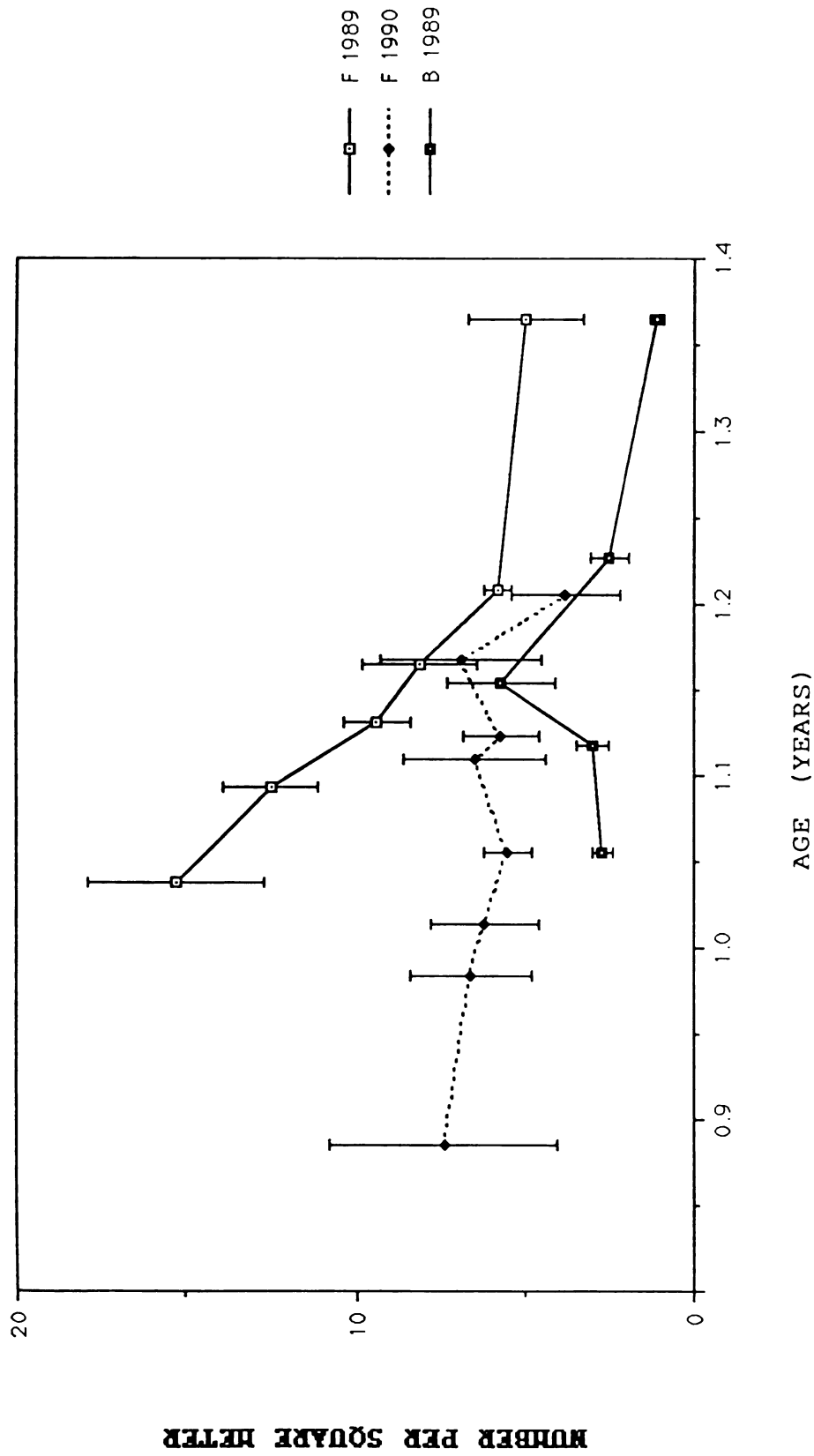


Figure 5. Density of y1 *O. propinquus* from the Ford River and Baraga Creek. Error bars indicate \pm S.E. F = Ford River, B = Baraga Creek.

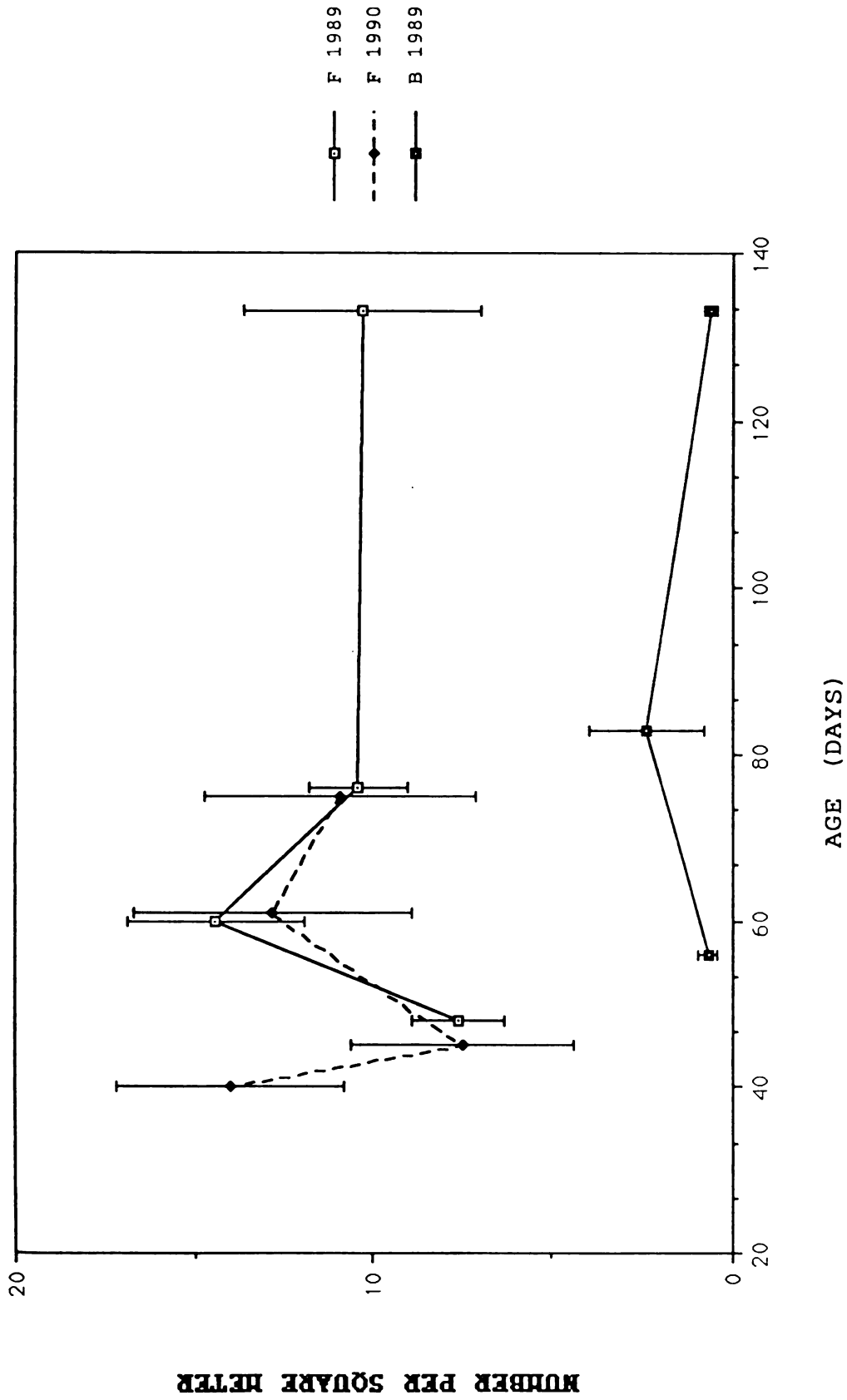


Figure 6. Density of YOY Q. propinquus from the Ford River and Baraga Creek. Error bars indicate \pm S.E.

Table 3. Mean individual dry weights (w), mean densities (d), and capture totals (N) for O. propinquus in Baraga Creek between 7/7/89-7/14/90.

Date	-----YOY-----			-----Y1-----			-----Y2-----		
	w(g)	d(#/m2)	N	w	d	N	w	d	N
7/7/89	---	---	---	1.147	2.7	115	2.970	0.1	4
7/30/89	0.030	0.1	3	1.049	3.0	100	3.599	0.3	9
8/12/89	0.056	0.7	16	1.115	5.7	116	2.837	0.2	5
9/8/89	0.111	2.4	77	0.996	2.5	81	2.871	0.3	12
10/28/89	0.180	0.6	23	1.080	1.1	39	3.345	0.2	5
5/5/90*				0.153	0.5	27	1.097	1.2	61
7/14/90	---	---	---	0.915	1.8	56	2.291	0.9	27

*- there were 0.2 y3s/m2, mean weight = 2.829 g, and N = 8 on this date.

>- dashed lines indicate cells with positive unknown values for the date indicated.

Early instar abundance

Early instar densities from longitudinal habitats were weighted according to the relative abundance of a given longitudinal habitat over the entire area of the Ford River site because densities from some of the longitudinal habitats were significantly different for some of the sampling dates (Table 4). Densities from latitudinal habitats were not used in the calculation of overall early instar density because they were not significantly different for any of the sampling dates (Table 4). Initial density of Ford YOY crayfish in 1990 was determined by the number of pleopod eggs/m² on 5/6/90. Considerable mortality occurred from the egg stage on 5/6/90 up until the time the vast majority of instars were independant of their mothers, 54 days later (Figure 7). Early instar densities stabilized for the next 3 weeks (54-76 days in Figure 7). An apparent increase in density of the cohort was realized when the YOY began being sampled with larger crayfish as part of the block net method (≥ 82 days in figure 7). The distribution of Ford O. propinquus early instars in the various microhabitats will be discussed in more detail later.

Growth

Crayfish growth was not continuous over time but incremental, since they must molt to grow. Thus, smooth growth curves were deceiving (Figure 8). Year 1 and y2

Table 4. Mean densities of Q. propinquus early instars from different habitats in the Ford River. Values are means \pm S.E.

Date	Longitudinal Position			Latitudinal Position	
	Run-T	Riffle	Run-H	Middle	Side
6/29/90	1.67 \pm 0.98a	4.29 \pm 2.52a	6.42 \pm 3.08a	4.56 \pm 1.97a	4.89 \pm 3.15a
7/4/90	2.37 \pm 1.07a	0.67 \pm 0.49a	2.45 \pm 1.34a	1.15 \pm 0.42a	2.92 \pm 1.33a
7/6/90	2.37 \pm 0.96a	0.20 \pm 0.20a	1.58 \pm 0.60a	1.31 \pm 0.35a	2.00 \pm 1.07a
7/10/90	2.00 \pm 0.65a	1.00 \pm 0.67a	1.50 \pm 0.82a	1.18 \pm 0.40a	2.13 \pm 0.93a
7/13/90	1.90 \pm 0.74a	0.25 \pm 0.16a	2.29 \pm 1.00a	1.57 \pm 0.61a	1.36 \pm 0.65a
7/18/90	2.11 \pm 0.86a	0.50 \pm 0.33ab	0.25 \pm 0.16b	1.07 \pm 0.56a	0.90 \pm 0.35a
7/21/90	3.00 \pm 0.69a	0.56 \pm 0.29b	0.25 \pm 0.25b	2.15 \pm 0.53a	1.17 \pm 0.67a

> any two means from the same habitat category (longitudinal or latitudinal position) and date with the same letter were not significantly different using Fisher's protected least significant difference ($\alpha = 0.05$).

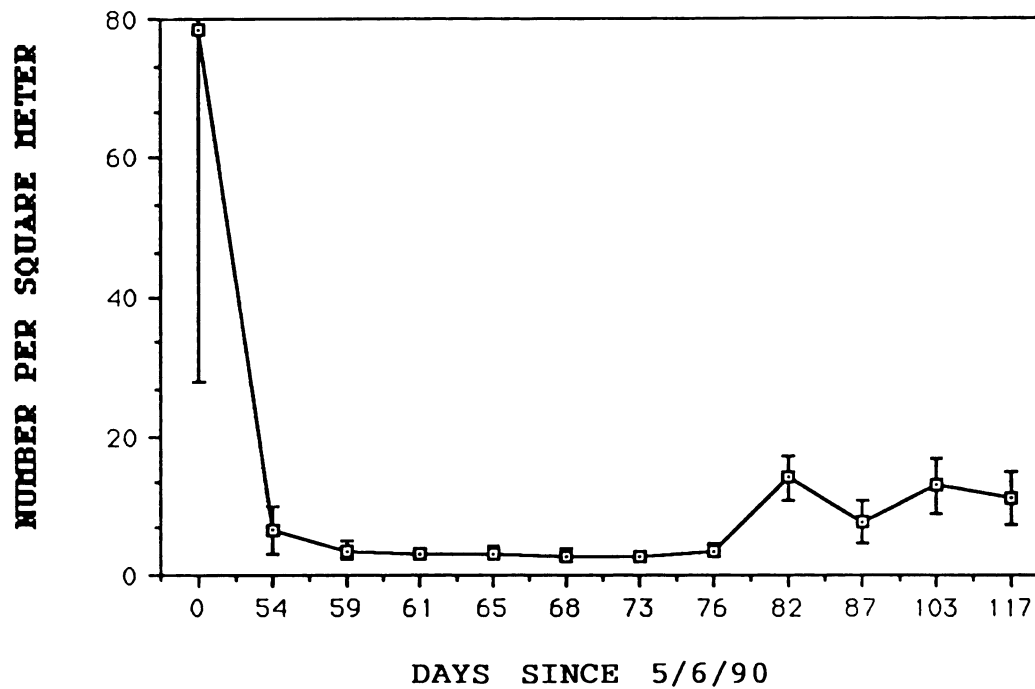


Figure 7. Change in mean density of O. propinquus early instars from the Ford River in 1990. Data point at zero days represents mean pleopod eggs/m². Data points at 54-76 days represent the grand mean of mean longitudinal densities (Figure 16) weighted for habitat relative abundance at the Ford site. Data points at 82-117 days represent mean densities obtained with the block net method. Error bars indicate \pm S.E. of means unweighted for habitat relative abundance on a given date.

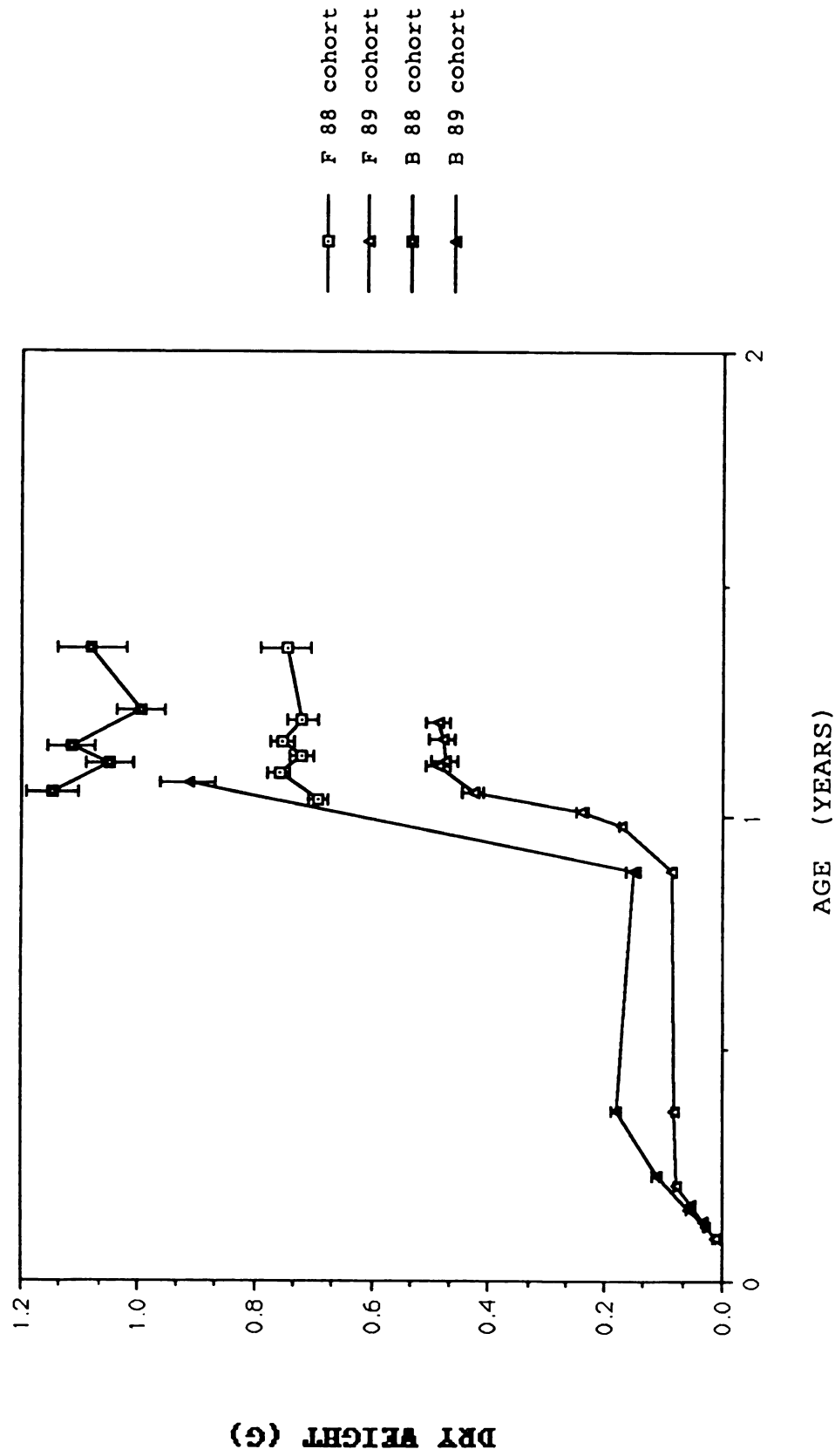


Figure 8. Change in mean individual size of Q. propinquus in 1988 & 1989 cohorts from the Ford River and Baraga Creek. Error bars indicate \pm S.E.

O. propinquus from the Ford River and Baraga Creek grew during the molting period of spring and early summer and stayed at a fixed size for the remainder of the year (Tables 3 & 5). Ford juveniles grew steadily during their first summer and fall and continued growth to maturity in their second summer (Figure 8). No appreciable growth occurred in YOY, y1, or y2 age classes from 10/28/89 to 5/6/90 in either population (t-tests $P > 0.05$, Tables 3 & 5). As with density, year-to-year differences in size (and by implication growth) were apparent among y1 individuals in the Ford River. Mean dry weight of 1990 y1's was 0.472 g compared to 0.729 g for 1989 y1's over the same interval (Figure 8). Growth comparisons of the two size classes could not be made because sampling began in the summer of 1989 after a sizeable amount of the growth in 1989 y1 individuals had already occurred. The mean size of y2 individuals in both populations was highly variable between samplings, probably a function of the small numbers collected (Tables 3 & 5). Comparisons between growth of YOY classes from the Ford River between years was possible. Individuals in 1990 grew faster over a common interval ($G = 0.0538/\text{day}$) than 1989 individuals ($G = 0.0419/\text{day}$) (Figure 9). Baraga 1989 and 1990 y1 O. propinquus achieved a larger size (1989 mean weight = 1.077 g) than Ford individuals from corresponding years and y1 1990 spring growth was clearly higher in Baraga Creek (Figure 8). Baraga YOY were also larger than Ford 1989 YOY and showed greater growth during their first year (Figure 9). Between 7/30-10/28/89 Baraga YOY growth rate was 0.0199/day compared to the interpolated Ford YOY growth rate of

Table 5. Mean individual dry weights (w), mean densities (d), and capture totals (N) for O. propinquus in the Ford River between 7/1/89-8/31/90.

Date	-----YOY-----			-----y1-----			-----y2-----		
	w(g)	d(#/m2)	N	w	d	N	w	d	N
7/1/89	---	---	---	0.692	15.3	496	2.414	1.1	38
7/21/89	0.013	0.7	14	0.759	12.5	251	1.952	0.6	11
8/4/89	0.033	7.6	147	0.722	9.4	189	2.369	0.3	7
8/16/89	0.053	14.4	261	0.754	8.1	155	1.933	0.2	4
9/1/89	0.079	10.4	196	0.720	5.8	111	1.645	0.3	5
10/28/89	0.083	10.3	101	0.747	5.0	42	1.481	0.1	1
5/6/90*				0.084	7.4	114	0.735	4.2	66
6/11/90				0.171	6.6	112	1.035	3.6	51
6/22/90				0.241	6.2	125	1.226	3.2	62
6/29/90	0.0017	26.1	114	---	---	---	---	---	---
7/4/90	0.0023	14.5	49	---	---	---	---	---	---
7/6/90	---	12.2	37	---	---	---	---	---	---
7/7/90	---	---	---	0.427	5.5	103	1.644	1.3	24
7/10/90	0.0037	12.7	36	---	---	---	---	---	---
7/13/90	0.0055	11.3	34	---	---	---	---	---	---
7/18/90	0.0115	10.4	25	---	---	---	---	---	---
7/21/90	0.0097	14.0	42	---	---	---	---	---	---
7/27/90	0.020	14.0	140	0.488	6.5	65	1.257	1.7	17
8/1/90	0.031	7.5	84	0.477	5.7	61	1.420	1.7	19
8/17/90	0.062	12.8	160	0.481	6.9	70	1.217	1.2	13
8/31/90	0.088	10.9	122	0.486	3.8	44	1.183	0.2	2

*- there were 0.2 y3s/m2, mean weight = 2.108 g, & N = 4, on this date.

>- dashed lines indicate cells with positive unknown values for the date indicated.

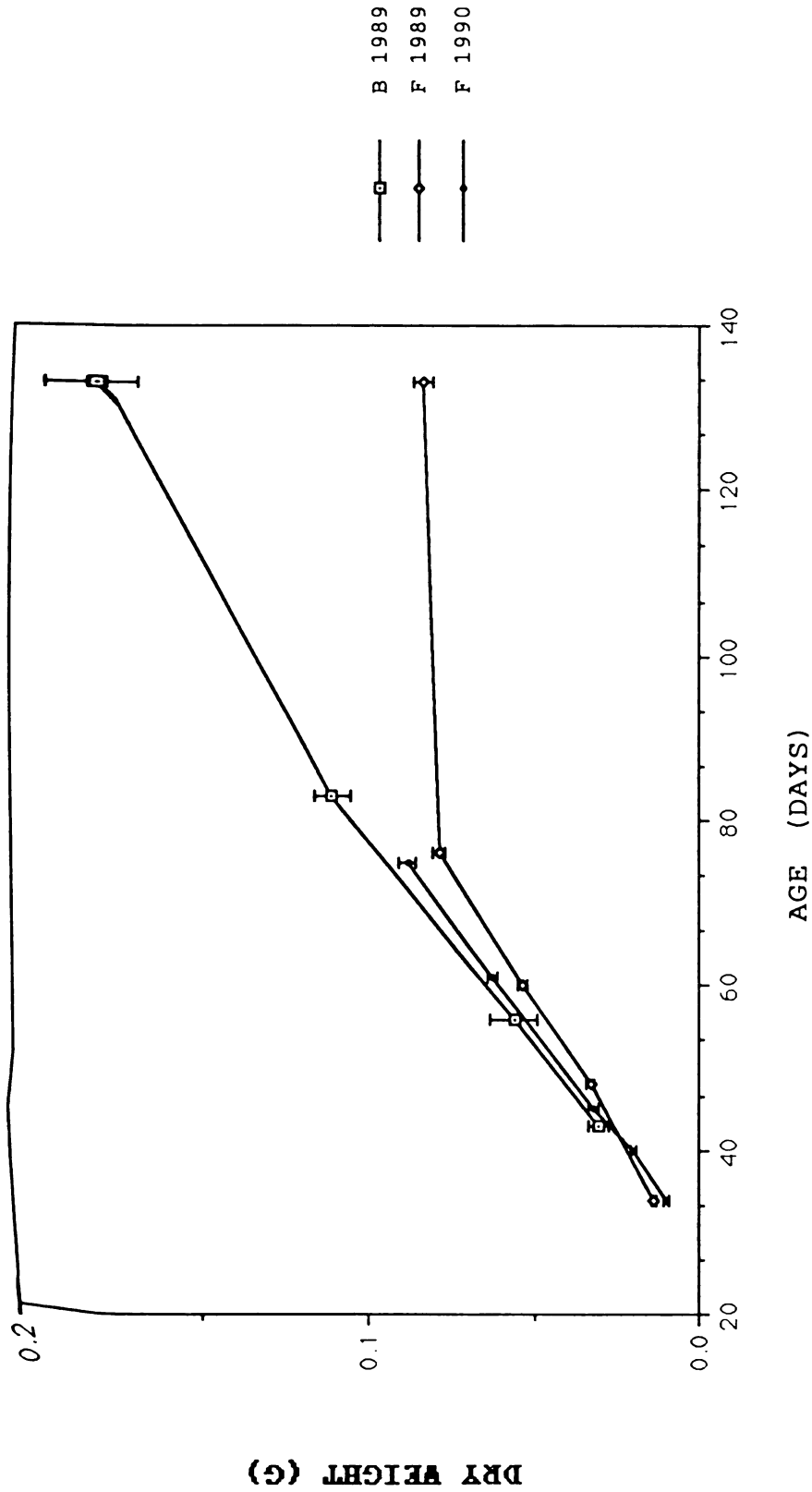


Figure 9. Change in individual weight of O. propinquus YOY from the Ford River and Baraga Creek. Error bars indicate \pm S.E. G/day values: 7/21-9/1: F 89 (0.0419), F 90 (0.0538); 7/30-10/28: F 89 (0.0130), B 89 (0.0199).

0.0130/day over the same interval. YOY growth was similar in both populations until 0.7 years of age. Ford crayfish grew very little during the fall of 1989 however, while Baraga individuals maintained nearly linear growth (Figure 9).

Production

The greater size and abundance of Ford y1 individuals in 1989 resulted in almost a threefold larger biomass than was present in 1990 (Table 6). Since early growth of O. propinquus was not sampled in 1989, production estimates from the Ford River were based primarily on 1990 data from spring and summer. Year 1 individuals contributed the greatest amount to total Ford crayfish production in 1990, followed by y2 and YOY age classes (Table 6). O. propinquus production in the Ford River was about 1.5 times higher than in Baraga Creek (5.0 g/m² vs. 3.0 g/m²) from 7/14/89-7/14/90 (Tables 6-7). Some interpolation was required, and production of Ford early instars and eggs was not included for comparative purposes. Total production in the Ford River over the same interval was 5.2 g/m² when egg and early instar production was considered, so the comparative data may be underestimated by 4 %. Although crayfish in the Ford River were over three times more numerous than in Baraga Creek, the larger size and faster growth of Baraga individuals resulted in sixty percent of the crayfish production in the Ford River. Production/biomass ratios were 1.04 and 1.11, for the

Table 6. Net production of *O. propinquus* in the Ford River between 7/1/89 and 8/31/90.

Time Period	-----YOY-----			-----Y1-----			-----Y2-----			Total P
	G ^a	B ^b	P ^c	G	B	P	G	B	P	
7/1-7/21/89	-----	-----	-----	0.005	10.0	0.9	0	1.9	0	0.9
7/21-8/4/89	0.063	0.1	0.1	0	8.1	0	0	0.9	0	0.1
8/4-8/16/89	0.041	0.5	0.2	0	6.4	0	0	0.5	0	0.2
8/16-9/1/89	0.024	0.8	0.3	0	5.1	0	0	0.4	0	0.3
9/1-10/28/89	0.001	0.8	<0.1	0	3.9	0	0	0.3	0	<0.1
10/28-5/6/90	<0.001	0.7	<0.1	0	3.4	0	0	0.3	0	<0.1
5/6-6/11/90	-----	-----	<0.1*	0.020	0.9	0.6	0.009	3.4	1.1	1.7
6/11-6/22/90	-----	-----	<0.1*	0.031	1.3	0.4	0.015	3.8	0.6	1.0
6/22-7/7/90	-----	-----	<0.1*	0.038	1.9	1.1	0	3.0	0	1.1
7/7-7/27/90	-----	-----	0.1*	0.007	2.8	0.4	0	2.1	0	0.5
7/27-8/1/90	0.116	0.3	0.1	0	2.9	0	0	2.3	0	0.1
8/1-8/17/90	0.043	0.5	0.3	0	3.0	0	0	1.9	0	0.3
8/17-8/31/90	0.025	0.7	0.2	0	2.6	0	0	0.8	0	0.2

a- instantaneous growth per day during time period

b- average biomass during period in g dry weight/m²c- net production during period in g dry weight/m²

*- estimated from values obtained in early instar sampling

>- dashed lines indicate cells with positive unknown values for the time period indicated.

Table 7. Net production of Q. propinquus in Baraga Creek between 7/7/89 and 7/14/90.

Time period	-----YOY-----			-----y1-----			-----y2-----			Total P
	G	B	P	G	B	P	G	B	P	
7/7-7/30/89	-----	-----	-----	0	3.1	0	0	0.7	0	-----
7/30-8/12/89	0.048	<0.1	<0.1	0	4.7	0	0	0.8	0	<0.1
8/12-9/8/89	0.025	0.1	0.1	0	4.4	0	0	0.7	0	0.1
9/8-10/28/89	0.010	0.2	0.1	0	1.8	0	0	0.8	0	0.1
10/28-5/5/90	0	0.1	0	0	1.3	0	0	0.6	0	0
5/5-7/14/90	-----	-----	-----	0.023	0.9	1.5	0.011	1.7	1.3	2.8

Ford and Baraga streams respectively, during the 7/14/89-7/14/90 interval.

Reproduction of *O. propinquus* from the Ford River

Ford *O. propinquus* were collected for pleopod egg counts on 5/6/90 as part of routine block net sampling. A carapace length/pleopod egg regression was constructed to estimate fecundities of all berried females (N = 14) sampled on 5/6/90 (Figure 10). Fifty-eight percent of mature females, or 8 % of the entire population, were reproductive on 5/6/90. The mean number of pleopod eggs per female declined from 85.5 on 5/6/90 to 66.5 on 6/11/90, although these means were not significantly different when subjected to a t-test ($P = 0.0737$), probably due to the low sample number and high variability of values on both dates.

Ten pleopod eggs each were chosen randomly from several berried females on 5/6/90 for egg diameter determination. Eggs were measured to the nearest 0.1 mm with vernier calipers. Mean Ford *O. propinquus* egg diameter was 2.0 mm. The relationship between carapace length and average egg diameter of this species is shown in Figure 11. The best fit in these reproduction regressions was realized when total egg volume (estimated from mean egg diameter) was regressed on carapace length (Figure 12).

$\gamma = -99.911 \pm 0.017^\circ$ $R^2 = 0.521$

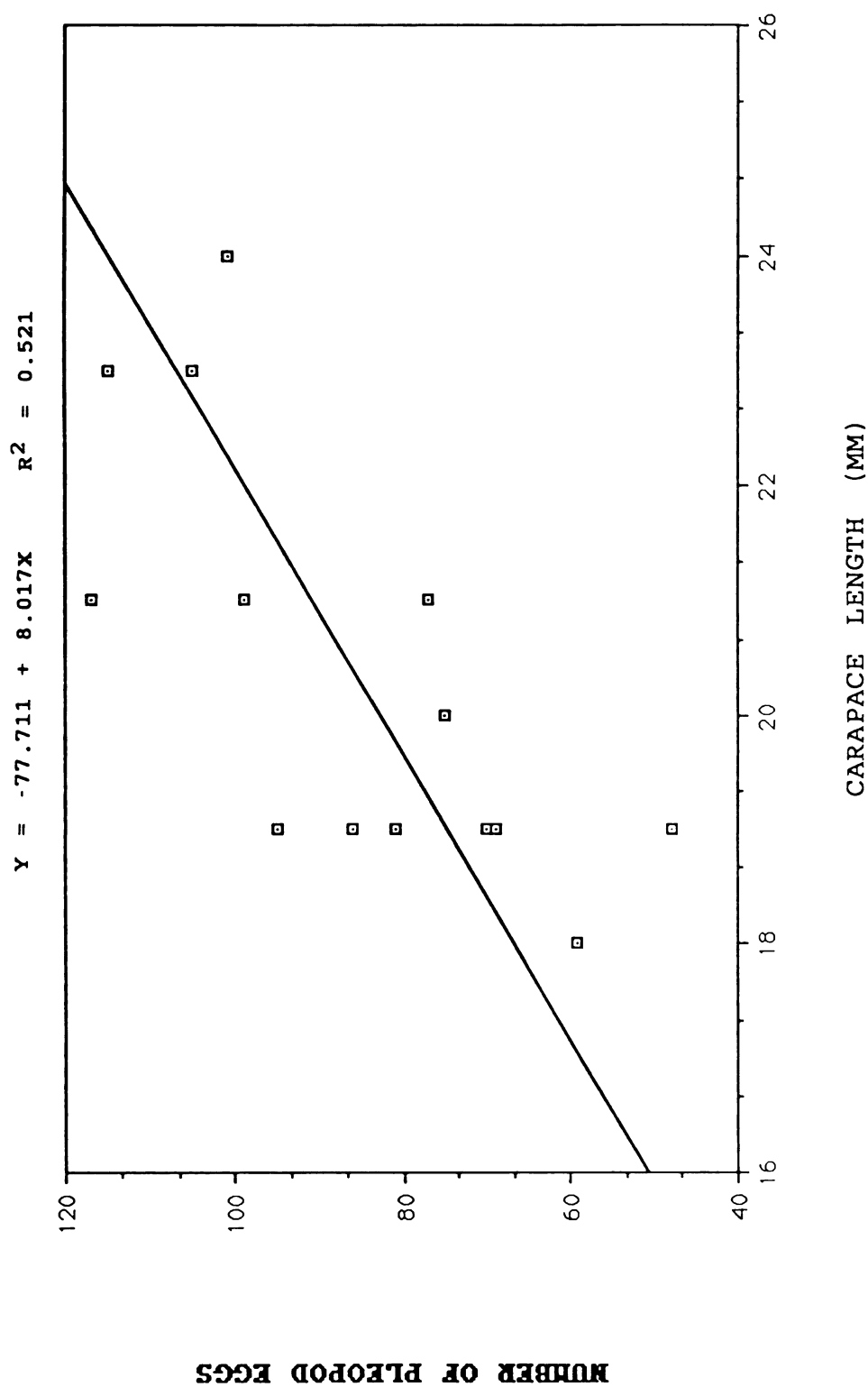


Figure 10. Carapace length-pleopod egg regression for O. propinquus from the Ford River on 5/6/90. $P = 0.0036$

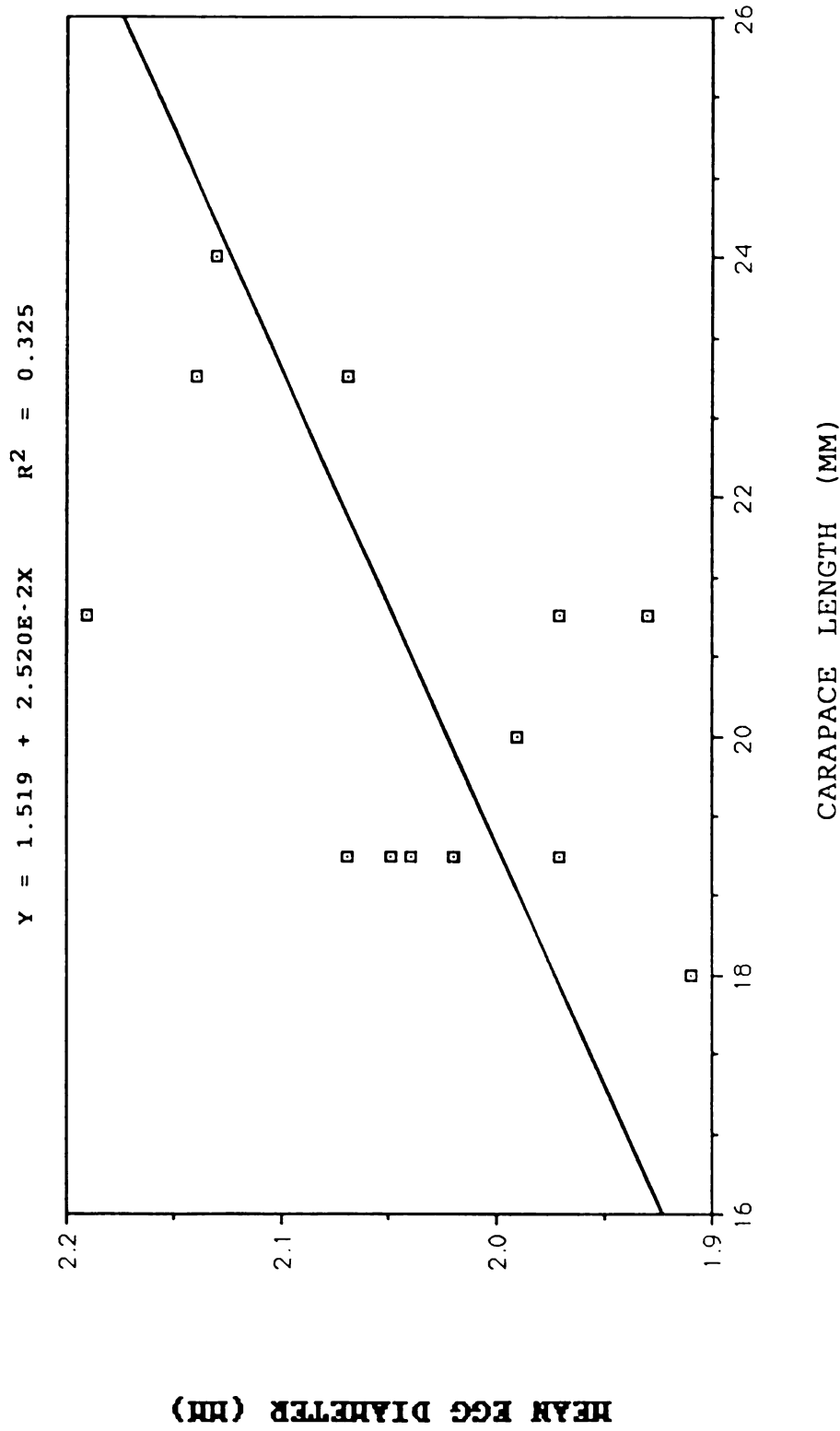


Figure 11. Regression of mean pleopod egg diameter on carapace length of Q. propinquus from the Ford River on 5/6/90. $P = 0.0332$

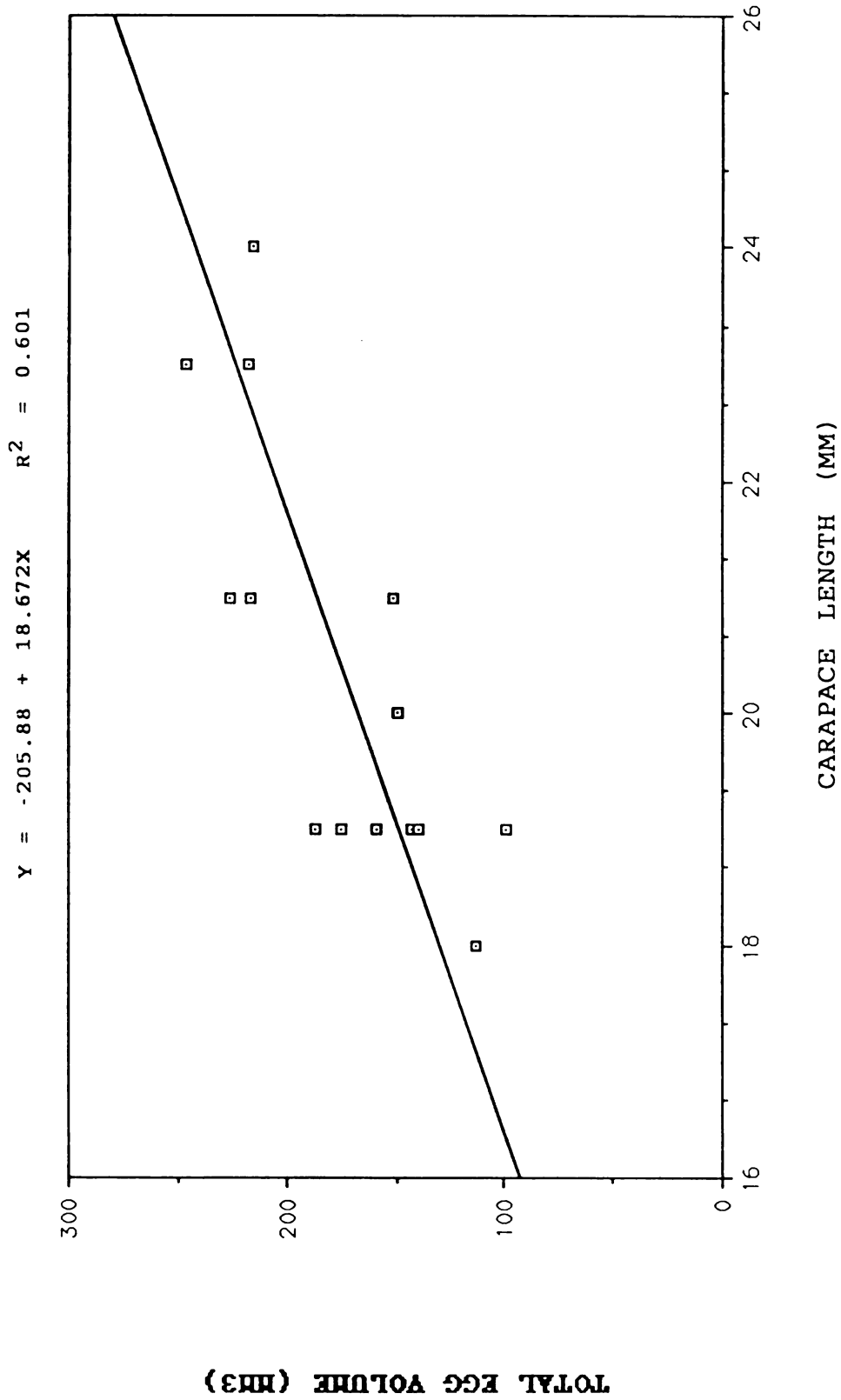


Figure 12. Regression of total pleopod egg volume on carapace length of *Q. propingus* from the Ford River on 5/6/90. $P = 0.0011$

Life Table for Ford River *O. propinquus*

A life table was constructed for *O. propinquus* from the Ford River to evaluate the population's stability (Table 8). The l_x column was constructed by estimating the number of females surviving to different ages, assuming each age class began as a brood equal to the total number of female age 0 individuals on 5/6/90. (An assumption of this analysis was that the number of age 0 females remains relatively constant from year to year.) This latter number was derived from the total number of age 0 individuals/m², or the number of pleopod eggs/m² on 5/6/90. By assuming a 50:50 sex ratio of age 0 individuals, halving the number of pleopod eggs/m² gave an estimate of the number of female age 0 individuals on 5/6/90. Survivorship of age 0.5, 1.5, and 2.5 females was estimated using densities obtained in population sampling on 5/6/90. The column P indicates the proportion of females found to be reproductive in each age class. One can not assume all mature females extruded eggs and contributed to the succeeding generation. The m_x values represent the empirically determined mean number of female pleopod eggs produced per female at each age class (assuming a 1:1 sex ratio). Data in the $l_x P m_x$ column (Table 8), indicated that y2 females were responsible for 93 % of the young production. This high proportion reflected the numerical dominance of y2 females relative to y3 females in the Ford River (Table 5). R_0 represents the reproductive rate per generation, or the number of eventual reproductive females produced per female. The R_0 of a population over many generations should be close

Table 8. Annual life table for female O. propinquus from the Ford River.

Age in years	l_x	P	m_x	$l_x P m_x$
0.0	1.000	0		
0.5	0.090	0		
1.5	0.055	0.411	41.0	0.927
2.5	0.001	1.0	57.3	<u>0.057</u>
				$R_0 = 0.984$

l_x = probability that a female survives to the indicated age based on the number of age 0 females & the number of females of the given age class on 5/6/90.

P = proportion of females reproductive at a given age.

m_x = potential number of female eggs an individual would produce if she were alive at the age indicated.

$R_0 = \sum l_x P m_x$ = the reproductive rate per generation.

to 1, providing the population is stable (Momot and Gowing 1977a). A R_0 well above or below one over time probably reflects an overall population increase or decrease, respectively. The Ford *O. propinquus* population appeared to be stable with a R_0 of 0.984; however, the population would have to be monitored for several years to determine if it is truly stable. A life table was not feasible for Baraga Creek due to the small number of berried females captured ($N = 4$) in the spring of 1990, a number insufficient for reliable fecundity estimates.

Life history

The following segment documents the life history of *O. propinquus* in the Ford River. Mature males and females were observed mating in the stream on 7/13/90, 7/27/90, and 8/1/90. (Males were considered sexually mature adults after they had successfully passed through their juvenile instar stages and attained the form I condition. Sexual maturity in females was recognized in females observed copulating with males in the stream, and in females bearing eggs and young in the spring). Mating was not observed in 1990 prior to 7/13/90. Sampling in the Ford River was terminated on 8/31/90 so it is unknown if *O. propinquus* mates in the fall in the Ford River. No appreciable growth occurred between 10/28/89 and 5/6/90 (Table 5). Females were first observed in berry in 1990 on 5/6/90, the first sampling trip of the year, and remained in berry through 6/1/90. On 6/22/90, the

eggs of the majority of ovigerous females had hatched and instars remained attached to the female pleopods. The smallest ovigerous female observed was 18 mm in carapace length. This indicates that individuals did not reach sexual maturity until after their first spring and did not mate and reproduce until into their second year, as y1s of both sexes were all under 18 mm during the entire spring of 1990.

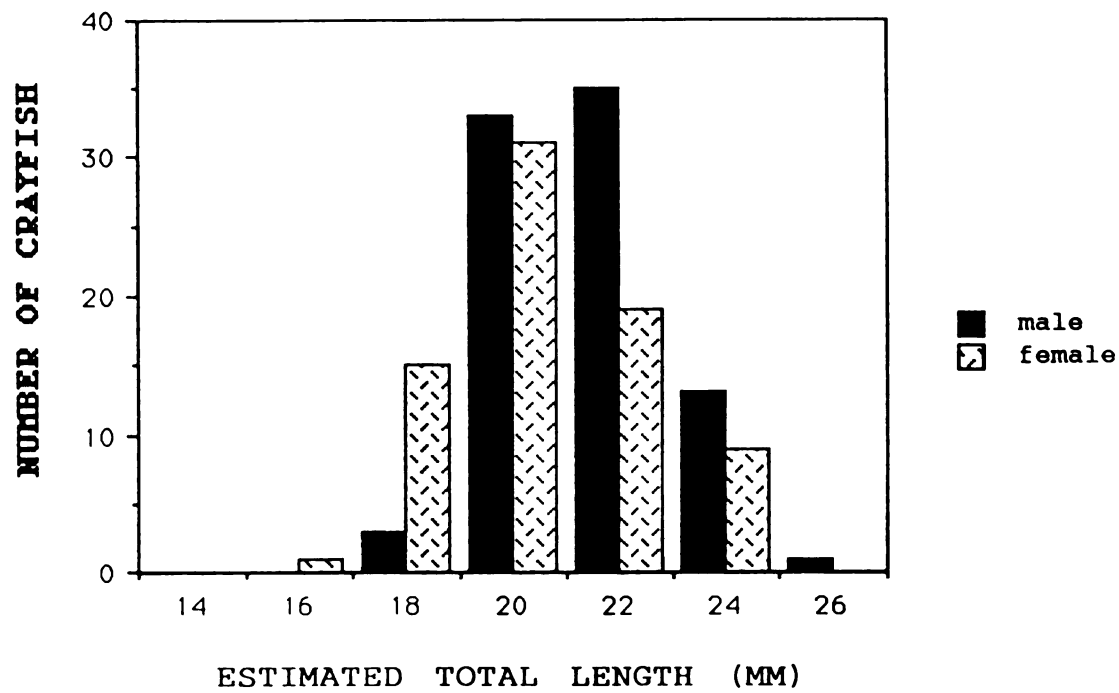
Mature males apparently molted synchronously twice a year. Mature males molted from form I to their nonsexual form, form II, between May and June, as all mature males examined on 5/6/90 were in form II, and 75 % of individuals examined in June and July of 1989 and 1990 were in form II. By August, mature males had molted back to form I. All individuals examined on 8/5/89 were in form I. Most individuals died after their second year (survivorship of y2's to 7/7/90 was 1.6 %). A few crayfish apparently lived to their third spring (survivorship of y3's to 5/6/90 was 0.2 %).

Year 1 and y2 O. propinquus from the Ford River generally maintained a 1:1 sex ratio throughout the year (Table 9). A noticeable exception occurred on 7/1/89 when males outnumbered females nearly 3:2. Males dominated the y1 and y2 sample more strongly and regularly in Baraga Creek than in the Ford River (Table 9). A small size difference between the sexes existed among both YOY and y1 & y2 Ford O. propinquus. Young-of-the-year males were 4.4% larger in total length on the two occasions they were compared (t-test, $P < 0.05$, Figure 13). Year 1 and y2 males were 4.3% larger on one occasion (t-test $P < 0.05$) and only 1.8% larger on another (t-test $P > 0.05$, Figure 14).

Table 9. Results of Chi-Square Goodness of Fit Tests
comparing numbers of y1 and y2 male and female
O. propinquus.

Site	Date	#Males	#Females	Chi-Square value	Significance
Ford	7/1/89	307	227	11.985	P<0.001
	7/21/89	131	131	0	NS
	8/4/89	100	96	0.082	NS
	8/16/89	77	82	0.157	NS
	9/1/89	58	58	0	NS
	10/28/89	20	23	0.209	NS
	5/6/90	35	35	0	NS
	6/11/90	24	27	0.176	NS
	6/22/90	33	29	0.258	NS
	7/7/90	16	8	2.667	NS
	7/27/90	43	39	0.195	NS
	8/1/90	48	28	5.263	P<0.05
	8/17/90	34	49	2.711	NS
	8/31/90	16	30	4.261	P<0.05
Baraga	7/7/89	80	39	14.126	P<0.001
	7/30/89	67	42	5.734	P<0.05
	8/12/89	82	39	15.281	P<0.001
	9/8/89	56	37	3.882	P<0.05
	10/28/89	26	18	1.455	NS
	5/5/90	61	8	40.710	P<0.001
	7/14/90	43	40	0.108	NS

A.



B.

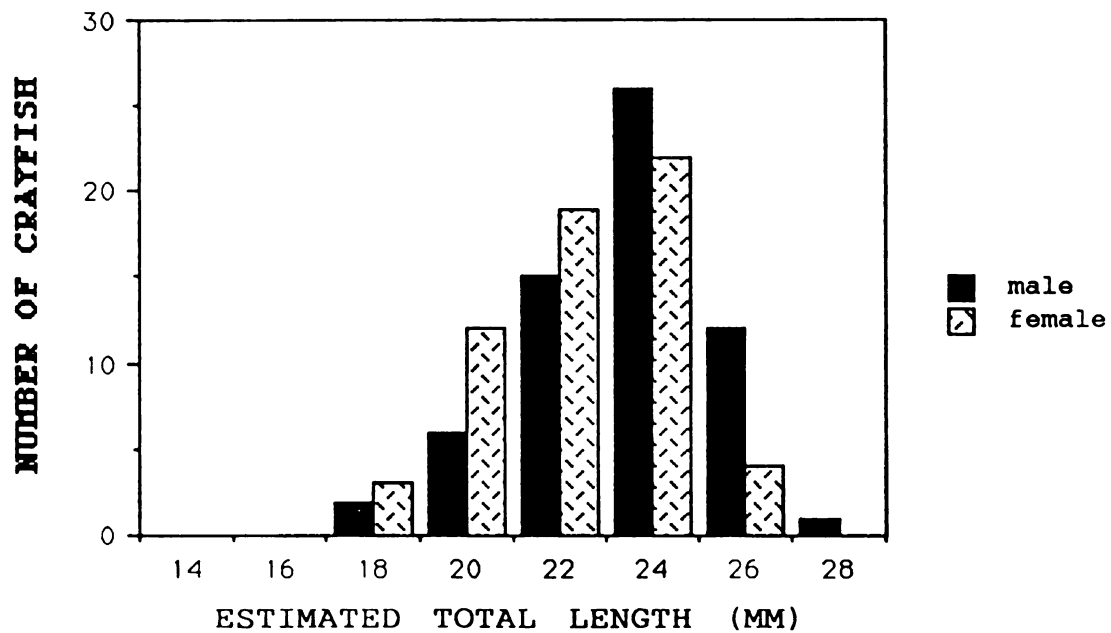


Figure 13. Size comparison of male and female YOY *Q. propinquus* from the Ford River. A. 8/17/90, males 4.4 % larger, $P = 0.0016$. B. 8/31/90, males 4.4 % larger, $P = 0.0091$.

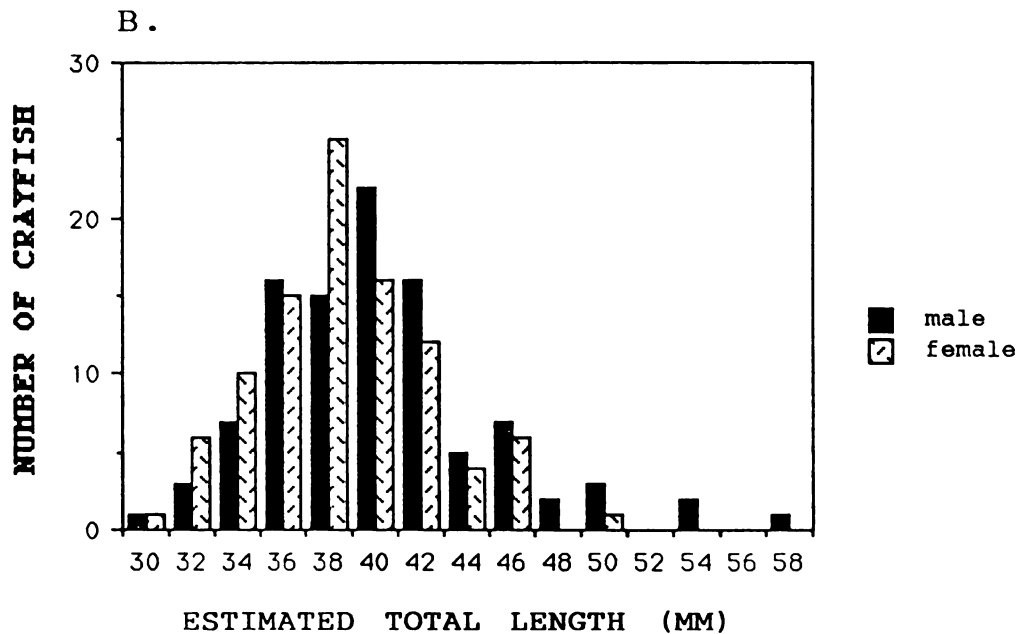
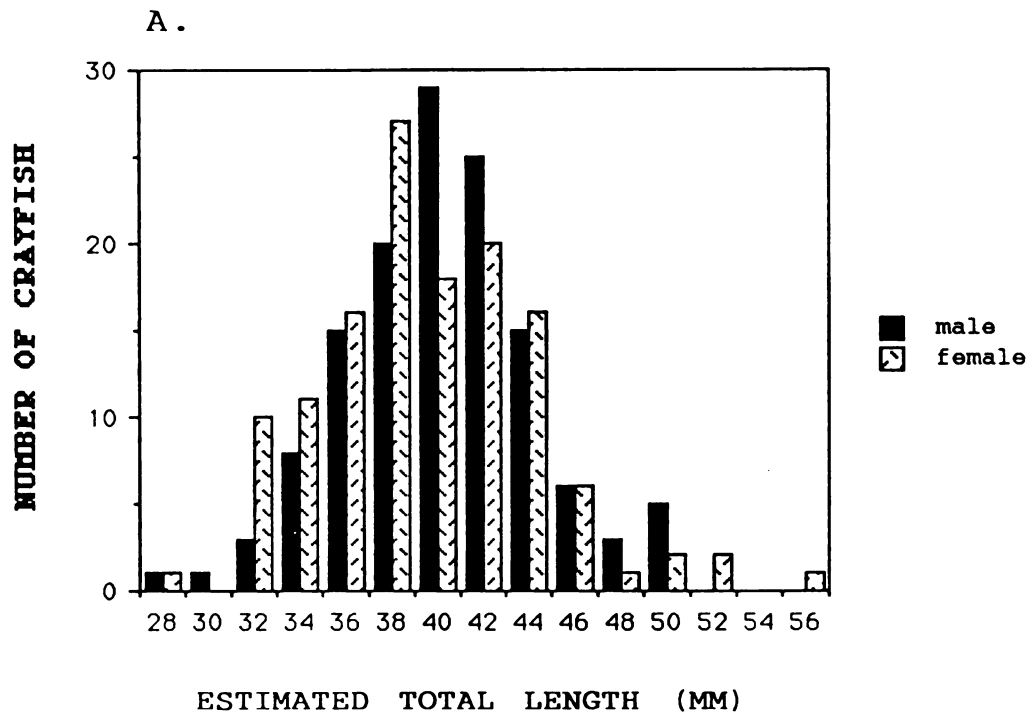


Figure 14. Size comparison of male and female adult *Q. propinquus* from the Ford River. A. 7/21/89, males 1.8 % larger, $P = 0.1933$. B. 8/4/89, males 4.3 % larger, $P = 0.0103$.

Ford early instar distribution

A three factor analysis of variance was performed to examine the effects of time (with seven levels corresponding to sampling dates), longitudinal position, and latitudinal position on early instar crayfish density in the Ford River (Table 10). No source in the ANOVA table sufficiently explained the variance in densities to be significant at the 95% confidence level. Time, with a P value of 0.112, seemed to be responsible for some of the variance. Densities generally decreased with time as one might expect in an organism that produces many eggs. That the three factor interaction had a low P value (0.0793) was a bit surprising. High densities early in the sampling regime at habitats that would later lose prominence in "attracting" young instars may have been attributable. Mean densities from latitudinal habitats on the same sampling date did not differ significantly ($P > 0.05$) when subjected to a multiple range test using Fisher's protected least significant difference (Table 4). Mean densities from longitudinal habitats on the same sampling date were significantly different ($P < 0.05$) on two occasions however, using the same statistical test (Table 4).

Considering longitudinal habitats, run-Hs had the highest overall mean density of early instars during the study ($2.48/\text{m}^2$), followed closely by run-Ts ($2.26/\text{m}^2$), with riffles being the least preferred habitat ($1.06/\text{m}^2$). Abundance in run-Ts was the most stable over the period (Figure 15).

Table 10. ANOVA table for a 3-factor analysis of variance on densities of early instar O. propinquus from the Ford River.

Source	df	Sum of squares	Mean square	F-test	P value
time (A)	6	146.402	24.400	1.734	0.118
long. pos. (B)	2	39.052	19.526	1.388	0.2533
AB	12	164.418	13.701	0.974	0.4772
lat. pos. (C)	1	1.851E-4	1.851E-4	1.315E-5	0.997
AC	6	37.341	6.224	0.442	0.8494
BC	2	31.793	15.896	1.13	0.3262
ABC	12	282.751	23.563	1.674	0.0793
error	133	1871.645	14.073		

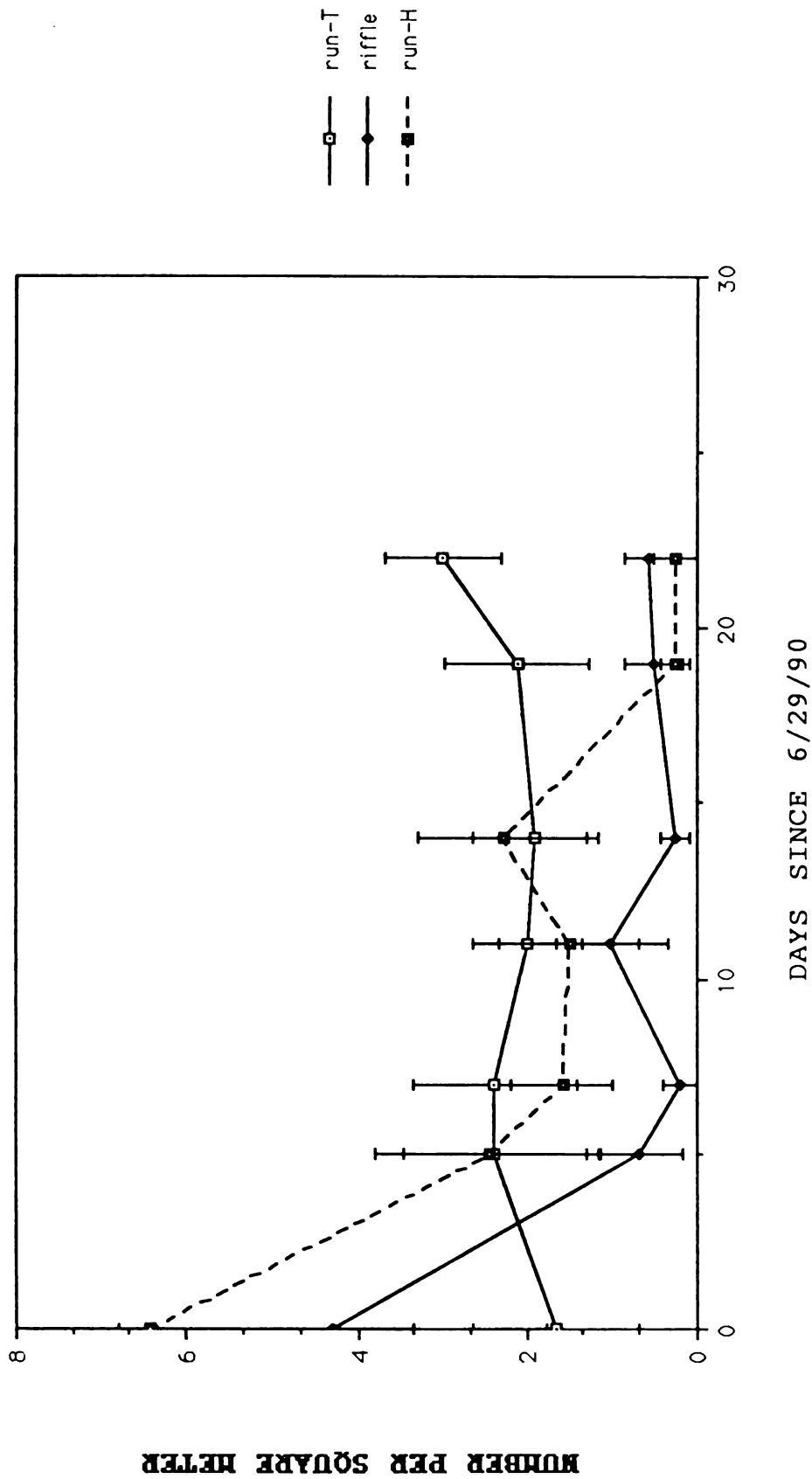


Figure 15. Mean densities of Ford *O. propinquus* early instars from run-T, rifle, and run-H habitats beginning 6/29/90. Error bars indicate \pm SE.

Densities in run-Hs and riffles were high initially, eventually declining to $< 1/\text{m}^2$ after 18 days, at which time nearly all individuals collected were from run-Ts. Overall mean densities from side ($2.41/\text{m}^2$) and middle ($1.87/\text{m}^2$) portions of the stream were quite similar. A decline in density over time was witnessed for both habitats (Figure 16). The crossing graph lines in Figure 16 suggest a possible lateral migration from side to middle positions, but because early instar crayfish densities were not significantly different between the two microhabitats, conclusions are speculative.

Other physical aspects of the stream environment were considered in their relationship to early instar abundance. No relationship existed between stream depth and crayfish density in the Ford River (Figure 17). Water velocity also was not significantly correlated with density (Figure 18), although crayfish generally achieved higher numbers in slower water and no individuals were found in water with a velocity greater than 0.440 m/sec.

DISCUSSION

O. propinquus growth and fecundity traits in the Ford River compared well with values reported for other populations of the species in the northern part of its range (Capelli 1975, Corey 1987). Growth, production, and fecundity were lower than most values reported for more southern populations of O. propinquus (Van Deventer 1937,

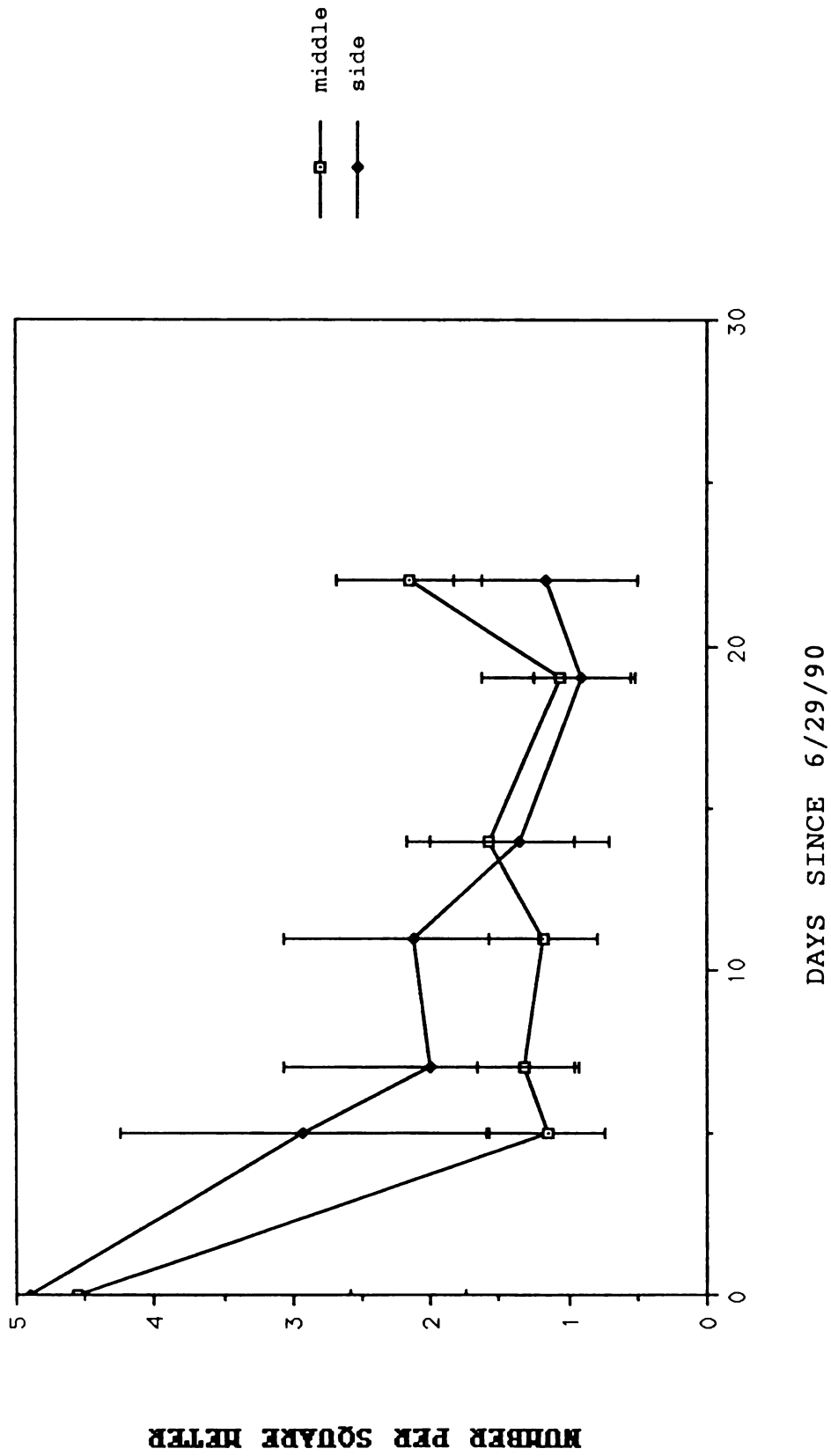


Figure 16. Mean densities of Ford *Q. propinquus* early instars from middle and side habitats beginning 6/29/90. Error bars indicate \pm S.E.

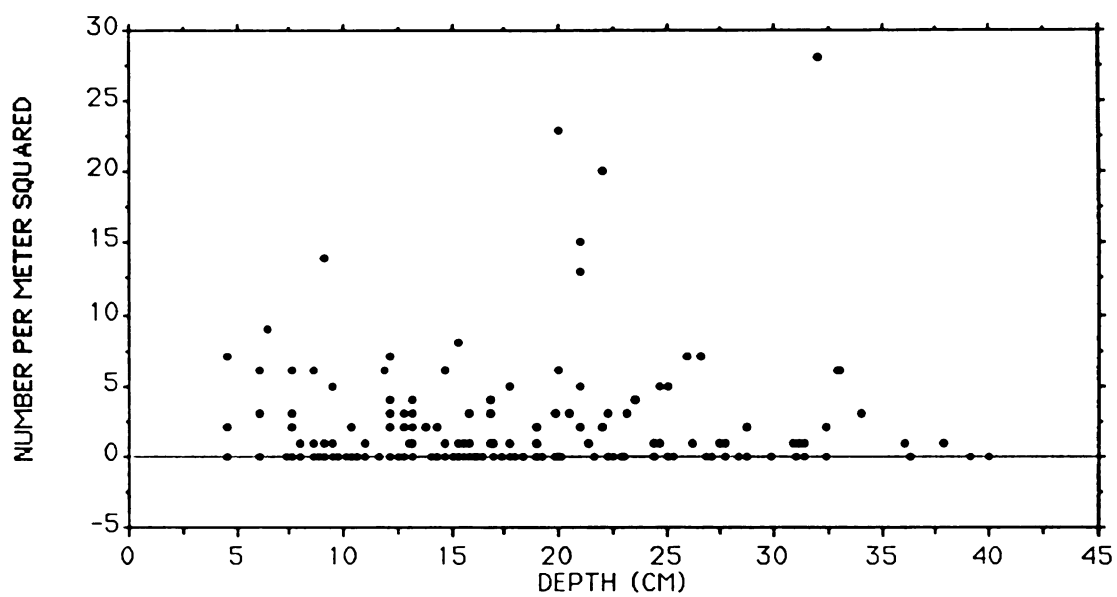


Figure 17. Relationship between water depth and density of early instar *Q. propinquus* from the Ford River.

$R^2 = 5.253 \text{ E-}3$.

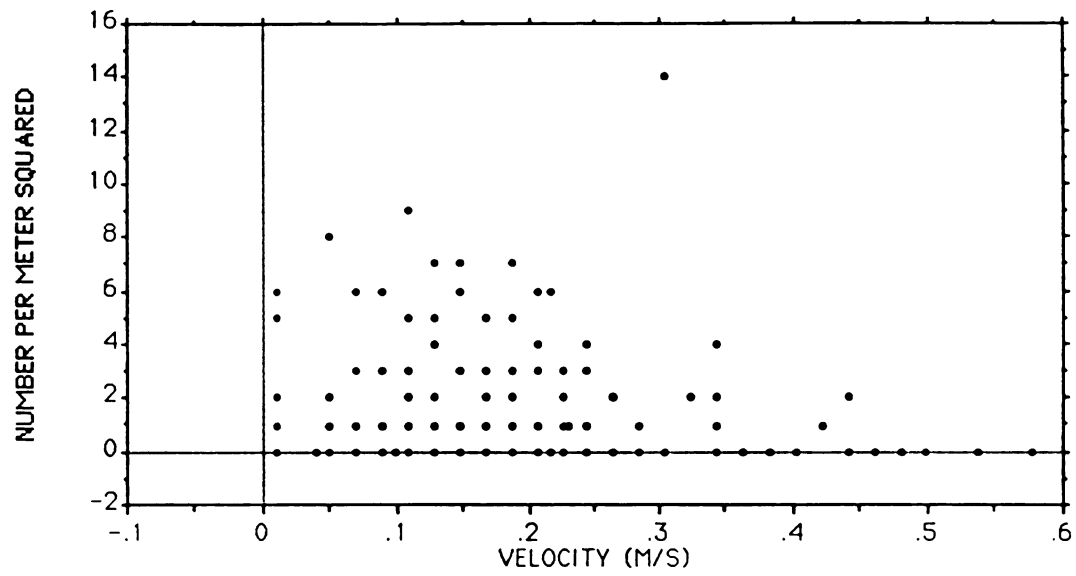


Figure 18. Relationship between water velocity and density of early instar *Q. propinquus* from the Ford River. $R^2 = 0.022$.

Vannote 1963), and in larger crayfish species (Langlois 1936, Momot 1967, Weagle and Ozburn 1972, Momot et al 1978, and Corey 1987). The sequence and timing of life history events in the Ford River were similar to those reported for O. propinquus in northern latitudes (Crocker and Barr 1968, Capelli 1975, and Corey 1988). Others who have studied O. propinquus in the southern reaches of its range found developmental events to occur earlier in the year (Van Deventer 1937, Bovbjerg 1952). For instance, Bovbjerg (1952) reported juveniles recruited into the population in late May and early June, while instars were not independent of their mothers in the Ford until late June. O. propinquus usually takes two years to mature over its entire range (Van Deventer 1937, Capelli 1975, and Corey 1988), while crayfish species in the southern United States tend to reach maturity within their first 8 to 16 months (Penn 1943). The absence of winter growth found for O. propinquus in the Ford River has been found in other temperate crayfish populations as well (Vannote 1963, Hopkins 1967, Flint 1975, Pratten 1980, France 1985, Corey 1988).

The deviation from the 1:1 sex ratio seen in the early summer Ford River population (Table 9) may have reflected a period of female seclusion during their postreproductive molt. A pattern of more males than females early in the growing season was observed in another O. propinquus population and was attributed to inadequate sampling of reclusive ovigerous females (Fielder 1972). Svärdson (1948) found the sex ratio of Astacus fluviatilis to deviate significantly from one in early June, with males being more

abundant. He found females to outnumber males in July, presumably related to the male molting period. The two occasions in August when sex ratios differed significantly from one in the Ford River (Table 9), did not coincide with molting periods. The deviant ratios may have been a product of small sample size. Sex ratios of Q. propinquus in the Baraga Creek population were more consistently different from one, also in favor of males (Table 9). The May and early June occurrences may be explained by isolation of reproductive females. The general consistency of the pattern throughout the summer however, may reflect a real difference in the numbers of males and females in the population.

Aspects of fecundity such as the percentage of ovigerous females in a population, size at first reproduction, number of eggs produced per female, and the amount of egg mortality can all influence the intrinsic rate of increase in a population. The values for these components of fecundity in Q. propinquus from the Ford River were generally similar to those found in other Q. propinquus populations at similar latitudes (Capelli 1975, Corey 1987, Corey 1988). Data on egg mortality were not given by these workers however. The figure of 57.7% of mature females ovigerous in the Ford River falls within the range of 44.4-78.3% reported in other species (Mason 1975, Woodcock and Reynolds 1988). The Ford value of 8.1% ovigerous out of the entire population is at the lower end of the 8.0-34.6% range given for Q. propinquus by Corey (1988).

The smallest gravid female in the Ford population was 18 mm in carapace length. The smallest gravid female in Capelli's

(1975) Wisconsin Q. propinquus population was also 18 mm in length. Corey (1988) found the species to bear eggs at a smaller size (12.8-14.3 mm) in four Ontario river populations. This smaller size may have reflected her method of measuring carapace length from the base of the eyestalk instead of the tip of the rostrum.

The mean number of pleopod eggs per reproductive female in Ford Q. propinquus (85.5) was within the range of 60-107.5 reported for the species at similar northern latitudes (Capelli and Magnuson 1974, Corey 1987). Van Deventer's (1937) mean of 132 for the species was exceptionally high and may have reflected a longer growing season in Illinois, compared to the shorter growing seasons in Wisconsin, Michigan, and Ontario.

Mixed reports of egg loss were found in the literature. Mason (1970) witnessed a 15-60% percent loss of the original brood of eggs in Pacifastacus trowbridgii and attributed it to cannibalization by the mother. Brown and Bowler (1977) also reported a considerable loss of eggs in A. pallipes. Conversely, Rhodes and Holdich (1982) found no relationship in the above species between egg number and time of collection during the brooding period. A trend towards lower egg number over time occurred in the Ford River but was not significant.

Q. propinquus annual production in the Ford and Baraga populations was lower than values found for more southerly Q. propinquus populations and larger crayfish species (Vannote 1963, Momot 1967, Momot and Gowing 1977b, Shimuzu and Goldman 1981). Vannote (1963) reported considerably

higher annual production figures of 41.5 g wet weight/m² (~13.8 g dry weight) for Q. propinquus in southern Michigan, perhaps related to a longer growing season. The larger Q. virilis had annual production figures in Michigan lower peninsula lakes ranging from 6.02-20.72 g dry weight/m² (Momot 1967, Momot and Gowing 1977b). Annual production:biomass ratios of Ford and Baraga Q. propinquus were similar to those reported for other short lived crayfish species. Vannote (1963) reported a 0.9 P/B ratio for Q. propinquus. Momot (1967) and Momot and Gowing (1977b) found a 0.94-1.53 range of P/B values in their Q. virilis studies. These ratios tend to be larger than the 0.32-0.90 range reported for longer lived crayfish species (Mason 1963, Shimizu and Goldman 1981, Brewis and Bowler 1983, Huryn and Wallace 1987, Cukerzis 1988). Longer lived species are often quite large and usually experience slow relative growth, lending to the lower P/B ratios.

The instantaneous mortality rate (Ricker 1975) of Ford early instars between 5/6/90 and 7/6/90 was 0.0531 / day (eggs hatched ~ 6/17/90). Instantaneous mortality rates of YOY crayfish from 6/20/90 to 7/14/90 (eggs hatched ~ 6/25/90) calculated from Capelli's (1975) data on a lentic population of Q. propinquus were lower than my value at 1 meter depths ($Z = 0.0123$ / day) but higher at 3 meters ($Z = 0.0561$ / day) and 5 meters ($Z = 0.1630$ / day). No researcher to my knowledge has attempted a detailed analysis of the survivorship of the earliest instars in a crayfish population. Capelli's (1975) estimate of mortality was based

on data from two sampling dates 25 days apart. Some have estimated the density of YOY individuals later in the growing season when crayfish were at a more catchable size (Momot 1967). Using this method and fecundity data, Momot and Gowing (1977b) found survivorship of YOY Q. virilis to the end of their first growing season to be 5-40 % over different lakes and years. Survivorship of Ford YOY to 8/31/90 was within this range at 13.9 %. Others have solely used pleopod egg counts to estimate the abundance of the YOY size class (Shimizu and Goldman 1981, Cukerzis 1988).

The survivorship curve constructed for Ford early instar Q. propinquus in 1990 was clearly an atypical survivorship curve (Figure 7). The initial steep decline of the curve, reflecting high initial mortality, was not unexpected. The increase in instar density at 82 days commensurate with the time early instars began being sampled in the block net however, seemed counterintuitive. One would expect the total numbers of a cohort to decrease with time as individuals succumbed to various forms of mortality. Two to five times more early instar crayfish were collected using the block net approach than were collected using kick screens. There is reason to believe that the kick screen method used to sample early instars during the first weeks of their lives was less efficient than the block net method. There was likely an increased probability of escape by YOY crayfish around the sides of the kick screen and underneath the bottom. Because of the nonpliable nature of window screen and the rough, mostly cobble substrate of the Ford River, it was sometimes difficult to position the bottom edge of the kick screen

flush with the stream bed. The block net, conversely, spanned the entire width of the stream and was equipped with lead weights on its bottom edge which were supplemented with rocks to effectively seal the net to the bed. Thus, potential escape of crayfish around or underneath the block net was largely prevented. The fact that O. propinquus YOY were quite small (< 7mm carapace length) and often difficult to locate among the mass of dislodged periphyton, invertebrates, leaf material, and other debris in the kick screen may have also contributed to the comparative low numbers of crayfish obtained using the kick screen method.

On 8/1/90 the kick screen method and the block net method were compared in order to determine a correction factor, Factor E, for the reduced catch-per-unit-effort of the kick screen method. The kick screen approach produced an unrealistically low density figure of $0.83/m^2$ however, so the methods were compared using a kick screen effort on 7/21/90 and a block net sampling on 7/27/90. For purposes of computing the correction factor, zero mortality was assumed between 7/21/90 and 7/27/90. Figure 19 is a modification of the survivorship curve shown in Figure 7 in which densities derived from kick screen sampling have been multiplied by Correction Factor E (3.99). This modified survivorship curve is more typical of the survivorship curve exhibited by a highly fecund short lived organism such as a crayfish.

Various workers have examined the distribution of juvenile and adult crayfish in different microhabitats within a single population (Flint and Goldman 1977, Gore and Bryant 1990). Rabeni (1985) found that juveniles of two sympatric

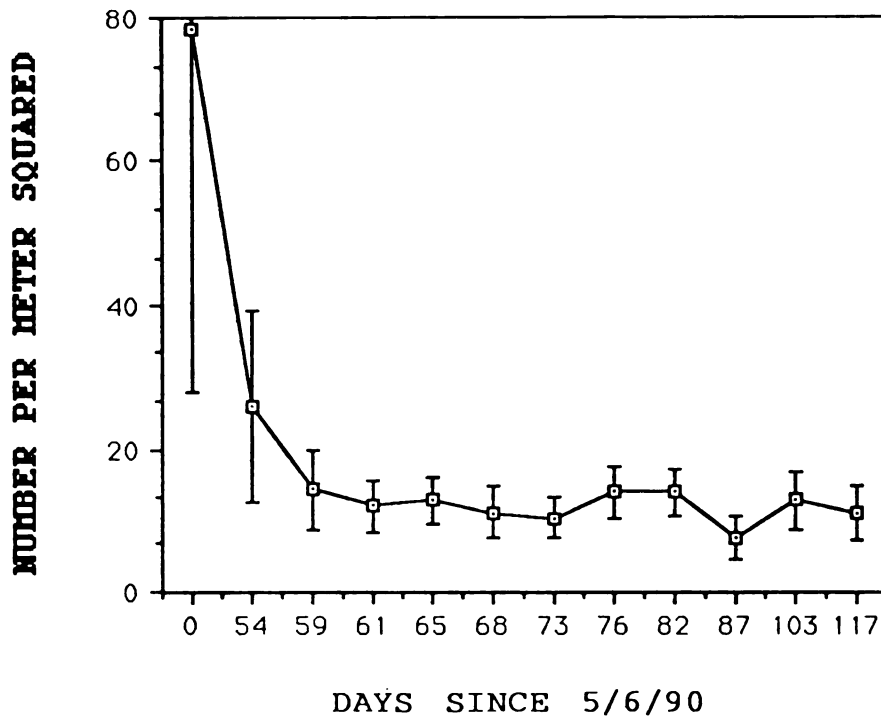


Figure 19. Revised survivorship curve of O. propinquus early instars from the Ford River in 1990. Data point at zero days represents mean pleopod eggs/m². Data points at 54-76 days represent the grand mean of mean longitudinal densities (Figure 16) weighted for habitat relative abundance at the Ford site and adjusted by Correction Factor E. Data points at 82-117 days represent mean densities obtained with the block net method. Error bars indicate \pm S.E. of means unweighted for habitat relative abundance on a given date.

Orconectes species used different microhabitats to some extent, and invoked competition as a mechanism explaining the differences. Ford O. propinquus early instars may be using different microhabitats during their first weeks of life. Because distribution of early instar crayfish tended to be rather clumped in all microhabitats examined, standard errors of mean densities for a given microhabitat were rather high. High standard errors were the main reason most densities were not significantly different between microhabitats. Keeping in mind that densities between microhabitats were not significantly different for most sampling dates, speculation will be made on the abundance trends observed. High densities of crayfish early instars in riffles and run-Hs initially (Figure 15) may have reflected the position of their mothers at the time the young became independent. Gore and Bryant's (1990) data on the habitat preference of adult O. neglectus in an Ozark stream suggested that while adults preferred backwater areas during most of the year, ovigerous females opted for riffle areas. This behavior of berried females presumably meets the high oxygen demands of their pleopod eggs, and could explain why Ford O. propinquus instars were initially the most abundant in riffles and run-Hs, which may have been more rich in oxygen. Ovigerous females in the Ford River were collected more commonly from runs than riffles during block net sampling however, a fact inconsistent with the preceding explanation. The decline over time in early instar densities from riffle and run-H habitats was probably due to various causes of mortality in the

cohort, but may have reflected some migration into run-T habitats, since run-T densities stayed fairly stable over time while overall densities declined (Figures 7 & 15). Rabeni (1985) reported his data as mean densities pooled over the course of his study, so there was no indication if the early instars changed their position in the stream as they grew.

There was considerable year-to-year variation and between stream differences in Q. propinquus abundance. It is not clear why densities of y1 individuals from the Ford River were so high initially in 1989 (Figure 5). It may have been that 1988 was an exceptional year for young production. Reasons for the steady decline in 1989 Ford River y1s are also unclear. Predation by fish or raccoons may have been responsible, or possibly intraspecific competition, in light of the initial high densities ($> 10/\text{m}^2$). Densities from 1989 were similar to those of most lotic crayfish populations that have been studied. Slack (1955) reported autumn crayfish densities in two Indiana streams between 23.2-29.2/ m^2 . Momot et al (1979) lists literature reports of stream crayfish density as high as 33/ m^2 , but it is not clear if this density represents only adults or all size classes. Others have reported annual mean adult densities in streams between 0.5-8.9/ m^2 (Vannote 1963, Shimuzu and Goldman 1981, Price and Payne 1984, Rabeni 1985). Even though many of these latter densities represent mean stream densities over a wider range of habitats than were used in the Ford River study, 1989 Ford crayfish densities were quite high, possibly high enough to foster intraspecific competition. The 1990 y1 size class in

the Ford River may have been at low enough numbers initially to prevent the effects of predation or competition, as densities were fairly stable over the 1990 sampling period. Baraga Creek 1989 yls, which were never more abundant than $5.7/\text{m}^2$, also experienced rather stable densities over the summer (Figure 5). Low densities on 10/28/89 in both Baraga and Ford populations (Figure 5), may have been partially due to decreased sampling efficiency of crayfish, since they tended to be sluggish due to low stream temperature.

The sampling efficiency of the block net method in general was determined using the results of a mark and recapture study in an area adjacent to the Ford site on 9/13/90. The study used an Adjusted Peterson Estimate of N (Ricker 1975). After partitioning a 10 m^2 area with upstream and downstream block nets, three kicking passes were made in the manner described earlier. Individuals were marked by clipping their left fifth periopod, released back in the enclosed area, and allowed to relocate for two hours. The recapture run consisted of three kicking passes. The total number of crayfish captured from the three initial kicking passes divided by the Peterson N represented the efficiency of the block net method. The block net method had a 58% efficiency in sampling crayfish $\geq 7 \text{ mm}$ in length. The 95% confidence interval on the block net method efficiency was quite large ($79\% > 58\% > 41\%$). The inverse of this efficiency value represented Correction Factor D (1.73) and could be applied to densities to result in adjusted densities. In adjusting crayfish densities using Correction Factor D, I would have preferred to use densities derived from the sum of the three

kicking passes, instead of depletion densities obtained using removal collection (Zippen 1958). This would have avoided adjusting densities that had already been adjusted (i.e. potentially compounding errors). Nevertheless, the percentage difference between crayfish totals derived from the sum of the three kicking passes and totals obtained using removal collection (Zippen 1958) was generally small. The mean difference over all the Ford and Baraga sampling dates was 4.7 ± 0.7 percent. Even though this difference becomes 8.1 ± 1.2 percent when multiplied through by Correction Factor D, the figure was within the error range of the block net efficiency. Figure 20 represents the two extremes for all 1989-90 Ford and Baraga subsites in the discrepancy between the two kinds of totals (labeled raw total and depletion total in the graph).

O. propinquus densities from the Ford River adjusted using Correction Factor D were clearly on the high end of densities reported for other stream crayfish populations. For instance, the mean adjusted density of yls in the Ford River between July and October of 1989 was $16.2/\text{m}^2$. Crayfish densities in Baraga Creek were adjusted using Correction Factor D obtained in the Ford River mark and recapture study. The assumption was made that Baraga Creek crayfish were sampled with the same efficiency as Ford individuals based on the similar substrate, stream width and depth, and flow regime of each stream. The adjusted mean density for Baraga Creek yls during 1989 was still fairly low at $5.2/\text{m}^2$.

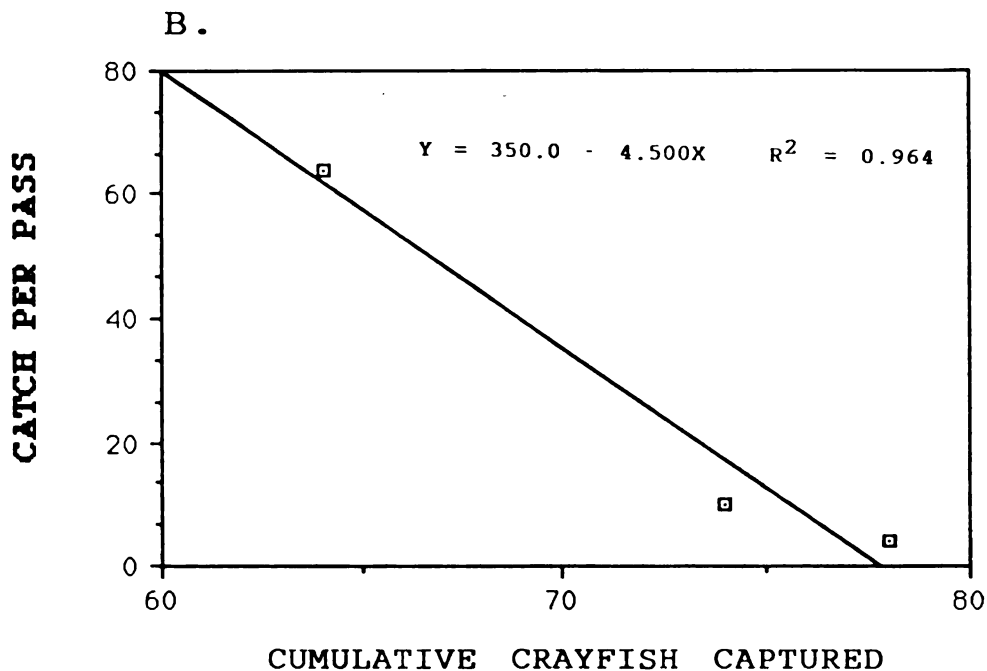
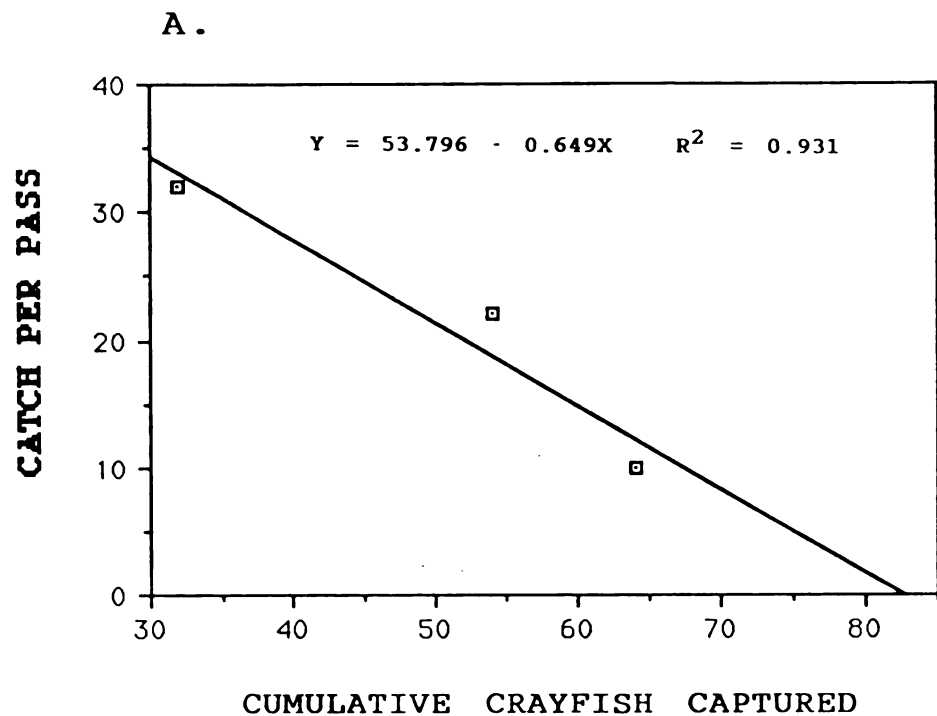


Figure 20. Ford River O. propinquus captured per kicking pass regressed on cumulative capture. A. 7/27/90: raw total = 64, depletion total = 83. B. 8/31/90: raw total = 78, depletion total = 78.

Differences in size (and therefore growth) of Ford y1 individuals between 1989 (1988 cohort) and 1990 (1989 cohort) may have been related to variable climates between the two years. Aiken (1967) found that molting (and therefore growth) in O. virilis ceased when water temperatures fell below 10 C. Therefore, mean water temperatures in the Ford River were examined for those periods during the crayfish growth season that could potentially be low enough to limit growth. The 1988 cohort experienced higher mean water temperatures and more days when mean water temperatures ≥ 10 C, for both the period at the end of its YOY growth season and the period of spring growth the following year, than the 1989 cohort during comparable intervals (Table 11). This data does not rule out other potential factors that may have been responsible for the year-to-year size differences observed. A paucity of data points makes conclusions about year-to-year size differences in Baraga y1 O. propinquus difficult, although 1989 individuals appeared to be slightly larger.

There was an inverse relationship between O. propinquus density and individual growth of YOYs in both Baraga Creek and the Ford River perhaps mediated by intraspecific competition. Growth of YOY individuals considered over an entire season was inversely correlated with the density of y1 individuals (Figure 9, Tables 3 & 5). In addition, growth of y1 individuals was substantially higher in the Baraga population compared to the denser Ford population in 1990 (Figure 8). If density was solely controlling individual growth in these crayfish populations one would have expected

Table 11. Ford River water temperature data¹ at the end of the YOY growing season and beginning of the y1 growing season for 1988 and 1989 O. propinquus cohorts.

Period	Mean temperature (C) \pm S.E.	Days ² > 10 C
<i>Sept9-Oct9 88</i>	<i>12.29 \pm 0.45</i>	<i>24</i>
Sept9-Oct9 89	11.57 \pm 0.59	21
<i>May 89</i>	<i>11.54 \pm 0.71</i>	<i>21</i>
May 90	9.87 \pm 0.49	15

1- data from Burton et al (1988-89) and Burton et al (1989-90).

2- number of days during time interval when the daily mean water temperature exceeded 10 C.

Ford 1990 yls to have been larger than the more numerous 1989 y1 individuals. This deviation might be explained by the lower stream temperatures in Fall 1989 and Spring 1990, however, and a case of physical factors overriding the influence of biological ones. Inverse relationships between density and individual growth in crayfish have been noted by many other investigators (Svårdson 1948, Abrahamsson 1966, Hopkins 1966, Momot 1967, Flint and Goldman 1977, Momot 1977b, France 1985, Sokol 1988, Hanson et al 1990).

Although water hardness could not be ruled out as a factor contributing to the greater abundance of O. propinquus in the Ford River compared to Baraga Creek, water hardness was apparently not affecting O. propinquus growth in either of the populations studied. If water hardness, and specifically calcium, was an important factor in growth, one would have expected individual growth to have been higher in the Ford River where calcium was plentiful (~20 ppm) compared to Baraga Creek where calcium was less abundant (~10 ppm). Although growth of Procambarus clarkii increased with hardness up to 200 ppm (de la Bretonne et al 1969) there are reports of individual crayfish in systems with equal or less amounts of calcium than Baraga Creek, growing as well as crayfish subject to much higher amounts of calcium (Capelli 1975, Goldman and Rundquist 1977). Capelli (1975) also determined experimentally that survivorship of O. propinquus juveniles in a lake with 2.8 ppm Ca^{++} was as high as that in a lake with three times more calcium. Conversely, de la Bretonne (1969) found that survivorship of Procambarus clarkii in plastic ponds was slightly lower in water with 50

ppm CaCO_3 (higher than the 25.0 ppm CaCO_3 in Baraga Creek) than in water with 100 ppm CaCO_3 . Thus, although it seems unlikely that calcium was limiting growth of Q. propinquus in Baraga Creek, it may have been affecting survivorship.

Chapter 2: Diet analysis of O. propinquus
in a northern Michigan stream

INTRODUCTION

A considerable number of diet studies have been performed on crayfish indicating that they are omnivorous generalists. Because of crayfish's wide feeding preferences they may act as primary consumers, secondary consumers, and as detritivores; in the latter case contributing to nutrient cycling by initiating the breakdown of allochthonous materials (Momot et al 1978, Huryn 1987). Although crayfish are omnivorous, plant material including vascular plants, algae, and detritus usually dominate their diet (Bovbjerg 1952, Vannote 1963, Momot 1967, Prins 1968, Capelli 1980, and Sokol 1988). Animal material usually represents a smaller percentage of their total diet. Exceptions are evident though, such as a population of Astacus leptodactylus cubanicus in the River Don in Russia which primarily consumed amphipods (Tcherkashina 1977). As crayfish often dominate the macroinvertebrate biomass of streams (Webster and Patten 1979, Momot et al 1978, Huryn and Wallace 1987), there is potential for them to regulate the abundance and distribution of various organisms. Experimental work has shown that crayfish can significantly reduce macrophyte (Lodge and Lorman 1987) and macroinvertebrate biomass (Hanson et al 1990), and reduce or increase periphyton production at high and low crayfish densities respectively (Flint and Goldman 1975). Different size classes of crayfish may affect community structure in different ways as evidence suggests that a crayfish's diet changes with age (Creaser 1934b,

Vannote 1963, Abrahamsson 1966, Mason 1975, Lowery and Holdicn 1988).

Diatoms compose varying percentages of a crayfish's diet in different systems (Prins 1968, Momot et al 1978, Capelli 1980). The kinds of diatoms eaten by crayfish however, have not been examined in any detail (but see Flint and Goldman 1975). Preliminary observation of O. propinquus diet in the Ford River indicated that diatoms were the predominant component. The objective of this study was to conduct a detailed diet analysis of O. propinquus to determine whether crayfish age and/or season affected the kind and relative amount of diatoms they consumed. Other components of O. propinquus' diet were analyzed with the same intent.

METHODS

Crayfish were collected for diet analysis during the summer of 1990 in a ~200 meter stretch of the Ford River approximately 200 meters downstream from the population sampling site (see site description, Chapter 1). Young-of-the-year (YOY) were collected on seven sampling dates beginning in late June and ending in early September. Adults were collected on three occasions between late June and early September. All individuals were obtained using hand held kick seines. Crayfish were placed on dry ice for 1-3 hours within an hour of collection, after which they were kept in a freezer until the contents of their stomachs were examined. All specimens were analyzed within four months of collection.

Frozen crayfish were allowed to thaw in ethyl alcohol for

at least 30 minutes before their stomachs were removed and examined. Stomachs were subjected to a sequential analytical regime. A Bausch and Lomb dissecting microscope (10-45x) was used initially to examine the total contents of a stomach for insects, larger algal material, and detritus. The stomach contents were then examined with a Leitz Laborlux 11 compound light microscope under 150x. This step allowed smaller items such as insect head capsules to be identified and counted. Semi-permanent wet mount slides were made by placing a subsample of the total stomach material (prior to any analysis) of a crayfish and a few drops of water on a glass slide, homogenizing the material by stirring it with the tip of a pipet, and securing a coverslip on the slide with household nail polish. These slides were also examined under 150x for insects and other material. Finally, the slides were examined for diatoms under 1500x using oil immersion. The first 50 valves encountered during horizontal searching passes across the slide were identified to genus (Prescott 1978, Wujek and Rupp 1980, Germain 1981) and recorded. Slides with less than 50 diatom valves were not included in the data analysis. All insects encountered during the various analysis steps were identified to order, or family when possible (Wiggins 1977, Coffman and Ferrington 1984, Edmunds 1984, Harper and Stuart 1984). The ability of a crayfish's gastric mill (Pennak 1978) to grind up food items made insect identification difficult. Some mangled insects were classified simply as unknown insects. A total count of all insects that could be identified as such was made for each stomach examined. For counting purposes, a piece of

insect was sufficient to conclude that at least one insect was present in a stomach. The assumption was made that a piece of insect in a stomach represented the remains of a whole insect ingested by the crayfish. The presence of two or more whole insects or insect pieces obviously not from a single individual (e.g. two head capsules), was necessary to confirm that two or more insects were ingested. Care was taken not to count the same insect or piece of insect twice. A qualitative note acknowledging the presence or absence of filamentous green algae, was made also for each stomach.

RESULTS

Diatoms, filamentous green algae, insects, detritus, and unicellular green algae were the major items found in both juvenile and adult O. propinquus stomachs. With the exception of adults on 9/7/90, filamentous green algae and at least 50 diatom valves each attained over 70 % incidence in crayfish stomachs examined for all dates during 1990 (Figure 21). Insects became increasingly abundant in YOYs as they grew over the summer (Figure 21). Well over 50 % of adult stomachs were empty on 9/7/90, in sharp contrast to earlier sampling dates. Because of difficulties in identifying fragmented algal filaments usually missing their chloroplasts, filamentous green algae were grouped together in a single category and reported as such. Unicellular green algae found in crayfish stomachs included Closterium, Staurostrum, Cosmarium, Scenedesmus, and Merismopedia. Sand

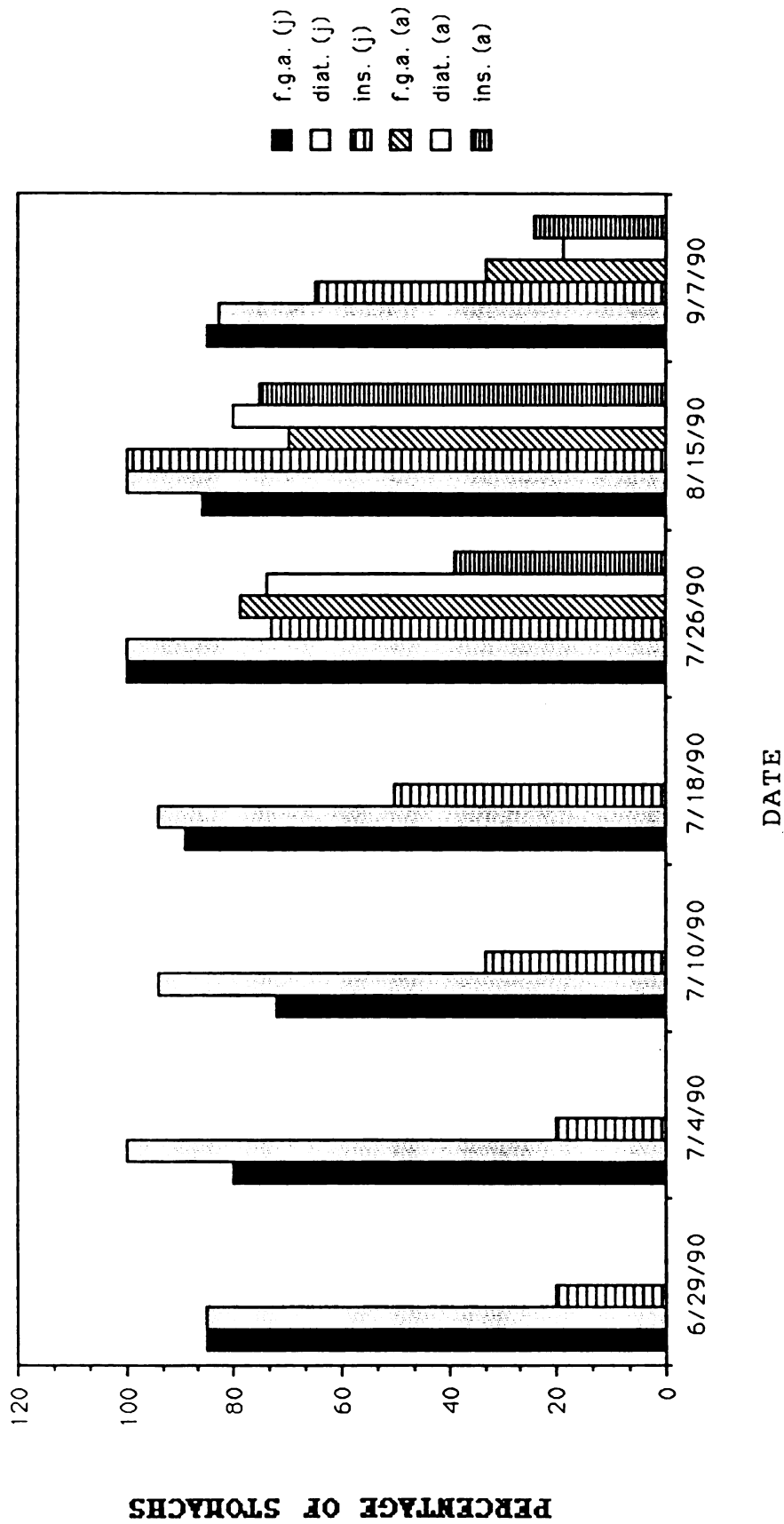


Figure 21. The percentage of *Q. propinquus* from the Ford River with various food items. f.g.a. = filamentous green algae. diat. = ≥ 50 diatom valves. ins. = insects. j = juvenile. a = adult.

grains and detritus, probably consisting mostly of leaf material, were also found in many stomachs.

Insects were considerably more abundant in juveniles than adults (Figure 22). Peak insect abundance occurred on 8/15/90 (47 days in Figure 22) in both age classes. Crayfish age and time of sample were both significant (ANOVA, $P = 0.0001$) in explaining the variation in insect abundance in stomachs when compared over 7/26/90 and 8/15/90. Diets on 9/7/90 were not included in the comparison because of the low incidence of food items in adults (Figure 21). Chironomidae dominated the insect fauna ingested in both age classes (Figure 23). Although juveniles contained more Trichoptera than adults, adults tended to eat more large insects including Plecoptera, Ephemeroptera, and insects in the "unknown" category.

Several diatom genera attained at least 7 % mean relative abundance in juveniles and adults when data was pooled over the summer. These included Achnanthes, Cocconeis, Cyclotella, Cymbella, Fragilaria, Gomphonema, Navicula, and Rhoicosphenia (Figure 24). A number of other genera occurred only rarely, never exceeding 3 % relative abundance. These included: Amphora, Diatoma, Epithemia, Eunotia, Frustulia, Gyrosigma, Meridion, Opephora, Stauroneis, and Synedra. Achnanthes, Cocconeis, and Navicula were more prominent in juvenile stomachs while Cyclotella, Cymbella, and Rhoicosphenia were more common in adults when summer data was pooled (Figure 24). The kinds of diatoms prevalent in stomachs changed over the summer. Figure 25 shows that certain genera such as Achnanthes dominated the diatoms

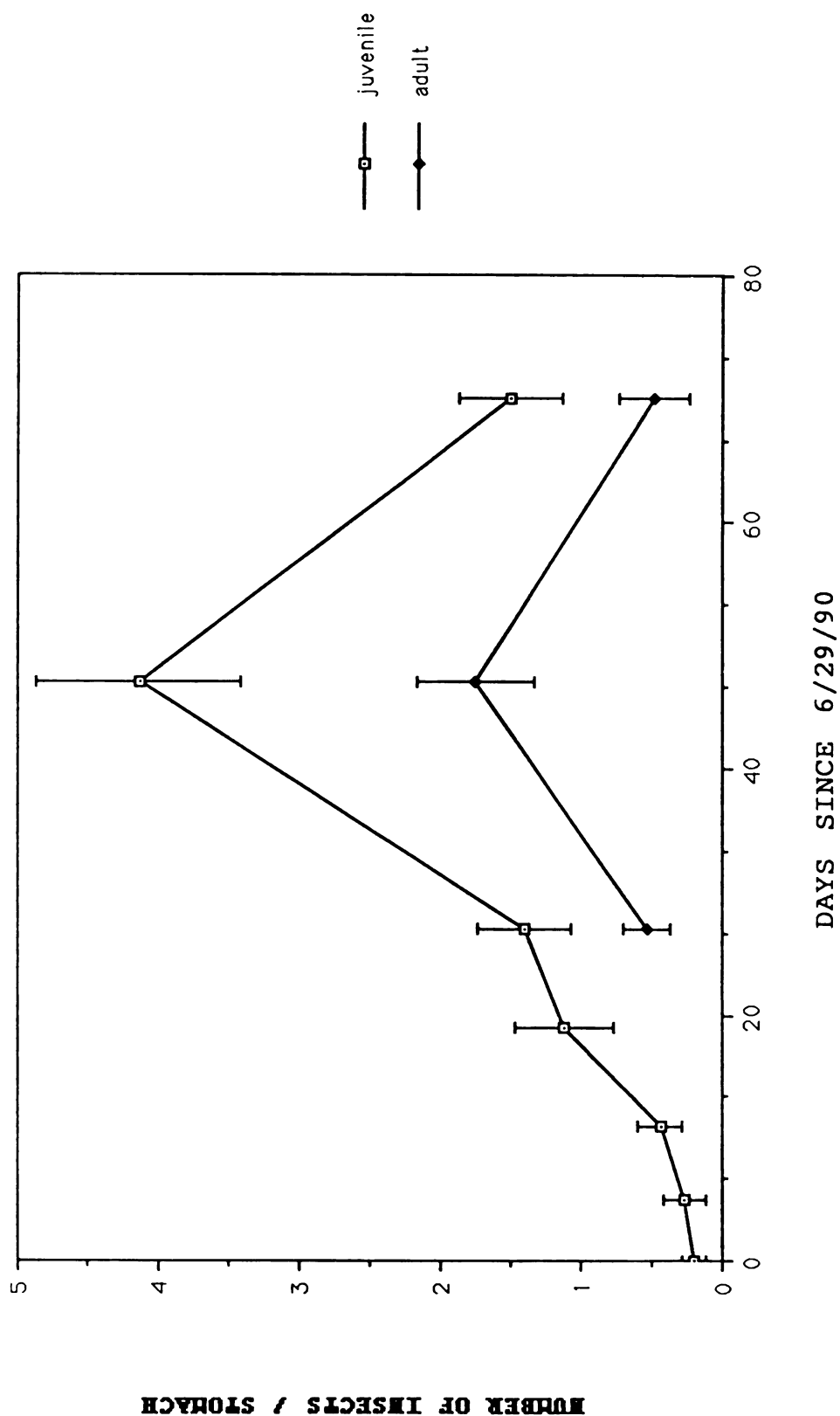
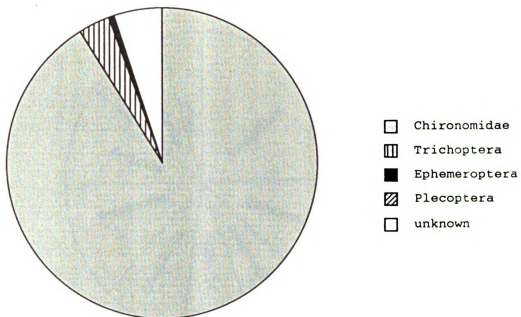


Figure 22. Mean number of insects in *Q. propinquus* from the Ford River. Error bars represent \pm SE.

JUVENILES



ADULTS

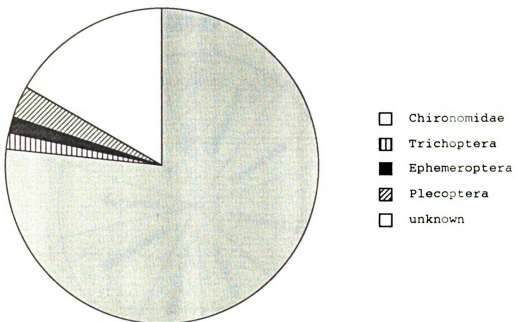


Figure 23. Mean relative abundance of insect types in the stomachs of *Q. propinquus* from the Ford River; data were pooled for the entire 1990 summer period.

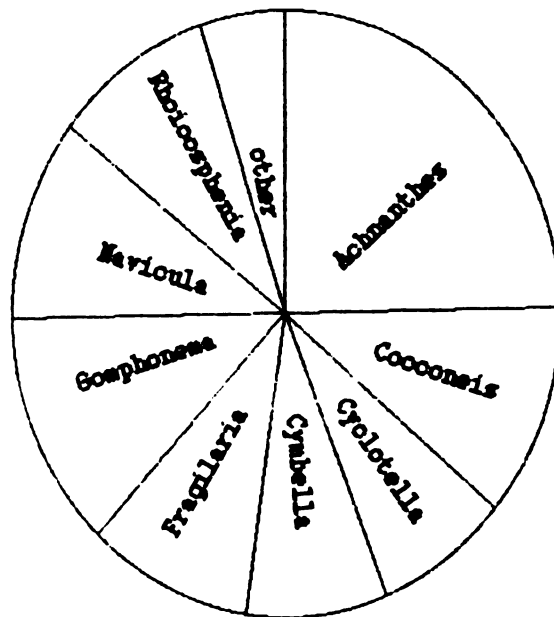
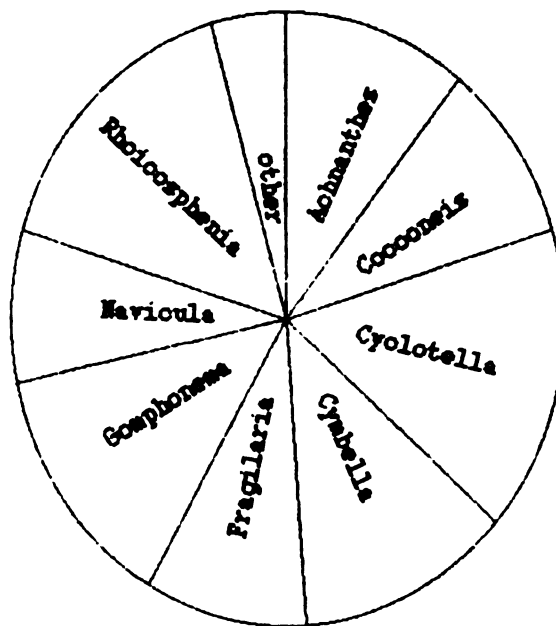
JUVENILES**ADULTS**

Figure 24. Mean relative abundance of diatom genera in Q. propinquus from the Ford River; data were pooled for entire 1990 summer sampling period.

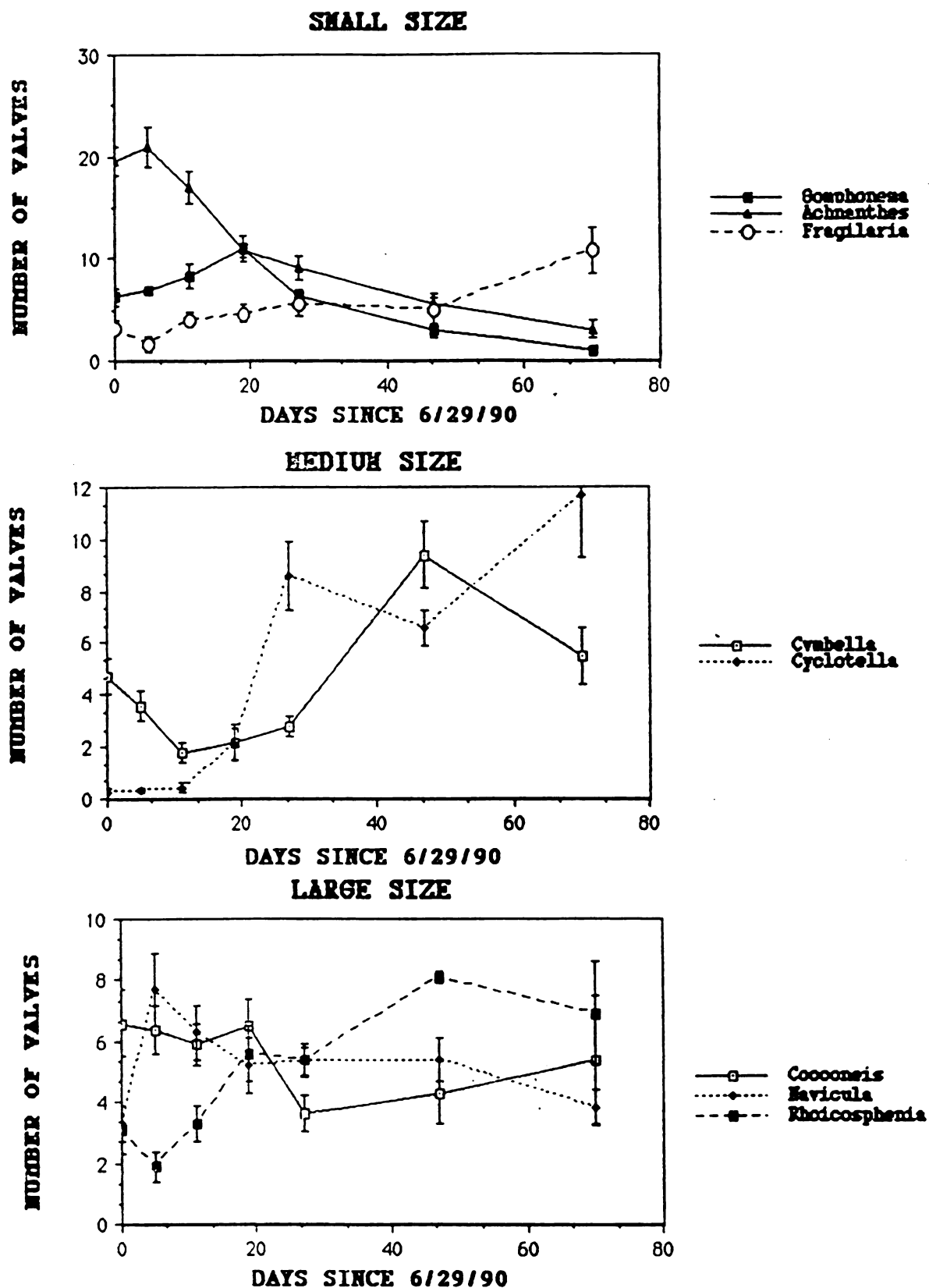


Figure 25. Relative abundance of small, medium, and large size diatom genera in *Q. propinquus* from the Ford River. The Y axis represents the number of diatom valves of a particular genus out of 50 total counted. Error bars indicate \pm S.E.

ingested early in the life of YOYs while others such as Fragilaria and Cyclotella increased in prominence in YOYs over the summer. Adults and juveniles generally appeared to be eating the same kinds of diatoms when compared over 7/26/90 and 8/15/90 (Table 12-13). When crayfish age and time of year were considered in a two factor ANOVA as possible influences on the relative abundance of common genera however, some significant differences were found (Table 14). Gomphonema was more abundant in adults ($P = 0.0021$) while Navicula was more common in juveniles ($P = 0.0289$). Additionally, Achnanthes was more common in juveniles but this difference was not significant at the 0.05 level ($P = 0.0633$). The ANOVA also showed that numerous diatom genera experienced significant changes in their relative abundance within the diet of a single crayfish age class between 7/26/90 and 8/15/90 (Table 14).

DISCUSSION

Although the relative proportions of different food items in O. propinquus stomachs were not quantitatively determined, diatoms appeared to be the most abundant food item by volume in both age classes. Filamentous green algae and insects were the second and third most common items in adults. Juveniles seemed to favor insects over filamentous green algae.

It is not clear why such a high proportion of adult O. propinquus stomachs were empty on 9/7/90 (Figure 21). High water at the time of sampling may have seen crayfish

Table 12. Relative abundances of small and medium size diatom genera in the stomachs of Q. propinquus from the Ford River. Values are means* \pm S.E.

Date	Age	N	<u>Achnanthes</u>	<u>Fragilaria</u>	<u>Gomphonema</u>	<u>Cyclotella</u>	<u>Cymbella</u>
6/29/90	J	17	19.5 \pm 1.4	3.2 \pm 0.7	6.3 \pm 0.9	0.2 \pm 0.2	4.7 \pm 0.7
7/4/90	J	15	20.9 \pm 1.9	1.5 \pm 0.8	7.0 \pm 0.1	0.3 \pm 0.1	3.6 \pm 0.6
7/10/90	J	17	16.9 \pm 1.6	4.0 \pm 0.7	8.3 \pm 1.1	0.4 \pm 0.2	1.8 \pm 0.4
7/18/90	J	17	10.9 \pm 1.3	4.6 \pm 0.9	11.1 \pm 1.1	2.1 \pm 0.6	2.2 \pm 0.7
7/26/90	J	15	9.0 \pm 1.2	5.5 \pm 1.1	6.3 \pm 0.6	8.6 \pm 1.3	2.8 \pm 0.4
8/15/90	J	14	5.5 \pm 1.0	4.9 \pm 1.3	2.9 \pm 0.7	6.6 \pm 0.7	9.4 \pm 1.3
9/7/90	J	15	3.0 \pm 0.9	10.8 \pm 2.3	0.9 \pm 0.5	11.7 \pm 2.4	5.5 \pm 1.1
7/26/90	A	20	6.5 \pm 0.8	4.1 \pm 0.8	8.7 \pm 0.8	10.4 \pm 1.3	3.9 \pm 0.6
8/15/90	A	16	4.4 \pm 0.9	3.8 \pm 1.2	5.1 \pm 0.6	5.7 \pm 1.1	9.0 \pm 1.1

* - mean number of diatom valves per individual crayfish out of 50 valves counted.

J - juvenile crayfish.

A - adult crayfish.

Table 13. Relative abundances of large size diatom genera in the stomachs of O. propinquus from the Ford River. Values are means \pm S.E.

Date	Age	N	<u>Cocconeis</u>	<u>Navicula</u>	<u>Rhoicosphenia</u>
6/29/90	J	17	6.6 \pm 1.1	3.3 \pm 0.6	3.1 \pm 0.8
7/4/90	J	15	6.4 \pm 0.8	7.7 \pm 1.2	1.9 \pm 0.5
7/10/90	J	17	5.9 \pm 0.7	6.3 \pm 0.9	3.3 \pm 0.6
7/18/90	J	17	6.5 \pm 0.9	5.2 \pm 0.9	5.6 \pm 0.9
7/26/90	J	15	3.6 \pm 0.6	5.3 \pm 0.5	5.4 \pm 0.5
8/15/90	J	14	4.3 \pm 1.0	5.4 \pm 0.7	8.1 \pm 0.2
9/7/90	J	15	5.4 \pm 2.1	3.8 \pm 0.6	6.9 \pm 1.7
7/26/90	A	20	4.3 \pm 0.7	4.5 \pm 0.9	5.3 \pm 1.1
8/15/90	A	16	5.3 \pm 0.7	2.7 \pm 0.7	11.2 \pm 1.7

Table 14. ANOVA tables for a 2-factor analysis of variance on the relative abundance of diatom genera in Q. propinquus stomachs. An asterisk indicates significance at the 0.05 level. Gomphonema had a higher relative abundance in adults. Navicula had a higher relative abundance in juveniles.

A. Achnanthes

Source	df	Sum of squares	Mean square	F-test	P value
age (A)	1	52.438	52.438	3.577	0.0633
time (B)	1	126.262	126.262	8.613	0.0047*
AB	1	7.545	7.545	0.515	0.4759
error	61	894.25	14.66		

B. Cocconeis

Source	df	Sum of squares	Mean square	F-test	P value
age (A)	1	10.125	10.125	1.076	0.3037
time (B)	1	11.63	11.63	1.236	0.2706
AB	1	0.148	0.148	0.016	0.9005
error	61	574.014	9.41		

C. Cyclotella

Source	df	Sum of squares	Mean square	F-test	P value
age (A)	1	3.821	3.821	0.162	0.6889
time (B)	1	177.989	177.989	7.535	0.0079*
AB	1	27.422	27.422	1.161	0.2855
error	61	1440.829	23.62		

D. Cymbella

Source	df	Sum of squares	Mean square	F-test	P value
age (A)	1	1.799	1.799	0.144	0.7056
time (B)	1	548.931	548.931	43.965	0.0001*
AB	1	9.324	9.324	0.747	0.3909
error	61	761.629	12.486		

Table 14 (cont'd.).

E. Fragilaria

Source	df	Sum of squares	Mean square	F-test	P value
age (A)	1	23.524	23.524	1.199	0.2778
time (B)	1	4.101	4.101	0.209	0.6491
AB	1	0.458	0.458	0.023	0.8791
error	61	1196.435	19.614		

F. Gomphonema

Source	df	Sum of squares	Mean square	F-test	P value
age (A)	1	85.535	85.535	10.315	0.0021*
time (B)	1	190.709	190.709	22.999	0.0001*
AB	1	0.224	0.224	0.027	0.8700
error	61	505.812	8.292		

G. Navicula

Source	df	Sum of squares	Mean square	F-test	P value
age (A)	1	46.001	46.001	5.008	0.0289*
time (B)	1	10.708	10.708	1.166	0.2845
AB	1	15.36	15.36	1.672	0.2008
error	61	560.312	9.185		

H. Rhoicosphenia

Source	df	Sum of squares	Mean square	F-test	P value
age (A)	1	37.514	37.514	1.488	0.2272
time (B)	1	288.92	288.92	11.463	0.0012*
AB	1	40.001	40.001	1.587	0.2126
error	61	1537.516	25.205		

secluded and not feeding, but this possibility does not explain why the vast majority of juvenile stomachs were quite full. A more likely reason for the high proportion of empty adult stomachs may involve the time of day crayfish were collected for analysis. Both juveniles and adults were collected during daylight hours. Feeding periodicity data collected during the summer of 1991 suggests that while juvenile crayfish feed with roughly equal frequency during daylight and after dark, adults show a strong preference for feeding after dark. Thus, the high proportion of empty adult stomachs on 9/7/90 may be the result of sampling adults during their daytime feeding lull. One would not expect a high percentage of empty stomachs in juveniles sampled during the daytime, since they apparently readily feed during this time. The preceding explanation does not account for why a comparatively small percentage of adult crayfish stomachs were empty of 7/26/90 and 8/15/90 (Figure 21).

Crayfish fragments were not seen in the 193 stomachs examined. This was a bit surprising as many others have reported crayfish remains in the stomachs of crayfish (Vannote 1963, Prins 1968, Mason 1974, Capelli 1980, and Growns and Richardson 1988). Perhaps evidence of cannibalism would have been found if adults were sampled for diet when the very small *O. propinquus* instars (4-5 mm carapace length) were abundant in the stream. On 7/26/90, the earliest date adults were sampled for diet, the early instar crayfish had obtained a mean size of 8 mm carapace length, a size perhaps at which they were less vulnerable to predation by adults.

Insects were clearly more abundant in juvenile stomachs than adult's on every sampling date when they were compared (Figure 22). Considering that the ordinate axis in Figure 22 represents absolute abundance of insects and that juveniles contained a substantially smaller total volume of material in their guts, the relative abundance of insect material was much greater in juveniles than adults. This may have reflected a greater protein need of juveniles during a period of active growth. Several others have also found juveniles to eat a higher percentage of animal material than adults (Creaser 1934b, Abrahamsson 1966, Mason 1975, Lowery and Holdich 1988). The similar pattern of insect absolute abundance in juveniles and adults over the 7/26-9/7/90 time interval (Figure 22) may indicate seasonal changes in the abundance of the insect community. The steady increase in the percentage of juveniles eating insects over the summer (Figure 21) could reflect an increase in the mobility and size of juveniles, as they become more adept at a predatory lifestyle. The fact that adult crayfish ate a higher proportion of larger insects than juveniles (Figure 23) may have been related to the larger mouth and chela size of adults.

Chironomids were the most common type of insect in either crayfish age class (Figure 23). Because the natural insect community was not sampled in 1990 however, it is not known if crayfish were actively selecting Chironomidae. Data from 1983 (Burton 1982-1983) on the summer insect community in the Ford River at a site immediately downstream from the current site suggests however, that O. propinquus may have been

selecting particular insects to consume among a mixed community (Table 15). The following assumption must hold if conclusions about O. propinquus selection in the Ford River are to be valid: the relative abundances of insect groups from the Ford River in 1990 at the current study site were generally the same as the relative abundances in 1983 at the downstream site. Aspects of stream morphology such as substrate, stream width and depth, and flow regime were similar when compared between 1983 and 1990 at the respective sites. Chironomidae had a higher relative abundance in the stomachs of juvenile and adult O. propinquus than in the 1983 natural stream community (Figure 23, Table 15). Juveniles may have been selecting Chironomidae, based largely on the insect's small size. It is not known why adult O. propinquus also apparently selected Chironomidae. A passive type of selection, where Chironomidae associated with the periphyton were ingested by grazing crayfish (Capelli 1980), may have been operating. Trichoptera and Ephemeroptera were underrepresented in the diet of O. propinquus. Although the larger size of these insects may have precluded their capture and ingestion by juvenile crayfish, it is unclear why they were not more common in adults.

There are a number of possible reasons for the differing relative abundances of diatom genera in adult and juvenile O. propinquus (Table 12-13). O. propinquus feed on the periphyton by grasping material with the chela of their periopods (personal observation). It seems possible that benthic diatoms such as Navicula may be less common in the diet of large crayfish (i.e. adult) than small crayfish (YOY)

Table 15. Relative abundance of various insect groups in the Ford River in 1983¹. Values are percent relative abundance.

Insect	Percent abundance
Chironomidae	61.9
Trichoptera	14.1
Ephemeroptera	14.5
Coleoptera	1.9
Other	7.6

1- data from Burton (1982-1983).

because of their tendency to adhere flat to the substrate, while an overstory form such as Gomphonema may be easier for larger individuals to harvest and hence appear more abundantly in their diets. Although Achnanthes, a benthic form, had a greater relative abundance in juveniles than adults (not statistically different however), Cocconeis, another benthic form, showed no significant difference in relative abundance between the two age classes (Table 14), counter to the explanation proposed above. A second possible explanation for the observed differences in diatom genera in Q. propinquus' diet involves active selection by crayfish for particular kinds of diatoms. Other invertebrates, including ciliates and snails, have been observed to selectively feed on particular diatoms (Patrick 1970, Patrick 1977). While it seems unlikely that adult Q. propinquus, due to their large size, could have been actively selecting diatoms, Q. propinquus juveniles, at 20 mm total length, may have been small enough to actively select particular diatoms; and, in the case of this study, may have selected Navicula. A third possibility for the perceived differences in diatom relative abundances in the diet of Q. propinquus involves adult and juvenile crayfish feeding in different areas of the stream. Diatom genera are known to favor particular substrates or flow regimes in a stream (Patrick 1977). As many diatom species attach to filamentous algae (Patrick 1977) there is also the possibility that diatoms were "accidentally" ingested by crayfish feeding on filamentous algae. Hence if filamentous algae were selected as a food source, certain

diatom genera may have appeared in greater abundance in a crayfish's stomach than if filamentous algae were not being eaten. As in the case of insects the natural diatom communities were not analyzed in this study, so any conclusions drawn about crayfish selecting particular diatom genera are speculative.

Previous diet studies of Q. propinquus also found the species to be omnivorous, with plant material generally comprising the bulk of the diet. Diatoms and other algae were the most frequent food items occurring in adults of a population from a Wisconsin lake, although mayflies and midges were also commonly eaten (Capelli 1980). Vegetation was preferred to animal material in an Illinois stream population of Q. propinquus (Bovbjerg 1952). Vannote (1963), as in the current study, found Q. propinquus juveniles to eat a larger percentage of animal material than adults.

CONCLUSIONS AND RECOMMENDATIONS

- 1) Q. propinquus was more abundant and experienced greater net production in the hard water Ford River than in the soft water Baraga Creek as I originally hypothesized (9.3 y1/m^2 vs. 3.0 y1/m^2 in 1989, 5.0 g/m^2 vs. 3.0 g/m^2 during 7/14/89 - 7/14/90).
- 2) Individual growth was greater in Baraga Creek than in the Ford River for YOY and y1 age classes. This result was contrary to my hypothesis that growth would be greater in the hard water Ford River.
- 3) The Ford River population appeared to be fairly stable as indicated by the R_0 (reproductive rate per generation) of 0.984 from life table analysis.
- 4) Mortality of early instar Q. propinquus from the Ford River was considerable from the egg stage through the first weeks of independence from the mother ($Z = 0.0531/\text{day}$ from 5/6/90 to 7/6/90).
- 5) Early crayfish instars from the Ford River appeared to use different microhabitats as they matured during their first weeks of independence. Some seemed to shift from run-Hs and riffles, where they were abundant early on, to run-Ts,

where most individuals were found on 7/18/90 and 7/21/90.

- 6) All size classes of O. propinquus from the Ford River predominantly ate diatoms during the summer of 1990. Filamentous green algae and insects were also commonly consumed.
- 7) Juvenile O. propinquus from the Ford River ate more insects than adults when compared over a common time period (2.7 insects/stomach vs. 1.0 insects/stomach).
- 8) Although juvenile and adult crayfish from the Ford River apparently consumed many of the same kind of diatoms in similar relative proportions, Gomphonema had a greater relative abundance in adult crayfish while Navicula had a greater relative abundance in juveniles.
- 9) O. propinquus of all age classes from the Ford River may be selectively consuming Chironomidae.

Many of the conclusions reached in this study suggest various avenues for further research in the systems. First of all, it would be worthwhile to investigate the mechanisms responsible for the individual size difference (or growth) and the differing abundances of O. propinquus in the Ford River and Baraga Creek. There are several factors that may be causing individual growth to be greater in Baraga Creek. There may be an inverse relationship between crayfish density and individual growth in these two systems. The

effects of crayfish density on growth could be examined through the use of in situ cage experiments in which crayfish are held in enclosures at predetermined densities along a continuum from low density (natural Baraga Creek crayfish density or lower) to high density (natural Ford River crayfish density or higher), and individual growth is measured. If individual growth is density-dependent in these streams, intraspecific competition for food may be involved. Baraga individuals may have more food available to them on a per individual basis. This possibility may be partially addressed by sampling the environmental food supply to see how it compares between the two rivers on a per crayfish basis. It may also be instructive to quantitatively compare the amount of food found in O. propinquus from each stream.

The other related question one could ask is why O. propinquus is over three times more numerous in the Ford River than in Baraga Creek. Because fecundity and survivorship of young can have profound effects on population size, these aspects should be compared between the two populations. Although low water hardness may not be affecting individual growth in this system, it may be affecting Baraga crayfish on the population level by interfering with reproduction or survivorship (France 1983). Predation represents a biological mechanism that could be affecting survivorship of O. propinquus in either stream and thus may ultimately be influencing population size. Various exclosure experiments could be performed in the stream to test this possibility. This type of experiment faces various problems however, one of which is controlling extraneous

variables. Habitat availability may be different between the Ford River and Baraga Creek and this represents another factor that could be limiting population size. This question could be addressed by completing a detailed substrate analysis in each stream.

In order to more adequately address the possibility that O. propinquus is selecting certain food types in the Ford River a study could be undertaken where crayfish diet and the biota are sampled at a single site over a common time period. It would also be interesting to see if food selection is taking place in Baraga Creek. This study could also separate individuals based on their microhabitat to determine if crayfish early instars are eating different things in different microhabitats. This analysis may provide insight as to the reasons for the apparent shifts in microhabitat use by early instars. The microhabitat distribution of adult crayfish could also be considered, to determine if juveniles and adults are segregating spatially in the stream. Finally, laboratory feeding studies could be used in conjunction with data on O. propinquus natural diet to determine if the crayfish actively selects particular insect and algal species among a mixed community.

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