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The Biology of Two Species of Crayfish in Southwestern Lake Michigan

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THE BIOLOGY OF TWO SPECIES OF CRAYFISH
IN SOUTHWESTERN LAKE MICHIGAN

by

John P. Quinn

A Thesis Submitted to the Faculty of the Graduate School
of Loyola University of Chicago in Partial Fulfillment
of the Requirements for the Degree of
Master of Science

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VITA

The author, John Patrick Quinn, is the son of John D. Quinn and Margaret (O'Hara) Quinn. He was born on November 19, 1956, in Evergreen Park, Illinois.

The author completed his secondary education at Marist High School, Chicago, Illinois in 1974. He began his undergraduate education at the University of Illinois, Chicago Circle for two years at which time he left to pursue other interests. He entered Loyola University of Chicago in August, 1978 receiving a Bachelor of Science in Biology in May, 1981.

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Publications:

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INTRODUCTION

Coexistence by resource partitioning is based on the competitive exclusion principle, that two species cannot coexist using the same limiting resource identically. For species to coexist there must be differences in how they utilize the resources or differences in the resources they utilize (Diamond, 1978). Competition can occur by depleting the shared resource or by interference with the ability of the other species ability to use the resource. MacArthur (1972) proposed the theoretical framework by which resources could be assigned by body size. This results in some minimum size ratio for congenics to be able to coexist. Body size as a method of resource partitioning has been proposed for many bird and mammal "guilds" (a group of species with similar requirements) (Wilson, 1975; Schoener, 1982). Others argue that body size alone is not sufficient to explain coexistence (Wiens, 1977, 1981; Simberloff and Boecklen, 1981; Simberloff, 1983).

Crayfishes are the dominant large invertebrates of the benthic fauna in the rocky areas of southwest Lake Michigan and are the most important food resource for yellow perch in that area (Janssen and Quinn, 1985). Two species of crayfish, Orconectes virilis and O. propinquus,

coexist in Lake Michigan, as well as in many lakes in Wisconsin (Capelli, 1975). O. virilis are the larger of the two species as adults, although there is overlap between the larger O. propinquus and O. virilis adults. O. virilis is considered by Capelli and Munjul (1982) to be the native species in Wisconsin lakes (and I assume Lake Michigan), being the first to invade the lakes in this area after the last glacier approximately 10,000 years ago. O. propinquus was first reported in the lakes of this area about 50 years ago, probably introduced by anglers as bait. The presence of O. propinquus has not totally displaced O. virilis either in Lake Michigan or Northern Wisconsin. This suggests that they are able to coexist, but the mechanism is not known (Lodge et.al., 1986).

Resource partitioning as described for birds by Wilson (1975) has resources divided by size of food with larger bird species utilizing larger food items. Size limits each species ability to exploit the available resources. Smaller birds are displaced by larger birds, so they forage on thinner branches that cannot support the weight of the larger bird. This type of resource partitioning requires the recruitment of new individuals into the population at adult size as occurs in most bird and mammal species. For animals with indeterminate growth a larger species may be recruited into the general population at a smaller size than the adults of a smaller

competing species so that a competitive bottleneck can occur (Neill, 1975) in which juveniles of the larger species compete with adults of the smaller species. In Neill's study zooplankton species that experienced a competitive bottleneck at an early life stage that reduced their relative abundance no longer competed with the other species once they grew larger than it. Other studies show that piscivorous fish are at a competitive disadvantage as juveniles when they are feeding on zooplankton and compete with obligate planktivorous fish (Werner, 1986; Crowder, 1980; Persson, 1986). The jaw structure of piscivorous fish is not adapted for feeding on zooplankton so they grow more slowly and remain juveniles longer than if the competition was not occurring. Once they reach adulthood they no longer compete with the planktivorous species.

My study suggests that Orconectes virilis and O. propinquus exhibit a predator mediated bottleneck type of competitive interaction. O. virilis are recruited into the crayfish population at a smaller size than adult O. propinquus. Shelters are a limiting resource for which the crayfish compete. Previous work (Capelli and Munjal, 1982) showed O. propinquus were better able to obtain available shelters when competing with a like size O. virilis. When O. virilis and O. propinquus are of similar size, my data suggest that O. virilis are more vulnerable to predation presumably because they are less likely to have adequate

shelter. This results in a differential survivorship to adulthood.

MATERIALS AND METHODS

Study Site:

Using SCUBA I sampled the crayfish in the rocky areas of Lake Michigan from Waukegan to Montrose Ave., Chicago. Most collections were from Wilmette to Hollywood Ave., Chicago, one kilometer to four kilometers off shore. The depth ranged from 6 m. to 10 m. The bottom in this area is composed of sections of glacial till with patches of sandy bottom. From July through September, part of this sandy portion is covered with thick Cladophora beds. Crayfish were mostly found under rocks but occasionally in these beds. In late September - Early October the Cladophora beds are destroyed by storms that churn up the bottom.

Density collections (Adults):

Crayfish were collected by hand one meter on either side of a 50m. long transect rope. Collections were random in the sense that I did not know the bottom characteristics before reaching the bottom due to low visibility from the surface. To determine population density, I collected all adult (defined in results) crayfish found within 1 m. on either side of the transect line, resulting in a 100 square meter sample area. Very few crayfish escaped as we followed and collected them if they swam out of the sample area. Only complete 50 m. transects were used for density

calculations.

Shelter:

In 1982 (June - September), I attempted to determine the number of potential crayfish shelters for each transect. A potential shelter was a rock not imbedded in substrate with one dimension greater than 10cm. Imbedded rocks are not suitable shelters as the substrate beneath is anaerobic as indicated by iron sulfide deposition. Potential shelters were recorded prior to checking them for crayfish. Potential shelters were tested for correlation with crayfish abundance using the Spearman's rho (Zar, 1974).

After collection, all crayfish were returned to the lab where they were measured. I recorded species, sex, reproductive state, carapace length, and weight.

Growth and Size Distribution:

I collected young of the year in the late summer and fall of 1983 to monitor their growth rate. I did not use the complete transects for young of year as young were too numerous and complete collection along an entire transect was not possible. Each collection date for young of the year individuals was considered separately, so that growth over time could be detected.

The size distribution of adults of both species was determined for the summer (July through August) and the fall (mid September through October). I used only

collections from the summer in which most adult males were form 2, or from the fall when most males were form 1. After males molt to form 1 they will not grow (molt) again until spring (France, 1985). Early September is when most of the crayfish molted from form 2 to form 1. I can then compare adults size distribution during both reproductive stages. All collections were pooled for all years.

Fecundity:

To determine fecundity I collected females with eggs and individually bagged them to avoid losing any eggs. I determined the site as above, but I did not limit collections to a the transect. Eggs were counted in the lab along with determination of species and carapace length.

Predation:

Yellow perch were collected by gill nets (1.3, 1.9, 2.5, 3.8, and 5.1 bar mesh) in July 1979, '80, '82 (seven sets). The nets were set overnight and pulled the following morning. The stomach contents of the perch were identified and the carapace length of measurable crayfish was recorded. Crayfish found in perch from July sets for the three years (seven sets) were pooled and compared to diver collected crayfish from the same period using Chi-square tests (Zar, 1974).

RESULTS

General Life History:

Life histories for Lake Michigan Orconectes were similar to that described by Payne (1978) for several Orconectes species, including Orconectes virilis, O. propinquus and four others (see also Aiken, 1975; Capelli, 1980; Momot, 1967; Momot et al., 1978; Weagle and Ozburn, 1972). The life histories of O. virilis and O. propinquus are similar. Both O. virilis and O. propinquus mate in the fall. The males insert a plug into the female after mating to hinder other males from copulating with her. By October most females have plugs present, indicating that they have mated. Eggs are deposited on the pleopods of the female in the spring and they are carried on the tail May through June. The eggs hatch in early July and stay attached to the pleopods through the first and second instar stages. The third and fourth instar stages are independent of the female but were too small to collect. The young molt several times throughout the summer, continuing to grow until late fall. They molt twice in the summer (June and early September) of their 2nd year and mate for the first time in the fall. Eggs are laid in the spring of their 3rd year. The crayfish molt twice during the summer and again mate in fall. Individuals of both species usually die at

the end of their 4th year.

Males have two distinct reproductive stages (Capelli, 1975): Form 1, in which they are capable of reproduction. Males are in this form most of the year (approx. August through June). Males molt into form 2 (non-reproductive) in early June. O. propinquus molts back to form 1 in late August, O. virilis molts back to form 1 in early September.

For the purpose of this study I am defining form 1 males and females with eggs as adult. Females without eggs and Form 2 males I define as adult when they are the same size or larger than the smallest females with eggs or form 1 males. On any collection date juveniles and adults can be easily separated by size.

Density and Relative Abundance:

The density of crayfish found in Lake Michigan ranged from .02 per square meter to .81 per square meter (Table 1). On one partial transect (6m² consisting of a pile of loose rocks) a density of 5.2 crayfish per m² was found.

Both species had patchy distributions. When sampling a fixed size area we expect a Poisson distribution in the number of crayfish collected per dive if they are randomly distributed. High variance/mean ratios of abundance (2.9-20.2, $P < 0.001$, chi-square test for contagion (Elliott 1971), except 1979 O. virilis, ratio is 0.98) in the number of crayfish collected on each transect indicate that they have a patchy distribution in Lake Michigan. As crayfish

were nearly always found under stones, which occur in patches, it appeared that the number of shelters (loose stones) may influence crayfish density and patchiness.

There was a strong correlation (Spearman's rho. = 0.89, $P < 0.001$) between the number of loose stones and the number of crayfish collected (Fig. 1) indicating that shelters appear to be the limiting factor on crayfish numbers. Loose stones are unevenly distributed on the lake bottom, which has areas of sand, stones imbedded in sand, loose stones on sand, and piled stones.

Averaged over four years O. virilis comprised 21.9% of all the crayfish collected (Table 2). The percent O. virilis ranged from 24.3% to 19.2% but did not differ significantly between years (chi-square = 5.46, 3 df $P > 0.10$).

Size distribution of both species of crayfish for the fall (Fig. 2a) shows young of year (year 0) O. propinquus are 9mm to 15mm. Adult O. propinquus (males form 1) are 16mm to 32mm in length. The juvenile O. virilis are 9mm to 19mm in length, with the adults (males form 1) being 20mm to 47mm in length. There is overlap between the larger O. propinquus and the smaller O. virilis adults. They are the same size the following spring indicating that they do not grow significantly over winter (also France, 1985). During the summer O. propinquus adults have the same size distribution as in the fall (Fig. 2b). O. virilis tend to

be smaller in the summer than the fall. 30% of O. virilis adults overlap with O. propinquus adults in the fall compared to 43% in the summer (chi-square = 4.6, 1 df $P > 0.05$).

Fecundity and Growth of Juveniles:

The larger body size of the O. virilis females produces more eggs per individual than the smaller O. propinquus females (Fig. 3). However O. virilis appears to fall on the same (or similar) regression line as O. propinquus (Fig. 3). The exponent of the regression is not significantly different from 2.0 ($P > 0.5$) suggesting that the area of the crayfish tail limits egg number. This indicates that females of both species that are the same size would produce a similar number of eggs. This makes intuitive sense since the eggs are carried on the underside of the tail.

Juvenile O. virilis grows faster than O. propinquus (Fig. 4). Growth is achieved by molting, so that an individual grows by steps rather than continuously. Both species are recruited into the population at about the same size and have been hatched for 4-6 weeks before first collection date. There was a significant difference in length for each collection date starting with August 24 (t-tests, $P > 0.05$) except for Sept. 26 when very few crayfish were collected. There was no difference between the length of juvenile males and females of the same species on

any of the collection dates.

O. virilis has a lower relative survival rate to adulthood than O. propinquus with the difference occurring during their second year. There is a decrease in the percentage of O. virilis at the transition from juvenile to adult (Fig. 5). The drop from approximately 40% to approximately 21% (chi-square = 13.861 1 df. $P < 0.001$) of the total number of crayfish occurs as the year 1 O. virilis are passing through the size range of the O. propinquus adults, during the summer. There is not a decrease in the percentage of O. virilis from their year one fall numbers to their year two spring numbers (chi-square = 1.75, 1 df, $P > 0.1$).

Predation:

Crayfish are an important prey item of yellow perch, 45% of the perch caught in July gill nets had crayfish remains in their stomachs. Not all crayfish remains could be identified to species and measured. The size distribution of the crayfish found in perch guts (Table 3), compared with the population as a whole indicates biased mortality due to predation. The mean size of O. virilis in the gut samples (21mm) is significantly smaller (t-test, $p < 0.002$) than the mean size of the randomly collected O. virilis adults (31.9mm). The mean size of the O. propinquus in the gut samples (20mm) is not significantly different from the collected mean (21.0). I infer from this that the

perch are not making prey selections by species but are selecting their prey based on size and availability. Crayfish in the 18-26mm size range appear to be the most vulnerable to predation (also Lodge et al., 1986).

Despite the preference by perch for crayfish in the size window of O. propinquus, O. virilis were more likely to be eaten. Most adult O. propinquus range in size from 18 to 30mm. This closely approximates the size range of the crayfish that perch prey upon. Of crayfish collected by divers in July in the vulnerable size range, 14.4% were O. virilis, but in the guts 30.6% were O. virilis. This shows an increased vulnerability to predation by perch for O. virilis (Table 3) (chi-square = 7.36, 1 df, $P < 0.01$). Of crayfish collected in the fall in the vulnerable size range only 9.3% were O. virilis.

DISCUSSION

Resource partitioning, predation, and disturbance have been identified as factors affecting co-existence. The relative importance of each is a matter of disagreement among ecologists (Schoener, 1982; Simberloff and Boecklen, 1981; France, 1985), but probably depends on the system. For that reason field studies should take into account all three variables before drawing any broad conclusions. Determinate growth species (birds and mammals) fledge into the population at adult size utilizing the same resources as adults. Bottlenecks can occur with species that exhibit indeterminate growth, because juveniles can compete with adults of another smaller species.

Bottlenecks have two basic criteria. First juveniles of one species must compete with adults of another species in which it is at a competitive disadvantage that results in increased mortality or decreased growth. Secondly the adults have a refuge from competition, so that as adults either they don't use the shared resource or they can out compete the other species for it.

O. virilis exhibit indeterminate growth and they are recruited into the population under 6mm and can grow to over 47mm (Fig. 2 & 3). O. propinquus enter the population at under 6mm and can grow to over 32mm (Fig. 2 & 3). For

juvenile O. virilis to reach adult size they must pass through the adult size range of O. propinquus during July of their second summer. Shelters are apparently limiting as they affect local density. Crayfish were observed fighting in front of potential shelters on several dawn dives. Their behavior was consistent with that described by Heckenlively (1970) for crayfish aggression (also Ameyaw-Akumfi, 1979), and I believe that the aggressive interaction was for possession of the shelter. When O. virilis competes with O. propinquus for shelter they are at a competitive disadvantage while juveniles and the same size as O. propinquus adults (Capelli and Munjal, 1982; Peck, 1985).

The size window juvenile O. virilis share with O. propinquus is about the same as the size window that perch select their prey. Perch are most abundant in our collecting area in July, with relatively few fish by August (pers. obs. and Abrant, in prep.). Perch appear to be in shallower water earlier in the season and in deeper water later. Year one O. virilis are the same size as O. propinquus adults during July (Fig. 2). They are competing with the more aggressive O. propinquus for shelter when the greatest danger from predation exists. As a result O. virilis suffers from a greater juvenile mortality compared to O. propinquus (Table 2 & 3).

Adult O. virilis have a refuge from predation,

probably because they are too large to eat. Stein (1977) showed that in the lab larger crayfish were less vulnerable to predation, as my field data also indicates. On pebble bottom in an aquarium crayfish 16 - 20mm are eaten first, those larger than 22mm or smaller than 14mm are less susceptible to predation by smallmouth bass (Micropterus dolomieu) (Stein, 1977). This closely matches the size that crayfish appear to be most vulnerable to predation by perch (Table 3). It also approximates the transition size range where O. virilis juveniles are competing with O. propinquus adults that are the same size (Fig. 4).

Predation increases crayfish shelter seeking (Clady, 1974; Stein and Magnuson, 1976; Stein, 1977; Hayes, 1977; Collins et al., 1983). Stein (1977) found that shelter is important for predator avoidance in O. propinquus. O. propinquus and O. virilis showed a high degree of activity and low shelter occupancy at night (Stein & Magnuson, 1976) and in Lake Michigan (personal obs.). In low predator lakes crayfish remained exposed during the day (Collins et al., 1983; Hazlett et al., 1979). In lakes with high predator densities, the crayfish remained inactive and concealed during the day (Collins et al., 1983).

There is an opportunity for crayfish in stream populations to avoid competitive bottleneck situations by occupying different microhabitats at various stages of their development. Jezerinac (1982) found O. propinquus

and O. virilis used different microhabitats, with large O. virilis in deep pools, small O. virilis and O. propinquus at pool edges, and smallest (young of the year?) O. virilis in shallows. Bovbjerg (1970) concluded that competition influenced the distribution of O. virilis and O. immunis in the Little Sioux River area. The O. immunis were excluded from the streams and lake margins by aggressive interactions with O. virilis. O. virilis are excluded from ponds and sloughs by periodic drying and low oxygen levels that O. immunis can tolerate. Similarly Rabeni (1985) found that O. punctimanus excluded O. luteus from its favored habitat into the swifter moving water.

Habitat partitioning for the two species similar to that which occurs in streams is not obvious in Lake Michigan. We have not detected any differences in microhabitat of O. virilis and O. propinquus and none were noted by Capelli (1975) for O. virilis and O. propinquus in Wisconsin lakes. O. virilis adults are larger than O. propinquus adults so presumably they use larger shelters (Flint and Goldman, 1977; Capelli and Magnuson, 1983). Juvenile O. virilis have no size advantage so they compete with like size O. propinquus. As a result resource partitioning can not occur based on size. If competition is occurring, it probably is for daytime shelter as shelter is strongly correlated with crayfish abundance both in my study and in lakes in Northern Wisconsin (Capelli and

Magnuson, 1983). Flint and Goldman (1977) found that transects with large amounts of cover produce greater numbers of crayfish. It is likely that, because larger crayfish require larger shelters, different size individuals may compete less for shelters. As a result the larger O. virilis probably are not competing for shelter with the smaller O. propinquus. We noticed that larger O. virilis seemed to be under loose boulders, but as noted by Berrill and Chenoweth (1982) they also occasionally dug cavities under some imbedded rocks. Data were not collected comparing rock size with individuals because only part of the rock bottom may be habitable.

It is possible that storm disturbance could selectively eliminate O. virilis. The greatest disturbance occurs during the winter storms, so we would expect any selective pressure by disturbance to manifest itself over the winter. There is not a decrease in the percentage of juvenile O. virilis from the fall to the spring indicating that there is not a disproportionate winter die-off compared to O. propinquus (Fig. 5).

In previous studies of juvenile bottlenecks food has been the limiting resource. For example, piscivorous fish are adapted to feed on other fish. They are at a competitive disadvantage as juveniles when they are feeding on zooplankton as obligate planktivorous fish are better adapted to exploit that food resource. This competitive

interaction with planktivorous fish is limited to the juvenile stage when they are using the same food sources. Those that survive to adulthood no longer compete with the planktivorous species (Werner, 1986; Persson, 1986). The competition in this case causes a decrease in growth rate, so that they are in the smaller size range longer and take longer to reach reproductive maturity. A competitive bottleneck at one stage of an organisms life history will manifest itself throughout subsequent stages. It will set an upper limit on the number of individuals at those later stages independent of the organisms ability to use resources at those stages (Neill, 1975). Persson (1986) found that when the bottleneck on juvenile perch was removed (by removal of the competitor) growth rate and maximum population size both increased.

Fecundity in crayfish is size dependent. Because O. virilis are larger as adults they have a much greater reproductive output compared to O. propinquus. To maintain themselves against its disproportionate juvenile mortality O. virilis must have a greater reproductive output per female than O. propinquus. If this were not the case then over time the percentage of O. virilis adult would decrease until O. virilis became locally extinct.

CONCLUSION

My data suggest that O. virilis has a refuge from competition and predation only when it is larger than O. propinquus. The juvenile O. virilis must pass through the adult O. propinquus size class to reach adult size (Fig. 2). This is also the size window that crayfish are most vulnerable to predation by perch (Table 3). It is while they are at the same size as the adult O. propinquus that the most intense competition for shelters occur; crayfish (primarily O. virilis) that do not obtain shelter suffer greater mortality from perch predation. To attain the refuge from competition they must survive a predator-mediated competitive bottleneck. The relatively greater mortality is offset by the greater individual fecundity of O. virilis due to its larger size. As a result fewer O. virilis need reach maturity and reproduce to produce sufficient offspring to maintain their numbers.

Table 1

Density of adult crayfish on 100 m² Transect

| Year | 1979 | 1980 | 1982 | 1983 |
|----------|--------------------|--------------------|--------------------|--------------------|
| # Trans. | 9 | 14 | 10 | 2 |
| Density | | | | |
| Mean | .28/m ² | .28/m ² | .41/m ² | .31/m ² |
| min. | .09/m ² | .02/m ² | .13/m ² | .16/m ² |
| max. | .56/m ² | .81/m ² | .73/m ² | .42/m ² |

Table 2

Summary of abundance of adult crayfish Collected on 100 m² Transect

| Year | 1979 | 1980 | 1982 | 1983* |
|---------------------------------------|-------|-------|-------|-------|
| No. of Transects | 9 | 14 | 10 | 5 |
| No. of <u>O. virilis</u> | 63 | 107 | 79 | 46 |
| No. of <u>O. propinquus</u> | 196 | 334 | 331 | 193 |
| % <u>O. virilis</u> total crayfish | 24.3% | 24.3% | 19.3% | 19.2% |

*includes 3 incomplete transects

Table 3

Crayfish with carapace length 18 to 30mm from July SCUBA collections and yellow perch collected in nets. A total of 454 fish were collected.

| Species | Number of crayfish | |
|----------------------|--------------------|------------------|
| | July Perch | July Collections |
| <u>O. propinquus</u> | 34 | 351 |
| <u>O. virilis</u> | 15 | 59 |

Figure 1

Correlation of crayfish abundance with numbers of loose stones for 13 transects in 1982. Spearman's $\rho = 0.89$, $P < 0.001$.

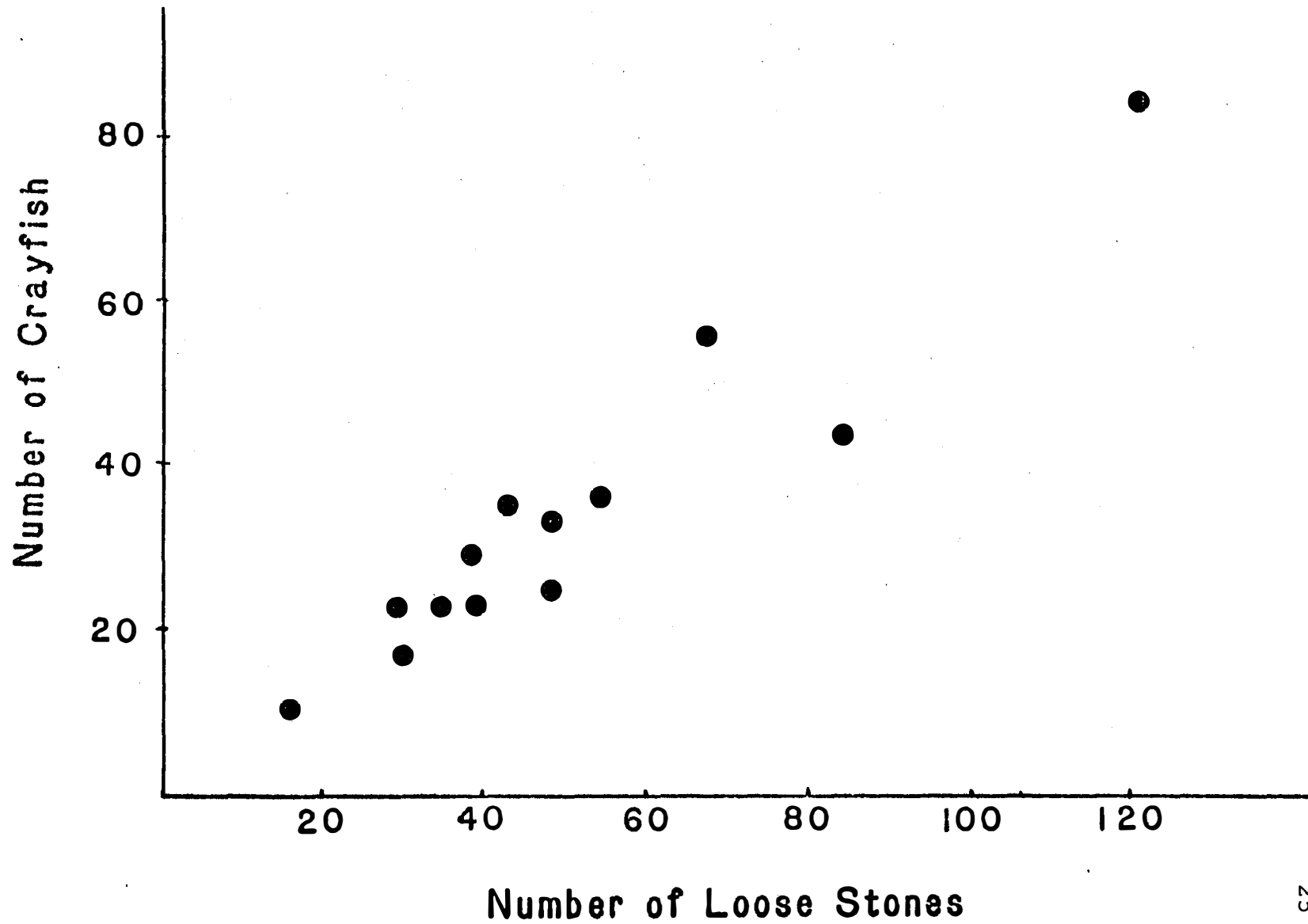
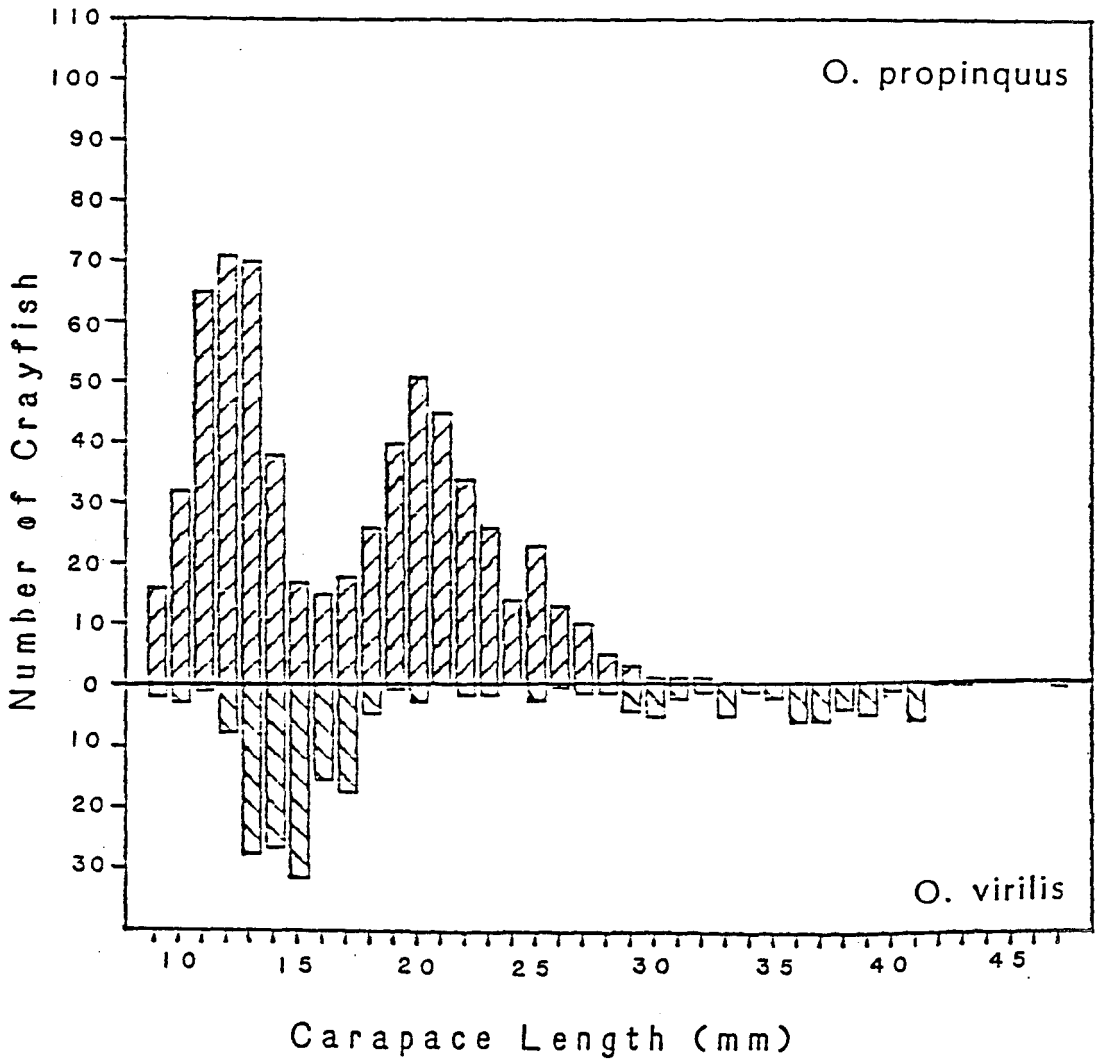


Figure 2a-b

Histograms of crayfish numbers by carapace size, all years pooled. Collections from the fall (mid-September-October) after most males have become form 1. Juveniles (year 0): O. virilis - less than 19mm, O. propinquus - less than 16mm. Adults (year 1+): O. virilis - greater than 19mm, O. propinquus - greater than 16mm. Summer collections (July - August) after most males become form 2. Year 0 not collected (too small) Adults (year 1+) O. virilis - 16mm to 47mm, O. propinquus - 13mm - 33mm.

FALL



SUMMER

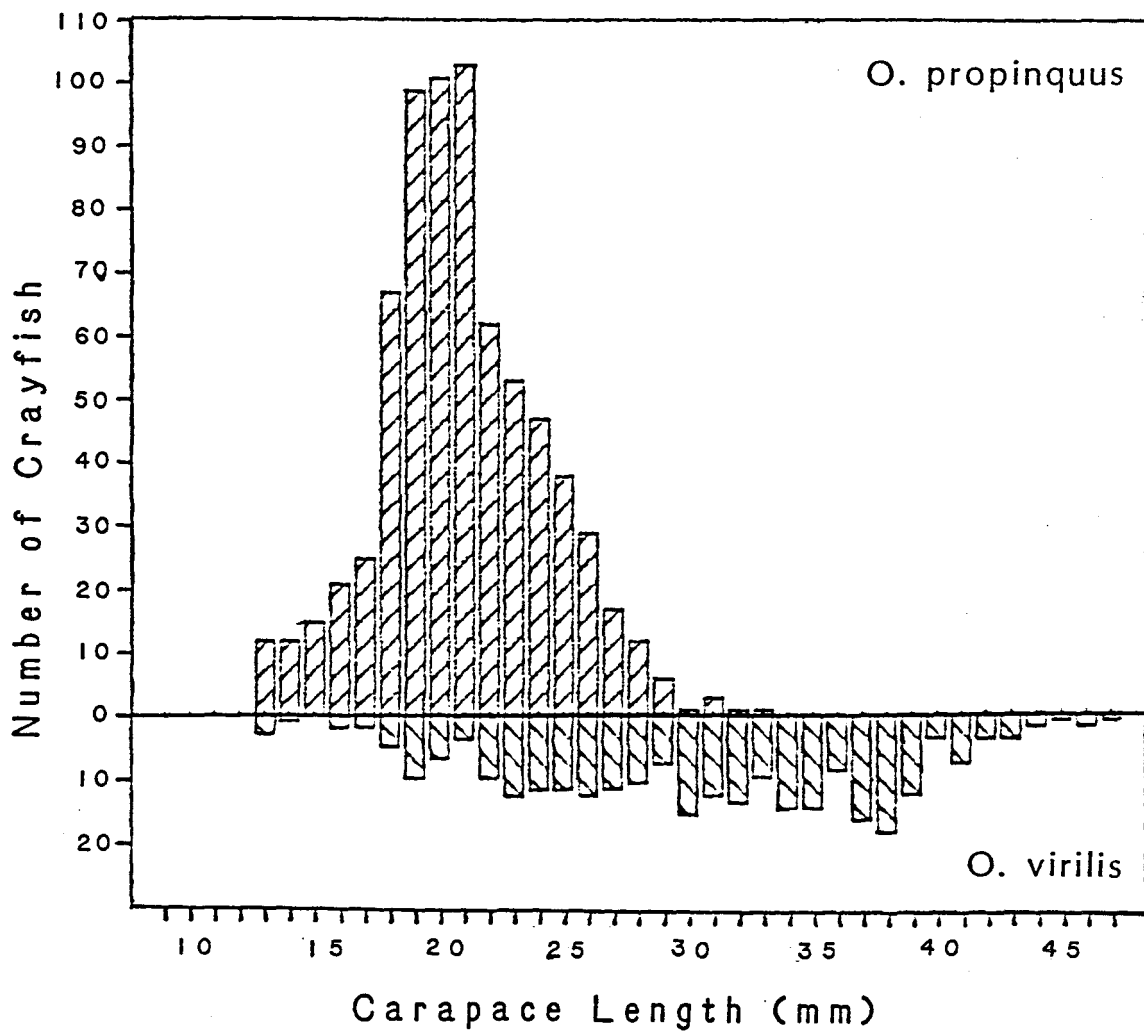


Figure 3

A log-log regression of egg number vs. carapace length. Both O. propinquus and O. virilis have similar regression lines (t-test, $P > 0.5$). Egg No. = $k(\text{length})^c$
O. virilis $c = 1.61$, O. propinquus $c = 1.71$,
pooled $c = 2.22$

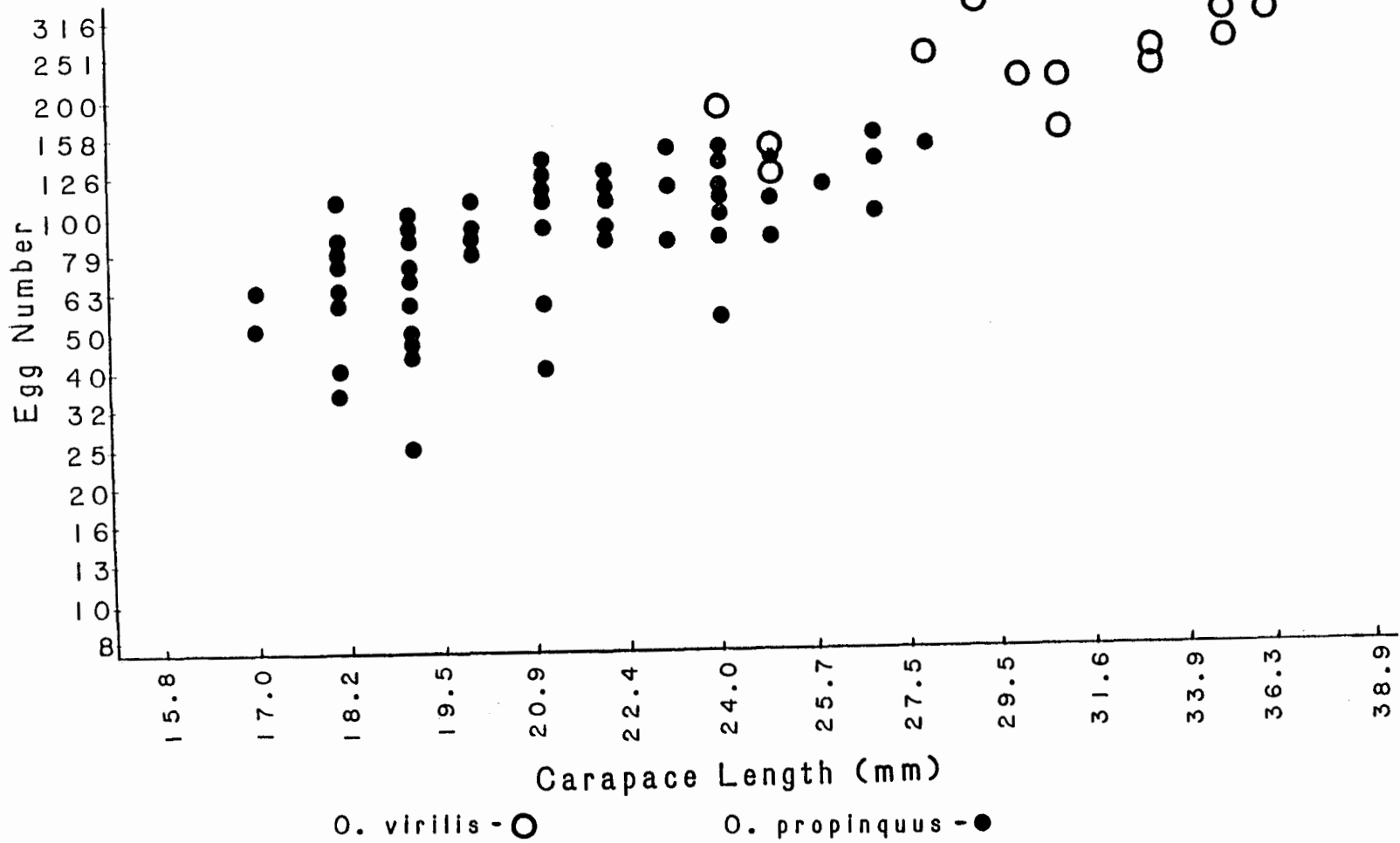


Figure 4

Plot of carapace lengths for year class 1983 O. propinquus and O. virilis, by collection date. Dates marked with * have a significant difference in the carapace length of O. propinquus and O. virilis.

Year Class 1983

Median Length

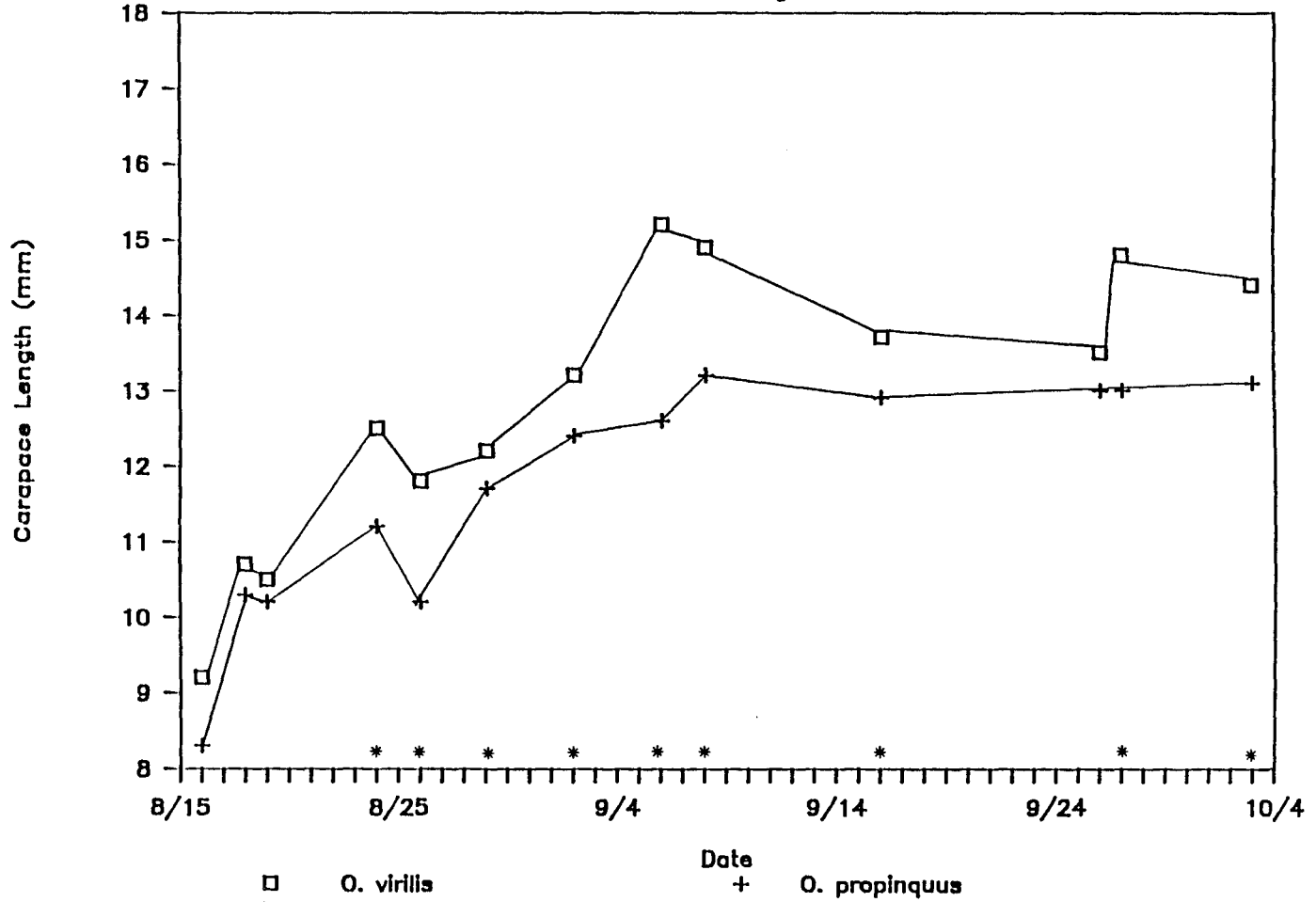
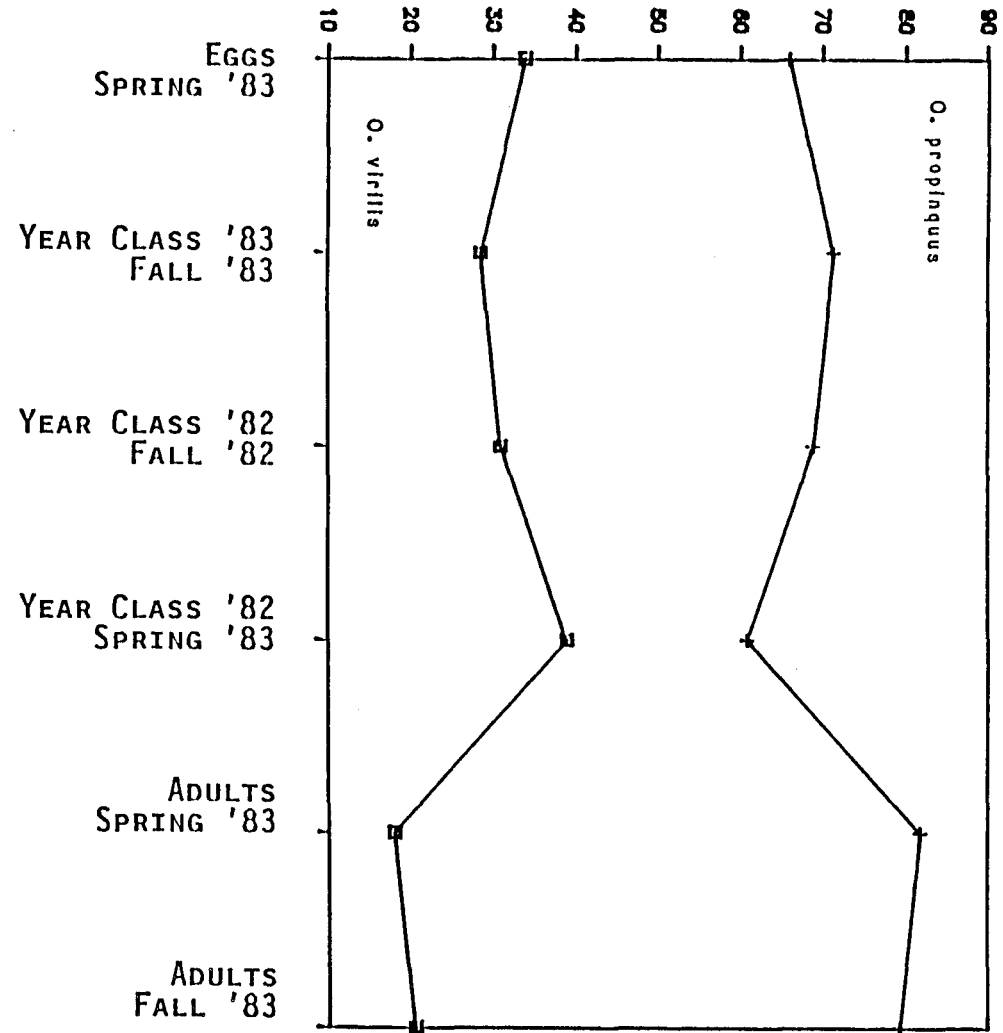


Figure 5

Percentage of total crayfish numbers each species. There is not a significant difference between the percentage of Year Class '82 from the fall to the following spring, nor is there a significant difference between adults from fall to spring. There is a significant difference between year 1 crayfish in the spring and adults in the fall.



PERCENT OF TOTAL POPULATION



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The thesis submitted by John P. Quinn has been read and approved by the following committee:

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The final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the thesis is now given final approval by the Committee with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Science.

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