EFFECTS OF SELECTED BIOTIC AND ABIOTIC FACTORS ON GROWTH AND SURVIVAL OF YOUNG CRAYFISH, *Orconectes virilis* (Hagen)

by

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ABSTRACT

The growth and survival of Orconectes virilis young was studied in 50 x 50 x 50 cm lake enclosures during the summer seasons of 1986 and 1987. The effects of density (12/m^2, 40/m^2, 160/m^2), substrate (mud, sand, no-substrate control), cover type (leaf-litter, muskgrass, plastic plant, no-cover control), treatment (control, food, fertilizer, 30 and 100 cm depth, and presence of adult crayfish were investigated.

When first placed in the enclosures, the young crayfish were 4.0 - 4.5 mm in carapace length (tip of the rostrum to the posteriomedial edge of the carapace). Experiments lasted two weeks, after which the surviving crayfish were counted and measured. In 1987, crayfish were returned to their cages after being measured, to permit sex determination at the end of the summer season and to provide further information on growth and survival.

Survival of crayfish was relatively high (75 - 100 %). It was reduced by the presence of adults (50 %) and was extremely low in cages lacking substrate and cover (6 - 15 %). It was not significantly influenced by any of the other factor combinations.

Mean carapace length after the two weeks experimental period ranged from 4.9 to 8.8 mm. Growth was poorest in cages lacking substrate and cover (4.9 - 6.4 mm) and in cages containing adult males (6.8 mm). Growth was inversely related to density, even though no difference existed between the low and the very low density after the first two weeks. Growth was also enhanced by

cover and a mud substrate. At the end of the summer season crayfish size was distinctly different at all three densities (16.1, 12.2 and 11.0 mm carapace length, respectively). Crayfish were also significantly larger in the fertilized cages (10.8 and 12.7 mm carapace length, respectively). Differences in growth are ascribed to food availability and feeding opportunity.

Sex ratio of crayfish that survived until the end of the summer, was 1 : 1.

Mortality of juvenile crayfish studied in Powell's lakes is mainly ascribed to intraspecific competition, moulting and oxygen deficiency. The extent of intraspecific competition is related to the size and quality of the nursery habitat.

This thesis is an original composition, based on research carried out by the author, and has not been previously submitted for credit toward any degree or diploma. Where the work of others has been included, it has been so acknoloedged and appropriately cited.

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INTRODUCTION

Crayfish populations are found in most parts of the world. In Europe, they have long been economically important (Brinck 1975, Hoffmann 1980). In North America, commercial interest in crayfish developed as the abundance of the European crayfish Astacus astacus (Linne) declined early in this century. The export market as well as increasing culinary acceptance, make aquaculture and commercial exploitation of wild stocks a worthwhile business. Louisiana now has approximately 50,000 hectares of ponds devoted towards production of crayfish, and Texas has 1,000 hectares (Gary 1975; de la Bretonne 1987). An intense fishery for wild stocks exists in California (Goldman 1973; McGriff 1983) and Louisiana (Comeaux 1975).

Little is known yet about the management of wild stocks. In Europe, severe season and size limits are in effect ostensibly to prevent overexploitation (Lindqvist 1977; Hofmann 1980). Recent discoveries from two northwestern Ontario lakes call these severe restrictions into question (Momot 1986). Despite intense trapping over several years, no reduction in production was observed. Compensatory increases in first year survival accounts for these relative stable yields.

In crayfish, first year survival can be affected by the availability of suitable nursery area (Momot and Gowing 1977a; Momot 1986). Quality and size of nursery habitat are related to availability of bottom substrate and aquatic vegetation, both of which determine the amount of available shelter. For example the

importance of Carex aquatilis, as modifier of aeshnid naiad predation, was demonstrated by Dye and Jones (1976) and Jones (1979). Stein (1977) observed that substrate availability modified susceptibility of intermoult crayfish (4 - 24 mm carapace length) to smallmouth bass (Micropterus dolomieui (Lacepede)) predation. On sand, crayfish were consumed in ascending order of body size, whereas on pebble substrate, intermediate size crayfish (16 - 20 mm carapace length) were by far the most susceptible. Mason (1978a) reported significantly higher survival in Pacifastacus leniusculus (Stimpson) young-of-the-year (YOY) on pebble substrate. He attributed this to visual isolation between individuals and a hypothetical behavioral response to the presence of pebbles. Both apparently serve to reduce cannibalism on soft shelled individuals. On pebbles, survival was density-independent, whereas on bare floor, survival was density-dependent.

Density-dependent survival is a commonly proposed mechanism for population regulation. Mortality, is usually related to predation and starvation, and is highest in young animals. Smitherman et al. (1967) studied the effects of supplemental food and fertilizer on production of Procambarus clarkii (Girard) in pools and ponds. In the ponds, no increase in production was noticed, probably due to the presence of sufficient natural foods. In pools, however, production of fed animals was significantly higher.

Crayfish feed upon a wide variety of food items. Therefore starvation is an unlikely cause of mortality. However, the food supply is of immense importance, since in the presence of predators, crayfish growth and survival are directly related. Crayfish below a certain size normally become vulnerable to predation, depending on the type of predator. Fast growing individuals are at an advantage if they rapidly outgrow their predators. For example predation of dragonfly naiads on YOY is only effective on YOY with a carapace length of less than 6 mm and only for a short period of one to two weeks (Dye and Jones 1976). Fish are capable of preying on larger crayfish (Reid 1972, Stein 1977). For example brook trout (Salvelinus fontinalis (Mitchill)) prey on young crayfish during their entire first year, with maximum consumption in late summer and midwinter (Momot 1967, Gowing and Momot 1979). Between October and June predation accounted for 56 % of the total mortality of YOY crayfish. The importance of crayfish in the diet has also been reported for other predatory fish species, such as smallmouth bass (Fedoruk 1966, Stein 1977), largemouth bass (Micropterus salmonides (Lacepede)) (Taub 1972), rock bass (Ambloplites rupestris (Rafinesque)) (Scott 1967) and white perch (Morone americana (Gmelin)) (Reid 1972).

Cannibalism is another possible source of mortality. Numerous reports document the existence of cannibalism amongst crayfish under experimental or cultural conditions (Westman 1973, Mason 1978a). Since soft shelled individuals were most

vulnerable to attacks, cannibalism was found to be directly related to moulting, which is most frequent in young, fast growing crayfish.

There has been little experimental work assessing the effect of predatory interactions among adult crayfish and their offspring. Capelli (1980) reported on predation by inshore male Orconectes propinquus (Girard) on newly hatched YOY. He found that YOY were only vulnerable to this kind of predation below the critical size of 8 mm carapace length. Dye and Jones (1976) noted cannibalism of adult Orconectes virilis (Hagen) on 4 - 6 mm YOY in laboratory experiments, but not in field enclosures. However, Morgan (1987) found a strong negative correlation for this species between YOY survival and density of two year old males in a northern Ontario marl lake, which implicates cannibalism as a possible source of population regulation.

Thus, biotic and abiotic factors appear to be of greater relative importance to first year survival than the size of the brood stock (Momot 1986). This study was therefore undertaken to measure the effects of several factors on first year crayfish growth and survival. Factors examined were density of crayfish, substrate, cover, temperature, supplemental feed and fertilizer and predation. An attempt has also been made to determine diet and feeding habits, since a food-growth relation is evident (Mason 1974 unpublished; Jones and Momot 1981). The relationship of these factors and their importance to crayfish culture is

examined. Possible enhancement techniques to improve first year survival are suggested, since higher recruitment to the adult population, would be of great benefit to an intensive fishery.

METHODS AND MATERIALS

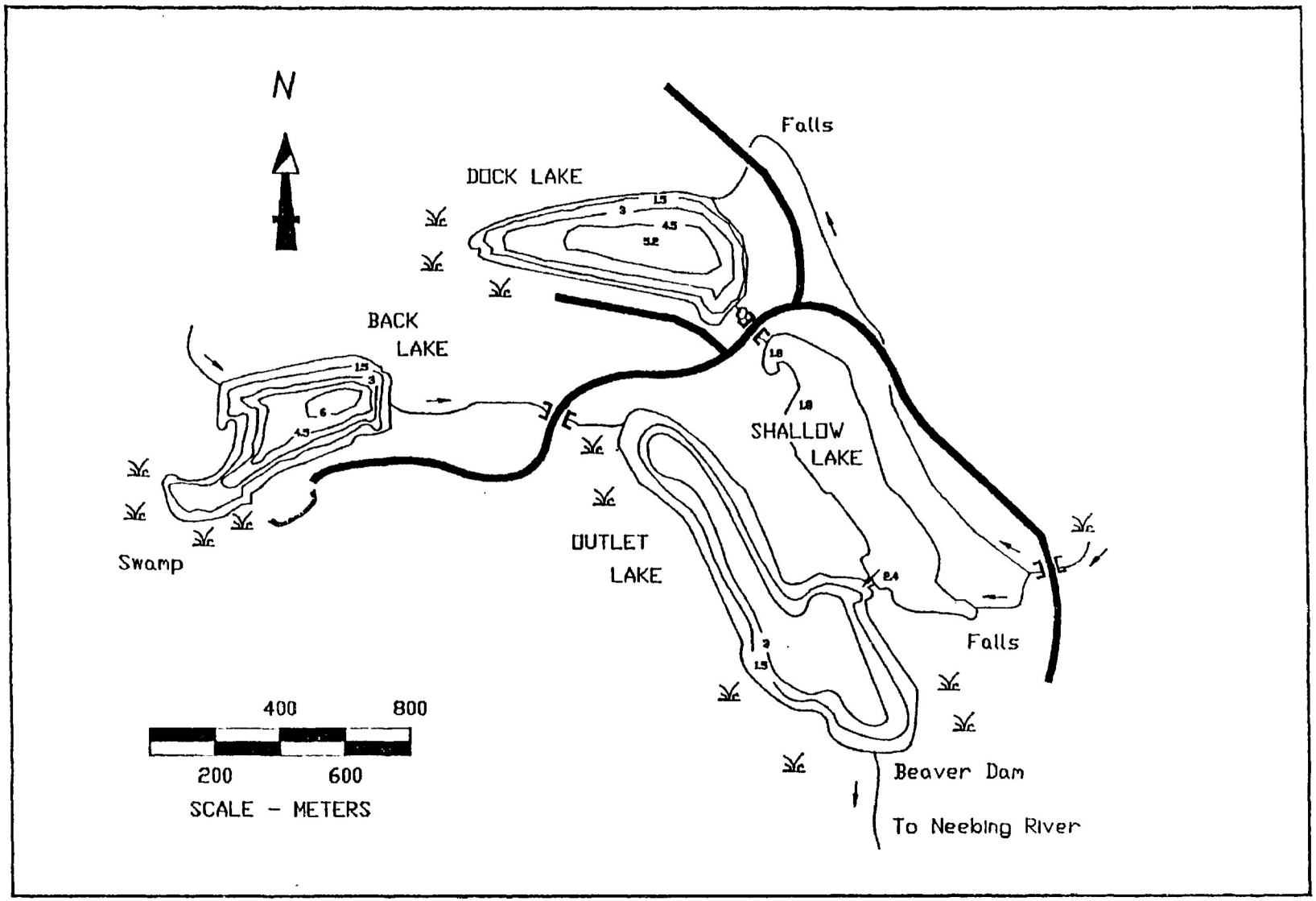
The subject of experiments was Orconectes virilis, a native North American crayfish widely distributed east of the Rocky Mountains, between the 40 and 55 ^{o}N latitude (Crocker and Barr 1968; Appendix I). Mating occurs mainly in late summer and early fall, but may also take place throughout the winter and in spring (Jones 1979; personal observation). Fertilization and extrusion of the eggs occurs in May. Young hatch after about two weeks, depending on temperature. The first and second instar still remain attached to the female. Time spans may vary according to temperature. During the first summer young moult at least five times, with a mean carapace length increase of about 2 mm per moult (Weagle and Ozburn 1972).

Experiments and data collection covered a two year period (1986 and 1987).

YOY for experimental purposes were obtained from females collected from a set of four marl lakes, Powell's Lakes, located within the municipal boundaries of Thunder Bay, Ontario (Figure 1). In 1986, some were also collected from a stretch of the McIntyre River, which passes through the Lakehead university campus.

Crayfish were collected with modified minnow traps (44.5 cm long x 23 cm at largest diameter, with both entrance holes expanded to 3 to 5 cm in diameter). In 1986, these traps were baited with frozen smelt (Osmerus mordax (Mitchill)). Since baiting resulted in a high percentage of males in the catch, it

Figure 1. Map of Powell's Lakes, McIntyre Township, Thunder Bay, Ontario. Depth contours are given in meters. (Momot 1978)


N
Falls
DOCK LAKE
1.5
3
4.5
5.2
BACK
LAKE
1.5
3
6
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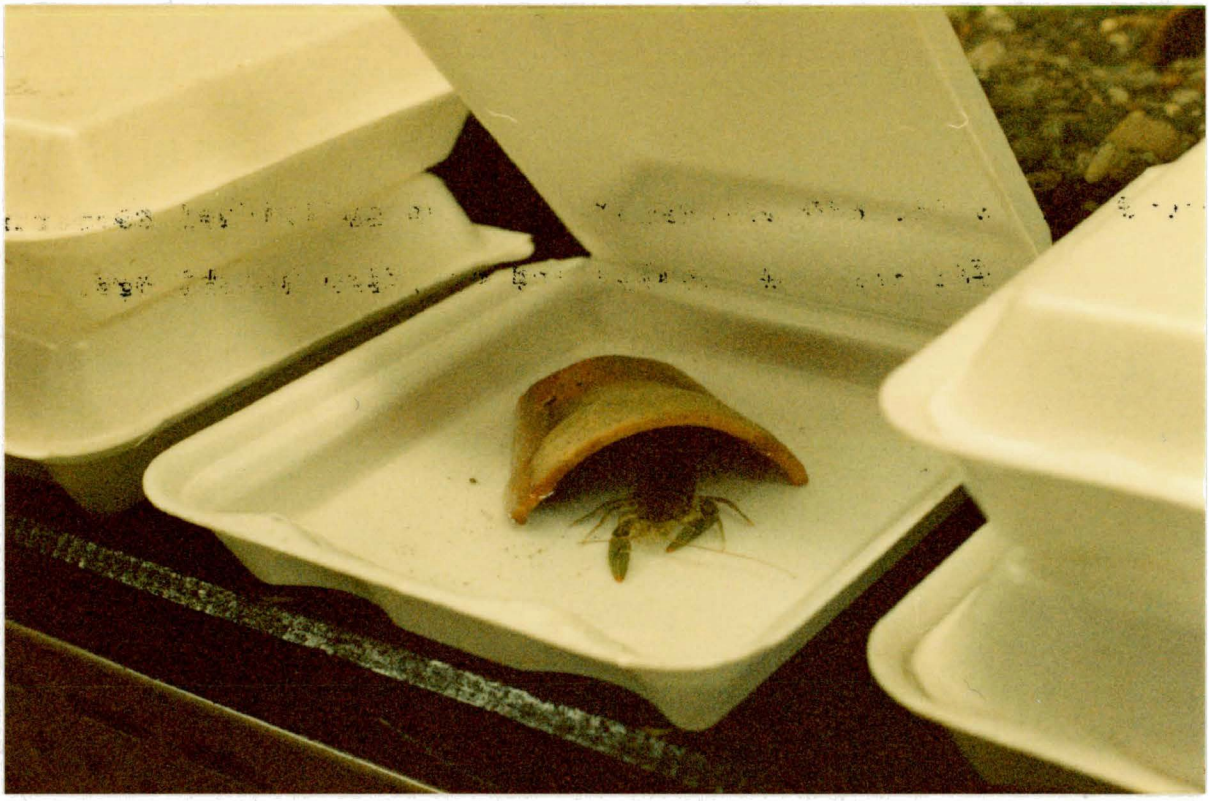
1.8
SHALLOW
LAKE
Swamp
OUTLET
LAKE
2.4
Falls
3
1.5
400
800
200
600
SCALE - METERS
Beaver Dam
To Neebing River

was decided to use unbaited traps in 1987. Females found under natural shelters as well as artificial shelters (longitudinally cut clay pots) were caught by hand.

In May 1986 about seventy females were caught and brought to the laboratory. At first they were kept in two 60 x 30 x 30 cm cages, which were suspended in two 91.5 x 45.5 x 46 cm glass aquaria, at densities of 35 females per cage. The cages were made of metal with a mesh size of 2 x 1 cm. The bottom of the cages was covered with artificial shelters, at least one per female. It was hoped that the young, once ready to leave the female, would fall through the mesh and could easily be collected for experimental purposes. However, after the first young had hatched, excessive losses were experienced due to fighting between individual adult females. Females were, therefore, transferred to separate containers (16 - 15 cm styrofoam food take out containers) (Figure 2). Females were fed very sparsely with algae, lettuce, frozen smelt and moist dog food (Gainsburger). The water was exchanged every second day.

For the 1987 experiments, forty-six females previously caught in late August of 1986, were kept in the laboratory. To guarantee that they were fertilized, each was placed over night in an aerated 30 x 20 cm compartment, together with a mature form I male. Usually, beginning of mating was observed within half an hour.

Figure 2. Styrofoam containers used as individual compartments for berried females and crayfish hatchlings.



To allow for ovarian maturation, female crayfish were kept in total darkness and at low temperatures (3 to 10 °C) for at least 4 months (Aiken 1969). Twenty-six of the fertilized females (group A) were therefore placed in a glass aquarium (dimensions as above) insulated with styrofoam (2.5 cm thick) and kept dark using a specially fitted lid. The aquarium was aerated and equipped with a "Hagen's" underground filter system to allow for continual waste removal (Lindsey 1986). The other twenty females (group B) were placed in a flow through holding tank (91 x 63.5 x 78.5 cm) (Figure 3), that was tightly wrapped with thick black plastic foil. In both cases, bottom substrate consisted of gravel, and clay pot shelters were provided in excess of the number of females. The water was cooled using frozen "Coleman ice-sub" freeze packs. Temperatures in the holding tank, however, could not be decreased sufficiently until the flow through water itself had declined to below 10 °C. When the flow through water had reached 6 °C, group A females were transferred to two separate flow through systems (Figures 4 and 5).

Group A was kept under winter conditions (darkness and temperature below 10 °C) from October 1, 1986 until February 28, 1987, and group B from November 20, 1986 until March 20, 1987. During this period only one group A female and 2 group B females died.

Figure 3. Flow-through holding tank, in which some of the females were kept during the winter.

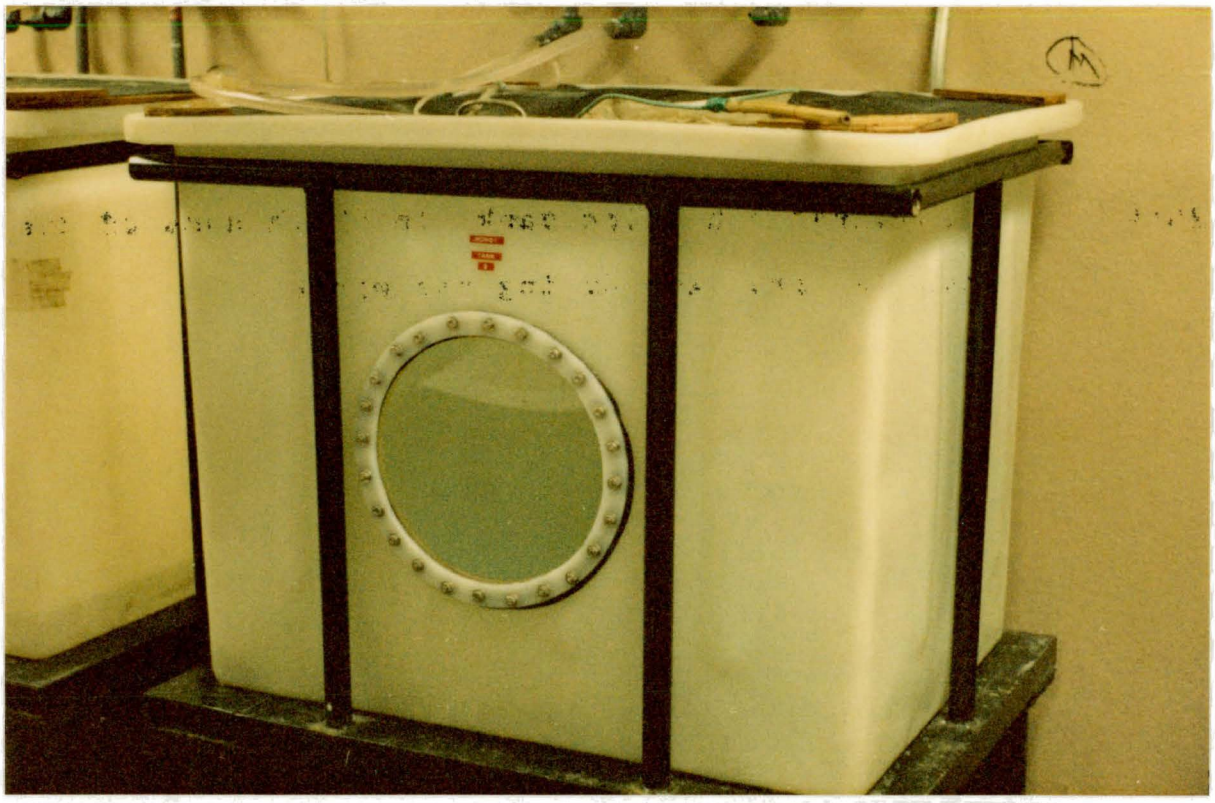
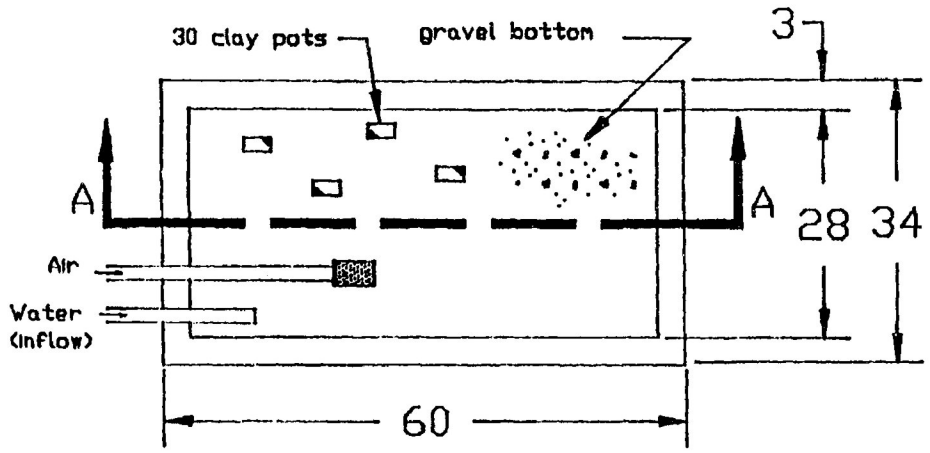
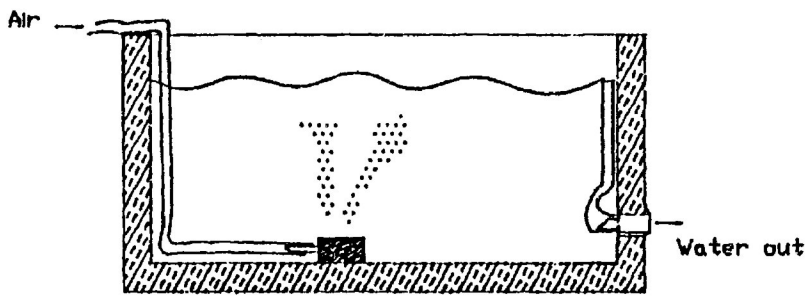


Figure 4. Technical drawing of a cooler, modified as a flow-through system. Shown is a top and side view, and a front section.



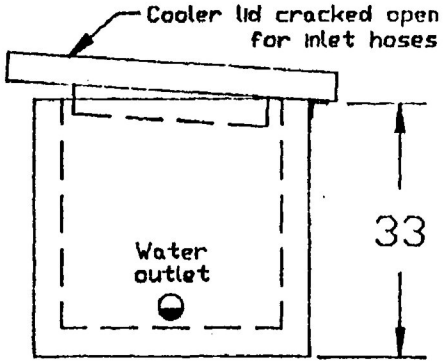
TOP VIEW (Lid Removed)

ALL DIMENSIONS IN CM



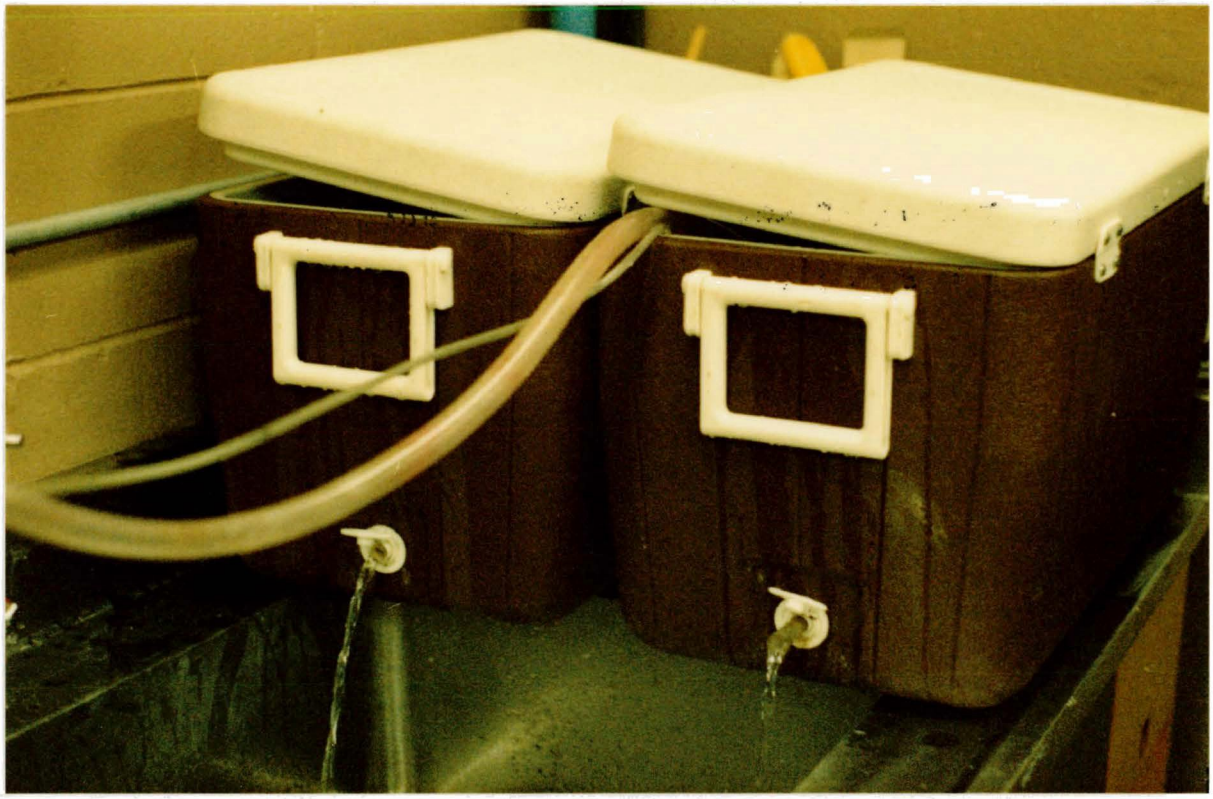
FRONT SECTION A-A

+ air & water ports



SIDE VIEW

Figure 5. Set-up of the two modified coolers in the laboratory.



Allowing the water to reach room temperature (about 15 - 16 °C), and setting the light/dark pattern (controlled by an automatic timer) to 16 hours light and 8 hours dark, simulated spring conditions. To avoid loss of eggs and attached young through spread of disease or fighting, group A females were immediately separated into single aquarium compartments or styrofoam containers. Within twenty days, most of them had extruded their eggs. In only one incident were the eggs diseased. In group B, the percentage of diseased eggs was higher (at least eight cases), since the females were not separated.

The first two instars are attached to the female (Figure 6), while third instar young may occasionally venture off the female (Crocker 1968). The young from all laboratory females were in both years separated from their mothers as soon as they became fully independent. They were kept in styrofoam containers at densities between twenty and forty per container. Food consisted of a mixture of moist dog food, trout pellets, brine shrimp, algae and lettuce. The containers were cleaned three times per week. Survival under laboratory conditions was excellent, but growth was extremely poor (4.0 - 4.2 mm carapace length at the start of the experiments).

Another forty females were collected for the 1987 experiments in May of that year. They were not brought back to the laboratory, but remained in the lake, where they were kept in

Figure 6. Lateral and ventral view of female Orconectes virilis with attached young.

cages at densities of four or five per cage. The cages, 50 x 50 x 50 cm in dimension, were made of mosquito screen with mesh size of 1.5 mm, held by a 28 gauge galvanized steel frame. Females were provided with adequate shelter and food. After the young were free-living, the adult females were removed.

No information has been gathered on survival of those young prior to experimentation. Growth, however, was noticeably better than under laboratory conditions (4.2 - 4.5 mm carapace length at time of stocking), even though they were not fed.

Data were analyzed using the SPSSX statistics package (SPSS Inc. 1986). T-Tests and ANOVA's were used to compare population means (Steel and Torrie 1980). IBM-software was used for graphics and tables.

EXPERIMENTAL PROCEDURES AND RESULTS

Both, field and laboratory experiments were conducted. For clarity of presentation, experiments are not always arranged in chronological order. Field experiments are presented first, followed by laboratory experiments.

A) Field Experiments

Field experiments were conducted in Dock Lake and Shallow Lake. Physical and chemical characteristics of both lakes are very similar (Momot 1978). Being marl lakes, mean values for pH, total dissolved solids, alkalinity and conductivity are high (Table 1). Predominant bottom substrate to a depth of 2 m is a sand/gravel mixture, partially overlain by silt and marl of varying thickness. At depths greater than 2 m, the substrate consists of organic matter, in Dock Lake turning into sapropel beyond 4 m. Predominant submerged vegetation consists of large beds of Chara sp., covering most of the lake bottom, where the depth does not exceed 1.5 m (Momot 1978; Morgan 1987).

Suitable shoal area for the field enclosure experiments, i.e., shallow and easily accessible, existed along the southeastern and eastern part of Dock Lake, along a short stretch of the southern shore of Shallow Lake and in the small pond between the two lakes (Figure 1). The objective of the enclosure experiments was to test the effect of several factors on growth and survival of YOY crayfish.

Table 1. Physical and chemical characteristics of two northwestern Ontario lakes, 1976-1977. (From Momot 1978)

MEASUREMENT	Dock Lake	Shallow Lake
Surface area (hectares)	1.2	1.6
Depth (m) Mean-max.	4.5 - 5.2	2.2 - 2.4
pH*	7.5 - 9.0	8.5 - 9.1
Total dissolved solids (mg/litre)*	240 - 247	187 - 195
Alkalinity (mg/litre)*	188 - 220	137 - 145
Conductivity (μmho/cm)*	215 - 360	225 - 295
Transparency (late summer) Secci disk (m)	1.5	0.75
Ortho PO_4 (mg/litre)	0.03	0.09
Nitrogen (mg/litre)		
NO_3	14.5	13.0
N_2	0.035	0.025
$CaCO_3$ (mg/litre)	145	130
Shoreline length (km)	0.61	0.64
Volume (m^3)	54,377	35,986
Size of littoral zone (Area in m^2 < 1.5 m)	6,292	8,094

*Data are ranges over two years.

The enclosures, 50 x 50 x 50 cm cages, were previously described. About two weeks prior to experimentation they were filled with experiment specific substrate and cover combinations and placed into the lakes. This allowed for settling of the cages and initiation of a typical "Aufwuchs" fauna and flora. In 1986 all cages were placed along the shore, whereas in 1987, most cages were suspended from stands into the water. This was done to avoid possible influences of overhanging shore-line vegetation, as well as to be able to position the cages horizontally and at a desired depth. In 1986 the young were counted out in the laboratory the night prior to initiation of the experiment.

In 1987, YOY came partially from laboratory females and partially from females kept in cages in the pond. Since YOY from the pond females were slightly bigger, the cages were stocked with half the young stemming from laboratory females, half from pond females. Counting of YOY for stocking was done on the day of stocking in the field. This also allowed for optimal mixing of laboratory YOY during transportation in a big plastic bucket.

Each experiment lasted two weeks, after which the survivors in each cage were counted and measured. Since most young were too small and delicate to be measured with Vernier calipers, two methods were used. In 1986 the young were grouped into eight size classes by comparison with precisely measured individuals. Precise measuring was done under a dissecting microscope with the

help of an ocular micrometer. All crayfish above a certain range were grouped together in the largest size class. This method caused problems with the statistical analysis. Therefore in 1987, the young were photographed in a glass container with a reference scale underneath. Measuring could then be done by computer, using the Apple software "Fiber".[1]

In 1987, once this procedure was completed, YOY were placed back into their cages. This was done to gather more information on their growth during the first growing season and to be able to determine their sex, since sex determination cannot be done with sufficient accuracy in very small crayfish.

Chara, one of the experimental cover types, was taken from the lakes. Therefore, it could not be prevented, that some undesirable lake organisms were introduced into the cages. Cages in which large dragonfly naiads of the families Libellulidae and Aeshnidae were found, had to be excluded from the habitat comparison. However, results were included to demonstrate the impact of dragonfly naiads as natural predators.

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[1]For information on the "Fiber" software, contact J. Wong in The School of Forestry, Lakehead University.

A time schedule for all field experiments is summarized in Table 2. Except for 1986, the variances of all carapace length data were homogeneous and only in a few instances were the data either skewed or kurtotic. In the case of skewness or kurtosis, data could most often successfully be transferred into a normal range. Since this did not substantially alter the ANOVA probabilities, probabilities given are based on the original data.

Table 2. Time schedule of field experiments and important sampling dates.

Experiment	Year	Time period (day/month)	Remarks
1	1986	25.6. - 9.7.	-
1	1987	18.6. - 2.7. (29.7.	- processing at end of summer)
2	1987	19.6. - 3.7. (28.7./29.7.	- processing at end of summer)
3	1986	25.6. - 9.7.	-
4	1986	25.6. - 9.7.	-
5	1986	8.7. - 22.7.	12 cages with adults
5	1986	27.7. - 12.8.	3 cages without adults
6	1986	25.6. - 2.7.	sampling period
6	1987	12.6. - 15.6.	sampling period
	1987	16.7.	size estimate of pond YOY

Experiment 1. Effects of density, substrate and cover.

Experimental procedure:

The 1986 main experiment tested the influence of density, substrate and cover on growth and survival of YOY. The design was a two by two by three factorial arrangement with three replications per treatment.

The cages were placed along the southeastern portion of the shoreline of Dock and Shallow lake (Figure 7).

Crayfish were stocked at two densities (ten or forty YOY per cage) representative of two extreme densities encountered under natural conditions (Dye and Jones 1976). The two substrate types were sand (obtained from a nearby sand pit) and black organic mud (sapropel), obtained from Dock Lake at a depth beyond four meters. The cover types were Chara sp., leaf litter, gathered from the trees around the lake (mainly alder, Alnus sp., and poplar, Populus sp.), and as control reference, no additional cover (i.e. sand or mud only).

Part of the experiment, involving Chara and a no cover control, was repeated in 1987. Cage locations are shown in Figure 8. In addition to the 1986 experiment, a density of three YOY per cage was tested on a sand substrate with no cover to find out whether a reduction in density would further increase growth or survival.

Figure 7. Section of Powell's Lakes, showing the cage locations in Dock and Shallow Lake in 1986. The inset shows the cage locations in Shallow Lake. Cages indicated by the numbers 4, 5, 6 and 8 are part of Experiment 1; cages indicated by the numbers 2, 7, 9 and 10 are part of experiment 3; cages indicated by the numbers 2 and 3 are part of experiment 4; cages indicated by the numbers 1 (females) and 11 (males) are part of experiment 5.

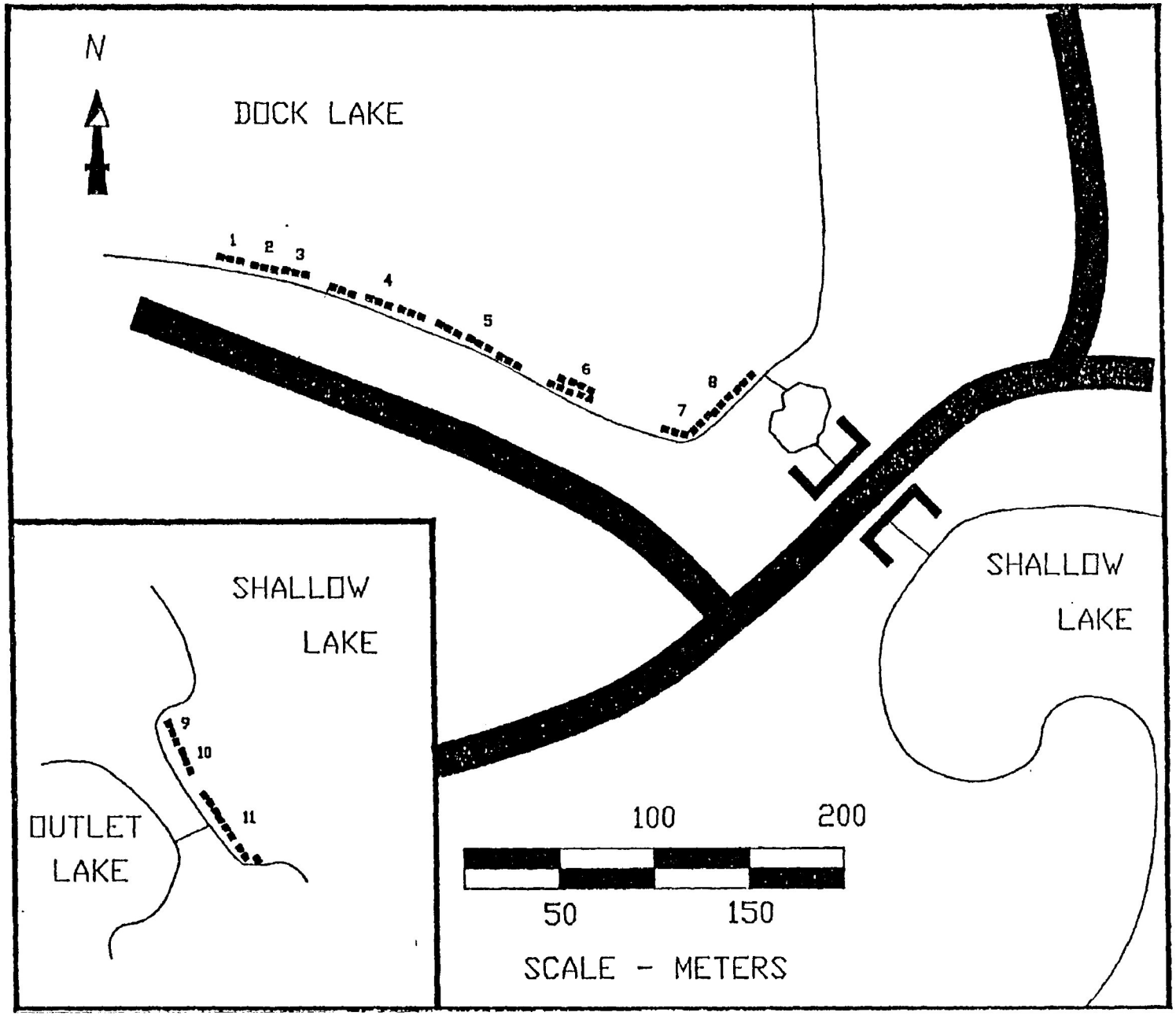
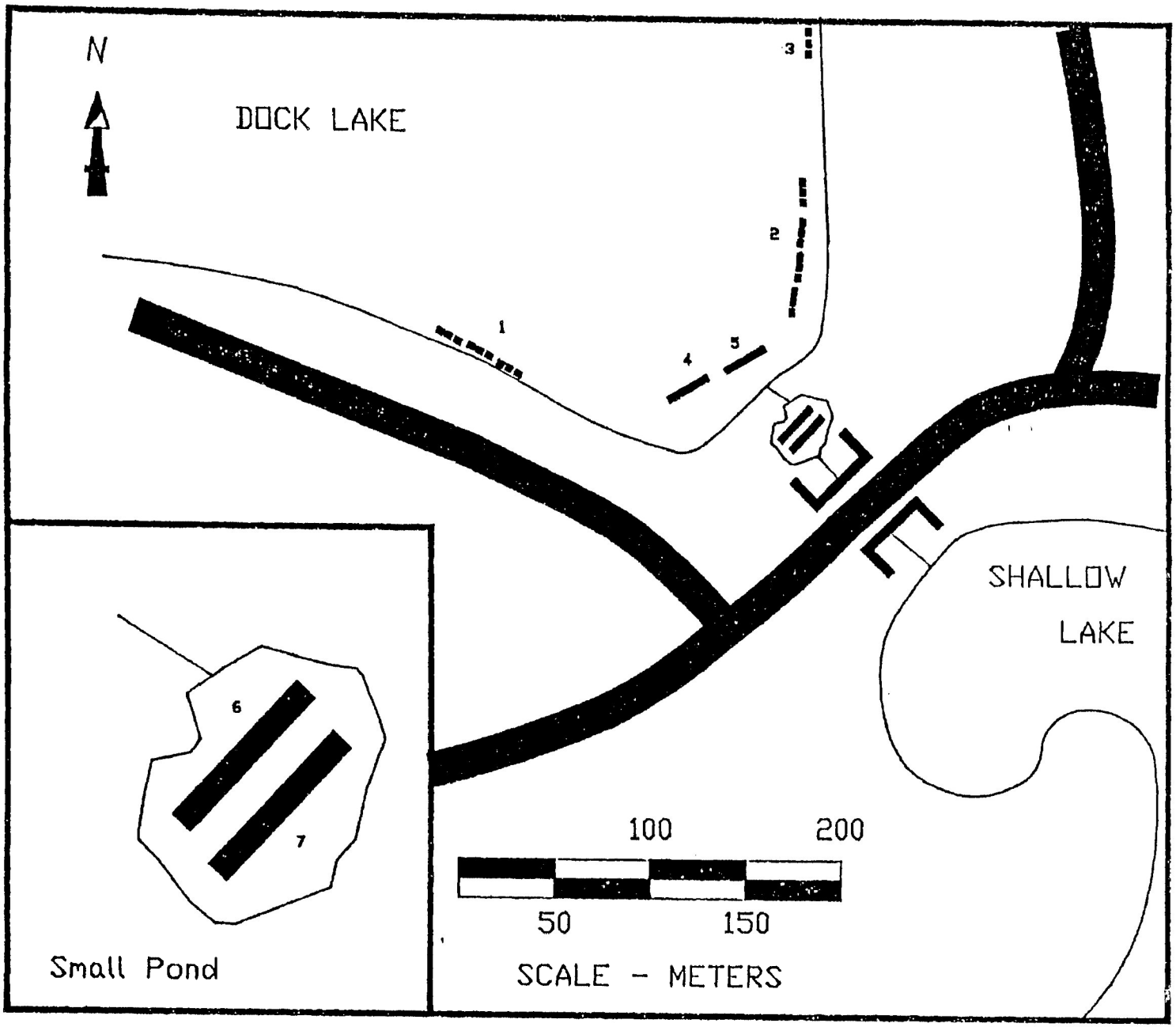

N
DOCK LAKE
1
2
3
4
5
6
7
8
SHALLOW
LAKE
9
10
11
OUTLET
LAKE
SHALLOW
LAKE
100
200
50
150
SCALE - METERS

Figure 8. Section of Powell's Lakes, showing the location of cages and stands in Dock in 1987. The inset shows the location of the fertilizer (6) and the food (7) stand. The numbers 4 and 5 indicate the control and the deep stand. Cages indicated by the numbers 1, 2 and 3 are part of experiment 1.


N
DOCK LAKE
1
2
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SHALLOW
LAKE
100
200
50
150
SCALE - METERS
Small Pond

Results:

By the end of the experiment, YOY had reached an average carapace length of 7.60 mm. All three factors, density ($P < .01$), substrate ($P < .01$) and cover ($P < .001$) significantly influenced YOY growth (Tables 3 and 4; Appendix II). Growth was best at the low density and with mud as substrate (Table 5). Growth was also enhanced by both cover types, leaf-litter and Chara. Without cover, YOY grew much more slowly (Table 6). Paired contrasts between carapace length means of the three cover types, leaf-litter/Chara, leaf-litter/nothing, and Chara/nothing, demonstrate that growth was equally enhanced by the presence of Chara or leaf-litter, whereas no difference was apparent between these two cover types (Table 7).

No significant two-way interactions between any of the factors were detected. However, a significant three-way interaction became apparent. This interaction is believed to be due to the small sample size for the cover type Chara and to the presence of small dragonfly nymphs in most Chara cages, which renders results for this cover type unreliable.

Optimum growth in this experiment was achieved with low density, mud substrate and leaf-litter cover. Under these conditions crayfish more than doubled their carapace length within the two week period (Table 8).

Table 3. ANOVA probabilities for carapace length and survivorship data of experiment 1, 1986, excluding cages containing large dragonfly naiads.

CARAPACE LENGTH AND % SURVIVORS BY
D DENSITY (10; 40)
S SUBTSRATE (SAND; MUD)
C COVER (LEAF-LITTER; CHARA; NOTHING)

	CARAPACE LENGTH			% SURVIVORS		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	4	22.584	0.000	4	1.560	0.228
D	1	7.089	0.008	1	1.812	0.195
S	1	7.933	0.005	1	2.962	0.102
C	2	36.908	0.000	2	0.648	0.533
2-WAY INTERACTIONS	5	0.851	0.514	5	2.349	0.083
D S	1	0.282	0.595	1	2.870	0.107
D C	2	0.300	0.741	2	0.249	0.782
S C	2	1.712	0.181	2	4.734	0.022
3-WAY INTERACTIONS	2	5.991	0.003	2	0.159	0.854
D S C	2	5.991	0.003	2	0.159	0.854
EXPLAINED	11	9.688	0.000	11	1.664	0.163
RESIDUAL	544			18		
TOTAL	555			29		

Note: Significance at $P < 0.01$

Table 4. ANOVA probabilities for carapace length and survivorship data of experiment 1, 1986, including all cages.

CARAPACE LENGTH AND % SURVIVORS BY
D DENSITY (10; 40)
S SUBTSRATE (SAND; MUD)
C COVER (LEAF-LITTER; CHARA; NOTHING)

	CARAPACE LENGTH			% SURVIVORS		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	4	23.298	0.000	4	2.875	0.046
D	1	7.999	0.005	1	0.044	0.835
S	1	10.121	0.002	1	1.699	0.205
C	2	37.034	0.000	2	5.063	0.015
2-WAY INTERACTIONS	5	0.927	0.463	5	1.103	0.386
D S	1	0.012	0.912	1	0.177	0.678
D C	2	0.301	0.740	2	0.569	0.574
S C	2	2.003	0.136	2	2.157	0.139
3-WAY INTERACTIONS	2	6.263	0.002	2	1.058	0.364
D S C	2	6.263	0.002	2	1.058	0.364
EXPLAINED	11	10.032	0.000	11	1.739	0.127
RESIDUAL	575			23		
TOTAL	586			34		

Note: Significance at $P < 0.01$

Table 5. Effects of density and substrate on young-of-the-year growth experiment 1, 1986. Given are mean carapace length in mm, number of individuals ( ), and standard error [ ].

DENSITY	SAND	MUD	TOTALS
10	7.67 (57) [0.14]	7.95 (53) [0.12]	7.89(110) [0.06]
40	7.45(233) [0.06]	7.66(213) [0.07]	7.55(446) [0.04]
TOTALS	7.49(290) [0.06]	7.72(266) [0.06]	7.60(556) [0.04]

(Cages containing large dragonfly naiads were excluded)

Table 6. Effects of density and cover on young-of-the-year experiment 1. 1986. Given are carapace length in mm, number of individuals ( ), and standard error [ ].

DENSITY	LEAF-LITTER	CHARA	NOTHING	TOTALS
10	8.15 (50) [0.10]	7.95 (16) [0.08]	7.35 (44) [0.18]	7.89(110) [0.06]
40	7.82(233) [0.06]	7.76 (79) [0.09]	7.17(177) [0.08]	7.55(446) [0.04]
TOTALS	7.89(240) [0.04]	7.79 (95) [0.08]	7.21(221) [0.08]	7.60(556) [0.04]

(Cages containing large dragonfly naiads were excluded)

TABLE 7. Contrast information for young-of-the-year (YOY) growth related to the three cover types, experiment 1, 1986. Probabilities are given for the pooled and the seperate variance estimate.

	Cover types and total means (no. of YOY)											
	Leaf-litter	Chara	Nothing		Pooled variance estimate				Separate variance estimate			
Contrast	7.89 (240)	7.78 (95)	7.21 (221)	Value	SE	T	DF	P	SE	T	DF	P
1	-1	1	0	-0.10	0.11	-0.93	553	0.352	0.09	-1.08	143.6	0.283
2	-1	0	1	-0.68	0.08	-8.20	553	0.000	0.09	-7.89	346.2	0.000
3	0	-1	1	-0.58	0.11	-5.31	553	0.000	0.11	-5.16	241.4	0.000

Note: Significance at $P < 0.01$

Table 8. Effects of density, substrate and cover on young-of-the-year growth, experiment 1, 1986. Given are carapace length in mm, number of individuals ( ), and standard error [ ].

		DENSITY	SAND	MUD	TOTALS
LEAF-LITTER	7.89(240) [0.04]	10	7.98 (27) [0.15]	8.36 (23) [0.12]	8.15 (50) [0.10]
		40	7.80(111) [0.05]	7.85 (79) [0.08]	7.82(233) [0.06]
CHARA	7.79 (95) [0.08]	10	8.31 (7) [0.17]	7.67 (9) [0.28]	7.95 (16) [0.08]
		40	7.17 (23) [0.28]	8.00 (56) [0.03]	7.76 (79) [0.09]
NOTHING	7.21(221) [0.08]	10	7.10 (23) [0.26]	7.63 (21) [0.22]	7.35 (44) [0.18]
		40	7.13 (99) [0.10]	7.23 (78) [0.14]	7.17(177) [0.08]
TOTALS			7.49(290) [0.06]	7.72(266) [0.06]	7.60(556) [0.04]

(Cages including dragonfly naiads were excluded)

Mortality was fairly low. Only 26.78 % of all crayfish had died during the two week experimental period. Losses were partially due to large dragonfly nymphs of the family Aeshnidae, which were found in several cages containing Chara as cover (Appendix II). Accordingly, mortality of YOY in cages having this cover type was higher (Tables 3, 9 and 10) than average. In one low density cage mortality was as high as 90 %. However, mortality was no longer influenced by any of the factors, when cages containing large dragonfly naiads were excluded from the analysis (Table 3). Except for the untrustworthy results obtained for cover type Chara, mortality was greater at the high density (Table 10) and on a mud substrate (Table 9). However, in both cases the differences were not significant (Tables 3 and 4).

The measurement method had, as already indicated, caused some complications. It resulted in an underestimation of the larger sized crayfish. Therefore the frequency distribution of carapace length was negatively skewed because of the restricted range of larger carapace length values (Figure 9). This is reflected in a highly significant Bartletts test of homogeneity (Bartlett-Box $F = 16.560$, $P = 0.000$) and a negative linear relationship between mean carapace length and standard deviation (Figure 10). With a transformation (x^4) skewness and kurtosis were transferred into a normal range, but variance remained heterogeneous. However, since the sample size is large and all

Table 9. Effects of density and cover on young-of-the-year survival, experiment 1, 1986. Given are mean survivorship in %, number of cages ( ), and standard error [ ].

SUBSTRATE	LEAF-LITTER	CHARA	NOTHING	TOTALS
SAND	92.92 (6) [1.98]	67.50 (3) [5.20]	80.00 (6) [4.79]	82.67 (15) [3.33]
MUD	71.25 (6) [7.52]	84.17 (3) [7.95]	72.50 (6) [6.02]	74.33 (15) [4.10]
TOTALS	82.08(12) [4.94]	75.83 (6) [5.65] { 60.23 (11) }	76.25(12) [3.84]	78.50 (30) [2.71] { 73.21 (35) }

(Cages containing large dragonfly naiads were excluded)
{ } = Cages containing dragonfly naiads were included.

Table 10. Effects of substrate and cover on young-of-the-year survival, experimet 1, 1986. Given are mean survivorship in %, number of cages ( ), and standard error [ ].

DENSITY	LEAF-LITTER	CHARA	NOTHING	TOTALS
10	85.00 (6) [5.00]	85.00 (2)[15.00]	78.33 (6) [6.01]	82.14 (14) [3.66]
40	79.17 (6) [8.89]	71.25 (4) [4.62]	74.17 (6) [5.19]	75.31 (16) [3.87]
TOTALS	82.08(12) [4.94]	75.83 (6) [5.65] { 60.23 (11) }	76.25(12) [3.84]	78.50 (30) [2.71] { 73.21 (35) }

(Cages containing large dragonfly naiads were excluded)
{ } = Cages containing dragonfly naiads were included.

Figure 9. Carapace length frequency distribution of crayfish from experiment 1, 1986. Sample size is shown at top of each bar.

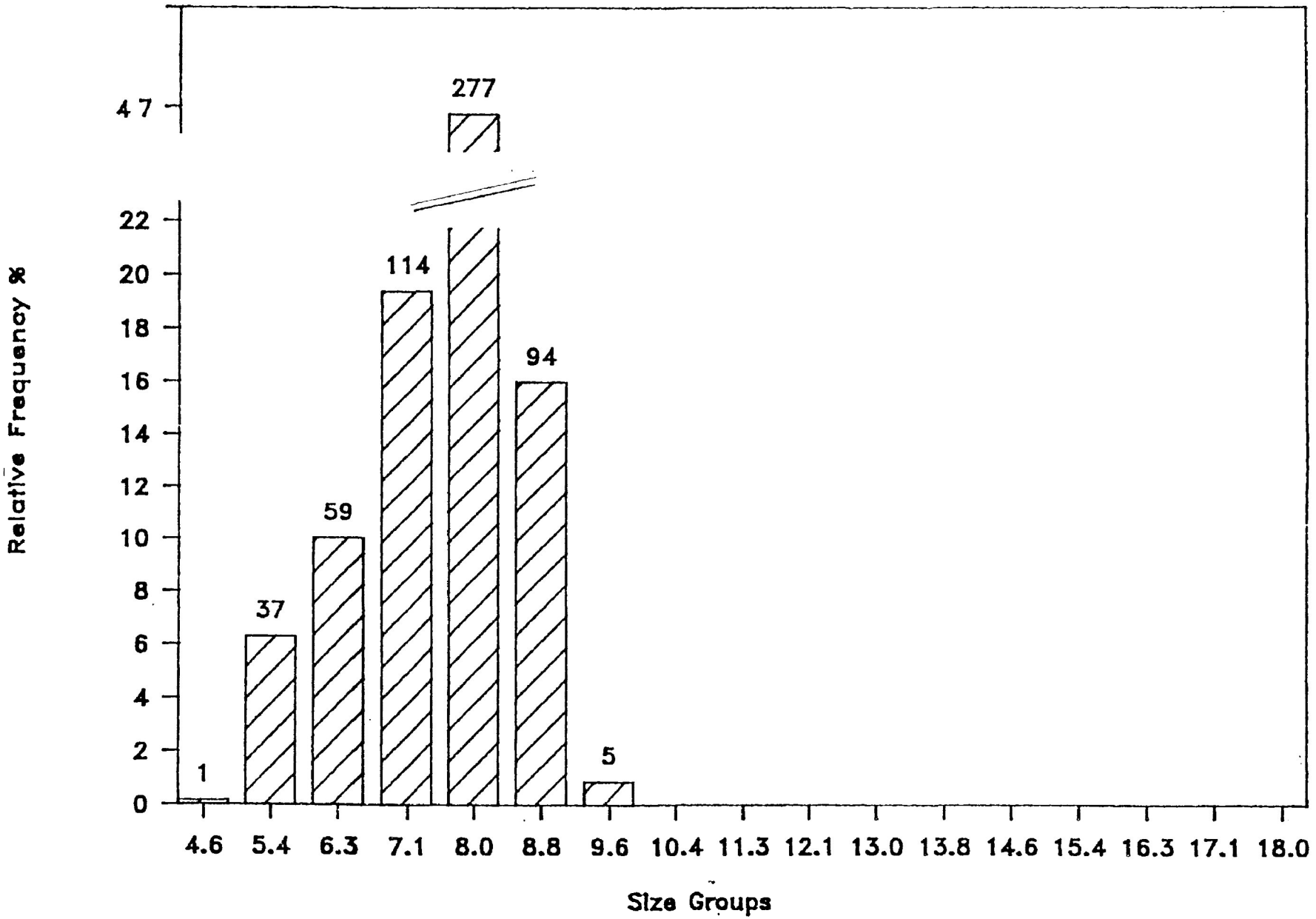
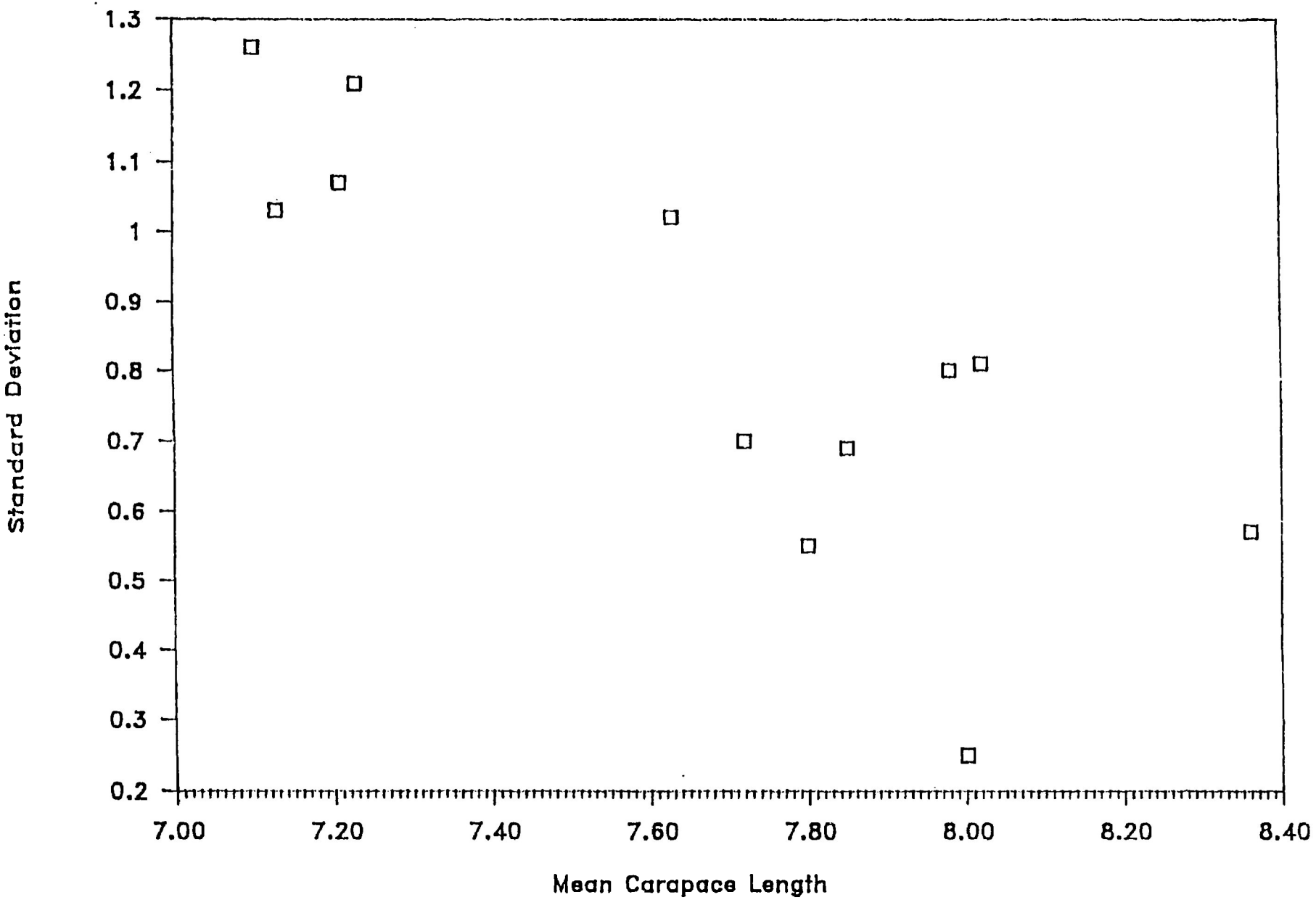

47
277
22
20
18
16
14
12
10
8
6
4
2
0
114
94
59
37
1
5
Relative Frequency %
4.6
5.4
6.3
7.1
8.0
8.8
9.6
10.4
11.3
12.1
13.0
13.8
14.6
15.4
16.3
17.1
18.0
Size Groups

Figure 10. Carapace length means (in mm) of crayfish from experiment 1, 1986, plotted against standard deviation.


Standard Deviation
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
7.00
7.20
7.40
7.60
7.80
8.00
8.20
8.40
Mean Carapace Length

findings were significant at the 99% confidence limit, the results are believed to be realistic. In addition, results are strengthened by the outcome of the 1987 experiments.

Table 11 summarizes the effects of the investigated factors on mortality. Apparently, none of the factors had a significant impact (Tables 12, 13 and 14). At low density, survival appears to be better on mud, but no ANOVA can be computed due to a lack of variance.

The carapace length frequency distribution obtained for 1987 reflects the true proportions much more accurately than the distribution obtained for 1986. Two additional large size groups were present in the 1987 distribution, and the data were neither skewed, nor kurtotic (Figure 11).

In agreement with previous year's results, growth was significantly better at low density ($P < 0.000$) (Tables 12, 13 and 15). No difference existed between the low and the very low density (Table 16). At high density, growth was enhanced by cover (Tables 12 and 15), whereas cover had no significant effect at low density (Tables 14 and 15).

Contrary to previous year's findings, substrate had no significant effect on growth in cages containing Chara as cover (Tables 13 and 15). Moreover, in cages without cover (only stocked at low density), YOY grew better on a sand substrate (Table 14 and 15).

Table 11. Effects of density, substrate and cover on young-of-the-year survival, experiment 1, 1987. Given are mean survivorship in %, number of cages ( ), and standard error [ ].

		DENSITY	SAND	MUD	TOTALS
CHARA	93.96 (12) [1.36]	10	90.00 (3) [0.00]	100.00 (3) [0.00]	95.00 (6) [2.24]
		40	92.50 (3) [2.89]	90.33 (3) [2.20]	92.92 (6) [1.63]
NOTHING	86.22 (12) [3.56]	3	77.78 (3)[11.11]	-	77.78 (3)[11.11]
		10	90.00 (3) [0.00]	100.00 (3) [0.00]	95.00 (6) [2.24]
		40	80.83 (3) [2.20]	-	80.83 (3) [2.20]
TOTALS			88.33(12) [1.55]	97.78 (9) [1.28]	90.56(24) [1.99]

Table 12. ANOVA probabilities for carapace length and survivorship data of experiment 1, 1987, comparing only cages with a sand substrate.

CARAPACE LENGTH
AND % SURVIVORS BY C COVER (NOTHING; CHARA)
D DENSITY (10; 40)

	CARAPACE LENGTH			% SURVIVORS		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	2	42.085	0.000	2	6.842	0.019
C	1	9.899	0.002	1	10.316	0.012
D	1	75.304	0.000	1	3.368	0.104
2-WAY INTERACTIONS	1	1.682	0.196	1	10.316	0.012
C D	1	1.682	0.196	1	10.316	0.012
EXPLAINED	3	28.617	0.000	3	8.000	0.009
RESIDUAL	257			8		
TOTAL	260			11		

Note: Significance at $P < 0.01$

Table 13. ANOVA probabilities for carapace length and survivorship data of experiment 1, 1987, comparing only cages with Chara as cover.

CARAPACE LENGTH
AND % SURVIVORS BY D DENSITY (10; 40)
S SUBSTRATE (SAND; MUD)

	CARAPACE LENGTH			% SURVIVORS		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	2	13.334	0.000	2	5.105	0.037
D	1	26.608	0.000	1	1.316	0.284
S	1	0.023	0.880	1	8.895	0.018
2-WAY INTERACTIONS	1	4.027	0.046	1	6.368	0.036
D S	1	4.027	0.046	1	6.368	0.036
EXPLAINED	3	10.231	0.000	3	5.526	0.024
RESIDUAL	272			8		
TOTAL	275			11		

Note: Significance at $P < 0.01$

Table 14. ANOVA probabilities for carapace length and survivorship data of experiment 1, 1987; comparing only low density cages.

CARAPACE LENGTH
AND % SURVIVORS BY C COVER (NOTHING; CHARA)
S SUBSTRATE (SAND; MUD)

	CARAPACE LENGTH			% SURVIVORS		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	2	6.096	0.003	2	-	-
C	1	0.962	0.329	1	-	-
S	1	11.109	0.001	1	-	-
2-WAY INTERACTIONS	1	0.287	0.593	1	-	-
C S	1	0.287	0.593	1	-	-
EXPLAINED	3	4.160	0.008	3		
RESIDUAL	108			8		
TOTAL	111			11		

(No ANOVA probabilities for % survivors were calculated because of lack of variation)
Note: Significance at $P < 0.01$

Figure 11. Carapace length frequency distribution of crayfish from experiment 1, 1987. Sample size is shown at top of each bar.

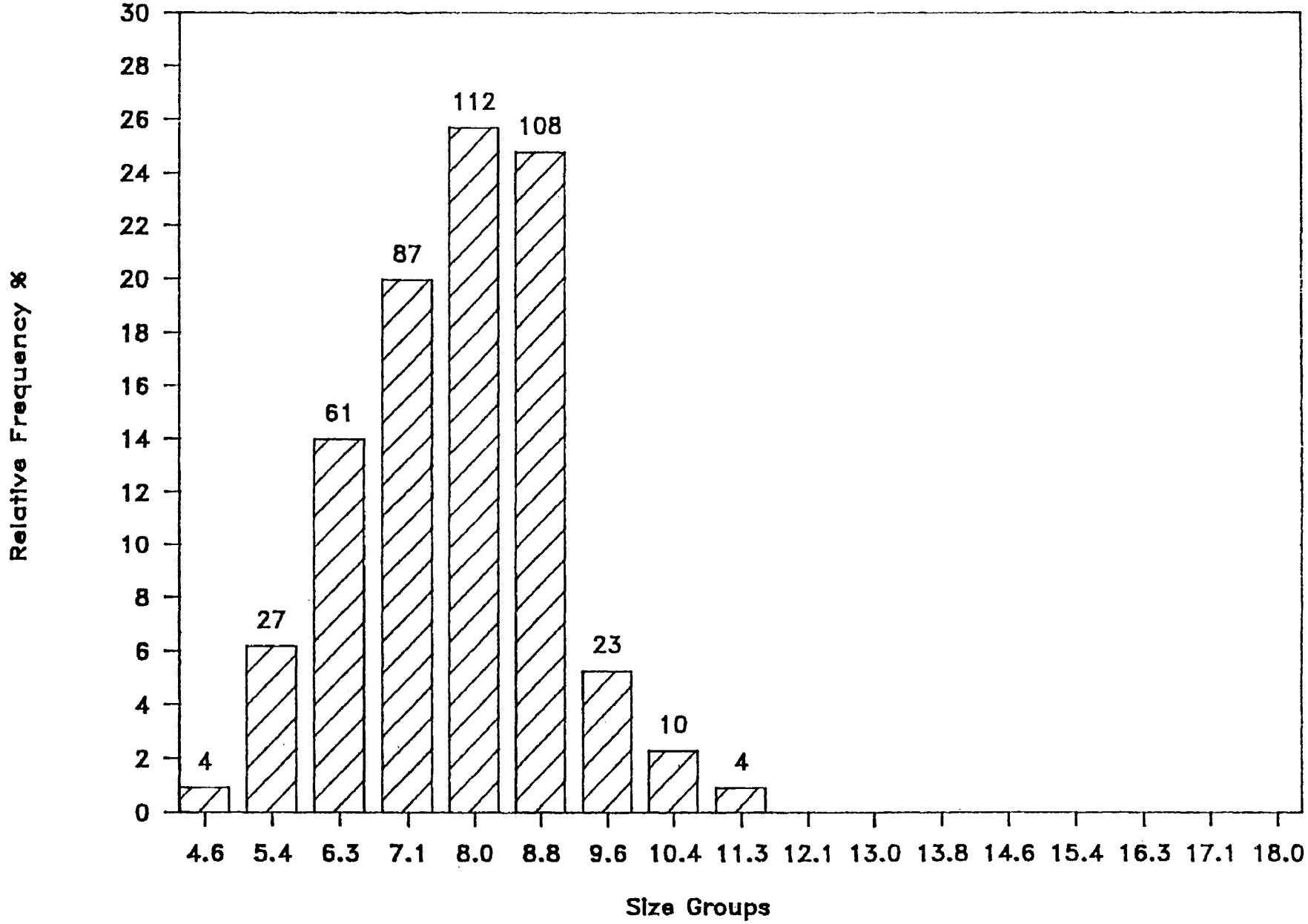

Relative Frequency %
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
4
27
61
87
112
108
23
10
4
4.6
5.4
6.3
7.1
8.0
8.8
9.6
10.4
11.3
12.1
13.0
13.8
14.6
15.4
16.3
17.1
18.0
Size Groups

Table 15. Effects of density and cover on young-of-the-year growth, experiment 1, 1987. Given are mean carapace length in mm, number of individuals ( ), and standard error [ ].

		DENSITY	SAND	MUD	TOTALS
CHARA	7.85 (276) [0.07]	10	8.84 (27) [0.23]	8.32 (29) [0.19]	8.57 (56) [0.15]
		40	7.59(111) [0.10]	7.75(109) [0.12]	7.67(220) [0.08]
NOTHING	7.60 (160) [0.10]	3	8.80 (7) [0.43]	-	8.80 (7) [0.43]
		10	8.76 (26) [0.02]	8.02 (30) [0.14]	8.37 (56) [0.13]
		40	7.07 (97) [0.11]	-	7.07 (97) [0.11]
TOTALS			7.67(268) [0.08]	7.90(168) [0.09]	7.76(436) [0.06]

Table 16. Contrast information for growth related to the three densities, experiment 1, 1987. Probabilities are given for the pooled and separate variance estimate.

	Densities and total means (no. of YOY)											
	3	10	40		Pooled variance estimate				Separate variance estimate			
Contrast	8.80 (7)	8.46(112)	7.49(317)	Value	SE	T	DF	P	SE	T	DF	P
1	1	-1	0	0.40	0.45	0.08	127	0.932	0.47	0.08	8.9	0.937
2	1	0	-1	1.73	0.42	4.15	127	0.000	0.44	3.93	6.8	0.006
3	0	1	-1	1.69	0.23	7.19	127	0.000	0.23	7.38	40.7	0.000

Note: Significance at $P < 0.01$

Growth remained density-dependent throughout the whole growing season, as became obvious by the end of the summer. No further dependence of growth on cover was found, but again a dependence of growth on substrate (Table 17; Appendix III). Growth was, as in 1986, enhanced by presence of a mud substrate (Table 18). A distinct size difference now had developed between all three densities of the sand/no cover cages, with means of 16.08 mm, 12.22 mm and 10.97 mm carapace length, in order of increasing density (Tables 18 and 19).

Table 17. ANOVA probabilities for end-of-summer carapace length data of experiment 1, 1987, separately for *Chara* cages and sand cages.

CARAPACE LENGTH BY	DENSITY (D) AND SUBSTRATE (S) D (10; 40) S (SAND; MUD) (For Chara cages only)			DENSITY (D) AND COVER (C) D (10; 40) C (NOTHING; CHARA) (For sand cages only)		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	2	46.320	0.000	2	26.603	0.000
D	1	79.444	0.000	1	52.823	0.000
S (C)	1	11.086	0.001	1	0.432	0.512
2-WAY INTERACTIONS	1	2.392	0.123	1	6.630	0.011
D S (C)	1	2.392	0.123	1	6.630	0.011
EXPLAINED	3	31.677	0.000	3	19.945	0.000
RESIDUAL	249			191		
TOTAL	252			194		

Note: Significance at $P < 0.01$

Table 18. Effects of density, substrate and cover on young-of-the-year growth by the end of the summer, experiment 1, 1986. Given are mean carapace length in mm, number of individuals ( ), and standard error [ ].

		DENSITY	SAND	MUD	TOTALS
CHARA	11.84(253) [0.13]	10	13.67 (27) [0.48]	13.75 (29) [0.38]	13.77 (56) [0.13]
		40	10.81 (94) [0.16]	11.73(103) [0.17]	11.29(197) [0.12]
NOTHING	11.84(107) [0.20]	3	16.07 (4) [0.47]	-	16.07 (4) [0.47]
		10	12.22 (16) [0.30]	12.99 (26) [0.33]	12.70 (42) [0.24]
		40	10.97 (61) [0.24]	-	10.97 (61) [0.24]
TOTALS			11.41(202) [0.15]	12.32 (158) [0.16]	11.84(360) [0.11]

Table 19. Contrast information for growth related to the three densities at the end of the summer, experiment 1, 1987. Probabilities are given for the pooled and separate variance estimate.

	Densities and total means (no. of YOY)											
	3	10	40		Pooled variance estimate				Separate variance estimate			
Contrast	16.07(4)	12.22(16)	10.97(61)	Value	SE	T	DF	P	SE	T	DF	P
1	1	-1	0	3.80	0.98	3.94	78	0.000	0.55	6.97	6.7	0.001
2	1	0	-1	5.10	0.90	5.66	78	0.000	0.52	9.72	4.8	0.000
3	0	1	-1	1.25	0.49	2.56	78	0.012	0.38	3.28	37.5	0.002

Note: Significance at $P < 0.01$

Experiment 2. Effects of cover and treatment.

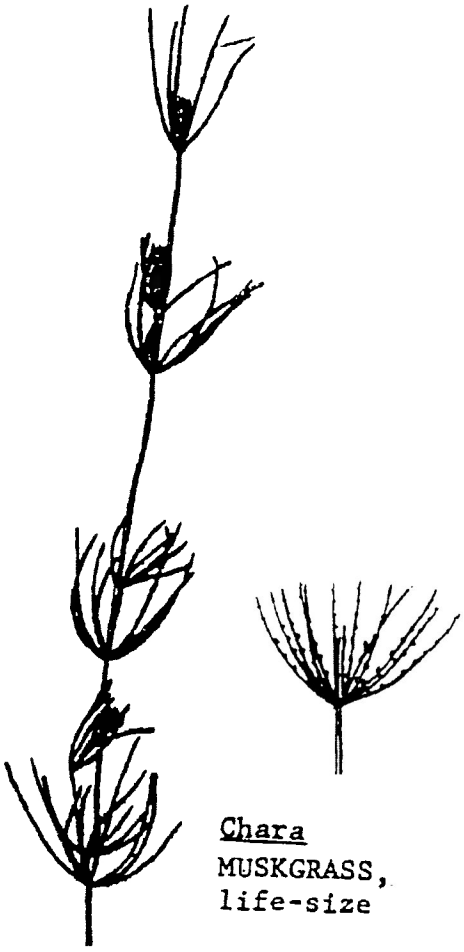
Experimental procedure:

The 1987 main experiment was a three by four factorial design, testing the influence of three cover types against four treatments. The cages were placed along the southeastern shore of Dock Lake and in the small pond between the lakes (Figure 8). The cover types were no cover, leaf-litter (this time collected from trees on the university campus) and an artificial plant. The treatments, besides the control, were food, fertilizer and temperature.

The replacement of Chara by an artificial plastic plant of similar structure was done to be able to distinguish between the the possible importance of Chara as food and Chara as shelter or additional space (Figure 12).

Cages of the control treatment, as well as of most other treatments, were suspended to a depth of only 30-40 cm, since YOY are mainly found in very shallow water. Only cages of the temperature treatment (temperature or deep set) were suspended to a depth of 1 m. This was hoped to produce a sufficient temperature difference. Only in the treatment "food" were the animals fed, again with moist dog food. Fertilizer consisted of 20 gram pellets (20% N, 10% P, 5% K) cut in half, with four halves per cage. The fertilizer was covered with approximately 3 cm of sand.

Figure 12. View of the macro-algae Chara compared to the plastic plant used in experiment 2, 1987.



Chara
MUSKGRASS,
life-size

PLASTIC PLANT,
life-size

The deep and the control set were placed into Dock Lake, far enough off the shore to prevent shading from trees growing along the shore. The other two sets could not be placed into Dock Lake because of spatial and technical problems. For easy access, they were placed in a small pond, about 6 m in diameter, that is sustained by a small outlet drain connecting the lakes (Figure 8).

All cages were stocked at a density of ten YOY per cage. Since there were not enough young from laboratory females, the deep set and four cages of the no food set could only be stocked with young from pond females.

Some technical problems were encountered during the experiment.

- Cages of the fertilizer set had to be moved in order to stabilize the stand. This not only disturbed the cages, but repeatedly increased turbidity of the water.

- When emptied at the end of the summer it was found, that the fertilizer pellets in the cages had hardly dissolved.

Results:

As in previous experiments, survival was not affected (Tables 20 and 21; Appendix IV). Mean survival after the two week experimental period was 75.28 %, which is comparable to the 1986 data of experiment 1 (78.50 %), but lower than the 1987 data of experiment 1 (90.56 %).

Growth was affected by treatment, but not by cover (Tables 20 and 22). Contrasting the four treatments revealed that YOY grew equally well in the control, the deep and the food set, but poorly in the fertilizer set (Table 23). This is believed to be due to stress caused by moving the cages and stirring up the water repeatedly.

A growth difference in the temperature set was not expected, since mean maximum and minimum temperatures at the two water depths were very similar (25.0 °C and 18.8 °C at 30 cm; 24.7 °C and 20.2 °C at 100 cm) (Table 24). Since surface waters respond quickly and more drastically to changes in air temperature, one would expect the maximum to be higher and the minimum to be lower in cages at the lesser depth. The recorded minimum temperatures correspond to these expectations, the recorded maximum temperatures do not. Whether this might be due to inaccuracy of the thermometers is not known. A definite drawback of minimum/maximum thermometers is surely that they do not record continuously, since a continuous record would be necessary in order to calculate mean daily water temperatures.

Table 20. ANOVA probabilities for carapace length and survivorship data of experiment 2, 1987.

CARAPACE LENGTH
AND % SURVIVORS BY C COVER (LEAF-LITTER; NOTHING; PLASTIC PLANT)
T TREATMENT (DEEP; CONTROL; FOOD; FERTILIZER)

	CARAPACE LENGTH			% SURVIVORS		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	5	3.973	0.002	5	1.889	0.132
C	2	1.728	0.180	2	0.827	0.449
T	3	5.455	0.001	3	2.613	0.075
2-WAY INTERACTIONS	6	1.820	0.096	6	1.008	0.443
C T	6	1.820	0.096	6	1.008	0.443
EXPLAINED	11	2.799	0.002	11	1.413	0.230
RESIDUAL	250			24		
TOTAL	261			35		

Note: Significance for $P < 0.01$

Table 21. Effects of cover and treatment on young-of-the-year survival, experiment 2, 1987. Given are mean survivorship in %, number of cages ( ), and standard error [ ].

	DEEP	CONTROL	FOOD	FERTILIZER	TOTALS
LEAF-LITTER	76.67 (3) [3.33]	73.33 (3) [12.02]	76.67 (3) [6.67]	56.67 (3) [3.33]	70.83 (12) [3.98]
NOTHING	60.00 (3) [15.28]	93.33 (3) [3.33]	80.00 (3) [5.77]	73.33 (3) [3.33]	76.67 (12) [5.12]
PLASTIC PLANT	70.00 (3) [10.00]	83.33 (3) [8.82]	86.67 (3) [6.67]	73.33 (3) [13.33]	78.33 (12) [4.74]
TOTALS	68.89 (9) [5.88]	83.33 (9) [5.27]	81.11 (9) [3.51]	67.78 (9) [4.94]	75.28 (36) [2.66]

Table 22. Effects of cover and treatment on young-of-the-year growth, experiment 2, 1987. Given are mean carapace length in mm, number of individuals ( ), and standard error [ ].

	DEEP	CONTROL	FOOD	FERTILIZER	TOTALS
LEAF-LITTER	8.34 (23) [0.39]	8.32 (22) [0.27]	7.68 (23) [0.29]	6.69 (17) [0.24]	7.83 (85) [0.17]
NOTHING	7.81 (18) [0.28]	7.90 (28) [0.27]	8.23 (15) [0.30]	7.27 (22) [0.22]	7.77 (83) [0.14]
PLASTIC PLANT	7.46 (21) [0.26]	7.33 (25) [0.33]	7.90 (26) [0.25]	7.16 (22) [0.27]	7.48 (94) [0.14]
TOTALS	7.89 (62) [0.19]	7.84 (75) [0.17]	7.90 (64) [0.16]	7.07 (61) [0.14]	7.68 (262) [0.09]

Note: Stocking density was 10 YOY per cage.

Table 23. Contrast information for growth related to the four treatments of experiment 2, 1987. Probabilities are given for the pooled and separate variance estimate.

	Treatments and total means (no. of YOY)												
						Pooled variance estimate				Separate variance estimate			
Contrast	Deep 7.89 (62)	Control 7.84 (75)	Food 7.90 (64)	Fertilizer 7.07 (61)	Value	SE	T	DF	P	SE	T	DF	P
1	-1	1	0	0	-0.05	0.23	-0.21	258	0.834	0.26	-0.19	130.4	0.848
2	-1	0	1	0	0.01	0.24	0.05	258	0.958	0.25	0.05	120.2	0.959
3	-1	0	0	1	-0.82	0.25	-3.29	258	0.001	0.24	-3.41	113.3	0.001
4	0	-1	1	0	0.06	0.23	0.27	258	0.790	0.24	0.26	137.0	0.793
5	0	-1	0	1	-0.77	0.24	-3.24	258	0.001	0.23	-3.39	133.2	0.001
6	0	0	-1	1	-0.83	0.25	-3.37	258	0.001	0.22	-3.82	122.1	0.000

Note: Significance at $P < 0.01$.

Table 24. Minimum and maximum water temperatures in cages at water depths of 30 and 100 cm, experiment 2, 1987.

DATE	TEMPERATURES (°C) at 30 cm water depth		TEMPERATURES (°C) at 100 cm water depth	
	MIN	MAX	MIN	MAX
June 23	22.0	25.0	23.0	26.0
June 24	21.0	28.0	22.0	27.0
June 25	22.0	29.0	23.0	30.0
June 26	20.0	25.0	22.0	28.0
June 29	22.0	25.0	22.0	27.0
June 30	12.0	25.0	18.0	23.0
July 2	17.0	22.0	19.0	23.0
July 3	17.0	23.0	20.0	20.0
July 4	12.0	23.0	15.0	22.0
July 6	18.0	24.5	20.0	23.0
July 14	16.5	22.5	19.0	21.0
July 15	16.5	20.0	16.0	22.0
July 17	18.0	23.0	19.0	23.0
July 20	17.0	25.0	19.0	24.0
July 21	18.0	25.5	20.0	25.0
July 22	22.0	26.5	22.0	26.0
July 24	19.0	28.0	21.0	26.0
July 27	24.0	29.0	22.0	26.0
July 28	24.0	26.0	21.0	27.0
MEAN	18.8	25.0	20.2	24.7

Obtaining the missing mean water temperatures from daily mean air temperatures was not possible since no correlation was found between the recorded water temperatures and either mean, minimum or maximum air temperatures.

No significant growth difference was found between the cover types (Table 20). However, it is somewhat unusual that in all sets growth was better with no cover, than with the plastic plant. For the control and the deep set, best growth achieved with leaf-litter as cover, as was expected (Table 22).

The carapace length distribution resembles very closely the one obtained for 1987 data of experiment 1 (Figures 11 and 13). The same size range is covered and the percentage per size group is similar.

By the end of the summer 52.5 % of the crayfish had died (Table 25), 27.78 % of which died in the four weeks following the actual experimental period. Taking into account that these 27.78 % had died over a four week period, mortality actually decreased by 50 %. No cover or treatment effects could be detected (Table 26).

Mean carapace length at the end of the summer was 10.92 mm. Growth was again not significantly influenced by cover, but by treatment (Table 26 and 27). Contrasting the treatments had a similar result; a significant growth difference existed between the fertilizer set and the other three sets. However, this time

Figure 13. Carapace length frequency distribution of crayfish from experiment 2, 1987. Sample size is shown at top of each bar.

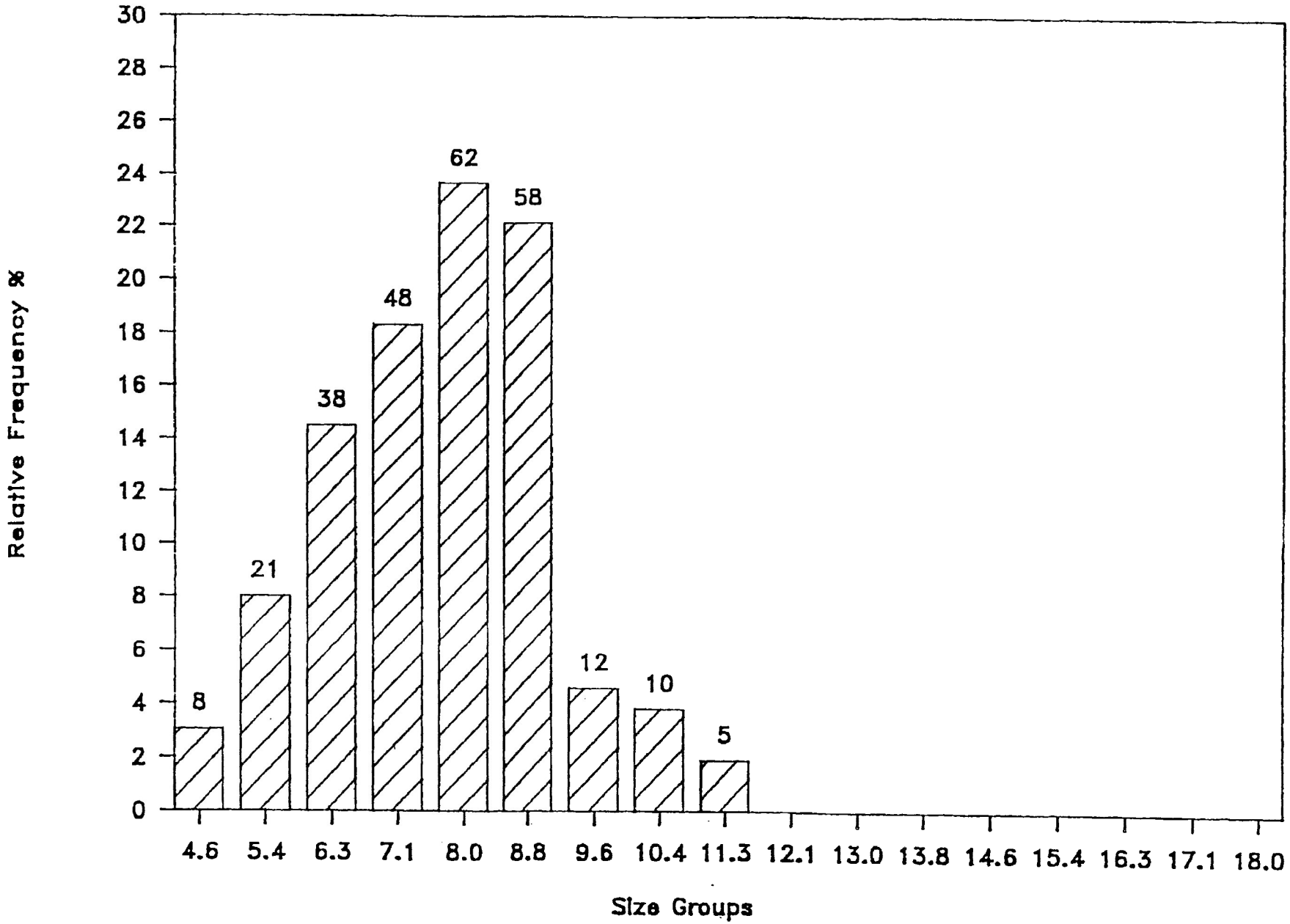

Relative Frequency %
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
8
21
38
48
62
58
12
10
5
4.6
5.4
6.3
7.1
8.0
8.8
9.6
10.4
11.3
12.1
13.0
13.8
14.6
15.4
16.3
17.1
18.0
Size Groups

Table 25. Effects of cover and treatment on young-of-the-year survival by the end of the summer, Experiment 2, 1987. Given are mean survivorship in %, number of cages ( ), and standard error [ ].

	DEEP	CONTROL	FOOD	FERTILIZER	TOTALS
LEAF-LITTER	53.33 (3) [6.66]	53.33 (3) [8.82]	50.00 (3) [17.32]	26.67 (3) [12.02]	45.83 (12) [6.09]
NOTHING	23.33 (3) [8.82]	76.67 (3) [8.82]	56.67 (3) [6.66]	53.33 (3) [8.82]	44.17 (12) [5.96]
PLASTIC PLANT	43.33 (3) [8.82]	53.33 (3) [14.53]	43.33 (3) [14.63]	36.67 (3) [14.53]	52.50 (12) [6.76]
TOTALS	40.00 (9) [6.01]	61.11 (9) [6.76]	50.00 (9) [7.07]	38.89 (9) [7.16]	47.50 (36) [3.57]

Table 26. ANOVA probabilities for carapace length and survivorship data of experiment 2 by the end of the summer, 1987.

CARAPACE LENGTH
AND % SURVIVORS BY C COVER (LEAF-LITTER; NOTHING; PLASTIC PLANT)
T TREATMENT (DEEP; CONTROL; FOOD; FERTILIZER)

	CARAPACE LENGTH			% SURVIVORS		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	5	7.029	0.000	5	1.730	0.166
C	2	0.656	0.520	2	0.600	0.557
T	3	11.486	0.000	3	2.483	0.085
2-WAY INTERACTIONS	6	0.369	0.898	6	1.448	0.238
C T	6	0.369	0.898	6	1.448	0.238
EXPLAINED	11	3.396	0.000	11	1.576	0.170
RESIDUAL	159			24		
TOTAL	170			35		

Note: Significance for $P < 0.01$

Table 27. Effects of cover and treatment on young-of-the-year growth by the end of the summer, experiment 2, 1987. Given are carapace length in mm, number of individuals ( ), and standard error [ ].

	DEEP	CONTROL	FOOD	FERTILIZER	TOTALS
LEAF-LITTER	10.80 (16) [0.46]	11.37 (16) [0.39]	11.11 (15) [0.45]	12.43 (8) [0.59]	11.29 (55) [0.24]
NOTHING	10.47 (13) [0.48]	10.41 (16) [0.41]	10.98 (13) [0.41]	12.71 (11) [0.54]	11.04 (53) [0.25]
PLASTIC PLANT	10.51 (7) [0.31]	10.81 (23) [0.34]	10.72 (17) [0.33]	12.84 (16) [0.64]	11.27 (63) [0.25]
TOTALS	10.62 (36) [0.27]	10.86 (55) [0.22]	10.93 (45) [0.22]	12.71 (35) [0.36]	10.92(171) [0.14]

Table 28. Contrast information for carapace length data of the four treatments of experiment 2 by the end of the summer, 1987.

	Treatments and total means (no. of YOY)												
	Deep	Control	Food	Fertilizer		Pooled variance estimate				Separate variance estimate			
Contrast	10.62 (36)	10.86 (55)	10.93 (45)	12.71 (35)	Value	SE	T	DF	P	SE	T	DF	P
1	1	-1	0	0	-0.23	0.37	-0.63	167	0.528	0.35	-0.66	75.0	0.509
2	1	0	-1	0	-0.30	0.38	-0.79	167	0.430	0.35	-0.86	72.4	0.394
3	1	0	0	-1	-2.08	0.40	-5.14	167	0.000	0.45	-4.65	63.9	0.000
4	0	1	-1	0	-0.07	0.34	-0.20	167	0.838	0.31	-0.24	96.4	0.823
5	0	1	0	-1	-1.85	0.37	-5.01	167	0.000	0.42	-4.42	59.3	0.000
6	0	0	1	-1	-1.78	0.38	-4.63	167	0.000	0.42	-4.22	59.2	0.000

Note: Significance at $P < 0.01$

YOY in the fertilizer set were the largest. Not only had they caught up in growth, but they were on average 1.9 mm bigger than in the other sets (Tables 22, 27 and 28). This means that they grew on average 2.5 mm more during this four weeks period, than YOY in the other sets.

Sex determination of YOY used in experiment 1 and 2 revealed approximately equal numbers of males and females (Figures 14 and 15; Table 29). No size difference between the sexes was apparent (Table 30). There was no significant size difference for pond YOY ($T = 1.70$; $P = 0.092$), even though males were slightly larger (Figure 16). The difference in sampling time (sampling of pond YOY was done two weeks prior to the final measuring of experimental YOY (Table 2)) prevents a direct growth comparison. Figure 17 shows the growth performance of experimental and pond YOY. The graph for experiment 1 only includes the low density cages, in order to allow comparison with experiment 2, in which all cages were stocked at the low density. The growth of pond YOY was somewhere between that of YOY from experiment 1 and experiment 2.

Figure 14. Carapace length frequency distribution of crayfish from experiment 1, 1987, by the end of the summer, separately for males (left bar) and females (right bar). The shaded area represents the portion of diseased individuals. Sample size is shown at top of each bar.

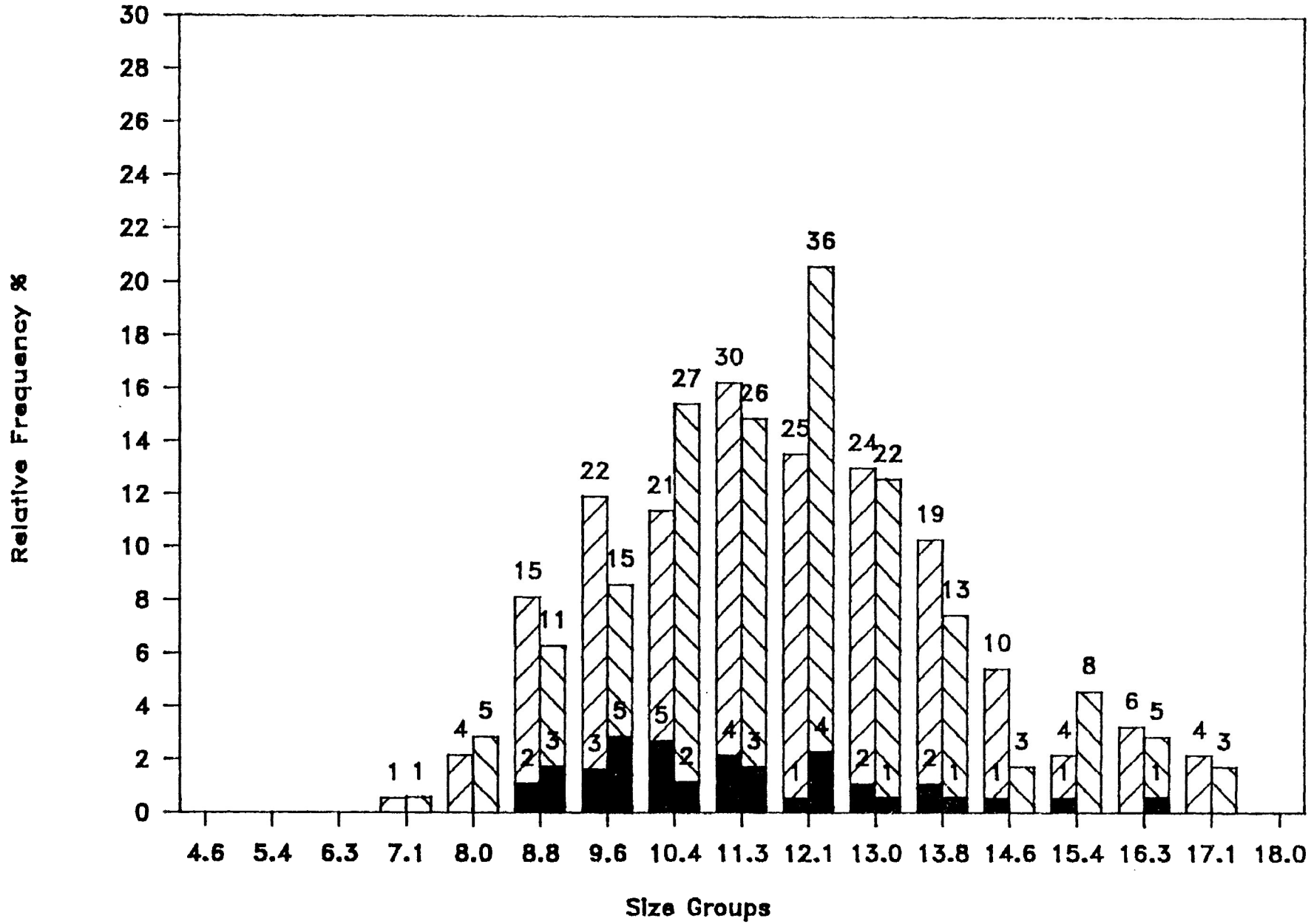

Relative Frequency %
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
1 1
4 5
15 11
22 15
21 5 27
30 26
25 36 4
24 22
19 13
10 3
4 8
6 5
4 3
4.6
5.4
6.3
7.1
8.0
8.8
9.6
10.4
11.3
12.1
13.0
13.8
14.6
15.4
16.3
17.1
18.0
Size Groups

Figure 15. Carapace length frequency distribution of crayfish from experiment 2, 1987, by the end of the summer, separately for males (left bar) and females (right bar). The shaded area represents the portion of diseased individuals. Sample size is shown at top of each bar.

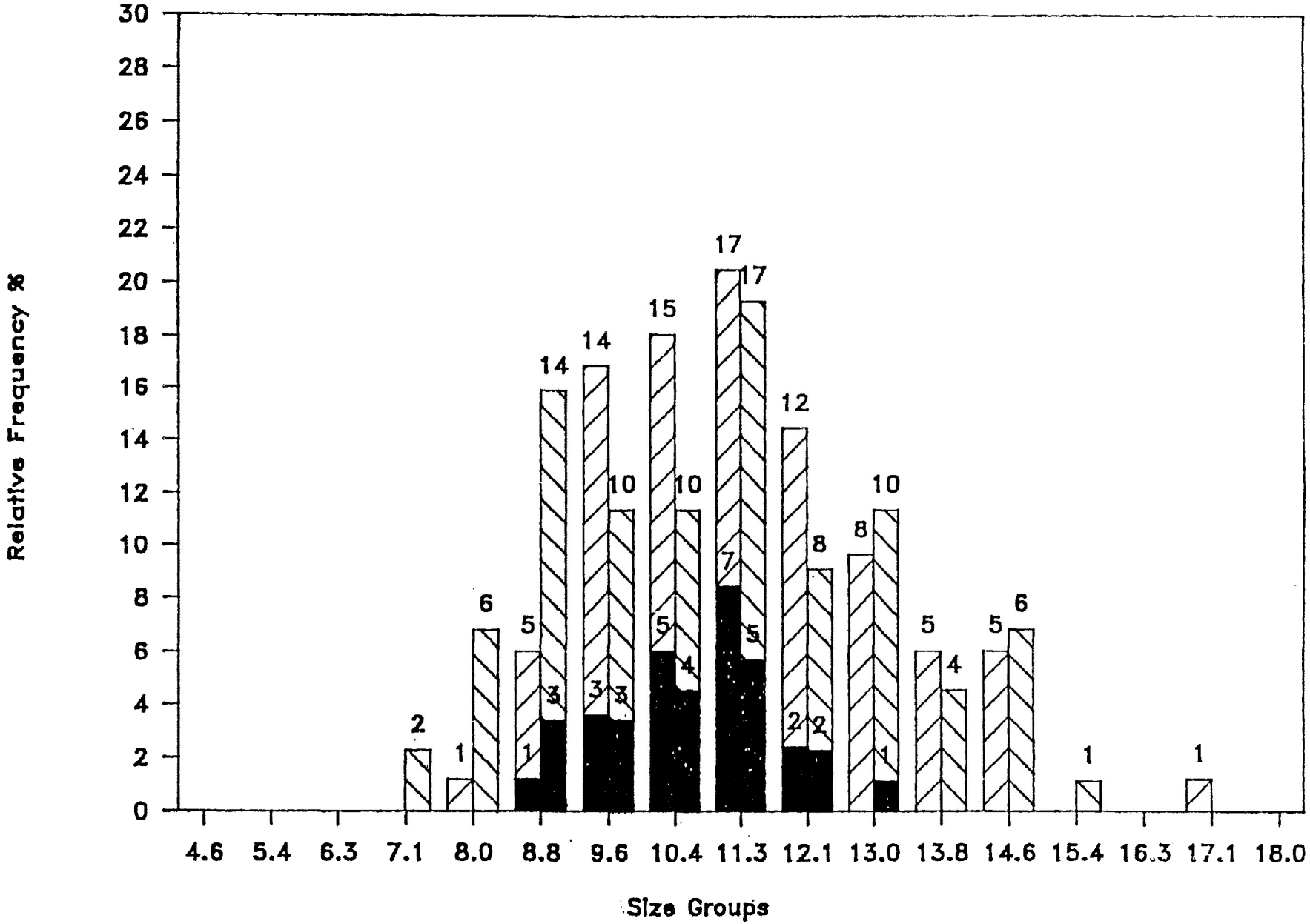

Relative Frequency %
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
4.6
5.4
6.3
7.1
8.0
8.8
9.6
10.4
11.3
12.1
13.0
13.8
14.6
15.4
16.3
17.1
18.0
Size Groups

Figure 16. Carapace length frequency distribution of young-of-the-year crayfish caught in Dock Lake in 1987.

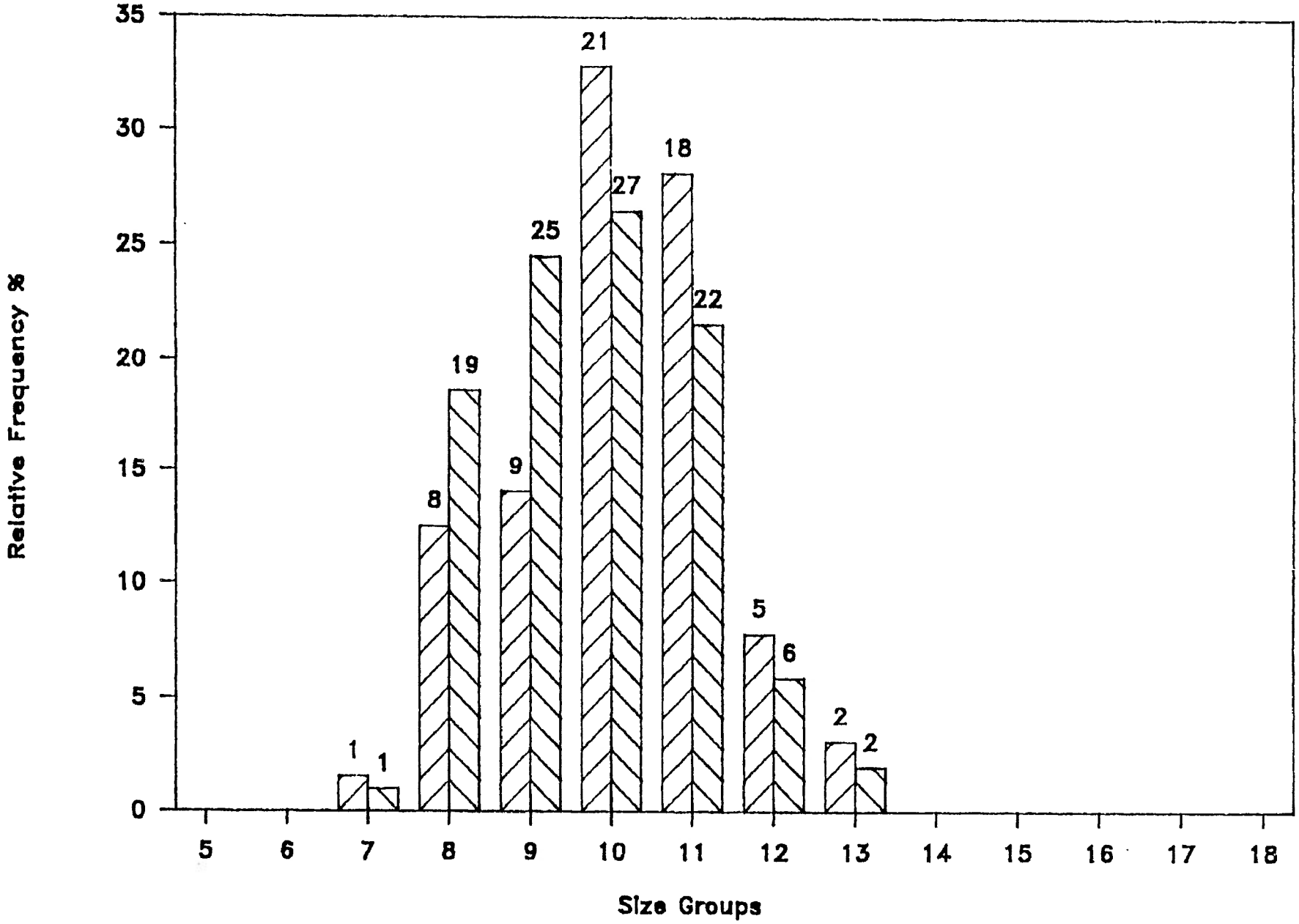
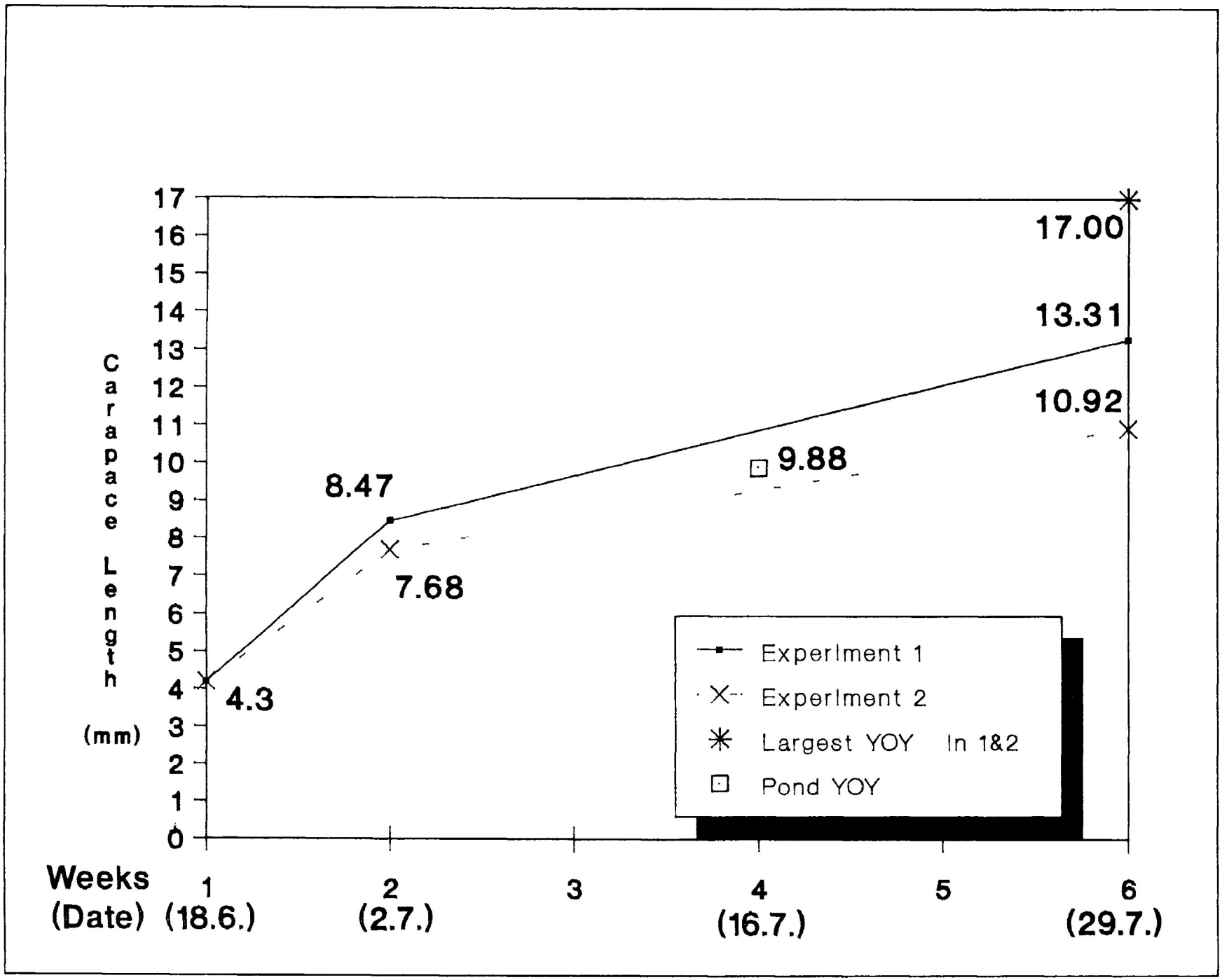

Relative Frequency %
35
30
25
20
15
10
5
0
1
1
8
19
9
25
21
27
18
22
5
6
2
2
5
6
7
8
9
10
11
12
13
14
15
16
17
18
Size Groups

Figure 17. Growth of juvenile crayfish from the lakes compared to those from experiment 1 and 2.


Carapace Length (mm)
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
17.00
13.31
10.92
9.88
8.47
7.68
4.3
Experiment 1
Experiment 2
Largest YOY In 1&2
Pond YOY
Weeks
(Date)
1
(18.6.)
2
(2.7.)
3
4
(16.7.)
5
6
(29.7.)

Porcelain disease was very prevalent among experimental YOY in 1987 (Figures 14 and 15; Table 29). Porcelain disease is an infection caused by the microsporidian Thelohania contejeani (Henneguy). Spores, similar to those described by Cossins (1972) were found, but could not be identified with certainty. However, recognition of the disease is possible because of the white colouration of the muscle tissue, which is most obvious on the ventral side of the abdomen (Figure 18). 11.45 % of the crayfish from experiment 1 and 21.05 % from experiment 2 were infected. Both sexes and all size groups were equally affected, even though there is a marginal tendency towards the smaller individuals (Tables 29 and 30).

Table 29. Sex ratio and prevalence of porcelain disease (p.d.) among 1987 experimental YOY by the end of the summer.

		MALES			FEMALES		
		TOTAL	without p.d.	with p.d.	TOTAL	without p.d.	with p.d.
Exp.1, 1987	NUMBER	185	164	21	175	155	20
	mean CL (mm)	11.85 [0.16]	11.91 [0.17]	11.40 [0.40]	11.82 [0.15]	11.92 [0.16]	11.03 [0.44]
Exp.2, 1987	NUMBER	83	65	18	88	70	18
	mean CL (mm)	11.43 [0.18]	11.61 [0.22]	10.81 [0.21]	10.99 [0.21]	11.09 [0.26]	10.58 [0.27]

Table 30. ANOVA probabilities for end-of-summer carapace length data from 1987 experiments in reference to sex and porcelain disease.

CARAPACE LENGTH by S SEX (MALE; FEMALE)
P PORCELAIN DISEASE (YES; NO)

	EXPERIMENT 1, 1987			EXPERIMENT 2, 1987		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	2	2.058	0.129	2	3.041	0.050
S	1	0.016	0.900	1	2.615	0.108
P	1	4.099	0.044	1	3.558	0.061
2-WAY INTERACTIONS	1	0.315	0.576	1	0.175	0.677
S P	1	0.315	0.576	1	0.175	0.677
EXPLAINED	3	1.477	0.220	3	2.086	0.104
RESIDUAL	108			8		
TOTAL	111			11		

Note: Significance at $P < 0.01$

Figure 18. Photograph showing a juvenile crayfish with a white abdominal muscle, indicative of porcelain disease, on the left, and a noninfected one on the right.

Experiment 3. Effects of lakes and "no" habitat.

Experimental procedure:

Twelve bare cages, i.e. lacking substrate and cover, were distributed between both lakes and stocked at both densities (Figure 7). They were intended to reveal possible differences between the lakes, and also to indicate the importance of substrate and cover.

Water fluctuations made objective comparison impossible. A beaver had blocked the outflow culvert, with the effect, that the water level was about 0.5 m above normal. On the second day of the experiment the dam was destroyed and the water level decreased. As a result, the cages were mostly out of the water and the YOY were crowded in small corners of remaining water. Two YOY had died and were replaced the following morning.

Results:

Growth, as well as survival was poor in both lakes, indicating the importance of substrate and cover. YOY in the bare cages reached an average carapace length of only 5.73 mm, compared to 7.60 mm in experiment 1 (Tables 7 and 31; Appendix V). Average mortality in the bare cages was as high as 89.17% compared to only 21.50% in experiment 1 (Tables 11 and 32).

After the two week experimental period YOY had grown significantly better in Dock Lake than in Shallow Lake (Table 33). Whether this is due to actual differences in location, or to stress caused by the water draw down is not known. Temperatures in Dock Lake are usually 1 - 2 ^{o}C below those in Shallow Lake. This might account for the growth difference (Table 34).

Mortality was equally high in both lakes (Table 32 and 33). In three of the six low density cages there were no survivors at all. Two of the three survivors of another low density cage, were probably those, replaced after the water draw down.

Table 31. Effects of lake and food on young-of-the-year growth, experiments 3 and 4, 1986. Given are mean carapace length in mm, number of individuals ( ), and standard error [ ].

	DENSITY	DOCK LAKE	SHALLOW LAKE	TOTALS
FOOD	10	5.00 (2) [0.40]	4.87 (3) [0.27]	4.92 (5) [0.20]
	40	6.19 (26) [0.19]	4.92 (10) [0.18]	5.84 (36) [0.17]
NO FOOD	40	6.44 (9) [0.30]	-	6.44 (9) [0.30]

Table 32. Effects of lake and food on young-of-the-year survival, experiments 3 and 4, 1986. Given are mean survivorship in %, number of cages ( ), and standard error [ ].

	DENSITY	DOCK LAKE	SHALLOW LAKE	TOTALS
FOOD	10	6.67 (3) [3.33]	10.00 (3) [10.0]	8.33 (6) [4.77]
	40	14.58 (6) [2.08]	8.33 (3) [2.20]	12.50 (9) [1.82]
NO FOOD	40	7.50 (3) [1.44]	-	7.50 (3) [1.44]

Table 33. ANOVA probabilities for carapace length and survivorship data of experiment 3, 1986.

CARAPACE LENGTH
AND % SURVIVORS BY D DENSITY (10; 40)
L LAKE (DOCK L.; SHALLOW L.)

	CARAPACE LENGTH			% SURVIVORS		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	2	9.428	0.000	2	0.523	0.607
D	1	1.782	0.190	1	0.676	0.428
L	1	13.854	0.001	1	0.214	0.653
2-WAY INTERACTIONS	1	1.780	0.190	1	1.048	0.328
D L	1	1.780	0.190	1	1.048	0.328
EXPLAINED	3	6.879	0.001	3	0.698	0.572
RESIDUAL	37			11		
TOTAL	40			14		

Note: Significance at $P < 0.01$

Table 34. Comparison between 1986/87 summer water temperatures from Dock Lake ans Shallow Lake for the experimental periods.

DATE	TEMPERATURES (°C) from Dock Lake MIN	MAX	TEMPERATURES (°C) from Shallow Lake MIN	MAX
June 25, 1986	13.0	24.0	17.0	21.0
June 26, 1986	17.0	20.0	-	-
June 27, 1986	16.0	22.0	18.0	22.0
June 30, 1986	16.0	25.0	15.0	24.0
July 2, 1986	16.0	24.0	16.0	23.0
July 4, 1986	14.0	24.0	16.0	23.0
July 15, 1986	15.0	25.0	15.0	24.0
July 18, 1986	17.0	24.0	16.0	24.0
July 21, 1986	19.0	30.0	22.0	25.0
July 22, 1986	19.0	25.0	24.0	25.0
July 23, 1986	19.0	26.0	23.0	25.0
July 24, 1986			22.0	25.0
July 25, 1986	20.0	27.0	21.0	24.0
July 28, 1986	22.0	26.0	20.0	24.0
July 29, 1986	19.0	28.0	20.0	25.0
July 30, 1986	20.0	27.0	22.0	27.0
July 31, 1986	19.0	26.0	22.0	25.0
August 1, 1986	19.0	25.0	21.0	25.0
August 5, 1986	17.0	24.0	18.0	23.0
August 6, 1986	17.0	21.0	19.0	22.0
August 7, 1986	17.0	24.0	19.0	23.0
August 8, 1986	17.0	23.0	19.0	21.0
August 11, 1986	16.0	26.0	-	-
August 12, 1986	-	-	16.0	24.0
August 13, 1986	18.0	25.0	18.0	23.0
June 23, 1987	22.0	25.0	24.0	26.0
June 24, 1987	21.0	28.0	23.0	27.0
June 25, 1987	22.0	29.0	25.0	25.0
June 26, 1987	20.0	25.0	22.0	23.0
June 29, 1987	22.0	25.0	20.0	28.0
June 30, 1987	12.0	25.0	12.0	23.0
July 2, 1987	17.0	22.0	16.0	23.0
July 3, 1987	17.0	23.0	16.0	18.0
July 4, 1987	12.0	23.0	18.0	21.0
July 6, 1987	18.0	24.5	14.0	27.0
July 14, 1987	16.5	22.5	17.5	28.0
July 15, 1987	16.5	20.0	16.0	22.0
July 17, 1987	18.0	23.0	20.0	23.0
July 20, 1987	17.0	25.0	19.0	23.0
July 21, 1987	18.0	25.5	18.0	23.0
July 22, 1987	22.0	26.5	-	-
July 24, 1987	19.0	28.0	21.0	28.0
July 27, 1987	24.0	29.0	22.0	27.0
July 28, 1987	24.0	26.0	-	-

Experiment 4. Effects of supplemental food.

Experimental procedure:

During experimentation, all crayfish were supplied with additional moist dog food (Gainsburger) about twice weekly. To determine the importance of supplemental food, YOY of three high density cages were not fed. These cages were lacking substrate and cover. For optimal comparison, they were placed next to the six high density cages of experiment 3, which were bare as well (Figure 7). Ergo, the experimental unit consisted of nine bare cages, of which only six were supplied with moist dog food.

Results:

Growth and survival in all bare cages was poor. No difference was apparent in growth or survival related to the additional food source (Tables 31, 32 and 35; Appendix V). The food was apparently not accepted, even though YOY were observed to feed on it in the laboratory.

Table 35. ANOVA probabilities for carapace length and survivorship data of experiment 4, 1986.

CARAPACE LENGTH
AND % SURVIVORS BY F FOOD (YES; NO)

	CARAPACE LENGTH			% SURVIVORS		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	1	0.459	0.503	1	4.922	0.062
F	1	0.459	0.503	1	4.922	0.062
EXPLAINED	1	0.459	0.503	1	4.922	0.062
RESIDUAL	33			7		
TOTAL	34			8		

Note: Significance at $P < 0.01$

Experiment 5. Effects of adults.

Experimental procedure:

This experiment was designed to test the influence of adults on growth and survival of YOY under different habitat conditions. Nine cages were set up in Shallow Lake, with combinations of sand and the three cover types (Figure 7). Only one medium density of twenty five YOY plus one adult male per cage was tested.

To determine whether male and female adult crayfish have a different impact on YOY growth and survival, three cages were set up with sand and no additional cover plus one female instead of one male. Because of lack of suitable shoreline in Shallow Lake, these cages had to be set up in Dock Lake (Figure 7). It was initially hoped to account for possible difference between location through comparison with the YOY in the bare cages. Since YOY in those cages performed so poorly, three cages were stocked with no adults at a density of 25 YOY per cage. Leaf-litter was chosen as cover.

Adults were supplied with moist dog food and live food organisms (mainly gammarid amphipods of varying sizes) to offer a food choice and prevent cannibalism due to starvation. The stomachs of those adults were not checked, since cages were not to be disturbed during the experimental period. To make up for this shortcoming, three cages were set up in 1987 with a sand substrate and two claypot shelters. Each cage was stocked with one female with attached young. When some of the young were

free-living, one male was placed over night in each cage. These males were caught in traps set the previous day. They ranged in size from 29 to 37 mm. The following morning they were preserved in 70 % alcohol. This was repeated on two subsequent days.

Results:

In the nine cages containing one adult male each, growth was comparable for all three habitat types (Tables 36 and 37; Appendix VI). The YOY reached a mean carapace length of only 6.77 mm. Growth was better in the cages containing one female (7.31 mm carapace length) and best in the cages containing no adults (8.19 mm carapace length) (Tables 36). Comparison is rendered difficult because of differences in time and location.

The "male" and the "no adult" cages were at the same location, but at different times. Since no striking differences in water temperatures are apparent (Table 34) and the growth difference is highly significant (Table 38), growth was actually suppressed by the presence of adult males.

The "male" and the "female" cages were at different locations (Figure 7), but at the same time. Since a growth difference between the two locations is possible (see experiment 3) and the growth difference between YOY from the two sets is only marginal (Table 39), male and female impact on YOY growth appears to be similar.

Table 36. Effects of adults and cover on young-of-the-year growth, experiment 5, 1986. Given are mean carapace length in mm, number of individuals ( ), and standard error [ ].

	DENSITY	LEAF-LITTER	CHARA	NOTHING	TOTALS
NONE	25	8.19 (37) [0.15]	-	-	8.19 (37) [0.15]
MALES	25	6.71 (50) [0.16]	6.86 (25) [0.22]	6.78 (34) [0.17]	6.77(109) [0.10]
FEMALES	25	-	-	7.31 (40) [0.17]	7.31 (40) [0.17]

Table 37. ANOVA probabilities for carapace length and survivorship data of experiment 5, 1986, including cages with one adult male only.

CARAPACE LENGTH
AND % SURVIVORS BY C COVER (LEAF-LITTER; CHARA; NOTHING)

	CARAPACE LENGTH			% SURVIVORS		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	2	0.164	0.849	2	2.511	0.176
C	2	0.164	0.849	2	2.511	0.176
EXPLAINED	2	0.164	0.849	2	2.511	0.176
RESIDUAL	106			5		
TOTAL	108			7		

Note: Significance at $P < 0.01$

Table 38. ANOVA probabilities for carapace length and survivorship data of experiment 5, 1986, comparing "male" and "no adult" cages.

CARAPACE LENGTH
AND % SURVIVORS BY A ADULTS (NONE; MALES)

	CARAPACE LENGTH			% SURVIVORS		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	1	43.615	0.000	1	3.596	0.131
A	1	43.615	0.000	1	3.596	0.131
EXPLAINED	1	43.615	0.000	1	3.596	0.131
RESIDUAL	85			4		
TOTAL	86			5		

Note: Significance at $P < 0.01$

Table 39. ANOVA probabilities for carapace length and survivorship data of experiment 5, 1986, including only cages with no cover.

CARAPACE LENGTH
AND % SURVIVORS BY A ADULTS (MALES; FEMALES)

	CARAPACE LENGTH			% SURVIVORS		
SOURCE OF VARIATION	DF	F	P	DF	F	P
MAIN EFFECTS	1	5.085	0.027	1	0.237	0.652
A	1	5.085	0.027	1	0.237	0.652
EXPLAINED	1	5.085	0.027	1	0.237	0.652
RESIDUAL	72			4		
TOTAL	73			5		

Note: Significance at $P < 0.01$

Mean survival was generally fairly low. It was only 54.5 % in the "male" cages, 53.3 % in the "female" cages and 49.3 % in the "no adult" cages (Table 40). The high mortality amongst YOY in cages with no adults is somewhat surprising. Comparison with the survival rate in experiment 1 demonstrates, that survival should be as high as 78.50 %. The YOY may have been in poorer condition due to the fact that they were kept in the laboratory longer than any of the other YOY. Being acclimated to laboratory conditions, they may also not have been able to adapt as well to the pond environment. No effect of adult males on YOY survival could be detected, due to this high mortality in the "no adult" cages (Table 38).

No difference was apparent between the impact of males and females (Tables 39 and 40). Even if adults do not actively prey on YOY, they may occasionally capture a few. Capture success is increased by the confinement, which may account for the lower survival.

Of the six stomachs analyzed in 1987, three were completely empty and three were nearly empty. All that was found were some plant fragments, which must have been ingested before the males were placed in the cages. This also gives evidence to the slow digestibility of plant matter.

Table 40. Effects of adults and cover on young-of-the-year survival, experiment 5, 1986. Given are mean survivorship in %, number of cages ( ), and standard error [ ].

	DENSITY	LEAF-LITTER	CHARA	NOTHING	TOTALS
NONE	25	49.33 (3) [5.33]	-	-	49.33 (3) [5.33]
MALES	25	66.67 (3) [7.42]	50.00 (2) [6.00]	45.33 (3) [7.42]	54.50 (8) [5.12]
FEMALES	25	-	-	53.33 (3)[14.67]	53.33 (3)[14.67]

Experiment 6. Cannibalism in the lakes?

Experimental procedure:

To investigate whether adults cannibalize YOY in the lakes, adults were collected in the spring along the shore in Dock and Shallow Lake in 1986 and 1987. Collection was done using wire traps, despite disadvantages inherent to trap fishing (Westman et al. 1979). Collection using SCUBA was unfeasible in these lakes, due to the dense growth of Chara and to turbidity caused by diver activity (Morgan, personal communication). Baiting the shore at dawn resulted in a meager catch of only two females. Shocking with a backpack electro-shocker was unsuccessful, because the shocker was malfunctioning. In 1986 it did not function at all, while in 1987 it functioned well during a trial run, but then failed to show any effect on crayfish on the actual sampling day.

Crayfish caught in the traps were preserved in 70 % ethanol. The stomach contents were analysed qualitatively, using a dissecting microscope.

In 1986 collecting was begun when the young were already off the female, in 1987 it was begun earlier, when most females were still carrying their young.

Seventy stomachs, thirty seven from 1986 and thirty three from 1987, from crayfish from both lakes were analyzed.

Results:

Stomach content analysis was restrained by the extent to which food items had been masticated. Plant matter and detritus appeared to constitute the bulk of the stomach contents. Fish remains were also frequently encountered. In 1986 these were most likely remains from the fish bait. In 1987, however, traps were not baited. In several occasions mudminnow (Umbra limi Kirtland) scales were detected. Midge larvae, mayfly nymphs and amphipods were only occasionally recognized. On no single occasion could any crayfish remains be detected.

B) Laboratory Experiments

Experiment 1. Habitat preferences.

Experimental procedure:

A preliminary experiment tested for habitat preferences. The bottoms of two glass aquaria (60 x 30 x 35 cm) were half covered with sand and half with mud. Twenty-nine YOY (corresponding to a density of 160 YOY per square meter) were placed in the tank. After six hours the two halves were separated by a barrier and the crayfish in each half were counted. This was repeated twice.

In one tank half of each substrate was then covered with leaf-litter, in the other tank with Chara sp., a large macro-algae that is extremely abundant in all four lakes. The next day, the habitats were separated by barriers and the YOY were counted. This as well was replicated twice.

Results:

On average, 93.1% of the crayfish young were recovered. Given only the choice between the two bare substrates, crayfish were found to prefer mud over sand ($T = 5.94$; $P = 0.001$). When offered cover, this was preferred over bare substrate, irrespective of cover and substrate type ($T = 5.67$; $P = 0.004$). However, when the cover types are regarded separately, this distinct preference for cover was only true for leaf-litter ($T = 6.03$; $P = 0.004$), not for Chara ($T = 2.949$; $P = 0.042$).

Table 41. Analysis of substrate preferences of young crayfish (YOY) in laboratory experiment 1, using T-Test.

Variable	Group	Number of cases	Mean	SD	SE	F Value	2-Tail Prob.	Pooled variance estimate T Value	DF	2-Tail Prob.	Separate variance estimat T Value	DF	2-Tai Prob
Mean no. of YOY per Substrate	Mud	4	62.20	5.81	2.90	1	1	5.94	6	0.001	5.94	6	0.00
	Sand	4	37.80	5.81	2.90								

Table 42. Contrast information for substrate and cover preferences of young crayfish in the laboratory, experiment 1.

a) Both cover types combined

	Substrate/Cover combinations & mean no. of YOY					Pooled variance estimate				Separate variance estimate			
Contrast	Sand 7.2	Mud 11.7	Sand/cover 38.8	Mud/cover 42.3	Value	SE	T	DF	P	SE	T	DF	P
1	-1	-1	1	1	62.23	10.97	5.67	12	0.000	10.97	5.67	6.6	0.001
2	-1	1	-1	1	7.94	10.97	0.73	12	0.483	10.97	0.72	6.6	0.494

Note: Significance at $P < 0.01$.

b) Cover type leaf-litter only

	Substrate/Cover combinations & mean no. of YOY					Pooled variance estimate				Separate variance estimate			
Contrast	Sand 7.3	Mud 14.4	Sand/cover 41.9	Mud/cover 36.4	Value	SE	T	DF	P	SE	T	DF	P
1	-1	-1	1	1	56.61	9.39	6.03	4	0.004	9.39	6.03	2	0.027
2	-1	1	-1	1	1.59	9.39	0.17	4	0.874	9.39	0.17	2	0.881

Note: Significance at $P < 0.01$.

c) Cover type Chara only

	Substrate/Cover combinations & mean no. of YOY					Pooled variance estimate				Separate variance estimate			
Contrast	Sand 7.14	Mud 8.93	Sand/Cover 35.71	Mud/Cover 48.21	Value	SE	T	DF	P	SE	T	DF	P
1	-1	-1	1	1	67.86	23.01	2.95	4	0.042	23.01	2.95	1.8	0.113
2	-1	1	-1	1	14.29	23.01	0.62	4	0.568	23.01	0.62	1.8	0.605

Note: Significance at $P < 0.01$.

Experiment 2. Cannibalism

Experimental procedure:

This experiment investigated the impact of adult male crayfish on the survival of YOY. Two glass aquaria, both divided into three separate 20 x 30 cm compartments, were stocked with females carrying young, one female per compartment. Shelter in the form of clay pot halves was provided, but compartments contained no bottom substrate. In one aquarium, one male of approximately same size as the female was added to each compartment.

To provide further information, a female with attached young and a male were placed in a 91.5 x 45.5 x 46 cm tank with sand as substrate and clay pots as shelter.

Results:

No analysis was possible, since females in all compartments lost most of their young prematurely. In the few aggressive interactions that were observed, the males retreated.

In the big tank as well, the female lost most of her young prematurely. These young, at least some of them visibly alive, but all still uncapable of locomotion, were later picked up and eaten by the male. No fighting between the female and the male was observed.

The male was never observed to stalk the remaining young, that reached the free-living stage several days later. On occasional encounters, the young had always time for retreat.

Loss of young was apparently stress induced, but not related to the presence of males. Stress might have been caused by transferring the females with hatched young to a strange environment.

Experiment 3. Aeshnid versus Libellulid predation

Experimental procedure:

This experiment tested the effectiveness of aeshnid versus libellulid dragonfly naiads predation on YOY. One large specimen of the family Aeshnidae (*Aeshna* sp.) was placed in a tank with no cover. A young crayfish (4.2 mm carapace length) was introduced. Subsequent behaviour was recorded on video tape. The same was repeated with a large libellulid.

Results:

The aeshnid nymph stalked and devoured the young crayfish within ten minutes. When the same was repeated with a large libellulid, the little crayfish was still alive after several days. On only one occasion was a libellulid observed to grab a young crayfish, but the crayfish escaped. Even though no cover was provided and the experimental set-up was highly artificial, observations show that aeshnids are severe predators, libellulids are not.

Experiment 4. Feeding mode and stomach analysis of laboratory YOY.

Experimental procedure:

Some YOY were transferred to a petri dish and fed Chlorella and brine shrimp (Artemisia salinus). Some were transferred to a small 8 cm x 18 cm glass aquarium, were they could feed on algae growing on a small stone. Their mode of feeding was filmed. Others were kept in an algal suspension of unknown composition.

For light microscopy, the crayfish were preserved in 70% ethanol. The specimens were dehydrated through a graded ethanol series and the stomach was dissected in xylene. The stomachs were mounted in Permount on a microscope slide (Budd et al. 1978).

For scanning electron microscopy, the crayfish were fixed in glutaraldehyde for six to twelve hours. The specimen were thoroughly rinsed with distilled water. The stomachs were dissected in water and transferred into a screen basket. They were dehydrated through a graded ethanol series and prepared for the vacuum with the critical-point drying method (Humphreys et al. 1979). The dried stomachs were carefully opened, mounted on a pedestal and coated with gold. Photographs were taken using Ilford PAN F 120 film.

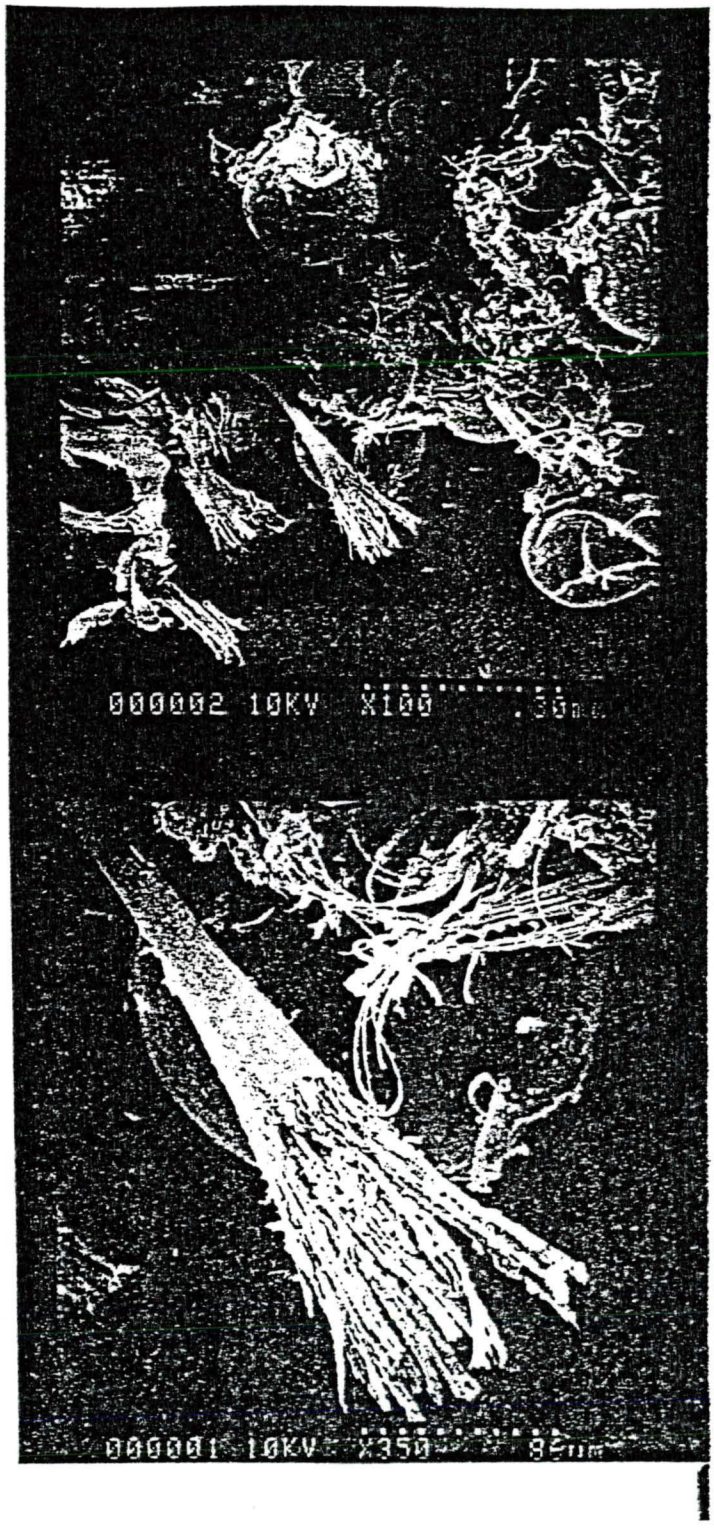
Results would determine the feasibility of stomach analysis of lake YOY.

Results:

Brine shrimp eggs and appendages could be identified under both microscopes (Figure 19). Chlorella could not be identified under either microscope, nor any other algae. A wide scale analysis was not thought to be feasible at this stage.

The young were filmed and observed to make extensive use of their tiny chelae to capture brine shrimp. They were also observed to thoroughly probe the bottom, when moving around on the algae covered stone. When feeding on soft bottom substrate they appeared to stir up material in order to ingest it by filtration, however, this could not be captured on film.

Figure 19. Scanning electron microscope photo showing brine shrimp eggs and appendages at two magnifications, upper x 100 and lower x 350.


000002 10KV X100
000001 10KV X350

DISCUSSION

Survival and growth of young crayfish depend on a number of factors such as: predators, food availability, temperature, and water chemistry. The relationship between growth and survival in the presence of predators has already been mentioned, as well as the correlation between growth and moult related mortality. This correlation makes difficult distinction between factors that enhance growth and those that decrease survival. Growth enhancing factors reduce moult related mortality by improving the overall physiological condition of the crayfish, but they also increase moult related mortality by increasing moult frequency. However, an increase in mortality may also be due to factors that adversely affect the overall physiological condition, in which case survival would be correlated with poor growth. This may be demonstrated using the fertilizer set of experiment 2 as example. During the first two experimental weeks, growth was rather poor and mortality was rather high, probably due to adverse conditions (movement of cages, turbidity, etc.). During the following six weeks, growth was excellent, but mortality remained high, indicating that the high mortality now was probably due to a high moult frequency. Whether moult related mortality is caused by cannibalism on soft-shelled individuals, or merely by mechanical or physiological moult related problems cannot be answered at this point.

In all my experiments YOY survival and YOY growth appeared unrelated, which is probably due to these opposing processes. Survival was only found to be affected by the presence of adults and accidentally introduced aeshnid dragonfly naiads, and was also exceptionally low in all bare cages. The reasons for the high mortality in the bare cages is not understood. Starvation is not likely to be a direct cause of mortality, since YOY can be starved for longer than two weeks with very low mortality (Dye and Jones 1976; personal observation). Procambarus clarki suffered from high mortality when cultured in vinyl-lined pools lacking a soil substrate, but this was found to be due to the low hardness of the water, rather than to the lack of substrate (Smitherman et al. 1967). Since all the cages were supplied with marl lake water, water hardness was not the problem. Mason (1977) observed female Pacifastacus leniusculus to make most use of shelter in lighted tanks, but also that they frequently sought shelter in darkened tanks. He ascribed this behaviour to a thigmotactic as well as a negatively phototactic response to shelter. Thigmotaxis was also described in Astacus leptodactylus (Esch.) juveniles, which consistently moved along aquarium walls, rather than in the open area (Burba 1987). In experiments with juvenile P. leniusculus, Mason (1978a) found survival to be significantly affected by substrate, being nearly twice as high on pebbles than on bare floor. Visual isolation was ruled out

since similar results were obtained in illuminated and in darkened tanks. He suggested that the presence of pebbles either reduced the probability of encounter between miss-matched individuals, or elicited some compensatory defense behaviour that served to reduce miss-match at encounter. I would suggest alternatively, that pebbles provided an appropriate thigmotactic clue, thereby reducing the frequency of encounter, which served to mitigate cannibalistic tendencies. The significant preference of YOY for cover in my experiment can also be interpreted as search for an appropriate thigmotactic cue. This behaviour exists already in second instars. When separated from the female, they formed aggregations by tightly clinging to each other (personal observation). Third instars immediately returned to their mother, or they sought shelter under other objects, forming close aggregations (Bovbjerg 1956: personal observation). Thigmotaxis is most likely an innate behaviour, which later in life may be modified in the presence of predators (Stein and Magnuson 1976; Stein 1977; Collins et al. 1983). However, the lack of shelter alone cannot explain the high mortality, since crayfish in cages containing only a mud or sand bottom substrate suffered no above average mortality. I hypothesized then, that the high mortality may be due to stress, related to solar radiation and reflection from the metal surface, a consequence of the lack of substrate and cover. However, no mortality was

experienced in eight YOY kept separately in white styrofoam containers and illuminated eight hours daily by a 60 Watt lamp for a two week period. Four of the YOY had a leaf as cover, and all were provided with food. Temperatures ranged between 20 and 26 ^{o}C. I suggest therefore, that a combination of several stresses, including lack of food, presence of congeners and solar radiation, all exerted at the same time, had a detrimental effect on survival.

Mortality of juvenile crayfish in experiment 1, 1986, averaged 25 %. In the presence of adults, mortality doubled. Assuming, that this additional mortality is a result of predation by adults on their offspring, YOY consumption by adults remains below one YOY every two days. Laboratory observations have shown that adults do not actively prey upon YOY, but readily pick up immobile individuals. Adult crayfish occasionally find a moulting individual by thoroughly probing the bottom for edible food items with their first two pairs of walking legs. Even though Morgan (1987) hypothesized cannibalism as a means of population regulation, based on a negative correlation between YOY survival and the abundance of two year old males, this hypothesis is neither substantiated by the cage experiments, nor by stomach content analysis of adults caught in the lakes. Investigations of food habits of adult Orconectes virilis

indicate as well, that this species thrives on a largely herbivorous diet (Momot 1967; Morgan, unpublished data). In contrast, stomach analysis of Orconectes propinquus, found to prey on their offspring, indicates the omnivorous diet of this species (Capelli 1980). Apart from algae and diatoms, which were found in most crayfish stomachs all year round, 60 % of the inshore crayfish contained crayfish parts (mainly from YOY) in late June, and in late September up to 90 % contained mayfly nymphs (Ephemeroptera, Heptageniidae). No such dietary shift has been thus far reported for Orconectes virilis.

Young of Orconectes virilis are not very aggressive. Fighting amongst 4 - 6 mm young was occasionally observed, but no cannibalism occurred on newly moulted individuals. Cannibalism on newly moulted, soft-shelled individuals in the cages cannot be totally ruled out, especially after a size divergence occurs. However, regarding high survival, cannibalism appears negligible. Only during the population estimate of pond YOY, when YOY were kept at extremely high densities for a short period of time, was cannibalism the rule, rather than the exception. This is in agreement with observations by Butler and Stein (1985), who found young of Orconectes sanborni (Faxon) and Orconectes rusticus (Girard) to be non-aggressive. The reason is that crayfish achieve about 50 - 60 % of their ultimate size during their first

growing season and therefore must feed rather than fight.

Supported by this convincing argument, I hypothesized, that growth is related not so much to the presence of food, but rather on the opportunity to feed on it. Predators suppress the feeding activity in crayfish (Collins 1983; Stein 1977; Stein and Magnuson 1976). It is therefore possible, that presence of predators reduced crayfish growth. If true, growth should be best in cages where food is not limiting and the feeding activity not impeded. The presence of adults might be comparable to the presence of fish predators. By moving around the cages, they forces the young crayfish to escape. Not only does this disturb the feeding activity, but force extra energy expenditure for each flight. Growth was indeed poor in all cages containing adults, but exceptionally so in those cages containing the more active males. In addition, a direct competition for food between adults and young could also be involved.

The better growth that results at a low density may also partially be due to fewer disturbing encounters amongst YOY, but food is surely of greater importance.

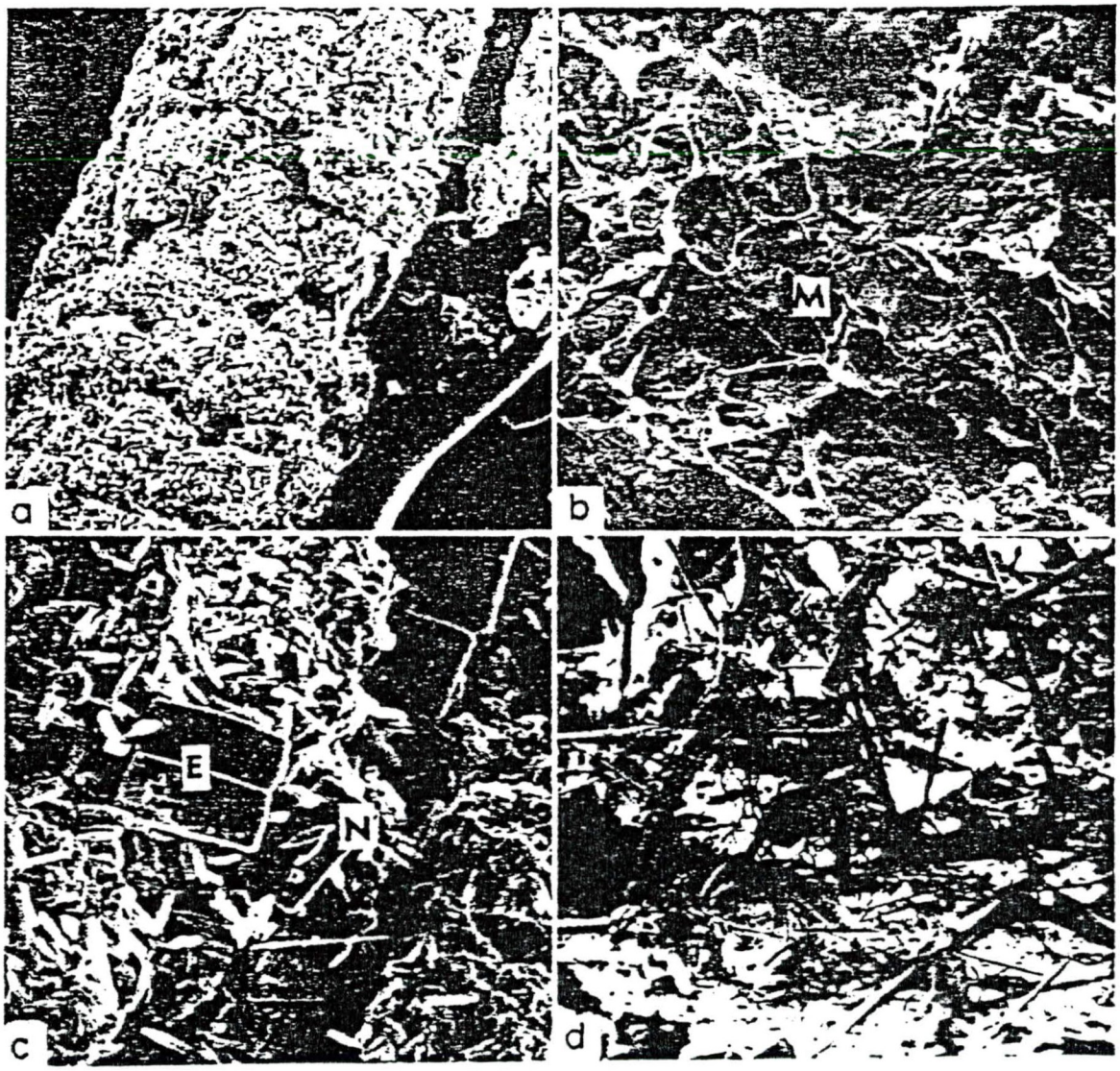
Experimental crayfish grew, with a few exceptions, much better on mud than on sand. Sapropel, the black organic mud used in these experiments, is deposited under anaerobic, reducing

conditions. Brought into aerobic condition, this mud forms an ideal substrate for colonization by decomposing microorganisms. On sand, which is much lower in nutrients, carrying capacity for those microorganisms is substantially lower. For example, bacteria, which increase about three to five orders in magnitude from the water to the surface sediments, are most numerous in littoral zones with a well-developed macrophyte community (Wetzel 1983). Protozoa are known to develope large population densities on aerobic, organic-rich sediments, where they feed on algae, bacteria, particulate detritus, and other protozoa (Wetzel 1983). The existence of a well developed mycoflora ensuring the breakdown of detritus is well documented (Wetzel 1983). Sediments are also colonized by numerous other organisms, including nematodes, oligochaetes, ostracodes and amphipods. These organisms, including their minute eggs and offspring, may be utilized as food by young crayfish, in search of a protein rich diet for optimum growth (Jones and Momot 1981). Numerous studies demonstrate, that crustaceans can thrive on a microflora diet. Gammarus pseudolimnaeus (Bousfield) and Gammarus minus (Say) achieved the best survival and highest assimilation efficiency on a diet composed of fungus enriched leaves and on mycelia from various fungi (Baerlocher and Kendrick 1975; Kostalos and Seymour 1976). Hyalella azteca (Saussure) ingesting epiphytic growth on Chara achieved very high assimilation

efficiencies (Hargrave 1970a). Most of the rich epiphytic microflora encrusting the Chara consists of diatoms and bluegreen algae (Figure 20) (Allanson 1973). Adult crayfish would benefit from this protein-rich microflora by feeding on macrophytes.

To my knowledge, nobody has studied the importance of microflora to the diet of macrophyte consuming crayfish. Numerous reports however exist, emphasizing the importance of allochthonous and autochthonous plant material (Momot 1984; Momot 1981; Caine 1975; Flint and Goldman 1975; Prins 1968). When submerged macrophytes are scarce, as is the case in Lake Tahoe, a large crayfish community still thrives by relying substantially on the periphyton of the littoral zone (Flint and Goldman 1975). An analysis of the microflora of the cage substrates and the fine mesh of the cages, which also served as substrate for periphyton, has not been done. However, cages containing Chara and leaf-litter harbor high densities of amphipods, especially gammarids (Gammarus sp.), indicative of the presence of a rich microflora. The positive growth response of crayfish to mud, as well as to the experimental cover types, Chara and leaf-litter, may be attributed to the richer "Aufwuchs" community, maybe as well as the presence of amphipod eggs and offspring as possible supplemental protein source.

Figure 20. The structure of the periphyton on the macro-algae *Chara* sp. from Wytham pond, Oxford. (a) x 75 and (d) x 250, upper storey appearance. (b) x 300, calcite surface after sonication showing mucoid sheets (M). (c) x 300, adnate diatom association upon calcite areas (E, *Eunotia arcus*; N, naviculoids). (Allanson 1973)


a
b
M
E
N
c
d

In experiment 2, 1987, crayfish grew slightly slower in cages in which Chara was substituted by a plastic plant, than in cages lacking cover. This is surprising, since cover supposedly reduces stress, which should in turn enhance growth. Probably, juvenile crayfish are faced with a trade-off between food acquisition and shelter occupancy. Since the plastic plants were placed in the cages the same day as the YOY were stocked, it initially did not support any periphyton growth. YOY hiding in the plant could therefore not feed. By the end of the summer, crayfish growth in these cages was slightly better than in cages without cover, indicating that periphyton had grown on the plastic plant as food source for hiding crayfish.

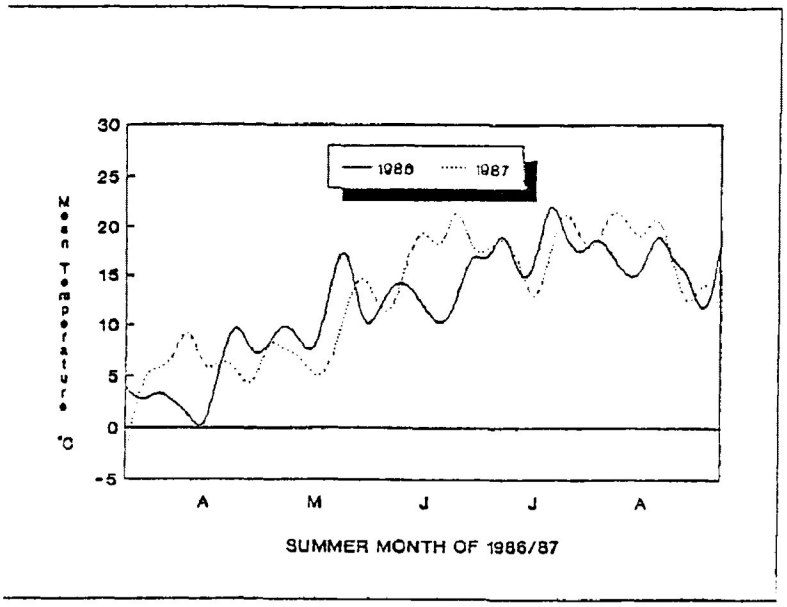
Substrate-choice experiments demonstrate, that crustaceans are quite capable of selecting sediments containing a viable microflora (Marzolf 1965; Hargrave 1970b). Prerequisite for this capability is the presence of chemoreceptors, which in crayfish are located on the antennular inner flagellum and on the dactyls of the first two pairs of walking legs (Ameyaw-Akumfi 1977). This agrees with my observations that crayfish, adults and young, thoroughly probe the substrate with their first two pairs of walking legs, most likely in search of agreeable food items. Most likely juvenile crayfish select the mud substrate for its greater food content, as well as for its darker colour.

Experimental results are rarely clear-cut. In experiment 1, 1987, no growth difference existed at low density between crayfish grown on Chara and those having no cover. Also, totally contrary to the 1986 results, YOY grew better on sand. These contrary results, however, refer only to crayfish at low densities during the first two experimental weeks. At high density YOY grew better on mud and with Chara, and by the end of the summer results corresponded to the 1986 findings. A relationship to food availability therefore appears very plausible. The productivity of an "Aufwuchs" community is increased at higher temperatures and light conditions (Wetzel 1983). Two weeks prior to the experiments, i.e. while the cages were placed in the lake to allow for colonization by lake microorganisms, the mean air temperature was indeed 3.5 ^{o}C higher in 1987 than in 1986. Similarly, during the two weeks experimental period itself, the mean air temperature was 1.7 ^{o}C higher in 1987 (Figure 21). Therefore, enough food must have existed on sand, making food no longer a limiting factor. I did not conduct experiments to determine why YOY did not grow equally well on both substrates under these circumstances. A possible explanation can be found in the different consistency of the substrates regarding the energy required for locomotion. Locomotion on mud is rendered difficult for small crayfish by the softness of the substrate. Also, extra energy is required to

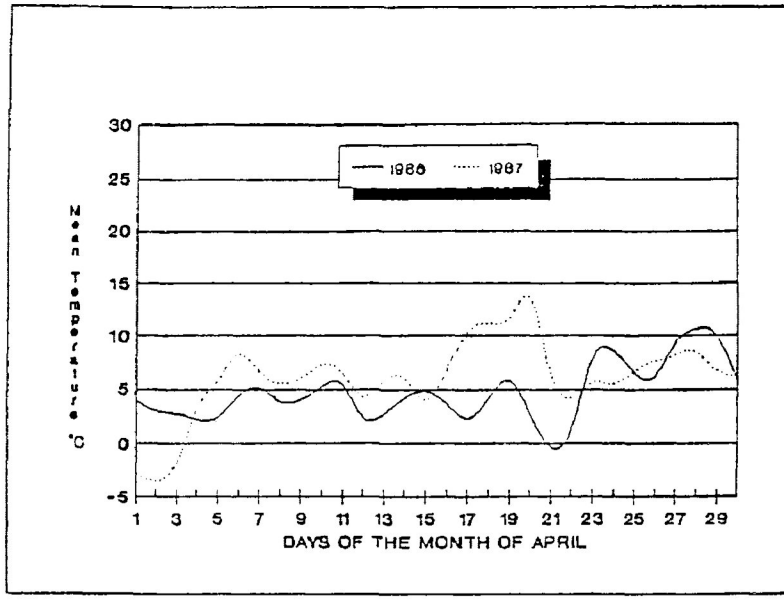
prevent sinking. Even though food supply would have been adequate, the extra energy required to navigate through soft substrate might have been sufficient to cause a growth difference.

Comparison of growth in the low density cages of experiments 1 and 2 demonstrates the indirect importance of temperature, by causing differential production of the "Aufwuchs" community influencing growth of YOY crayfish. Both, mean air and measured water temperatures were lower in 1986, than in 1987 (Table 34; Figure 21). Accordingly, YOY did not grow as well, perhaps in response to the lower microflora production. Average carapace length in the low density cages of experiment 1 in 1986 was only 7.89 mm, compared to 8.47 mm in 1987. However, average carapace length in experiment 2, 1987, during which all cages were stocked at a low density, was only 7.68 mm, i.e. even lower than in 1986. This can be explained through differences in the experimental arrangement. In experiment 1, all cages were placed along the shore in direct contact with the lake bottom. In experiment 2, cages were suspended from stands, approximately 80 cm above the lake bottom (20 cm in the deep set). Although members of the benthic microflora can occasionally be found in the phytoplankton (Wetzel 1983), this particular arrangement makes initial colonization of the suspended cages very difficult. Once initial colonization occurred, the microflora responded positively to

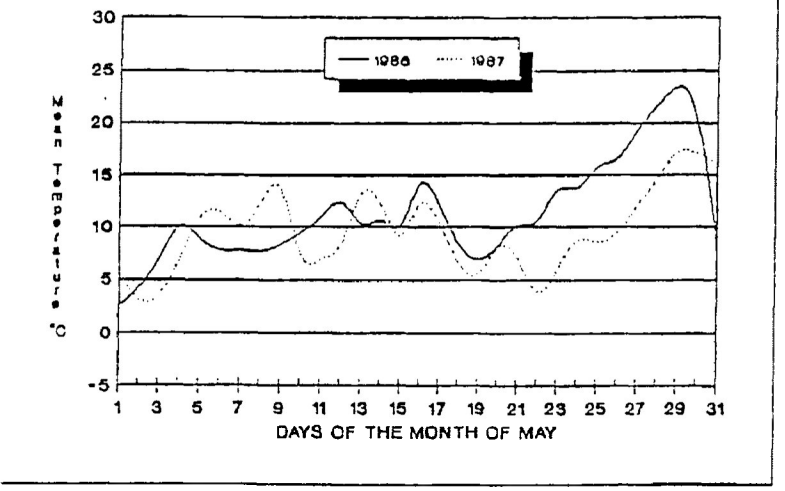
Figure 21. Mean daily air temperatures at Thunder Bay, Ontario, for the months April to August after records from the Ministry of Environment. (Anonymous 1986 and 1987)



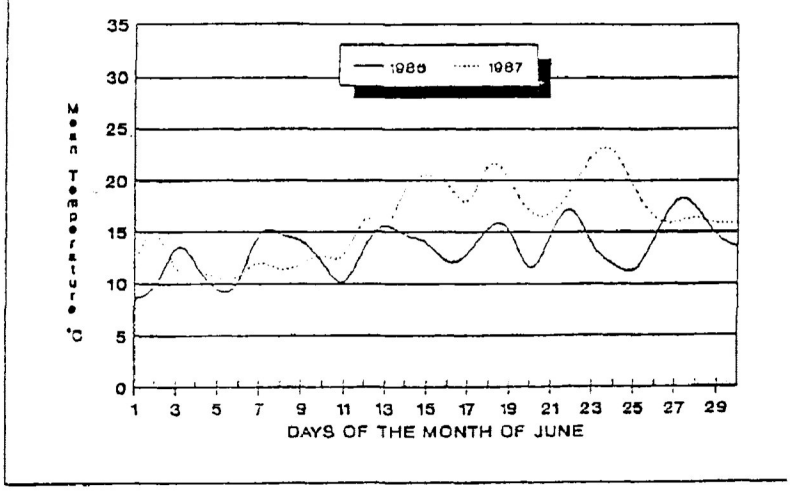
SUMMER MONTH OF 1986/87



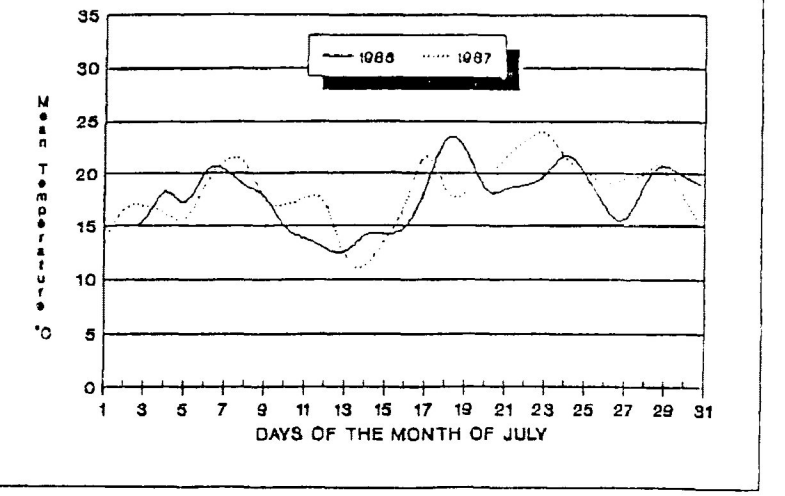
DAYS OF THE MONTH OF APRIL



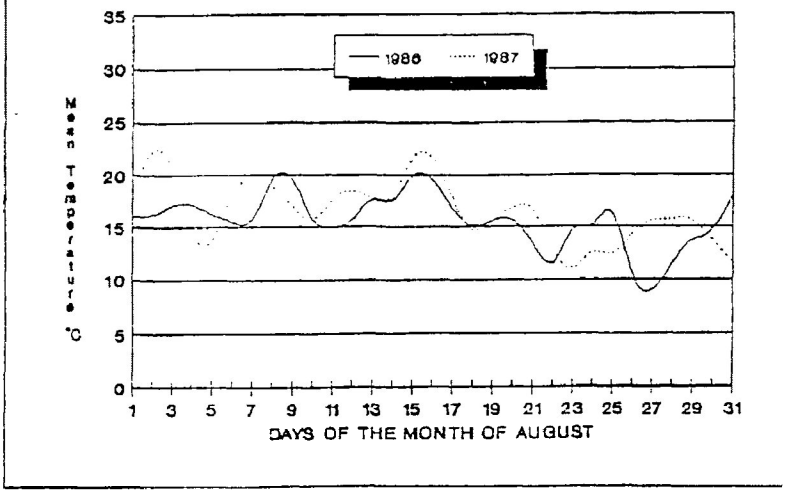
DAYS OF THE MONTH OF MAY



DAYS OF THE MONTH OF JUNE



DAYS OF THE MONTH OF JULY



DAYS OF THE MONTH OF AUGUST

fertilization. This produced an even better growth in the suspended sand/no cover cages of experiment 2, than in the sand/no cover cages of experiment 1.

Growth differences discussed so far referred to mean carapace length values in respect to the experimental set-up. Even though often highly significant, these differences are small compared to growth differences encountered between individual YOY within the same cage. Whereas the mean values vary seldom more than 1 mm between treatments, differences encountered within cages are mostly above 3 mm, and in the extreme reach 5 mm. How can these differences be explained? Unfortunately, individual crayfish could not be marked so that size, individual growth and interactions between individuals could not be assessed. Therefore, it is not known whether these growth differences develop after hatching, or prior to it. Mason (1978b) found that although larger, heavier eggs resulted in heavier second instars, no relationship was evident between egg-size and subsequent growth and survival during thirty days of culture. Females from Dock Lake do produce significantly larger eggs than females from Shallow Lake, most likely in response to reduced competition in Dock Lake due to heavy exploitation (Morgan 1987). However, whether these differences in egg size are indeed a determinatant for later growth seems doubtful in light of Mason's findings. It certainly does not explain a size difference of such magnitude.

A potential source of early size determination may occur at the time of hatching, as well as prevalent biotic and abiotic conditions present at that time. It takes several days for the brood of the same female to hatch, and hatching of YOY from all females present at one location takes place over several weeks. As soon as the yolk supply is exhausted, young are forced to feed exogenously. If temperature and food supply are favorable, the first young to hatch moult first, thereby gaining an initial growth advantage. Momot (1986) and Jones and Momot (1981) pointed out the importance of size and quality of the nursery habitat to the survival of YOY. Bovbjerg (1964) demonstrated density-related dispersal in crayfish, as a result of aggression. In juvenile crayfish dispersal begins with an avoidance reaction which gradually develops into aggressive behaviour (Bovbjerg 1956). This avoidance reaction or spacing behaviour begins immediately after the young become independent of the female. Evidently, YOY are forced to disperse at a very early life history stage. Should the carrying capacity of the nursery area be exceeded, surplus young would be forced into lesser quality habitats, were they may die from either predation or an accumulation of numerous stresses.

In the cages, the situation is somewhat different. Inferior young cannot be driven away. In the enclosed environment, they are subjected to aggression from larger individuals, since

dominance in crayfish is size-related (Bovbjerg 1956). This harassment, as well as disturbance by adult crayfish (experiment 5) and the presence of predators, may be sufficient to explain any growth differences.

Momot (1986) attributed the better survival of YOY in Dock Lake to the presence of beds of the emergent sedge, Carex aquatilis var. substricta. These beds were denser, wider, and over firmer substrate in this lake than in nearby Shallow Lake. He and other researchers found, that the availability of firm substrates is essential for good crayfish survival. This is in contrast to the outcome of my experiments, in which survival was not influenced by substrate. However, the softer mud substrate did have a positive effect on growth. How could this be explained? The presence of a mud substrate is often correlated with stagnant, oxygen-poor water. Orconectes virilis is very sensitive to oxygen depletion (Bovbjerg 1970). Low oxygen levels may result in high mortalities. The cages, however, were located over firm substrates in water with a sufficient oxygen supply. Periphyton growth is also suppressed on a soft mud substrate. In the cages however, periphyton could grow on the screen. In addition, periphyton was also likely stimulated in the mud cages by the greater nutrient release. No experiments have been conducted, testing for substrate preferences in larger YOY.

Should these preferences change, YOY could always utilize the screen as a firm substrate.

Not enough is known concerning the food requirements and mode of feeding of juvenile crayfish, let alone newly released instars. Crayfish are most often described as generalized feeders, consuming a wide variety of dead and live plant materials, detritus and animal matter (Capelli 1980; Crocker and Barr 1968; Prins 1968).

Investigations of the setal armature has, however, shown that both, adult and fourth instar, have the structural apparatus for filter feeding (Budd et al. 1978; Thomas 1979). Laboratory feeding experiments showed crayfish fry fed on solid diets had poor survival, whereas those fed a rich algal suspension had good survival. This led to the opinion that young crayfish are filter feeders (Budd et al. 1978; Budd et al. 1979; Thomas 1979). These researchers also declare that newly released crayfish cannot effectively capture food with their chelae, since the chelae are too delicate in structure, not yet allowing for firm muscle attachment (Jahromi and Atwood 1977). However, even second instars are already capable of clinging to the female using their tiny chelae (Andrews 1907; Kossakowski 1966; Crocker and Barr 1968; Cukerzis 1986). They are also known to consume their egg capsule and their stage one exuviae (Mason 1978b). From personal observations I know that young crayfish

are quite capable of using their chelae to capture food (brine shrimp). It appears, that young crayfish use their tiny chelae very much like adults use their chelate walking legs, i.e. for the prehension of food (Thomas 1979). This is also believable in view of the relative proportions of the chelae and the chelate walking legs in adults and young (Bovbjerg 1956). However, until definite evidence has been produced, one can only surmise the relative importance of filter feeding versus active food capture in very young crayfish. A filter feeding apparatus would be of great benefit in the presence of a dense plankton suspension. In most fast flowing rivers and clear lakes, however, it is doubtful whether crayfish could secure sufficient nutrients to sustain growth through filter feeding. In water bodies that are poor in plankton juvenile crayfish likely rely on both, periphyton, as well as all minute animal matter that can be ingested, but might switch to filter-feeding in the presence of a rich plankton bloom.

In Powell's Lakes, plankton production is low, even though the lakes are highly eutrophic. Food abundance is not likely the limiting factor, since dense beds of Chara and other aquatic plants are abundant (Momot 1978). Information on survival of YOY in Dock and Shallow Lake is obtained from spring and summer estimates. The first day's catch is measured and the sex ratio determined, to obtain the size distribution. The initial number

of YOY in the ponds is estimated by pleopod egg counts, multiplied by the number of mature females. Differential egg production by female year classes has been taken into account. The spring estimate may be somewhat high, due to losses of eggs and attached hatchlings. Females are supposedly very seclusive while carrying their eggs and hatching their young (Mason 1977; Stein 1977; Payne 1978). However, many berried females, as well as females with attached young were caught in traps, a definite indication of their activity. Mortality prior to hatching may be as high as 80 - 90 % in Astacus (Strempl 1975) and as high as 40 - 50 % in Pacifastacus (Mason 1975). Losses in Orconectes virilis are not as high, but must not be ignored. Often, less than 1 % of the initial number of hatchlings survive until the summer estimate (Momot and Gowing 1975), which is obtained by mark and recapture (Momot and Gowing 1975).

What factors are responsible for this high mortality rate? Experimental YOY suffered a 50 % mortality until the end of the summer. This mortality was due to moulting, and possibly cannibalism and further unknown stresses. Under natural conditions, a certain additional percentage will die from predation. The only known predators in the lakes are aeshnid dragonfly naiads. Even if the fish present in these lakes would account for some mortality as well, predation does not appear to be the main cause of mortality. Momot and Gowing (1977) believe

that crayfish eaten by fish and dragonfly nymphs would die anyway. But from what? Oxygen depletion in large areas of the lake may play an important role. Oxygen depletion, related to microbial decomposition of organic sediments is a well known problem (Poole et al. 1977; Dupree and Huner 1984). Momot (1984) suggested, that this results in the formation of physically unstable and chemically detrimental microhabitats for juvenile crayfish. Naturally, the higher the density of YOY crayfish, the more intense becomes the competition for suitable habitat.

In deeper lakes, crayfish populations are stratified. After hatching, YOY are found in the shallowest water, while females start moving into deep water. Males occupy the intermediate zone (Momot 1967).

In Dock and Shallow Lake such a stratification is not possible due to the shallow basin and oxygen deficiency in lower depths. In respect to nursery habitat, the two lakes are distinctly different. The shoreline in Dock Lake slopes gradually. As a result, the lake has more shallows and a larger beds of Carex. Shallow Lake has little suitable nursery habitat. The shoreline in most parts is very steep, with water depths being immediately 30 cm and above. YOY are therefore forced early to compete with adult crayfish for suitable habitat and food. This may explain the strong inverse relationship between YOY abundance and density of two year old males in this lake.

Apart from predation, a certain number of crayfish die from disease. Crayfish are hosts to a number of parasites, such as bacteria, fungi, protozoa and worms (Johnson 1977). Records of Thelohania sp. infections, the microsporidian parasite that had infected a considerable number of experimental YOY in 1987, exist for decapod crustaceans from all over the world (Graham and France 1986; McGriff and Modin 1983; Mazylis 1978; Cossin 1972; Iverson and Kelly 1976). According to Graham and France (1986),

> most researchers accept the "typical microsporidian plan" of Kudo (1924) that no intermediate hosts exist and that disease transmission occurs when the recipient host consumes infected muscle of a dead animal. Once ingested, the infective spore extrudes a polar filament in reaction to the host's digestive juices ( ). Amoeboid sporoplasm then emerges through the polar filament, penetrates the intestinal epithelium, and is transported to the muscle fibres via the hemocoele. Infection eventually leads to death of the host, release of non-mobile spores, and repeat of the life cycle.

Mazylis (1978) successfully infected Astacus astacus by injecting a homogenate made from diseased animals into the stomach or directly into the abdominal tissue of the host. Symptoms of the disease occurred 5-6 months after such treatment. However, an increasing number of failures to transmit Thelohania spores directly through feeding, and successful transmission after spores were conditioned by passage through a fish gut, indicate, that spores may require a secondary host to complete their life cycle (Graham and France 1986; Iverson and Kelly 1976).

Altogether 77 infected YOY were recovered from the cages, with no obvious correlation to the experimental set-up, i.e. a few were found in nearly all cages. The infection could not have started by YOY feeding on dead infected crayfish, since they were only in contact with supposedly healthy congeners and their mothers. Contamination of cages by fish feces is equally unlikely, since the ichthyofauna of the lakes is rather limited, consisting mainly of minnows (Cyprinidae) and stunted white sucker (Catostomus commersoni (Lacepede)), which are not known to prey on crayfish. Also, if fish feces were involved, the occurrence of Thelohania infection should be higher in the lakes, since fish were excluded from the cages. However, only the occasional diseased YOY was found in the lakes. Whether this low occurence is due to lower infection rates in the lakes, or merely to higher mortality and susceptibility to predation under natural conditions, is not known.

The 77 diseased young may represent the brood of one single female. Since the young were thoroughly mixed before being placed into the cages, the occurrence of this disease in YOY from so many cages may be explained by transmission of spores from one infected female to her offspring. However, nowhere in the literature could I find records of this microsporidian being transferred directly from the mother to the young. In contrary, no mating occurred in diseased Astacus astacus, and diseased

females, fertilized by a healthy male, did not lay eggs (Mazylis 1978). In infected shrimps (Crangon sp.), ovaries did not develop beyond a very early stage (Breed and Olson 1977). In Orconectes virilis, I did observe conjugation between diseased animals, but whether this would have resulted in viable offspring is not known, since all infected animals were destroyed. Also, I found evidence, that deviations from the typical "microsporidian plan" exist. Spores of Nosema bombycis (Naegli), a microsporidian infecting the silkworm (Bombyx mori), are normally transmitted through ingestion by silkworm larvae (Marquardt and Demaree 1985). In cases of heavy infection, larval silkworm die or are unable to produce a cocoon (silkworm disease). In cases of light infection, however, the insect may complete its life cycle, transmitting spores to the offspring through the egg.

More experimental work is necessary to answer the question of Thelohania transmission. The knowledge of the ways by which it is would certainly be of great benefit to crustacean culture world-wide.

The aquaculture potential of freshwater crayfish is receiving an increasing commercial interest (Stechey and Somers 1983). Problems encountered in almost all culture systems are disease, predation, oxygen deficiency and particularly in crayfish, cannibalism. Suitability for culture therefore depends

on disease resistance, susceptibility to predation, tolerance to low oxygen level and interspecific aggression. Interspecific aggression is high in all crayfish species, but losses can be reduced by providing shelter and by stocking equal-sized individuals. Growth rates, final size and meat yields also of great importance. Recently, Stechey and Somers (1983) have examined the suitability of four Ontario crayfish for aquaculture. They favoured Orconectes immunis (Hagen), a pond-dwelling species, based on its greater tolerance to low dissolved oxygen and temperature fluctuations.

CONCLUSION

Growth in the enclosures as well as in the lakes is related to food availability and feeding opportunity. Availability of food, in particular periphyton, is largely temperature and nutrient dependent, while feeding opportunity is associated with the presence of predators as well as congeners.

In the enclosures, mortality was apparently moult-related. Moulting success seems to depend on the physiological state of the individual, i.e. on nutrition and stress.

In the lakes, moulting, as well as adverse chemical and physical conditions, were the factors most responsible for the mortality amongst juvenile Orconectes virilis. Sufficient oxygen supply appears to be of utmost importance.

For culture, equal-sized young should be stocked on a substrate providing numerous shelters. Great care must be taken to find a balance between food supply and oxygen consumption, since oxygen deficiency is absolutely detrimental.

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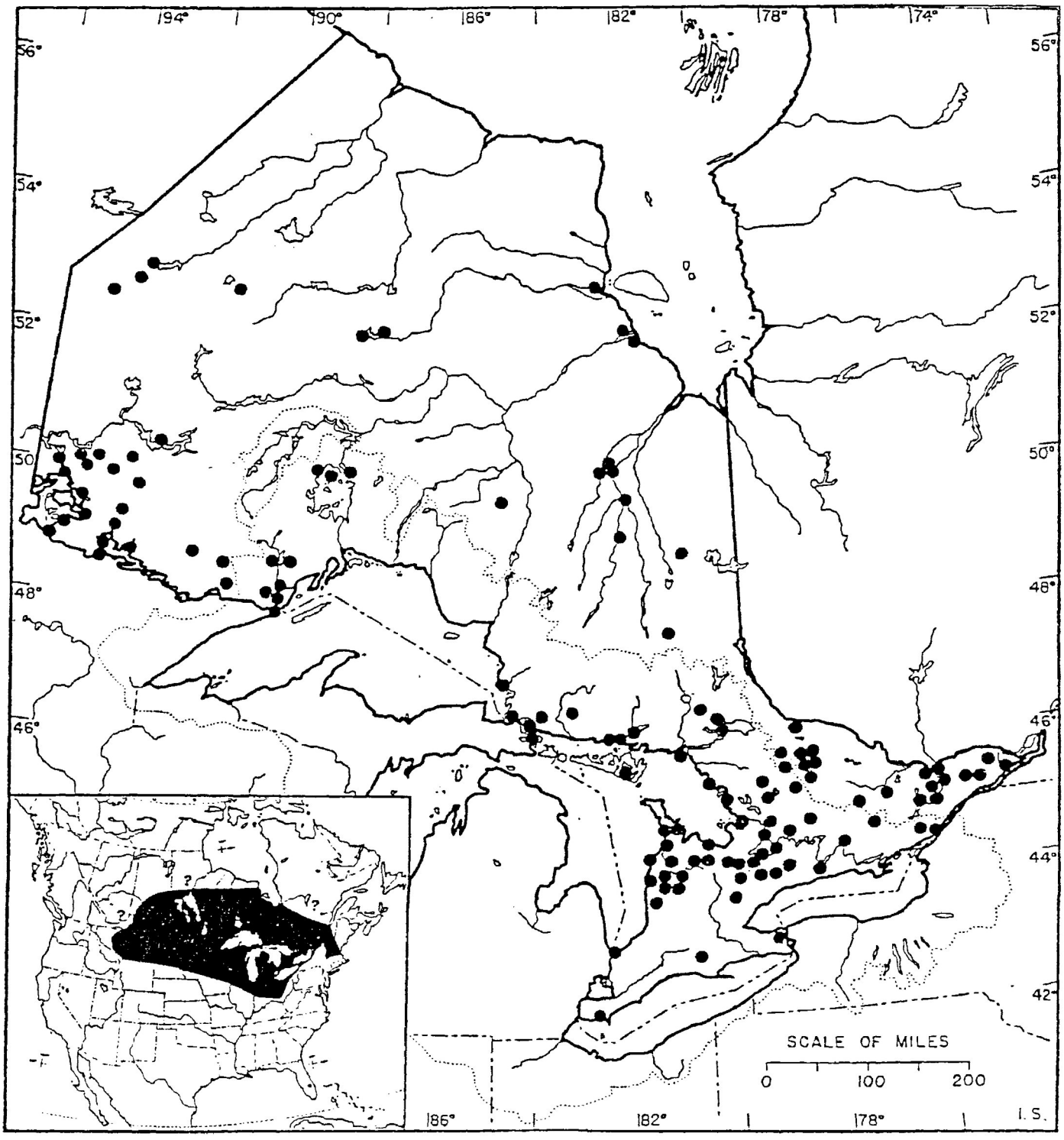
APPENDIX I. Distribution of Orconectes virilis in Ontario. Inset shows total range of the species (Crocker and Barr 1968).



APPENDIX II. Growth and survival of YOY per individual cage, Experiment 1, 1986.

CAGE NUMBER	INITIAL DENSITY	SUBSTRATE	COVER	MEAN CARAPACE LENGTH (mm)	+/- SE	SURVIVORS	% SURVIVORS
1	10	SAND	LEAF-LITTER	8.06	+/- 0.11	8	80.0
2	10	SAND	LEAF-LITTER	8.46	+/- 0.17	10	100.0
3	10	SAND	LEAF-LITTER	7.38	+/- 0.32	9	90.0
*4	10	SAND	CHARA SP.	7.61	+/- 0.34	5	50.0
*5	10	SAND	CHARA SP.	8.01	+/- 0.52	5	50.0
6	10	SAND	CHARA SP.	8.31	+/- 0.17	7	70.0
7	10	SAND	NONE	5.82	+/- 0.29	6	60.0
8	10	SAND	NONE	7.10	+/- 0.43	9	90.0
9	10	SAND	NONE	8.06	+/- 0.19	8	80.0
10	10	MUD	LEAF-LITTER	7.95	+/- 0.26	7	70.0
11	10	MUD	LEAF-LITTER	8.68	+/- 0.12	7	70.0
12	10	MUD	LEAF-LITTER	8.42	+/- 0.15	9	90.0
13	10	MUD	CHARA SP.	7.67	+/- 0.28	10	100.0
*14	10	MUD	CHARA SP.	7.78	+/- 0.25	4	40.0
*15	10	MUD	CHARA SP.	7.95	+/- 0.00	1	10.0
16	10	MUD	NONE	8.23	+/- 0.18	6	60.0
17	10	MUD	NONE	7.67	+/- 0.42	6	60.0
18	10	MUD	NONE	7.19	+/- 0.39	9	90.0
19	40	MUD	LEAF-LITTER	7.84	+/- 0.19	16	40.0
20	40	MUD	LEAF-LITTER	7.88	+/- 0.11	36	90.0
21	40	MUD	LEAF-LITTER	7.82	+/- 0.14	27	67.5
22	40	MUD	CHARA SP.	7.92	+/- 0.03	31	77.5
23	40	MUD	CHARA SP.	8.09	+/- 0.06	25	62.5
24	40	MUD	CHARA SP.				
25	40	MUD	NONE	7.45	+/- 0.28	24	60.0
26	40	MUD	NONE	7.16	+/- 0.20	30	75.0
27	40	MUD	NONE	7.10	+/- 0.25	24	60.0
28	40	SAND	LEAF-LITTER	7.90	+/- 0.07	37	92.5
29	40	SAND	LEAF-LITTER	7.76	+/- 0.12	35	87.5
30	40	SAND	LEAF-LITTER	7.73	+/- 0.08	39	97.5
*31	40	SAND	CHARA SP.	7.27	+/- 0.12	15	37.5
32	40	SAND	CHARA SP.	7.17	+/- 0.28	23	57.5
33	40	SAND	CHARA SP.			30	75.0
34	40	SAND	NONE	7.30	+/- 0.17	30	75.0
35	40	SAND	NONE	7.07	+/- 0.22	33	82.5
36	40	SAND	NONE	7.03	+/- 0.14	37	92.5

* Cages containing large dragonfly naiads.

APPENDIX III. Growth and survival of YOY per individual cage, Experiment 1, 1987.

CAGE NUMBER	INITIAL DENSITY	SUBSTRATE	COVER	MEAN CARAPACE LENGTH (mm) +/- SE	SURVIVORS	SURVIVO
49	40	SAND	CHARA SP.	7.36 +/- 0.12	39	97.5
50	40	SAND	CHARA SP.	7.95 +/- 0.22	35	87.5
51	40	SAND	CHARA SP.	7.49 +/- 0.19	37	92.5
52	10	SAND	CHARA SP.	9.10 +/- 0.43	9	90.0
53	10	SAND	CHARA SP.	8.68 +/- 0.35	9	90.0
54	10	SAND	CHARA SP.	8.74 +/- 0.43	9	90.0
61	40	SAND	NONE	6.79 +/- 0.20	31	77.5
62	40	SAND	NONE	7.36 +/- 0.19	32	80.0
63	40	SAND	NONE	7.06 +/- 0.17	34	85.0
55	10	SAND	NONE	8.30 +/- 0.32	8	80.0
56	10	SAND	NONE	8.66 +/- 0.35	9	90.0
57	10	SAND	NONE	9.28 +/- 0.33	9	90.0
*58	3	SAND	NONE	8.85 +/- 0.45	2	66.7
59	3	SAND	NONE	7.55 +/- 0.05	2	66.7
*60	3	SAND	NONE	9.60 +/- 0.60	3	100.0
64	10	MUD	NONE	8.11 +/- 0.31	10	100.0
65	10	MUD	NONE	7.80 +/- 0.17	10	100.0
66	10	MUD	NONE	8.16 +/- 2.43	10	100.0
67	10	MUD	CHARA SP.	8.41 +/- 0.41	9	90.0
68	10	MUD	CHARA SP.	8.05 +/- 0.34	10	100.0
69	10	MUD	CHARA SP.	8.47 +/- 0.25	10	100.0
70	40	MUD	CHARA SP.	7.80 +/- 0.24	35	87.5
71	40	MUD	CHARA SP.	7.46 +/- 0.21	39	97.5
72	40	MUD	CHARA SP.	8.03 +/- 0.15	35	87.5

* All YOY are from pond females.

APPENDIX IV. Growth and survival of YOY per individual cage, Experiment 2, 1987.

CAGE NUMBER	TREATMENT	INITIAL DENSITY	SUBSTRATE	COVER	MEAN CARAPACE LENGTH (mm) +/- SE	SURVIVORS	% SURVIVORS
13*	DEEP	10	SAND	LEAF-LITTER	8.63 +/- 0.72	8	80.0
14*	DEEP	10	SAND	LEAF-LITTER	9.10 +/- 0.47	8	80.0
15*	DEEP	10	SAND	LEAF-LITTER	7.14 +/- 0.67	7	70.0
16*	DEEP	10	SAND	ARTIF.PLANT	7.51 +/- 0.47	8	80.0
17*	DEEP	10	SAND	ARTIF.PLANT	7.74 +/- 0.36	5	50.0
18*	DEEP	10	SAND	ARTIF.PLANT	7.23 +/- 0.49	8	80.0
19*	DEEP	10	SAND	NONE	7.68 +/- 0.24	8	80.0
20*	DEEP	10	SAND	NONE	7.70 +/- 0.41	7	70.0
21*	DEEP	10	SAND	NONE	8.40 +/- 1.41	3	30.0
22	CONTROL	10	SAND	LEAF-LITTER	8.97 +/- 0.42	9	90.0
23	CONTROL	10	SAND	LEAF-LITTER	8.11 +/- 0.43	8	80.0
24	CONTROL	10	SAND	LEAF-LITTER	7.50 +/- 0.45	5	50.0
25	CONTROL	10	SAND	ARTIF.PLANT	6.95 +/- 0.63	8	80.0
26	CONTROL	10	SAND	ARTIF.PLANT	7.03 +/- 0.57	10	100.0
27*	CONTROL	10	SAND	ARTIF.PLANT	8.20 +/- 0.39	7	70.0
28*	CONTROL	10	SAND	NONE	7.48 +/- 0.65	9	90.0
29*	CONTROL	10	SAND	NONE	7.66 +/- 0.34	10	100.0
30*	CONTROL	10	SAND	NONE	8.60 +/- 0.37	9	90.0
31	FOOD	10	SAND	LEAF-LITTER	8.07 +/- 0.71	7	70.0
32	FOOD	10	SAND	LEAF-LITTER	7.27 +/- 0.43	9	90.0
33	FOOD	10	SAND	LEAF-LITTER	7.83 +/- 0.35	7	70.0
34	FOOD	10	SAND	ARTIF.PLANT	8.10 +/- 0.44	8	80.0
35	FOOD	10	SAND	ARTIF.PLANT	7.64 +/- 0.54	8	80.0
36	FOOD	10	SAND	ARTIF.PLANT	7.95 +/- 0.38	10	100.0
37	FOOD	10	SAND	NONE		9	90.0
38	FOOD	10	SAND	NONE	7.86 +/- 0.34	8	80.0
39	FOOD	10	SAND	NONE	8.64 +/- 0.51	7	70.0
40	FERTILIZER	10	SAND	NONE	7.34 +/- 0.27	8	80.0
41	FERTILIZER	10	SAND	NONE	7.61 +/- 0.39	7	70.0
42	FERTILIZER	10	SAND	NONE	6.84 +/- 0.50	7	70.0
43	FERTILIZER	10	SAND	ARTIF.PLANT	7.80 +/- 0.41	6	60.0
44	FERTILIZER	10	SAND	ARTIF.PLANT	6.93 +/- 0.46	10	100.0
45	FERTILIZER	10	SAND	LEAF-LITTER	6.86 +/- 0.49	5	50.0
46	FERTILIZER	10	SAND	LEAF-LITTER	6.78 +/- 0.39	6	60.0
47	FERTILIZER	10	SAND	LEAF-LITTER	6.47 +/- 0.43	6	60.0
48	FERTILIZER	10	SAND	ARTIF.PLANT	6.90 +/- 0.48	6	60.0

* All YOY are from pond females.

APPENDIX V. Growth and survival of YOY per individual cage, Experiments 3 and 4, 1986.

CAGE NUMBER	INITIAL DENSITY	LAKE	FOOD	MEAN CARAPACE LENGTH (mm) +/- SE	SURVIVORS	% SURVIVORS
40	40	DOCK L.	NO	7.10 +/- 0.00	3	7.5
41	40	DOCK L.	NO	6.68 +/- 0.42	2	5.0
42	40	DOCK L.	NO	5.84 +/- 0.54	4	10.0
37	40	DOCK L.	YES	5.28 +/- 0.25	6	15.0
38	40	DOCK L.	YES	5.58 +/- 0.31	5	12.5
39	40	DOCK L.	YES		9	22.5
43	40	DOCK L.	YES	7.10 +/- 0.00	5	12.5
44	40	DOCK L.	YES	6.98 +/- 0.12	7	17.5
45	40	DOCK L.	YES	5.70 +/- 0.74	3	7.5
46	10	DOCK L.	YES	4.60 +/- 0.00	1	10.0
47	10	DOCK L.	YES	-	0	0.0
48	10	DOCK L.	YES	5.40 +/- 0.00	1	10.0
49	10	SHALLOW L.	YES	-	0	0.0
50	10	SHALLOW L.	YES	4.87 +/- 0.27	3	30.0
51	10	SHALLOW L.	YES	-	0	0.0
52	40	SHALLOW L.	YES	5.42 +/- 0.48	3	7.5
53	40	SHALLOW L.	YES	4.76 +/- 0.16	5	12.5
54	40	SHALLOW L.	YES	4.60 +/- 0.00	2	5.0

APPENDIX VI. Growth and survival of YOY per individual cage, Experiment 5, 1986.

CAGE NUMBER	INITIAL DENSITY	ADULT	COVER	MEAN CARAPACE LENGTH +/- SE		SUR	% SUR
55	25	MALE	LEAF-LITTER	6.91	+/- 0.33	13	52.0
56	25	MALE	LEAF-LITTER	6.82	+/- 0.22	18	72.0
57	25	MALE	LEAF-LITTER	6.48	+/- 0.29	19	76.0
58	25	MALE	CHARA SP.	6.64	+/- 0.37	11	44.0
59	25	MALE	CHARA SP.	6.25	+/- 0.00	1	4.0
60	25	MALE	CHARA SP.	7.04	+/- 0.27	14	56.0
61	25	MALE	NONE	6.43	+/- 0.33	10	40.0
62	25	MALE	NONE	7.04	+/- 0.19	15	60.0
63	25	MALE	NONE	6.73	+/- 0.40	9	36.0
76	25	FEMALE	NONE	7.55	+/- 0.24	17	68.0
77	25	FEMALE	NONE	7.15	+/- 0.26	17	68.0
78	25	FEMALE	NONE	7.10	+/- 0.49	6	24.0
64	25	NONE	LEAF-LITTER	7.87	+/- 0.24	11	44.0
66	25	NONE	LEAF-LITTER	8.25	+/- 0.32	11	44.0
71	25	NONE	LEAF-LITTER	8.39	+/- 0.21	15	60.0