Natural History and Microdistribution Near Shore of Two Co-Occurring Crayfish, *Orconectes propinquus* (Girard) and *Orconectes virilis* (Hagen)

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ABSTRACT

Natural History and Microdistribution Near Shore of Two Co-Occurring Crayfish, Orconectes propinquus (Girard) and Orconectes virilis (Hagen)

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Populations of the crayfish Orconectes propinquus and Orconectes virilis were observed to be equally abundant and to occupy the same habitat near the shore of the St. Lawrence River. Closer examination revealed a spatial separation between the two species. Most O. propinquus were found between 2 and 3 meters from shore, whereas most O. virilis were found less than 2 meters from shore. Field studies and laboratory experiments were performed in order to determine (1) differences in life histories of the two species, (2) differences in preferred physical environment, (3) differences in behavior, and (4) whether microdistribution in the study area is controlled more by physical conditions or biotic factors.

Crayfish were sampled twice a week between May and November, 1980. Orconectes propinquus was found to

have a reduced growth rate after its first summer. The maximum size attained by O. propinquus (8.3 mm areola length or 24.4 mm carapace length) is much lower than maximum sizes recorded in the literature for that species. Orconectes propinquus individuals were found to have a higher aggression level, were better able to defend shelters, and were more capable of protecting themselves against fish predation than similar sized O. virilis individuals.

Laboratory results suggest that substrate particle size, predation pressure and water temperature are possible factors controlling microdistribution of the two crayfish species in the study area.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

INTRODUCTION

The natural histories of the crayfish Orconectes propinquus and Orconectes virilis have been previously studied in Ontario and northeastern United States, and it is known that these two species have similar habitats and life histories. However, there have been no detailed studies on the timing of life history events or specific interactions between O. virilis and O. propinquus when they are co-occurring, even though they are the most common and widespread crayfish in Ontario and Quebec (Crocker and Barr 1968) and are frequently found together (Bovbjerg 1952; Capelli and Magnuson 1975; Jordan and Dunham 1981). Momot et al. (1978) state: "Often O. propinquus and O. virilis are found in the same type of habitat, ie., rocky streams with moderate to rapid current, yet little is known about the possible competition between these species."

Over the years there have been numerous published studies concerning crayfish distribution in the field. Some have investigated the natural distribution of several species of crayfish over a wide area (Aiken 1965; Berrill 1978; Smith 1979), while others have looked at movement of crayfish using mark and recapture experiments (Black 1963; Momot 1966; Hazlett et al. 1974).

Microdistribution of crayfish, on the other hand, has been looked at by very few authors. Stein and Magnuson (1976) and Stein (1977) have observed microdistribution of crayfish in relation to fish predation. Stein and Magnuson (1976) found that in a lake with fish predators, more large crayfish than small, and more males than females were exposed on top of the substrate. It is believed that this occurs because these individuals are better able to protect themselves from the predator. Stein (1977) showed that in two lakes studied, crayfish densities on sand were inversely related to the densities of fish in the lakes. It seems that crayfish shift their microdistribution from sand to pebble substrate in the presence of a fish predator.

The immediate shoreline has not been studied in detail in the past. Depth distribution research has focused on a wide depth range in order to study crayfish distribution in relation to temperature (Capelli and Magnuson 1975) or oxygen concentration (Fast and Momot 1973), or to examine seasonal migration of crayfish (Momot and Gowing 1972).

The shoreline zone is an important area in terms of crayfish survival, and it is the best area to observe life histories, since this is where female crayfish brood and release their young (Momot 1967; Capelli and Magnuson 1975; Momot 1978). In a lake in northeastern Wisconsin at the end of May, 84% of the female O. propinquus in one meter of water carried eggs, whereas at 8 meters only 13% did so. In July, the density of young-of-the-year at a depth of one meter was almost $100/m^2$, but at 3 meters was less than $20/m^2$ (Capelli and Magnuson 1975). In two northern Ontario lakes, young-of-the-year O. virilis were found along the shoreline in the area of emergent vegetation which usually grew to a depth of only 0.5 meters (Momot 1978).

The immediate shoreline has also been found to be very important as a nursery for young-of-the-year O. virilis (Momot and Gowing 1977a, 1977b). Since this area near the shore seems to be the preferred habitat for both adult and young crayfish during the summer, it is probable that this is where species interactions would be most noticeable.

Objectives and questions asked

The present study concerns itself with the natural history and microdistribution of the two crayfish species, O. propinquus and O. virilis in a section of the St. Lawrence River within a few meters from shore, the maximum water depth not exceeding one meter. Upon close examination of the habitat in which these organisms live, a difference in the microdistribution of the two species was observed.

This phenomenon meant that there were differences between the two species. Therefore, this study set out to determine whether there were differences in (1) natural history, (2) behavior and (3) preferred physical environment, in this population of crayfish in the study area. The information gained would then be used to attempt to determine the possible cause, or causes, of the observed differences in microdistribution.

The following questions were asked:

1) Is the crayfish population under investigation stationary or constantly moving? This information is necessary in order to be sure that a cross-section of the whole population in the area, and not just a few individuals, is being studied.
2) Is any form of competition taking place between the crayfish of the two species? The answer may aid in establishing causes of the observed difference in microdistributions.
3) What are the life histories of each crayfish species in this habitat? This information will determine whether timing of events change when two crayfish species share the same habitat.
4) What physical environment does each crayfish species prefer? This will determine possible physical factors affecting crayfish microdistribution in the study area.

5) What are the behavioral differences between the two crayfish species?

6) Are the two crayfish species subject to different predation pressure? The information from questions 5 and 6 will determine possible biotic factors influencing crayfish microdistribution in the study area.

7) Is microdistribution of the two crayfish species, in the study area, controlled more by physical conditions or by biotic factors?

General comparison of the two species

Orconectes propinquus is found in the northeastern United States, eastern Ontario, and southern Quebec. Its northern range has not been reported past the southern tip of James Bay (Fitzpatrick 1967; Crocker and Barr 1968). *Orconectes virilis* has a wider distribution, being found throughout the northern United States and southern Canada from eastern Alberta to eastern Quebec. Its northern limit in Quebec slightly exceeds that of *O. propinquus* (Aiken 1968). The only other crayfish species in large numbers in Quebec is *Cambarus bartoni* (Fabricius), but its habitat is mainly limited to swift, cool, rocky streams (Crocker and Barr 1968).

Orconectes propinquus does not grow to as large a size as *O. virilis* and has a life span of 2 to 3 years (Crocker and Barr 1968; Stein and Magnuson 1976) compared to 3 to 3.5 years for O. virilis (Momot 1967; Crocker and Barr 1968; Momot and Gowing 1975) in northern latitudes.

Orconectes propinquus and O. virilis have similar mating periods and life cycles. To give an idea of the type of life cycle that these organisms have, a short generalized life history follows:

Mating occurs between mid-July and October and eggs are laid the next spring between late April and mid-June. Eggs are carried by the female on the ventral side of the abdomen for several weeks and hatch between mid-May and mid-July. The young are then carried for approximately another two weeks before becoming free-swimming in June or July. These crayfish will usually reach sexual maturity in their second summer (Crocker and Barr 1968; Weagle and Ozburn 1972; Capelli and Magnuson 1975; Stein 1977). The intervals mentioned above will vary depending on the seasonal temperatures and the location of the habitat in North America.

STUDY AREA

The majority of the field work for this research was carried out during 1980 and 1981 along the south-eastern shore of Nun's Island (Isle des Soeurs) which is located adjacent to the Island of Montreal (45°31'N 73°34'W), Quebec in the St. Lawrence River (Fig. 1). The waters in this area appear to be one of the least polluted around Montreal, even though downtown Montreal is only a few kilometers away. This observation was confirmed by performing total bacteria counts in different areas along the southern shore of Montreal Island (Appendix I). The relatively low pollution level may be partly due to the fact that the St. Lawrence River widens at this point causing a diluting effect of pollutants. Another reason is that all the sewage from downtown Montreal enters the river on the northern side of Nun's Island, effectively by-passing the study area on the southern side.

Nun's Island has been increased in size by land-fill operations and, therefore, the study area is composed of landfill, but it has been undisturbed for many years enabling the natural flora and fauna of the area, both aquatic and terrestrial, to colonize.

A large portion of the southern shore of Montreal Island southwest of Nun's Island, including the Lachine Rapids and Lake St. Louis, was also examined in 1980.

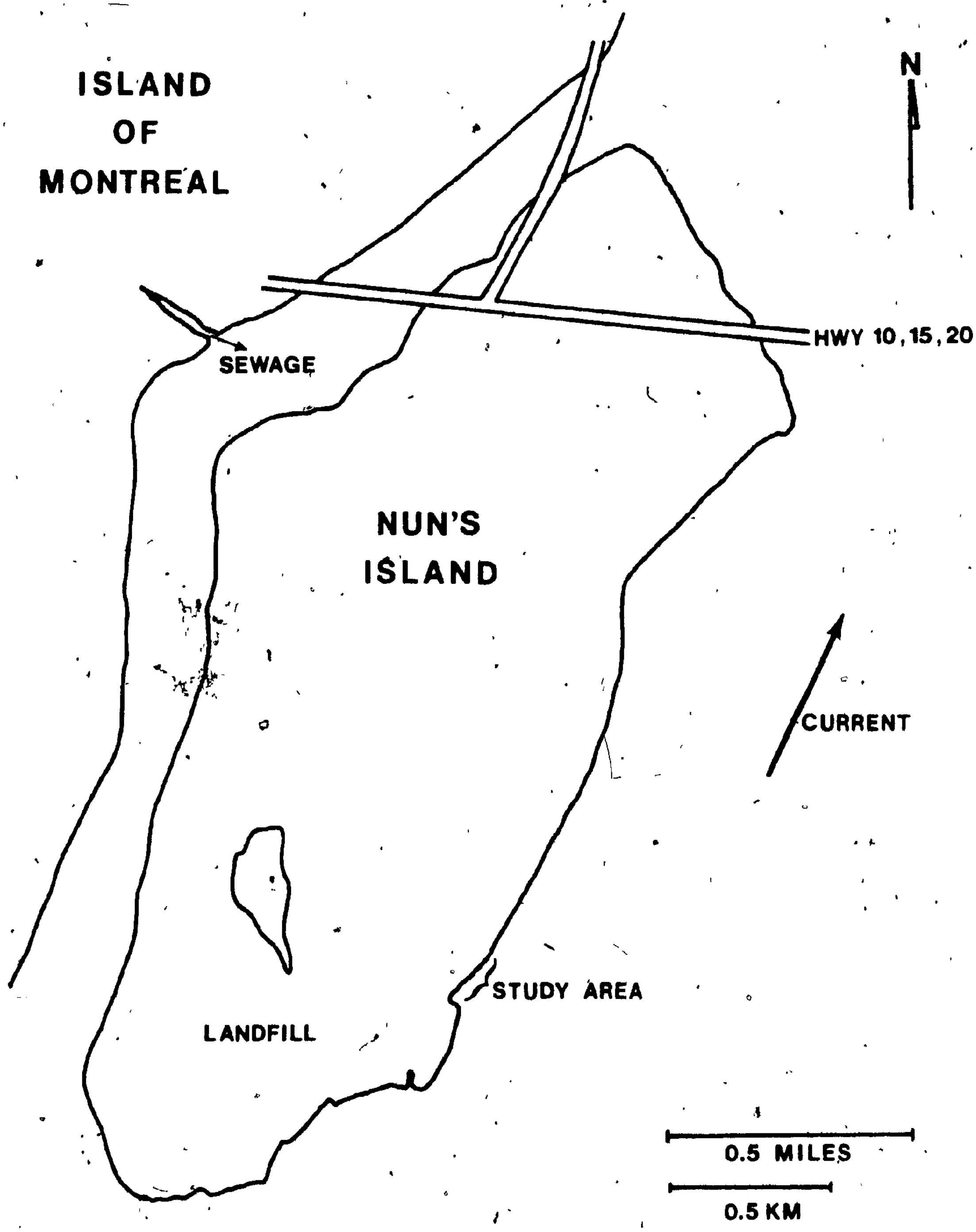

FIG. 1. Map of Nun's Island (Ile des Soeurs). (Modified from map of Lachine, Ministère des terres et forêts du Québec, 1978).

Appendix I compares chemical and physical properties among some of the different sites studied. Crayfish were not uniformly distributed along the shoreline. The southeast shore of Nun's Island had the most abundant crayfish population of all the sites studied. Orconectes propinquus and O. virilis were found in only a few other areas, since neither was observed in heavily polluted water, rapidly flowing water, in Lake St. Louis, or in regions with a muddy or a shale substrate. Only four C. bartoni were seen in two years of sampling the St. Lawrence River, indicating that C. bartoni is not in its optimal habitat here.

In 1980, the microhabitat of a small region of the St. Lawrence River at Nun's Island was studied intensively. This portion of the river bottom is gently sloping (11° angle) and has a gradient of particle sizes starting from gravel (2 cm diameter) near the shore to rocks (15 cm diameter) a few meters from shore. Another gradient occurs along the shore, since the particles become increasingly smaller toward the southwest, until only silt and a few rocks are found 30 meters away. The speed of the water current near the shore is moderate (mean = 0.24 m/sec). The maximum water temperature at one meter from shore was 25°C in August, 1980. The chemical and physical properties of the water are listed in Appendix II.

Filamentous algae, mainly *Cladophora* and some *Microspora*, started growing in early May, 1980 and remained through the summer and fall in abundance. Macrophytes started growing in early June, 1980 and increased in number and distribution through the summer, but remained at least three meters from the shore. The main plant species present were: *Vallisneria americana*, *Sagittarius teres*, *Potamogeton crispis*, *Potamogeton gramineus*, and *Myriophyllum* spp.

The crayfish share their habitat with many other benthic organisms such as: several snail species, flatworms, amphipods (*Gammarus*), the mudpuppy (*Necturus maculosus*), darters (*Etheostoma* spp.), and the spoonhead sculpin (*Cottus ricei*). Both adult and young smallmouth bass (*Micropterus dolomieui*), yellow perch (*Perca flavescens*), young brown bullhead catfish (*Ictalurus nebulosus*), and young pumpkinseed sunfish (*Lepomis gibbosus*) were also frequently seen near the shore. Many frogs, as well as water birds such as: the ring-billed gull (*Larus delawarensis*), the herring gull (*Larus argentatus smithsonianus*), the killdeer (*Charadrius vociferus vociferus*), and on one occasion, the common loon (*Gavia immer*), were seen in the vicinity of the study area. Therefore, there may be a fair amount of predation on crayfish in the study area, since almost all of the organisms mentioned above are predators of crayfish.

MATERIALS AND METHODS

FIELD STUDIES

In the spring of 1980, three quadrats measuring 3 meters x 3 meters were marked using painted rocks in the shallow water along the shore of Nun's Island. These quadrats were positioned approximately ten meters apart, the first (A) being located on rocky substrate, the second (B) on fewer and slightly smaller rocks, and the third (C) on silty substrate with a few large rocks. Chemical tests of the water were performed on an average of every two weeks from June to October 1980 (dissolved oxygen concentration determinations were begun in April) using the Hach DR-EL water test kit.

Crayfish sampling

Crayfish sampling took place twice weekly from May 15 to November 14, 1980. By wading upstream, gently turning over all the rocks in the three quadrats and capturing by hand or with a hand-held net, 341 adult and 812 young-of-the-year crayfish were collected. (In the present study, "adult" refers to all crayfish in at least their second summer, for this is when both species reach sexual maturity (Weagle and Ozburn 1972; Stein 1977)). Few crayfish escaped using this procedure, and if one did, it could usually be followed and subsequently captured. Since crayfish are mainly nocturnal (Huxley 1880), they remain hidden under shelter until uncovered and, therefore, their natural daytime distribution is not disturbed by the collector's movements.

Ordinary cylindrical minnow traps baited with fish were also used in an attempt to sample the deeper waters that could not be reached by wading. This method for catching crayfish has been successfully used by others (Momot and Gowing 1972; Fast and Momot 1973). This procedure, however, was abandoned since it proved to be virtually ineffective (only ten crayfish were caught with ten traps over 50 days in May and June). The poor capture rate was most likely due to the low crayfish density in the study area and the abundant plant growth in June which prevented the traps from reaching the bottom of the river.

For all the adult crayfish captured in 1980, the following information was noted: the quadrat in which it was caught, species, sex, presence or absence of eggs or young, missing appendages, and areola length. All measurements were taken with vernier calipers and were rounded to the nearest 0.1 mm. In contrast to most published studies which use carapace length (c.l.), the distance from the anterior portion of the abdomen to the tip of rostrum, this study uses areola length (a.l.), the shortest distance from the anterior portion of the abdomen to the cervical groove, as the standard measure of crayfish size. Areola length is a more accurate measure since the rostra of crayfish vary in length and are sometimes broken (one crayfish was found missing the entire rostrum) thus rendering it impossible to measure. This rationale was also used by Berglund (1980) for measuring prawns. Areola length can easily be converted to carapace length or vice versa since the two are directly proportional to one another, as shown in Appendix III.

After the crayfish were measured, they were released at the center of the quadrat in which they were found. Since most crayfish disperse randomly from a density center (Bovbjerg 1959), it was assumed that they would redistribute themselves randomly throughout the quadrat. It should also be noted that after each rock was turned over during sampling, it was returned to the same position as before, thereby keeping the habitat unaltered.

From mid-July to October, each quadrat was split into three 3 x 1 meter subquadrats, 0 to 1 meter, 1 to 2 meters, and 2 to 3 meters from shore. During regular sampling, the water temperature just above the substrate in each of these subquadrats was taken.

In order to take a small sample and note the crayfish density in deeper sections of the river, a SCUBA diver collected specimens twice in the month of July at a depth of approximately five meters.

Mark and recapture

A total of 250 adult crayfish were marked with blue Bell-Mark numbering-machine ink according to the methods of Slack (1955). A small amount of ink was injected between the thin cuticle and muscle on the ventral surface of the abdomen, thus forming a small discrete spot which was easily discernable since the thin cuticle of the abdomen is transparent. By marking different segments on the left and right sides of the abdomen, the crayfish were coded so that when recaptured it was possible to tell which month and from which quadrat the crayfish was first captured. This method of marking has no detrimental effect on the subject and the spot is still perceptible after several molts (Slack 1955; Black 1963). Since adult crayfish molt only once or twice in a summer (Weagle and Ozburn 1972; Capelli and Magnuson 1975), there was no danger of losing the markings during this study. Crayfish were marked and recaptured twice a week from May to August, 1980.

Feeding habits

To determine whether there were any differences in the feeding habits of the two crayfish species in June and July, when crayfish were most numerous, 11 to 12 adults of each species were collected from along the shore and were immediately preserved in 80% ethyl alcohol. These specimens were brought back to the laboratory for stomach content analysis. The stomachs were removed, and the contents were examined under a dissecting microscope at 50x magnification.

Bacterial counts

In July and August, 1980, water samples were taken from the Nun's Island study area and from other sites along the southern shore of the Island of Montreal. These samples were kept on ice until they were returned to the laboratory where total bacteria counts were performed.

Substrate sampling

When all the crayfish sampling was completed in November, 1980, substrate samples from each of the nine subquadrats were taken. Large rocks were removed and the greatest diameter measured. A subsample of underlying substrate was removed with a shovel and brought to the laboratory where it was divided into size classes using sieves of varying mesh size. The amount of small pebbles, sand and silt was measured by the volume of water they displaced.

Sampling 1981

In 1981, crayfish were collected between April and July from the southeastern shore of Nun's Island in order to obtain females of each species with attached eggs. These individuals were brought to the laboratory where the eggs were removed, counted and their diameters measured under a dissecting microscope.

As a check to see if the sampling technique of the previous year was accurate, especially if any larger size classes were undetected, chelae (claws) that were washed-up onto the shore by storms were collected. Since these chelae originated from dead crayfish and were not molts, they should represent the population of mature individuals and may indicate the average size at death. It is possible to determine the species of the chelae but not the sex. This makes it difficult to convert chela length to areola length even though they are directly proportional, since males and females of the same areola length have different chela lengths (Appendix IV).

LABORATORY EXPERIMENTS

Crayfish were collected from the study area and were kept in large 55 x 208 cm and 56 x 116 cm holding tanks with many rocks covering the bottom for shelter. These tanks were aerated and had dechlorinated water flowing through them at room temperature (19 to 23°C). Lighting was provided by overhead fluorescent lights on a 12 hour photoperiod. Crayfish were fed three times a week with pellet food (formula GRT G size 3/32, Martin

Feed Mills Inc.). In all experiments performed, water temperature, photoperiod and feeding were kept constant unless otherwise stated, and male and female crayfish were used in equal numbers. Sizes of O. propinquus used ranged from 3.8 - 7.7 mm a.l., whereas O. virilis sizes ranged from 4.8 - 8.8 mm a.l. (third year O. virilis were not used in experiments). These sizes were representative of the majority of the population in the field. All crayfish used were active, had intact chelae and had not recently molted.

Substrate particle size preference (gradient)

The bottom of large polyethylene tubs measuring 65 x 170 cm were covered with rocks from the Nun's Island study area. The rocks were arranged in such a manner as to duplicate the gradient in the study area. The substrate was divided into three regions (small rocks < 30 mm in diameter; medium rocks 30 to 100 mm; large rocks 100 to 200 mm). The water was 15 to 20 cm deep covering all the rocks and was constantly aerated. Fluorescent lights hung directly overhead so that no shadows would be present. Crayfish were placed in the center of the tubs and were allowed to radiate outward in a random manner. After an acclimation period of 24 hours, observations were made daily by counting the number of crayfish on or under the small and medium-sized rocks, the remainder being under the large rocks. Crayfish under the large rocks were not counted since removal of all the large rocks would cause a great disturbance and would affect the distribution of crayfish. The medium-sized rocks, however, could be lifted and replaced one at a time with very little disturbance to the crayfish. At the end of each experiment, all the rocks were removed and all the crayfish were accounted for.

Before observations were made, fiberglass dividers were placed between the three different substrate areas preventing individuals from fleeing to another region if disturbed. Since crayfish are mainly nocturnal, leaving their shelters at night (Bovbjerg 1970b), only one observation was made per day to allow the crayfish to redistribute themselves overnight after having been disturbed. Ten crayfish ($9/m^2$) of each species were placed in separate tubs and observed for four days. This procedure was repeated for 20 ($18/m^2$), 30 ($27/m^2$) and 40 ($36/m^2$) crayfish of each species, but the 40 crayfish were observed for a period of ten days. A duplicate experiment with 40 crayfish was performed for ten days, then, as a control, the tubs were rotated 180° and observed for another ten days to see if the observed distribution was caused by any outside agent, such as room wall color.

To see if species interactions would alter the distribution of crayfish, duplicate experiments were performed with 20 of each species together, maintaining the same total crayfish number, in the same tub for ten days under the same conditions.

Substrate particle size preference (extreme)

These experiments were performed to test crayfish preference to extremely different substrate particle sizes. A 65 liter aquarium measuring 30 x 60 cm was divided into three substrate types as follows: sand (<1 mm in diameter), gravel (5 to 20 mm), and rock (60 to 100 mm). Crayfish were placed in the center of the tank, acclimated for 24 hours, then observed once a day without disturbing the substrate. Experiments were performed with each crayfish species and with both species together at crayfish densities of 33, 67, 100 and $133/m^2$, in order to detect interspecific competition for shelter. Observations were made for two days at each density with each species separate, and for four days at each density with both species together.

The above experiment utilized crayfish that had been in captivity for several months. To see if these crayfish had changed their behavior since capture, duplicate experiments were performed with newly obtained crayfish from the study area, as a control.

Distribution with a predator

Twenty crayfish of each species were placed together in a tub containing a rock gradient, identical to that used in the substrate particle-size preference (gradient) experiments. The only change in procedure was the following: crayfish were observed for seven days with no predator (control), then a 16 cm long smallmouth bass (Micropterus dolomieui) was introduced for twelve days.

Aggression studies

For these experiments a 20 liter aquarium measuring 19 x 40 cm had its sides and bottom covered with black plastic to avoid external stimuli. To eliminate the corners of the aquarium as a possible refuge, two long pieces of fiberglass were bent into U-shapes and placed in the aquarium end to end. This formed an oval-shaped arena, and since one piece of fiberglass fit inside the other, the area of the arena could be increased or decreased as desired simply by moving one of the U-shaped pieces of fiberglass. The ratio of crayfish size to arena area was kept constant so that the probability of contact between crayfish species would remain the same regardless of the size of the individuals. The bottom of the tank was covered with white aquarium gravel to allow the crayfish a foothold but not shelter. One crayfish of each species (male versus male or female versus female) was placed in the arena and observed for 15 minutes from overhead. An aggression contact is defined as a head-on encounter between two individuals that results in one crayfish retreating from the other. These contacts were noted as being one of the following: avoidance, threat, strike, or fight, as described by Bovbjerg (1953).

Three sizes of O. virilis (5.5, 6.5 and 7.5 mm a.l. ± 0.2 mm (range)) and seven sizes of O. propinquus (4.5, 5.0, 5.5, 6.0, 6.5, 7.0 and 7.5 mm a.l. ± 0.2 mm (range)) were utilized in these experiments, since these sizes represent the sizes of the majority of crayfish in the field. These sizes were matched in all possible combinations in an attempt to discover the size difference at which the two crayfish species were equally aggressive. Male and female crayfish were tested in duplicate or triplicate for each of the size combinations, and the water was changed between each size combination in order to remove any pheromones that may cause increased aggressive behavior in the next crayfish pair that is placed in the same "conditioned" water (Thorp and Ammerman 1978). Before the crayfish were introduced into the arena, their wet weight and chela length were determined. Chela length, the distance from the tip of the propodus to the carpus, was measured with vernier calipers.

Shelter occupation

These experiments were performed to see if aggression and shelter occupation were related. Twenty liter aquaria were divided in half with heavy plastic partitions, the bottoms covered with white aquarium gravel, the sides covered with black plastic, and the water aerated. Shelters were constructed by placing three stones in each half of the tank in such a way that they formed a tunnel large enough to accomodate only one crayfish. Orconectes virilis (6.5 mm a.l.) were used in combination with five sizes of O. propinquus (4.5, 5.0, 5.5, 6.0 and 6.5 mm a.l. ± 0.1 mm (range)). Observations were made 15 minutes and 4 hours after the addition of crayfish, and then twice a day for the next two days to see which species occupied the shelter. Experiments were performed in duplicate or in quadruplicate for some size combinations.

Temperature preference

The temperature gradient apparatus measured 8 x 96 cm and was made of plexiglass (Fig. 2). At one end of the apparatus was a heater and at the other end was an aluminum coil which had cold water running through it. Water was 3 cm deep and was aerated by an air hose with pin holes in it at intervals. This aeration allowed mixing of the water in order to prevent thermal stratification, but did not disturb the temperature

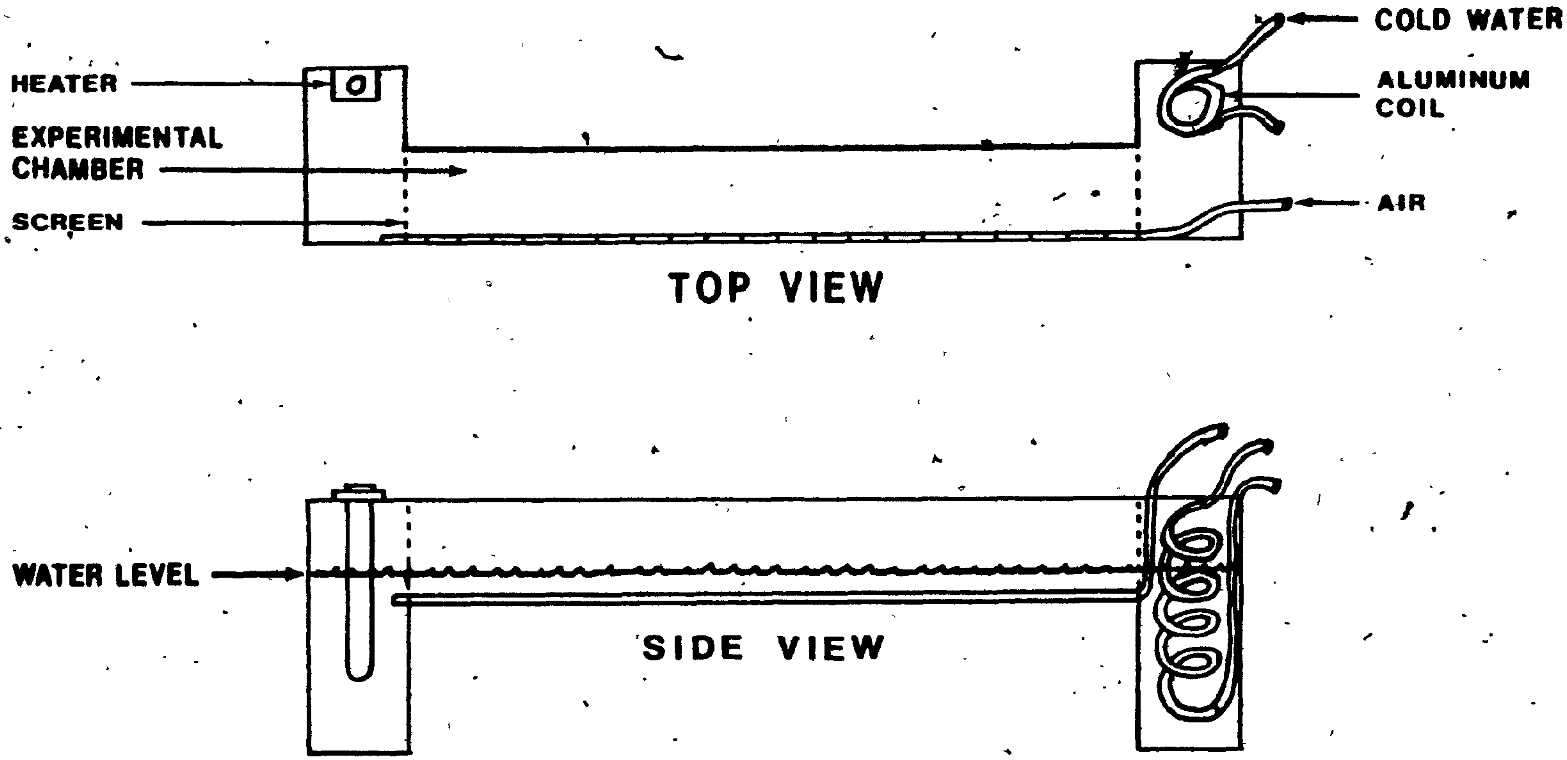

FIG. 2. Temperature gradient apparatus.

gradient. The sides of the apparatus were covered with black plastic and the bottom with black aquarium gravel. The experimental chamber was marked off into ten sections. A temperature gradient of 19 to 31°C was set up, or approximately one degree per section. The apparatus was covered overnight to prevent crayfish from escaping. Crayfish were not fed throughout the duration of the experiment in case feeding would interfere with crayfish distribution along the gradient. Orconectes virilis individuals utilized in these experiments were between 5.5 and 8.0 mm a.l., whereas O. propinquus were between 4.0 and 5.0 mm a.l. A small rock (approximately 2 cm in diameter) was placed in each of the ten sections along the side of the experimental chamber. These rocks afforded similar shelter in each section, thereby eliminating the need for crayfish to seek shelter in the corners of the chamber.

Six temperature gradient experiments were performed simultaneously with a single adult crayfish per gradient. Individuals were placed in the center of the gradient, at which point the temperature was approximately room temperature. Subjects were acclimated for 24 hours, then their positions were noted every hour for 7 to 8 hours. The temperature gradient was then reversed by switching the heater and the cooling coil. The crayfish were again acclimated for 24 hours and observed as before.

Predation by fish

To determine if fish predators prefer one crayfish species over another, a 16 cm long smallmouth bass (*Micropterus dolomieui*) was placed in a flow-through holding tank measuring 56 x 116 cm with no substrate. Twenty *O. virilis* ranging in size from 5.0 to 8.8 mm a.l. and 20 *O. propinquus* ranging in size from 3.8 to 7.1 mm a.l. were then placed into the tank without any shelter. These crayfish sizes correspond directly to the range of sizes of each species found in the study area in June and July, 1980 and 1981. The experiment was left undisturbed for two weeks. The remaining crayfish were then removed and measured.

Another experiment was performed using the same fish predator to see if the results would change when crayfish had shelters to hide in. The bottom of half the tank was covered with rocks measuring approximately 70 to 150 mm in diameter. Twenty *O. virilis* (5.0 to 8.8 mm a.l.) and 20 *O. propinquus* (4.7 to 7.1 mm a.l.) were placed in the sheltered half of the tank at night so that the fish would not see its prey until they had a chance to hide and acclimate. After two weeks, the crayfish were removed, measured, then returned to the tank as before. After another two weeks, the remaining crayfish, having undergone four weeks of predation, were removed and measured. Unfortunately, due to an insufficient quantity of crayfish of the proper size and health, these experiments could only be performed once.

Starvation

In order to determine whether crayfish death during experimentation was due to starvation, the following experiment was performed:

Eight 4 liter glass jars were filled 3/4 full of dechlorinated water, constantly aerated, and covered with black plastic to prevent algal growth. Air hoses were put through pieces of cardboard at the mouth of the jars to prevent crayfish from escaping by climbing up the air hose. Four O. propinquus and four O. virilis were placed in the jars (one crayfish per jar). Orconectes propinquus individuals measured between 5.7 and 7.1 mm a.l., and O. virilis individuals measured between 7.2 and 8.9 mm a.l. Equal numbers of males and females were utilized. All crayfish were fed the day the experiment began, but were not fed afterward. The jars were checked daily for deaths and as the water evaporated, fresh dechlorinated water was added.

RESULTS

FIELD STUDIES

Temporal changes

On May 6, 1980, crayfish were first observed along the shore of the study area. The temperature of the water along the shore was 10°C and filamentous algae of the genus Cladophora had begun to grow on the substrate. Crayfish may have reached the shore before this date since the previous sample day was April 10, at which time no crayfish were seen and the water temperature was 4.5°C. (In the spring of 1981, which was warmer than 1980, a few crayfish were observed along the shore in 5°C water on April 3.) After the first observation in 1980, the density of adult crayfish observed in the three quadrats along the shore increased during the month of May, reached a peak in June and July, then decreased until there were no adults present in the study area in late August (Fig. 3).

Young-of-the-year crayfish become free-swimming in July, then dramatically increased in number to a peak, which exceeded the adult peak threefold, in late August to mid-September. The number of young-of-the-year crayfish decreased gradually until November 14, at which time no crayfish were observed (Fig. 3). The water temperature at this time was 3.5°C.

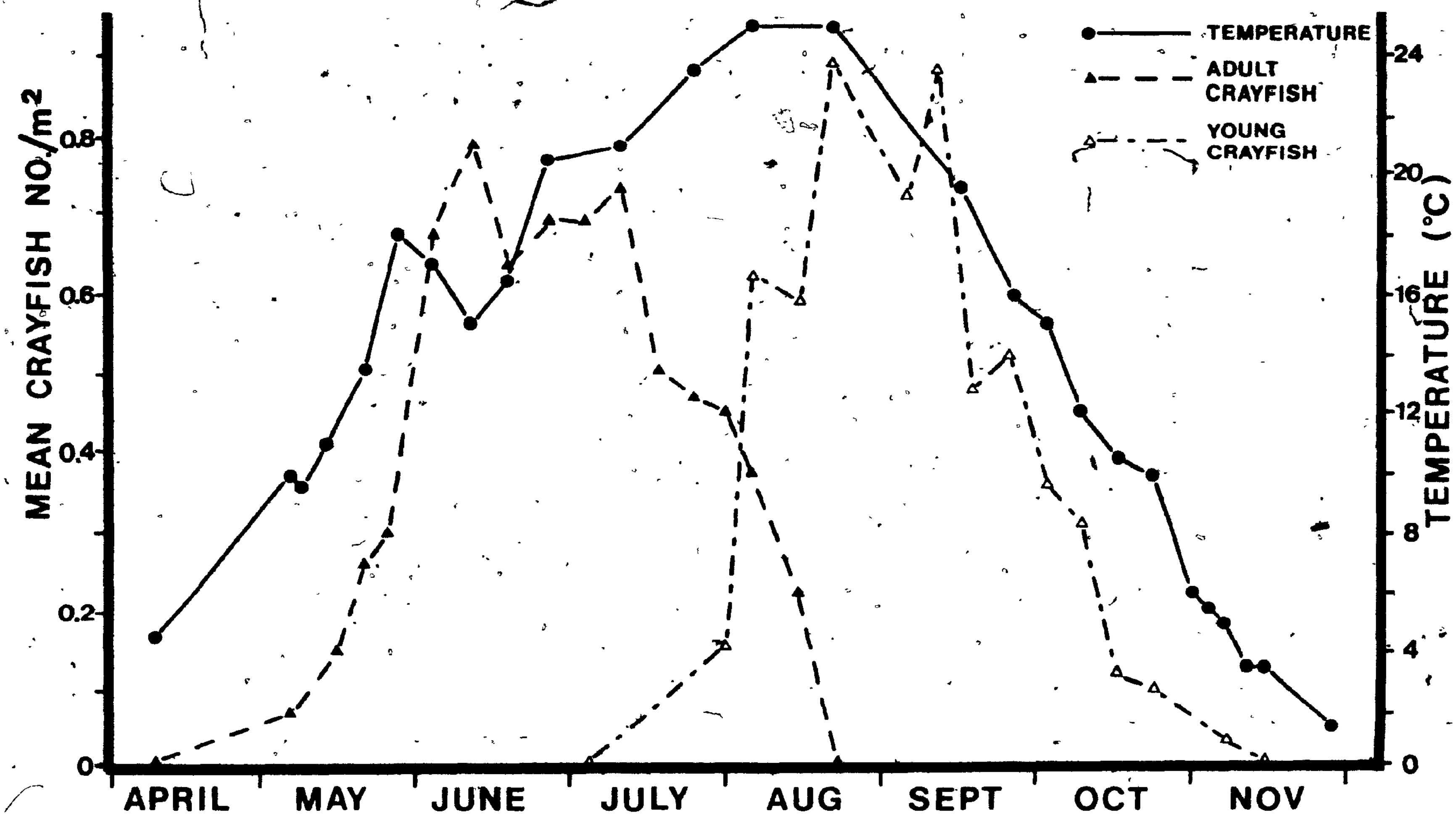

FIG. 3. Temporal changes in crayfish density and temperature in the study area in 1980. Mean young crayfish density has been divided by 3 for suitable scaling. Values are means of two sample days.

Temperature readings were taken just above the substrate, two meters from the shore, and the highest recorded temperature for the summer of 1980 was 25°C.

The mean water current 2.5 meters from shore was 0.29 m/sec, with a minimum of 0.20 m/sec in mid-June, following the growth of macrophytes in early June.

The mean adult crayfish density for the three quadrats combined changed monthly as follows: May, 0.3/m^2; June, 0.7/m^2; July, 0.6/m^2; and August, 0.3/m^2. The mean young-of-the-year densities in quadrats A and B combined were as follows: August, 2.0/m^2; September, 2.9/m^2; October, 0.8/m^2. Six crayfish, all O. propinquus, were collected during the day at a depth of approximately 5 meters by a SCUBA diver on two separate occasions in July. This small number indicates a low density of crayfish in the deep water far from shore, but the low sample number does not allow a proper comparison of near-shore and deep water crayfish densities.

Figure 4 displays the temporal change in density of adults and young of both crayfish species. Points on the graph are averages of two sample days a week. Fluctuations in mean crayfish number captured from week to week may be due, in part, to varying degrees of visibility, which depended on weather conditions, during sampling. Even with these fluctuations, the

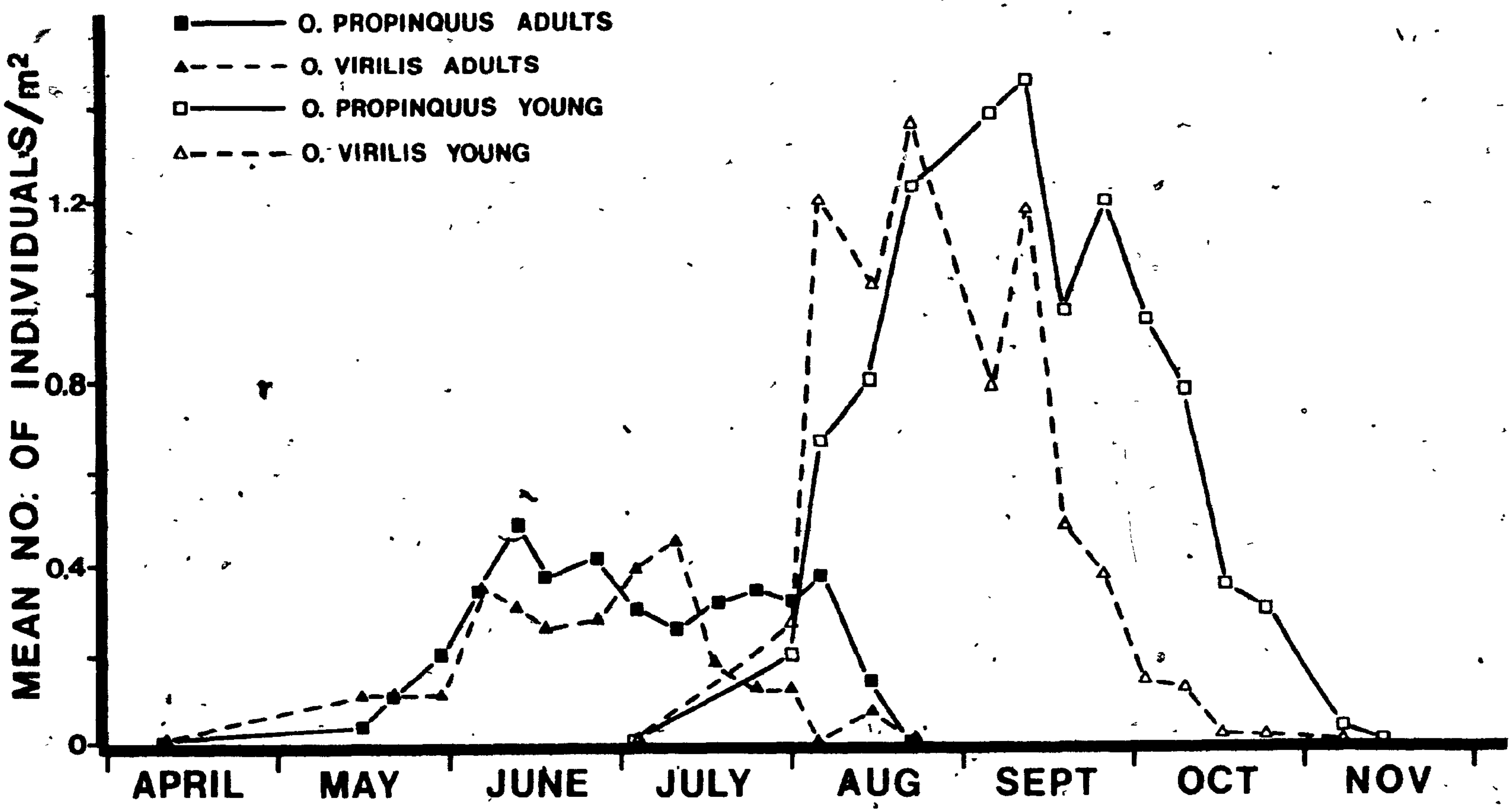

FIG. 4. Temporal changes in density of adult and young O. propinquus and O. virilis. Values are means of two sample days.

trend that *O. virilis* declined in number sooner than *O. propinquus* is still evident.

Crayfish movement

Crayfish were marked with a different code each month, but there is uncertainty as to the length of time that crayfish were actually present in the area. They may have been there since the last marking day or for the whole month. Only the least number of days spent in the study area can be known by noting the recapture date in the next month. When the least number of known days is divided into classes, an estimate of the duration of the presence of the crayfish population in the study area can be obtained (Table 1). The crayfish seemed to be constantly moving in and out of the study area since 24% of all the crayfish marked were recaptured on the next sample day, whereas only 8% were subsequently recaptured. It should be noted that adult crayfish were being marked every two to four days from May 15 to August 15, thus there was always a number of marked individuals in the population. The fact that very few of the 250 marked crayfish were recaptured suggests that the crayfish population was constantly moving, possibly with new crayfish entering and others leaving the area on a daily basis, which further implies that the population was very large.

TABLE 1. Crayfish movement in the study area. Adult crayfish were marked and recaptured twice weekly from May to August.

Least number of days spent in study area	Number of crayfish: *O. propinquus*	*O. virilis*	Total	% of marked[a]
1	142	108	250	100
2 - 4	33	26	59	24
5 - 15	7	10	19	8
16 - 33	0	3	3	1
Number moved upstream	3	4	7	3
Number moved downstream	2	6	8	3

[a]Total number marked = 250

The data also show that there was no definite migration of crayfish along the shore since they moved both upstream and downstream equally. This observation was also noted by Hazlett et al. (1974) for O. virilis.

Loss of appendages

During the sampling, adult crayfish were examined for missing appendages in order to obtain information on the hardiness of each species. Appendages were recorded as missing even if they had been lost at some previous time and were in the stage of regeneration. The results for both species of crayfish were tabulated in Table 2. Out of 168 O. propinquus adults sampled, 44% had missing appendages, whereas 62% of 137 O. virilis adults had missing appendages. The difference between percent appendages lost for each species was found to be significant ($P < 0.002$) using the test for equality of two percentages (Sokal and Rohlf 1969).

Feeding habits

Adult O. propinquus and O. virilis had similar feeding habits in June and July, as shown in Table 3. Based on stomach content analyses, both species were found to feed mainly on filamentous algae (mostly Cladophora) which was in abundance in the study area. The two crayfish species also ate macrophytes and snails, both of which existed in large quantities in

TABLE 2. Between species comparison of the number of appendages missing in whole or in part.

Appendage	Number with missing appendages: *O. propinquus*	Number with missing appendages: *O. virilis*
Antenna	34	36
Cheliped	30	32
Periopod	9	16
Other	1 (Rostrum)	1 (Uropod)
Total number	74	85
Number of crayfish sampled	168	137
Percent with missing appendages	44	62

TABLE 3. Feeding habits of adult *O. propinquus* and *O. virilis* in June and July, 1980.

Stomach contents	Percent occurrence	
	O. propinquus (n=12)	*O. virilis* (n=11)
Filamentous algae	75	64
Macrophytes	25	18
Snails	25	18
Chironimid larvae	0	9
Caddisfly larvae	8	0
Crayfish parts	8	0
Sand	92	91

the study area. Chironimid larvae, caddisfly larvae and crayfish parts were observed in the guts of some crayfish. Almost all of the crayfish examined had sand present in their stomachs and intestines. The sand had probably been ingested with the food (Capelli 1980).

Life histories

The life histories of O. propinquus and O. virilis are very similar to each other and to the generalized life history described in the INTRODUCTION. Both species laid eggs and carried them from early May to early June. The eggs hatched in June and the young were free-swimming by early July. The major differences observed between these two crayfish species included the size at which they attained sexual maturity, the number of eggs produced, egg diameter, and the rate of growth. Some aspects of reproduction of the two crayfish species are compared in Table 4. Orconectes propinquus females reached sexual maturity and extruded their eggs at much smaller sizes than O. virilis females. They also produced considerably fewer, but slightly larger eggs than O. virilis. The difference in egg diameter of the two species is significant ($F=19.68$, $P<0.001$) using one way analysis of variance (Sokal and Rohlf 1969) on 90 O. virilis and 40 O. propinquus egg diameters.

TABLE 4. Comparison of reproduction data for O. propinquus and O. virilis in the study area.

	O. propinquus		O. virilis	
	Mean±S.E.	N	Mean±S.E.	N
Size of females with eggs (mm) (areola length)	6.2 ± 0.2	23	12.4 ±0.4	15
Egg diameter (mm)	1.80±0.01	40[a]	1.72±0.01	90[b]
Egg number per female	50±8	5[c]	250±31	9[d]

[a]From 4 individuals with size range 6.2-6.4 mm a.l.
[b]From 8 individuals with size range 10.6-14.0 mm a.l.
[c]Size range of individuals: 5.4-6.4 mm a.l.
[d]Size range of individuals: 10.6-14.3 mm a.l.

Figures 5A and 5B illustrate the increase in egg number and diameter with increasing size of O. virilis. There are insufficient data to attain similar conclusions for O. propinquus. The linear regression of areola length versus egg number for O. virilis has a correlation coefficient of 0.735 (significant at $P<0.02$ using Z* transformation (Sokal and Rohlf 1969)), and the correlation coefficient for areola length versus mean egg diameter is 0.703 (significant at $P<0.05$).

Orconectes virilis grew at a faster rate than O. propinquus, as can be seen from the growth curves of young-of-the-year for each species (Fig. 6). By using cohort analysis, the growth of each crayfish species can be followed through its entire lifespan. This is done by constructing a histogram which divides all the crayfish captured each month into size classes, making it possible to see the different cohorts that were present (Figures 7 and 8). It is difficult to distinguish third or fourth year cohorts due to the lack of sufficient individuals. The numbers of young-of-the-year (1st summer) crayfish in Figures 7 and 8 are low because they are based on a one day sample, whereas the adult numbers are based on six to nine sample days. The number of crayfish in April, 1981 was very large due to a massive storm which washed vegetation and crayfish ashore, trapping the crayfish under the vegetation. From the cohort analysis one can

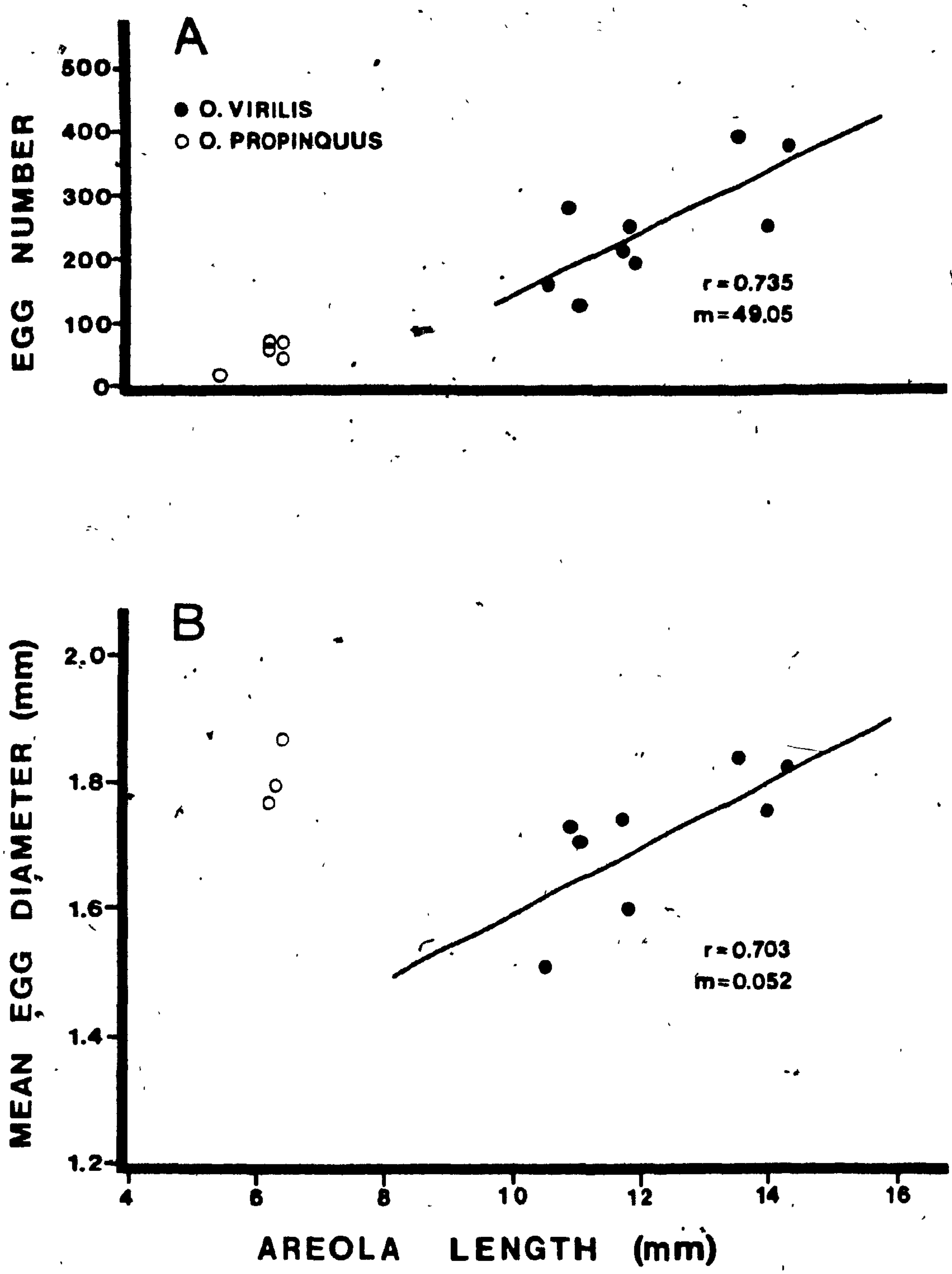

FIG. 5. Changes in (A) egg number and (B) egg diameter with crayfish size. Egg diameter values are means of 10-20 measurements per female crayfish and the standard error for all the values is ± 0.01.

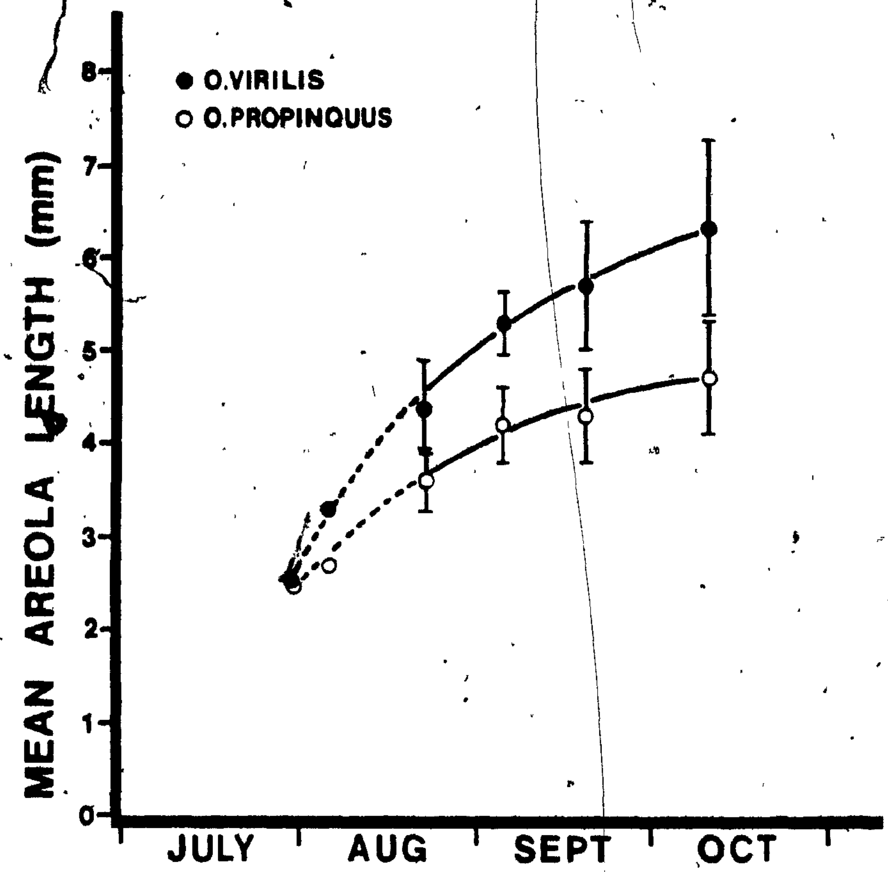

FIG. 6. Differences in growth between O. propinquus and O. virilis young-of-the-year in the study area in 1980. Values of July 30 and August 6 were estimated. Values for O. virilis are means of 15-29 individuals and values for O. propinquus are means of 27-44 individuals. Vertical lines indicate standard error.

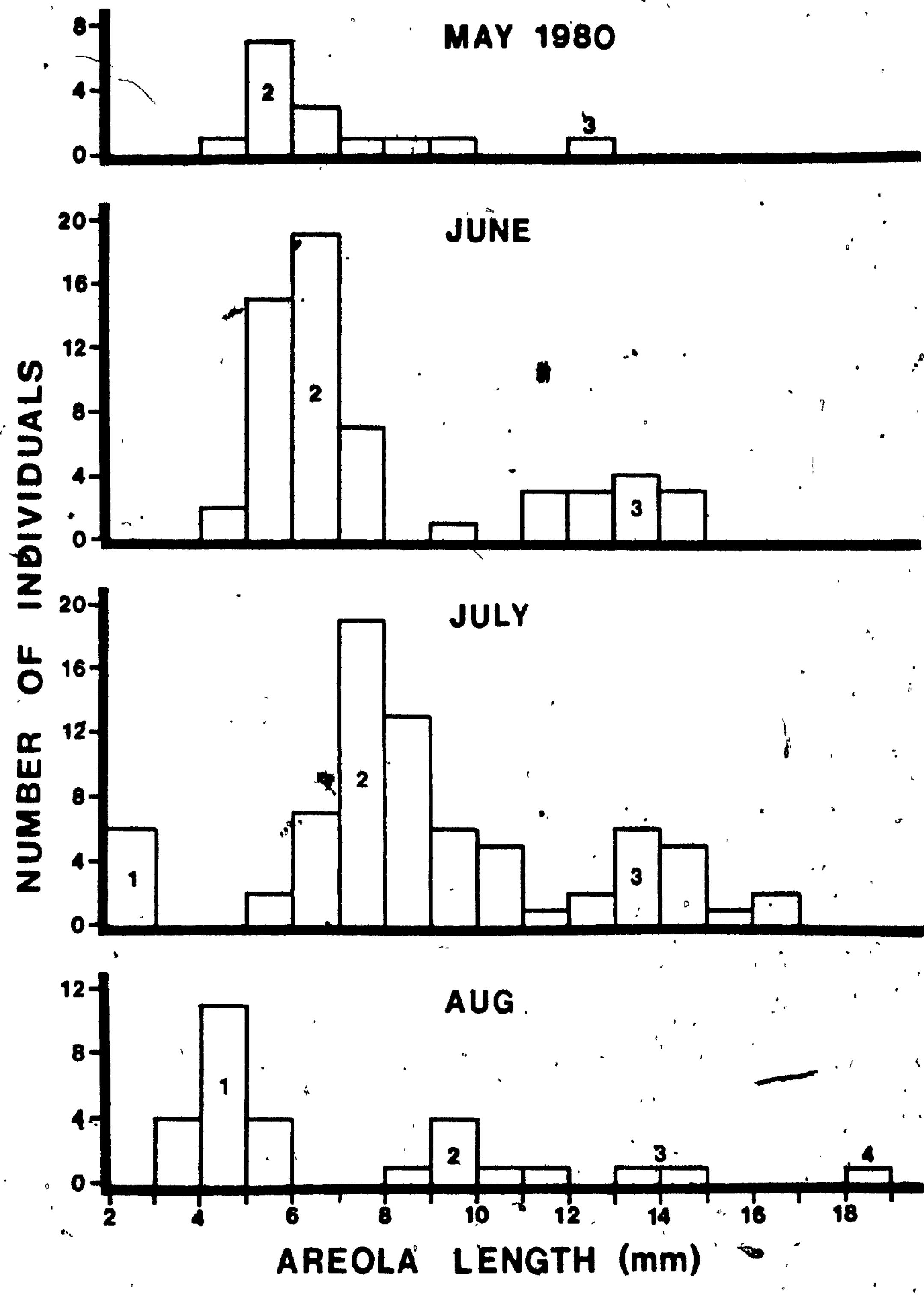

FIG. 7. Size-frequency distribution of O. virilis captured in the study area. Numbers represent cohorts in their 1st, 2nd, 3rd or 4th summer (Continued on next page).

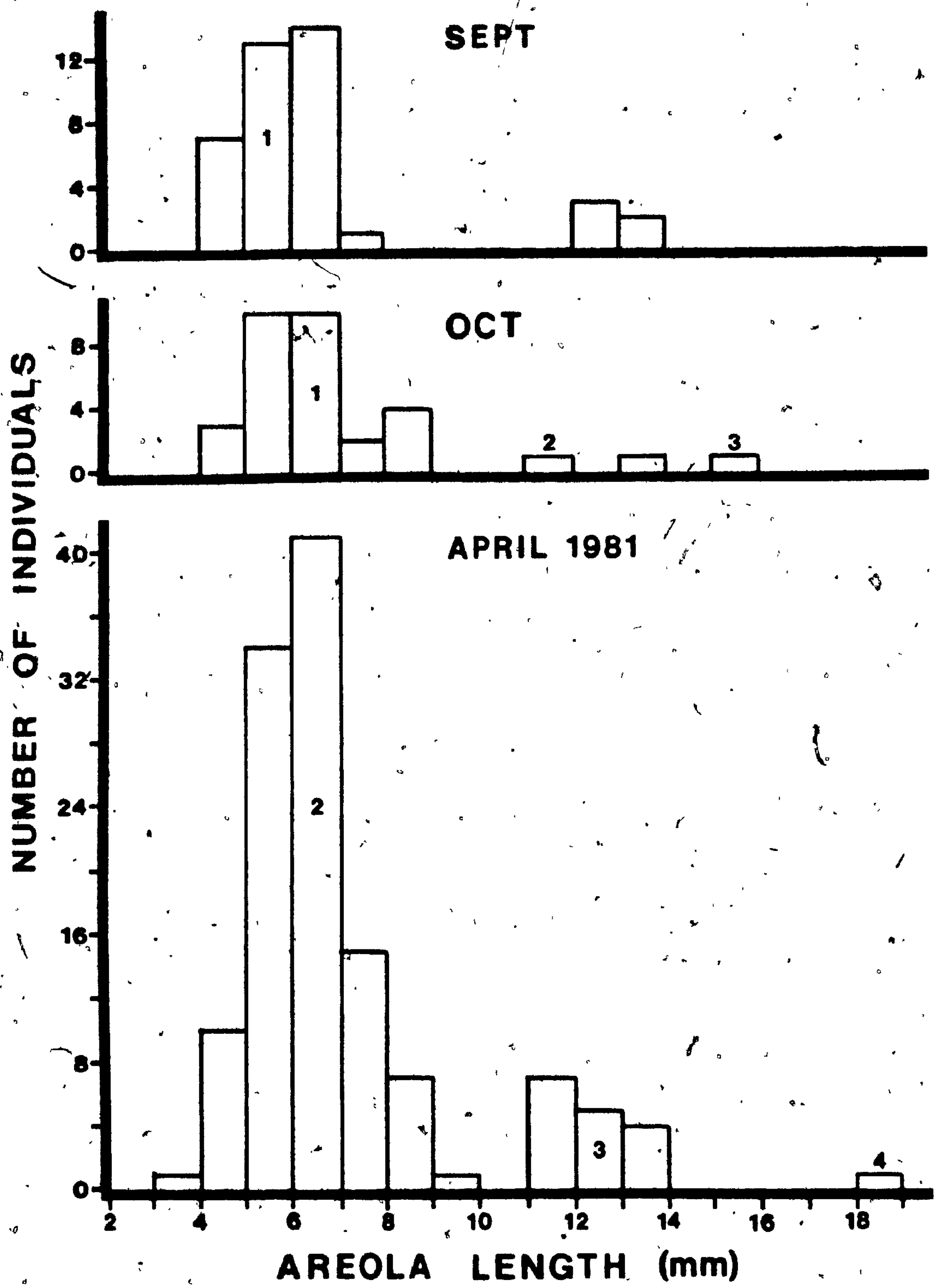

FIG. 7. (Continued)

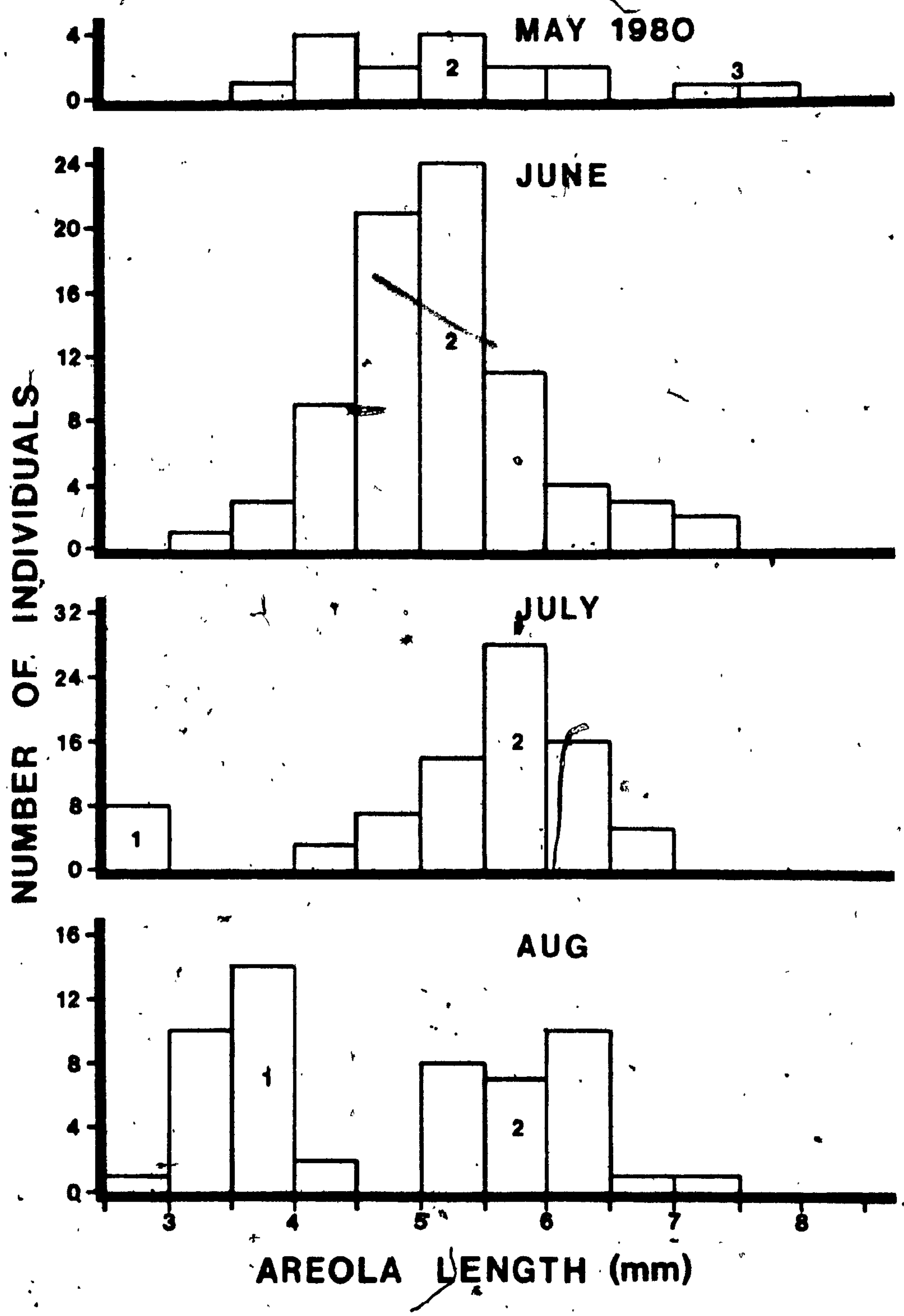

FIG. 8 Size-frequency distribution of O. *propinquus* captured in the study area. Numbers represent cohorts in their 1st, 2nd or 3rd summer. (Continued on next page).

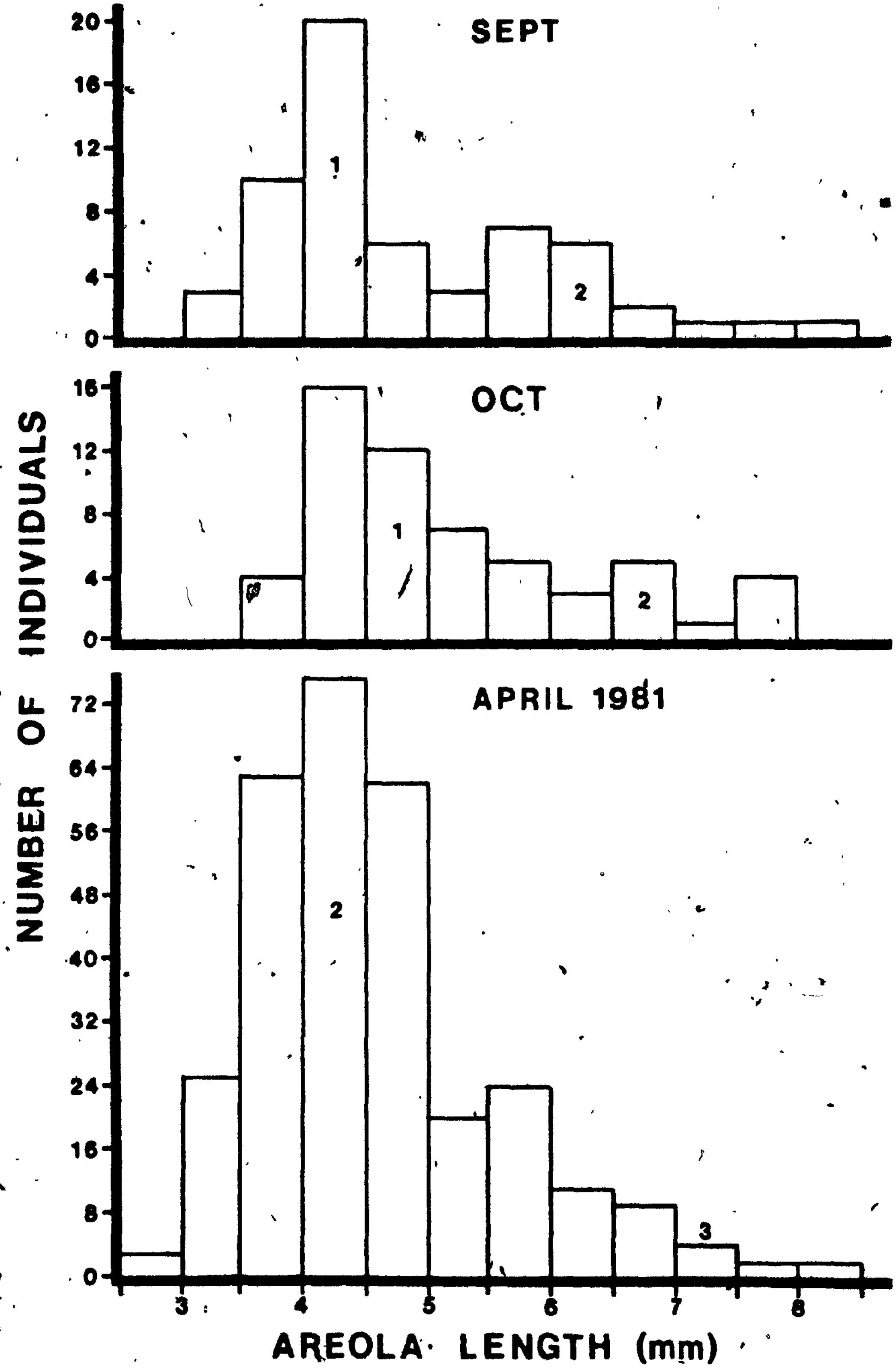

FIG. 8.A (Continued)

see that there was a large variation in individual growth rate, and that no growth occurred over the winter months. The latter is obvious since the majority of O. propinquus young-of-the-year measured 4.0 to 5.0 mm a.l. in October, 1980 and 3.5 to 5.0 mm a.l. in April, 1981. Similarly, the majority of O. virilis measured 5.0 to 7.0 mm a.l. in October, 1980 and the same in April, 1981.

During 1979, 1980 and 1981 the longest O. virilis individual captured was a female, 18.1 mm a.l. (50.2 mm c.l.), and the largest O. propinquus individual was a male, 8.3 mm a.l. (25.4 mm c.l.). This maximum size of O. propinquus, observed in the study area, is much smaller than sizes reported in the literature (Table 16).

In order to prove that my sampling methods (hand capture near shore) represented a true cross section of the crayfish population, washed-up chelae from dead crayfish, which should indicate the largest size attained by each species, were collected from not only the study area, but from along the entire southeastern shore of Nun's Island. As mentioned in MATERIALS AND METHODS, the sex of the chelae is difficult to determine, therefore, Figure 9 shows two curves. One curve assumes that all chelae belonged to male crayfish, whereas the other curve assumes that all chelae belong to female crayfish. The actual crayfish size range

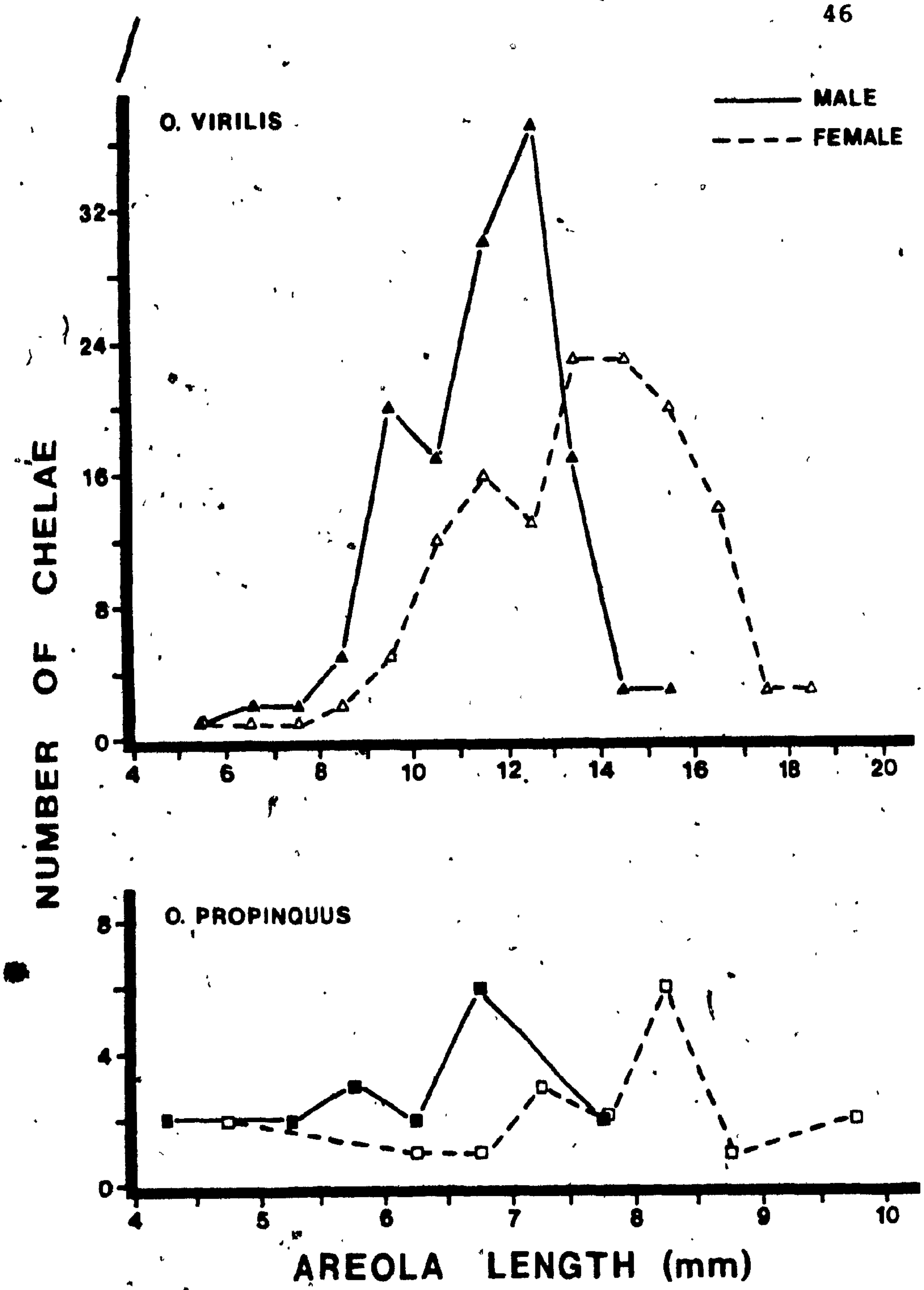

FIG. 9. Possible range of crayfish sizes in the study area inferred from chelae washed-up on shore. See text for explanation. Points are mean values of the size intervals.

lies somewhere between the range of the two curves shown. For Figure 9, chela lengths were converted to areola length using the graphs in Appendix IV. More O. virilis chelae than O. propinquus chelae are represented because numerous O. virilis chelae were found in an area other than the study area.

Microdistribution

Crayfish in the study area certainly were not randomly distributed. Tables 5 and 6 list the total number of both crayfish species captured in each quadrat in all of 1980. Orconectes propinquus (both adult and young) were more prevalent in quadrats A and B, which contained the most rocks, whereas more O. virilis were found in quadrat C, where there were few rocks. Greater numbers of both species combined (adult and young) were found in quadrat A than in either quadrats B or C.

Not only was there a difference in microdistribution along the shore (crayfish numbers decreased from quadrat A to C), but there was also a difference with distance away from the shore (Fig. 10). The majority of O. virilis were observed less than two meters from the shore, while the majority of O. propinquus were found 2 to 3 meters from the shore. Statistical analysis of the data using the chi-square test shows that the observed distributions of adult and young of each

TABLE 5. Total number of adult O. propinquus and O. virilis captured in each quadrat along the shore in 1980.

Quadrat	Adult crayfish number			
	O. propinquus	O. virilis	Total	P/V Ratio[a]
A (many rocks)	115	69	184	1.67
B (less rocks)	63	39	102	1.61
C (few rocks)	17	38	55	0.45
Totals	195	146	341	

[a]Ratio of O. propinquus number to O. virilis number.

TABLE 6. Total number of young *O. propinquus* and *O. virilis* captured in each quadrat along the shore in 1980.

Quadrat	Young crayfish number			
	O. propinquus	*O. virilis*	Total	P/V Ratio[a]
A (many rocks)	336	189	525	1.78
B (less rocks)	140	111	251	1.26
C (few rocks)	11[b]	25[b]	36	0.44
Totals	487	325	812	

[a]Ratio of *O. propinquus* number to *O. virilis* number.
[b]Sampled in August only.

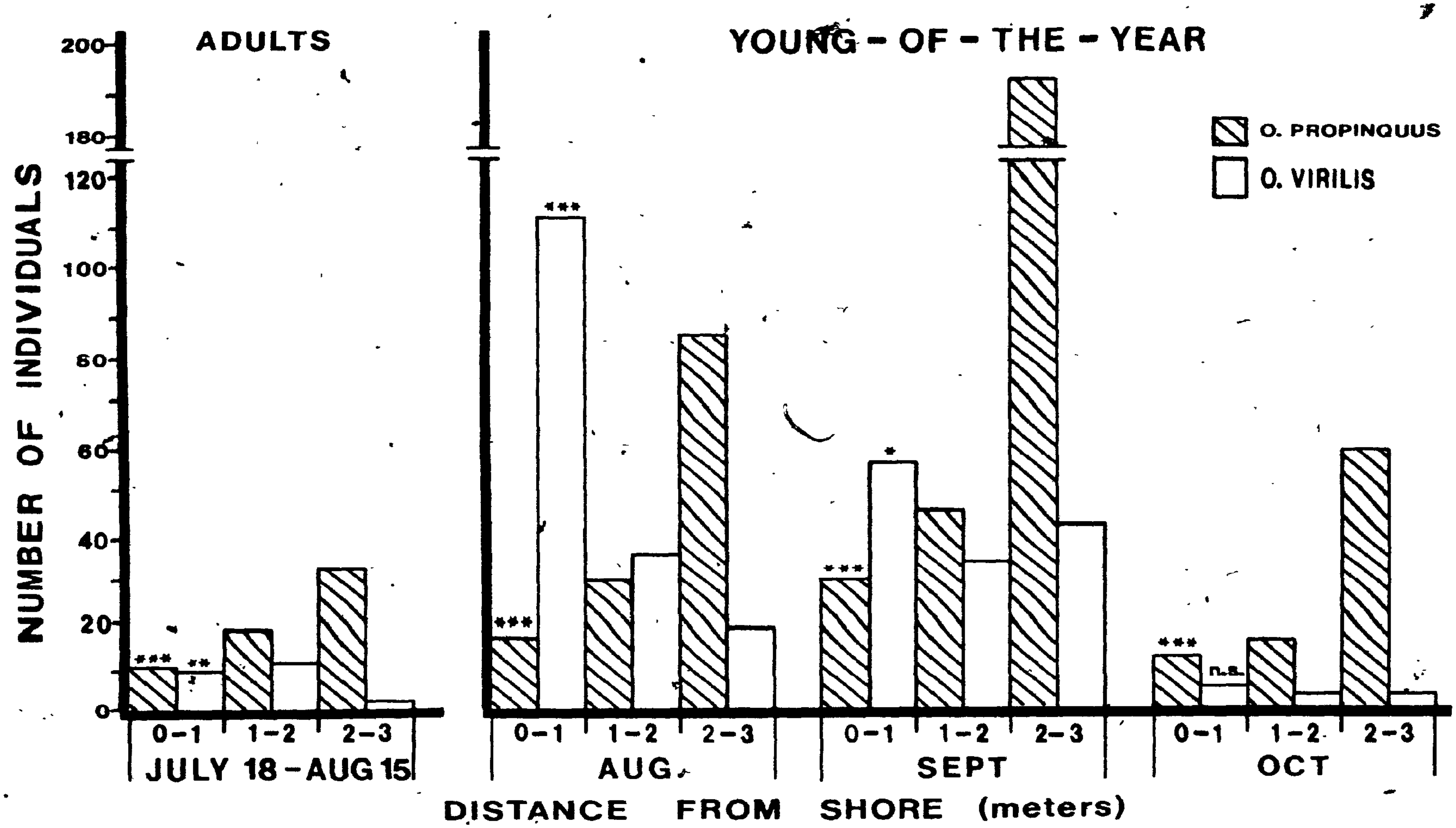

FIG. 10. Microdistribution differences between O. *propinquus* and O. *virilis* with increasing distance from shore. * indicates the probability of randomness for that species among the 3 distances from shore. n.s.=not significant; *<0.05; **<0.01; ***<0.005.

species deviated significantly from random distributions in all instances, except for in October (O. virilis).

In the summer of 1981, two other areas of the shore at Nun's Island, with different substrate particle sizes than the study area, were sampled. Unlike the particle size gradient of the study area, the stretch of shore just northeast of it had a very rocky substrate at all distances from the shore. Three days of sampling at this location yielded 29 O. propinquus, but only 7 O. virilis. In contrast to this finding, a region at the northeastern end of Nun's Island, which had relatively small substrate particles with a few very large rocks, yielded 2 O. propinquus and 35 O. virilis on one sample day. Many O. virilis were found in this area, regardless of the fact that the substrate contained large quantities of oil, but they were not found at the very polluted northern tip of the island. This indicates that there may be differences in substrate preference between the two crayfish species, O. propinquus preferring a very rocky substrate, and O. virilis preferring a less rocky substrate.

Physical factors

Since O. propinquus individuals with areola lenths of 6.0 mm have total body length of 38 to 41 mm and O. virilis individuals with areola lengths of 7.5 mm have total body lengths of 47 to 48 mm, and considering laboratory observations, it was estimated that adult O. virilis would require rocks greater than 70 mm in diameter to provide adequate shelter, whereas O. propinquus would find smaller rocks adequate. The number of rocks suitable for shelter, along with the amount of silt in each subquadrat is tabulated in Table 7. The number of large rocks increases along the shore from quadrat A to quadrat C. There is also a direct relationship between the number of rocks suitable for shelter and the distance from shore, since more are found away from shore. The amount of silt present is inversely related to the number of large rocks. Most silt is found in quadrat C and close to shore in quadrats A and B. Figure 11A, using information from Tables 5 and 6A, suggests that the number of adult O. propinquus is more closely associated with large rock number than is O. virilis (the slope of the line drawn by eye is closer to 1.00). Figure 11B, using information from Figure 10 and Table 6A, shows that O. propinquus number is directly related to large rock number away from shore, while O. virilis number is not.

On sunny days, the mean water temperature just above the substrate was warmer near shore (25.6°C) than at 1.5 (24.4°C) or 2.5 (23.6°C) meters from shore (Table 8). The 2°C temperature difference between 0.5 and 2.5 meters was shown to be significant

TABLE 7. Differences in the number of rocks suitable for shelter and amount of silt in each quadrat in relation to distance from shore.[a]

(A)

Distance from shore (meters)	Number of rocks 70mm in each quadrat along shore			
	A	B	C	Total
0-1	84	38	4	126
1-2	96	56	16	168
2-3	148	74	20	242
Total	328	168	40	536

(B)

Distance from shore (meters)	Amount of silt (volume displaced) in each quadrat along shore (mls)			
	A	B	C	Total
0-1	750	1740	1710	4200
1-2	390	240	840	1470
2-3	330	135	2550[b]	3015
Total	1470	2115	5100	8685

[a]Values are per 3 m^2.
[b]High volume due to accumulation of silt among macrophytes.

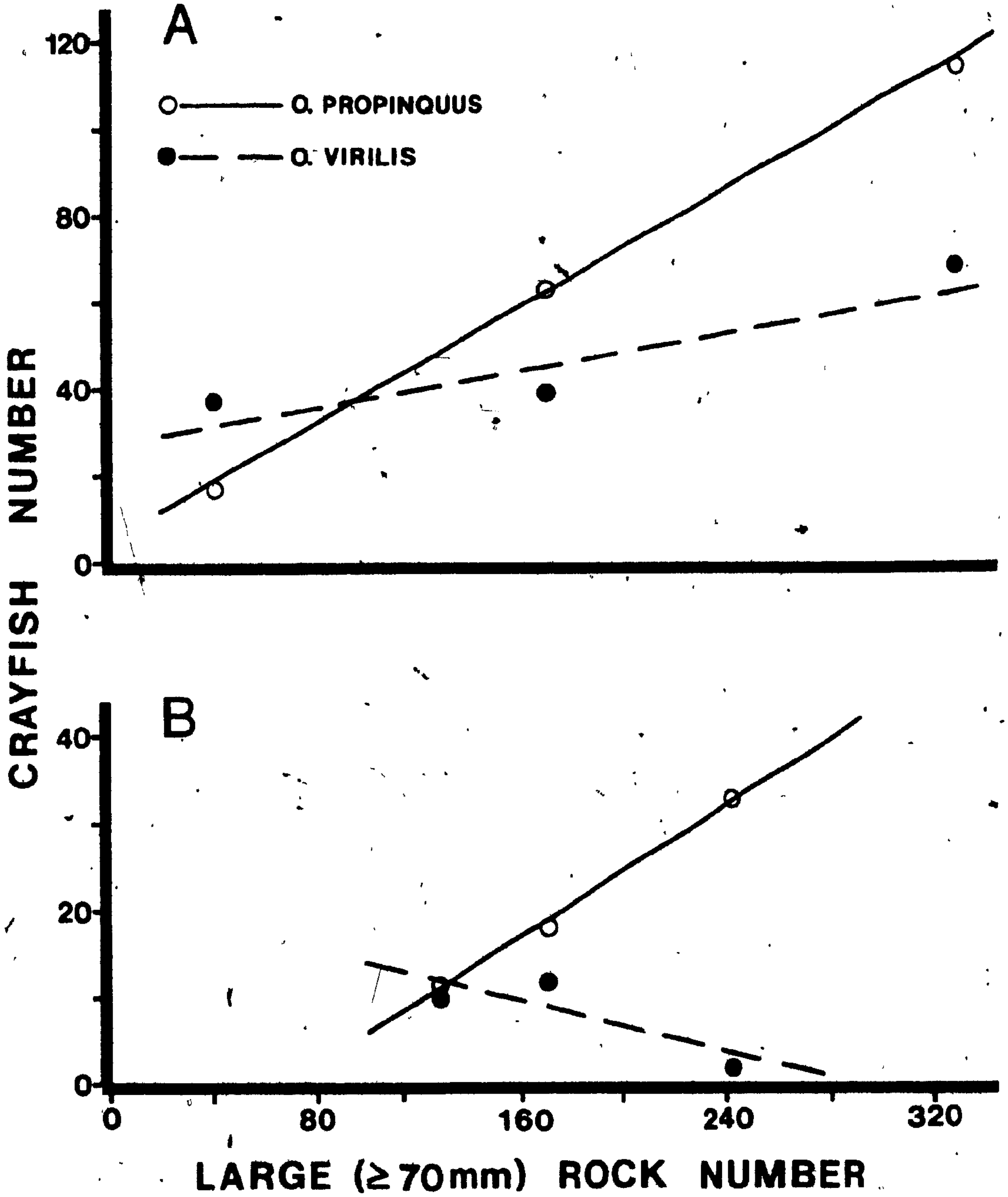

FIG. 11. Relationship between total number of adult crayfish found and total number of large rocks present. A. In each quadrat along shore. B. With distance from shore.

TABLE 8. Water temperature in relation to distance from shore on sunny days in 1980. Temperature was taken just above the substrate.

	Water Temperature (°C)			
	Meters from shore			Difference between
Date	0.5	1.5	2.5	0.5 and 2.5 meters
July 18	25	23	22	3
July 25	25	23.5	23	2
August 1	25	24.5	24	1
August 5	27	26	25	2
August 22	26	25	24	2
Mean:	25.6	24.4	23.6	2

(t=6.33, $P<0.005$) using a t-test for paired comparisons (Sokal and Rohlf 1969).

LABORATORY EXPERIMENTS

Substrate particle size preference

When placed on a size gradient of rocks, O. virilis always preferred larger rocks, at crayfish densities of 9, 18 and $27/m^2$ (Fig. 12). The distributions were found to be significantly different from random distributions by using the chi-square test. Orconectes propinquus, on the other hand, did not always show a significant preference for any one substrate particle size, although more individuals were observed on the large rocks.

When 40 crayfish were used ($36/m^2$), and when the experimental tubs were reversed, O. virilis still displayed the same significant preference for large rocks, whereas, O. propinquus showed a preference for only the large rocks in two out of three cases (Fig. 13).

To see if the observed distributions above would change when both crayfish species were together, 20 of each species were placed in the same tub, in duplicate experiments (Fig. 14). The result was a distribution similar to those previously observed. Orconectes virilis showed a highly significant preference for the large rocks, whereas O. propinquus did not.

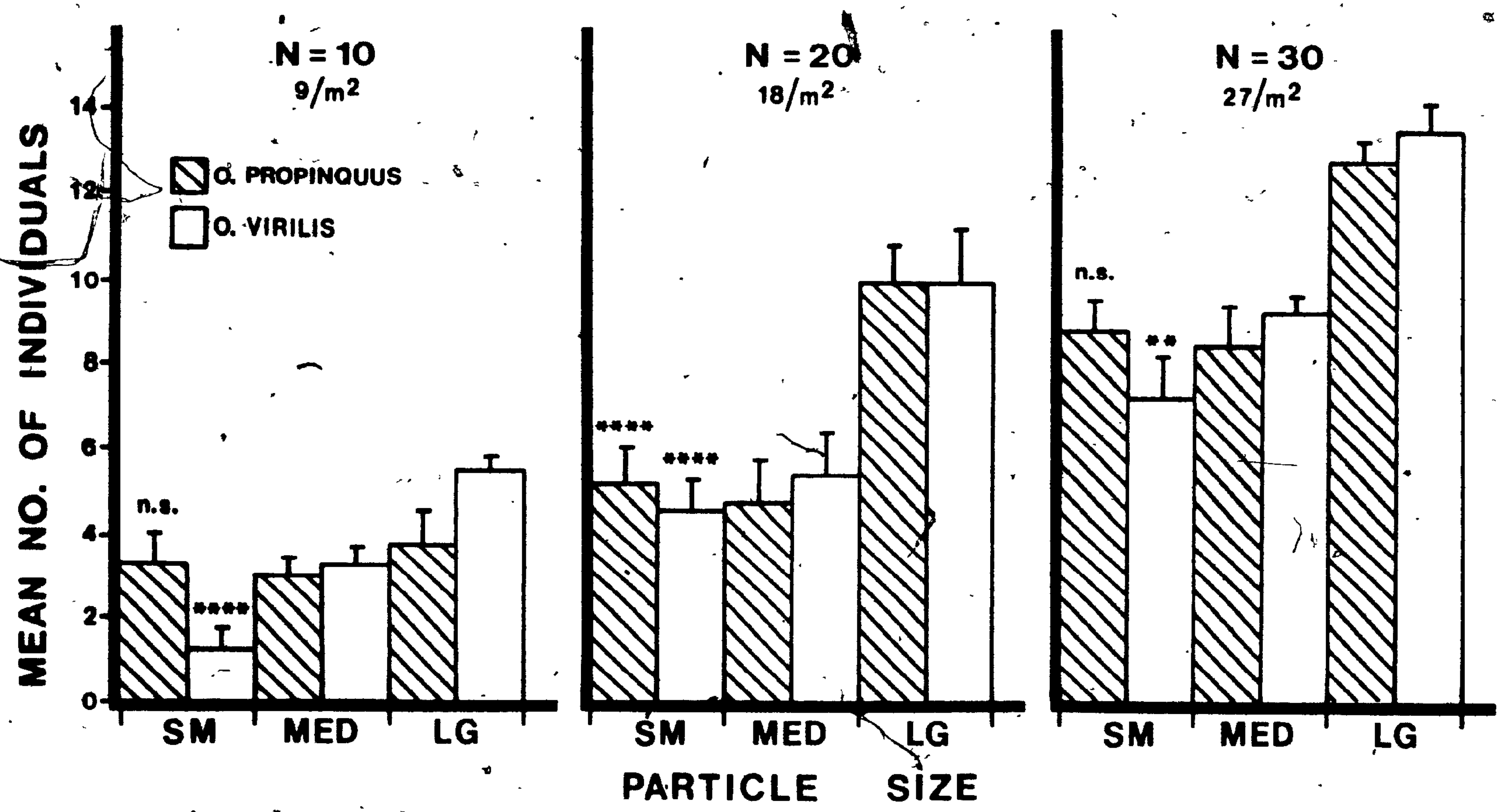

FIG. 12. Substrate particle size preference at different crayfish densities (each species separate). *Above a column indicates that the distribution of that species is non-random. n.s.=not significant; *<0.1; **<0.025; ***<0.01; ****<0.005. SM<30mm diameter; MED=30-100mm diameter; LG=100-200mm diameter. Values are means of 4 observations (one per day). Vertical lines indicate standard error.

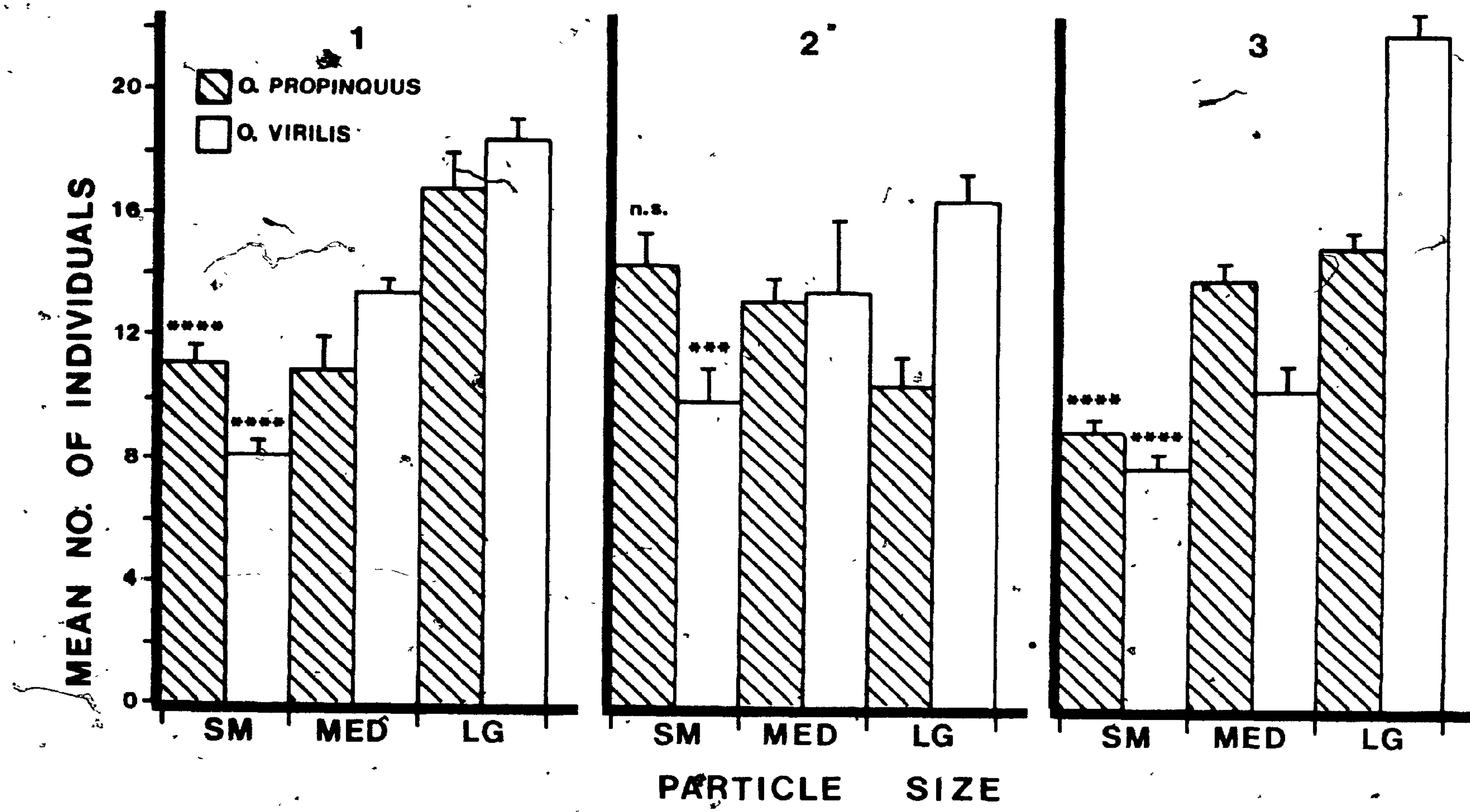

FIG. 13. Substrate particle size preference in 3 experiments (each species separate.) N=40 ($36/m^2$). In experiment 3, experimental tub was reversed. For explanation of significance levels (*) and substrate particle sizes, see Fig. 12. Values are means of 10 observations (one per day). Vertical lines indicate standard error.

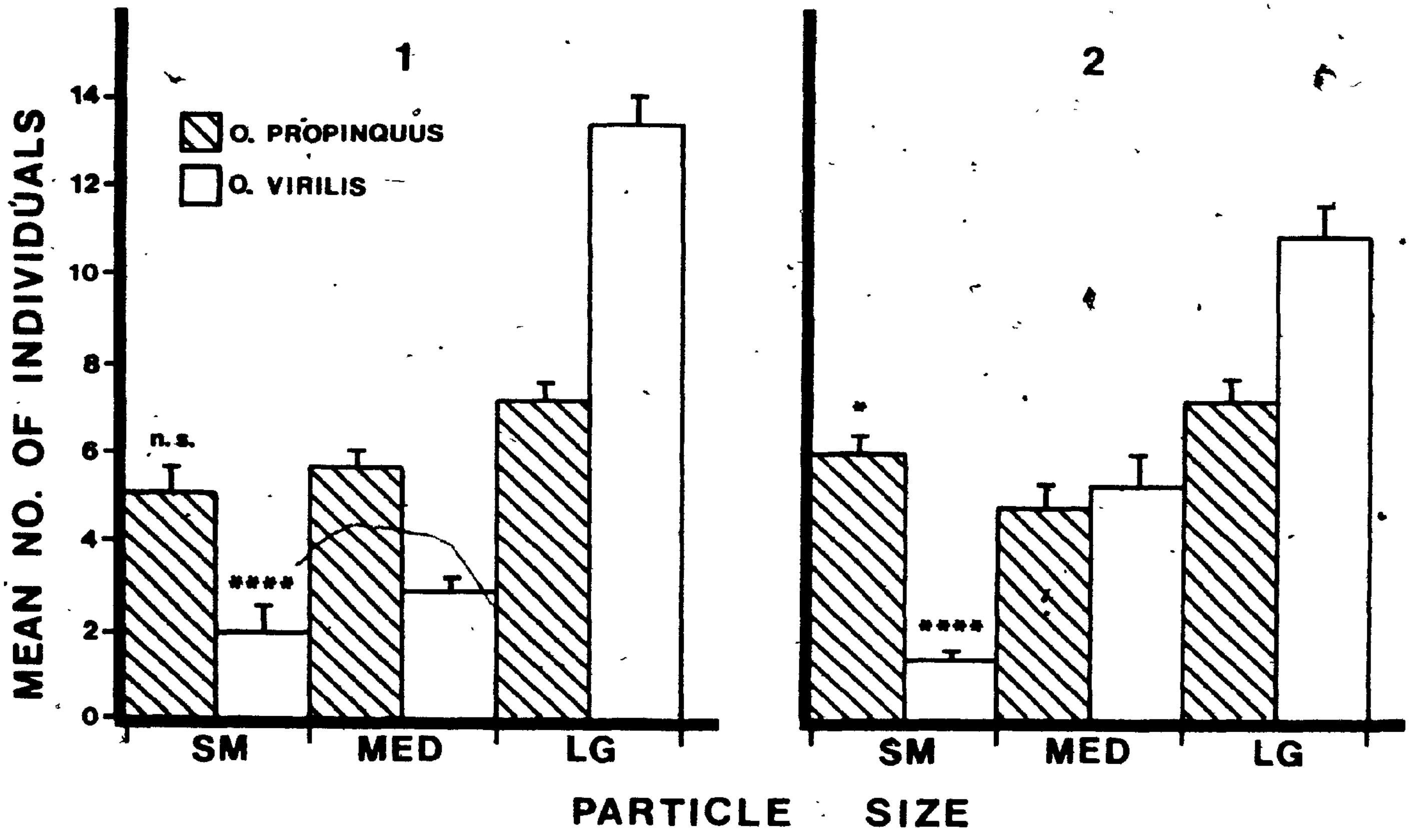

FIG. 14. Substrate particle size preference in duplicate experiments (both species together). N=20+20 ($36/m^2$). For explanation of significance levels (*) and substrate particle sizes, see Fig. 12. Values are means of 10 observations (one per day). Vertical lines indicate standard error.

When different substrate types (sand, gravel and rock) were offered, both crayfish species chose the rock substrate, although O. virilis preferred it more than O. propinquus, since more of the latter were observed on the sand and gravel substates than were O. virilis (Fig. 15). As the density of crayfish was gradually increased from 33 to 133/m^2, no significant change in distribution was noted. Figure 15 shows the mean number of crayfish, over all the densities, that was observed on each substrate type. When each species was separate, the crayfish that had been newly captured from the study area (Figure 15B) distributed themselves in a manner essentially identical to those crayfish that had been kept in captivity for several months (Figure 15A). When each species was separate, more newly captured O. propinquus were observed on the gravel than captive O. propinquus because they were smaller than the captive individuals and were, therefore, able to find shelter among the gravel particles. When both crayfish species were placed together, the newly captured individuals distributed themselves differently than the crayfish held in captivity. Seventeen percent more O. propinquus and 24% less O. virilis were observed occupying the rock substrate than crayfish that had been kept in captivity. This pattern more closely resembled the distribution in the field than did the observations illustrated in Figure 15.

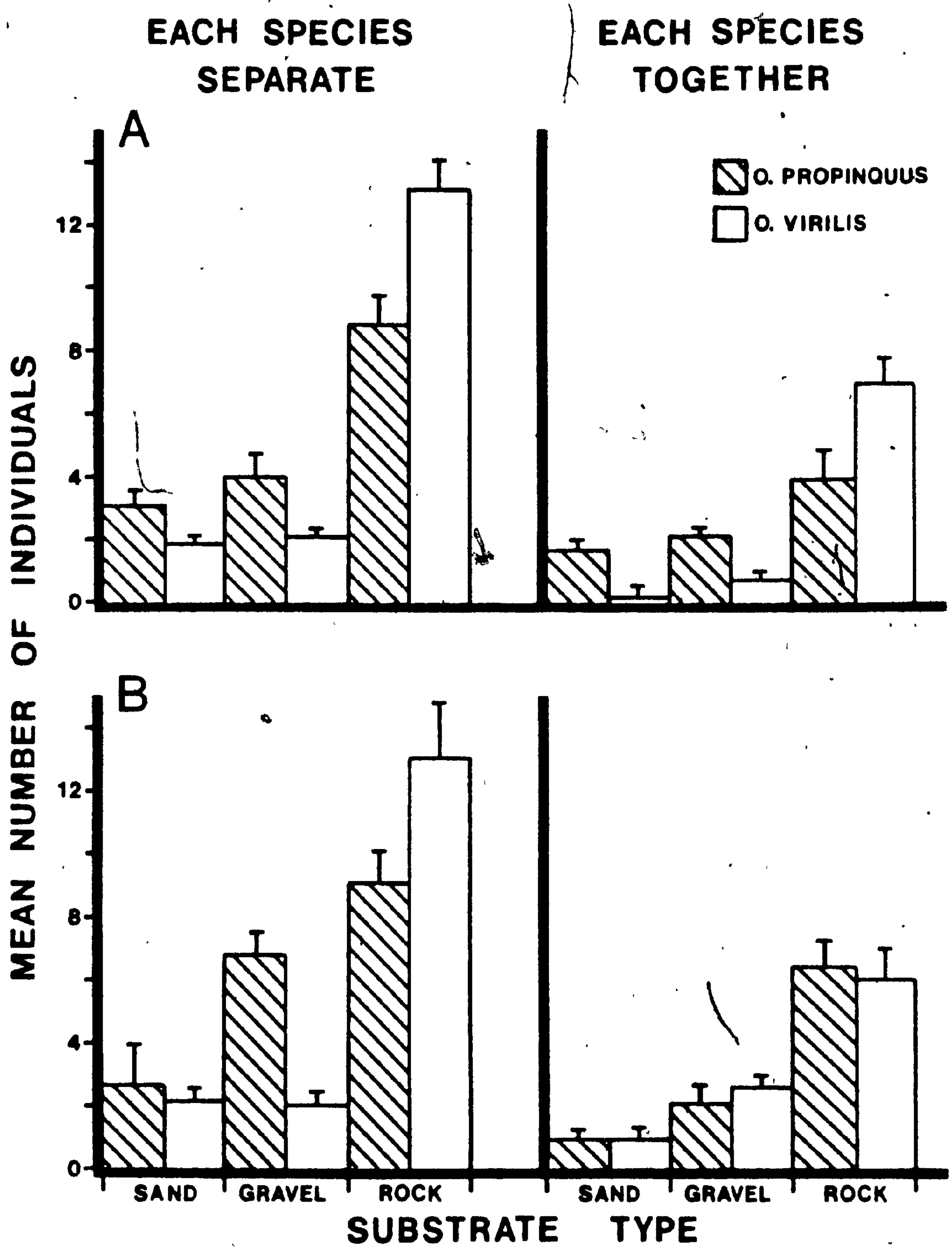

FIG. 15. Substrate preference on different substrate types.
A. Crayfish in captivity for several months.
B. Newly captured crayfish. All distributions are significantly non-random (P<0.005). Sand<1mm diameter; gravel=5-20mm diameter; rock=60-100mm diameter. Values are from 4 different density experiments (33, 67, 100 and 133 crayfish/m²) combined. Values are means of 8 observations (one per day) for each species separate and 16 observations (one per day) for each species together. Vertical lines indicate standard error.

Distribution with a predator

When a smallmouth bass (Micropterus dolomieui), a predator of crayfish, was introduced into a tub which contained both crayfish species, the number of individuals on the small rocks declined drastically (Table 9). The number of crayfish on the large rocks could not be determined by counting the number of crayfish on the small and medium sized rocks, since some of the crayfish were eaten by the bass, the significance of the changes in crayfish numbers after predation were obtained by performing one way analyses of variance on the raw data.

Aggression studies

Crayfish dispersal may be an innate tendancy found in some species with intra-specific aggression (Bovbjerg 1959; Mobberly and Owens 1966). A difference in dispersal behavior between the two crayfish species in the present study was noted each time they were placed in a tank which contained rocks. Orconectes virilis individuals would find the nearest shelter and remain there, even though they were close to others of the same species (sometimes two under the same rock), and moved very little. Most O. propinquus individuals, on the other hand, moved to the ends of the tub within one minute. Then for ten minutes or so they would move about greatly, and aggressive displays were common when

TABLE 9. Change in crayfish distribution with a fish predator, on a substrate particle size gradient. N=40. Values are means of 7 observations (one per day) for the control, and 12 observations (one per day) with the predator. (S.E. = standard error, N.S. = not significant).

	Mean number of crayfish observed ± S.E.		Significance level of change
	Before predation (control)	During predation (exp.)	
Small rocks:			
O. virilis	7.1 ± 0.7	0.8 ± 0.4	0.001
O. propinquus	3.4 ± 0.4	0.3 ± 0.2	0.001
Medium rocks:			
O. virilis	6.9 ± 0.6	5.7 ± 0.8	N.S.
O. propinquus	6.7 ± 0.4	4.8 ± 0.4	0.01

another individual was encountered. Less movement took place after this period. The O. propinquus individuals that remained in the area where they were introduced did not stay close to any other individual. Orconectes propinquus was also observed to be more active than O. virilis during the night, when examined under red colored light.

To study the level of aggressive behavior in each crayfish species, individuals of each species were "pitted" against one another in an arena and the winners of the aggressive contacts were noted. A total of 59 experiments were performed in duplicate or triplicate using 16 size combinations of females and 12 size combinations of males. The mean number of successful aggression contacts for each species, as well as mean weights and mean chela lengths, were plotted against the mean size difference between the two species for each size class of males and females (Figures 16A-E). Orconectes virilis size was kept constant while O. propinquus size was varied. The graphs demonstrate that, as O. propinquus decreases in size in relation to O. virilis, its weight, chela length, and number of successful aggression contacts decreases. Size, weight and chela length are all significantly correlated with the number of successful aggression contacts (Table 10).

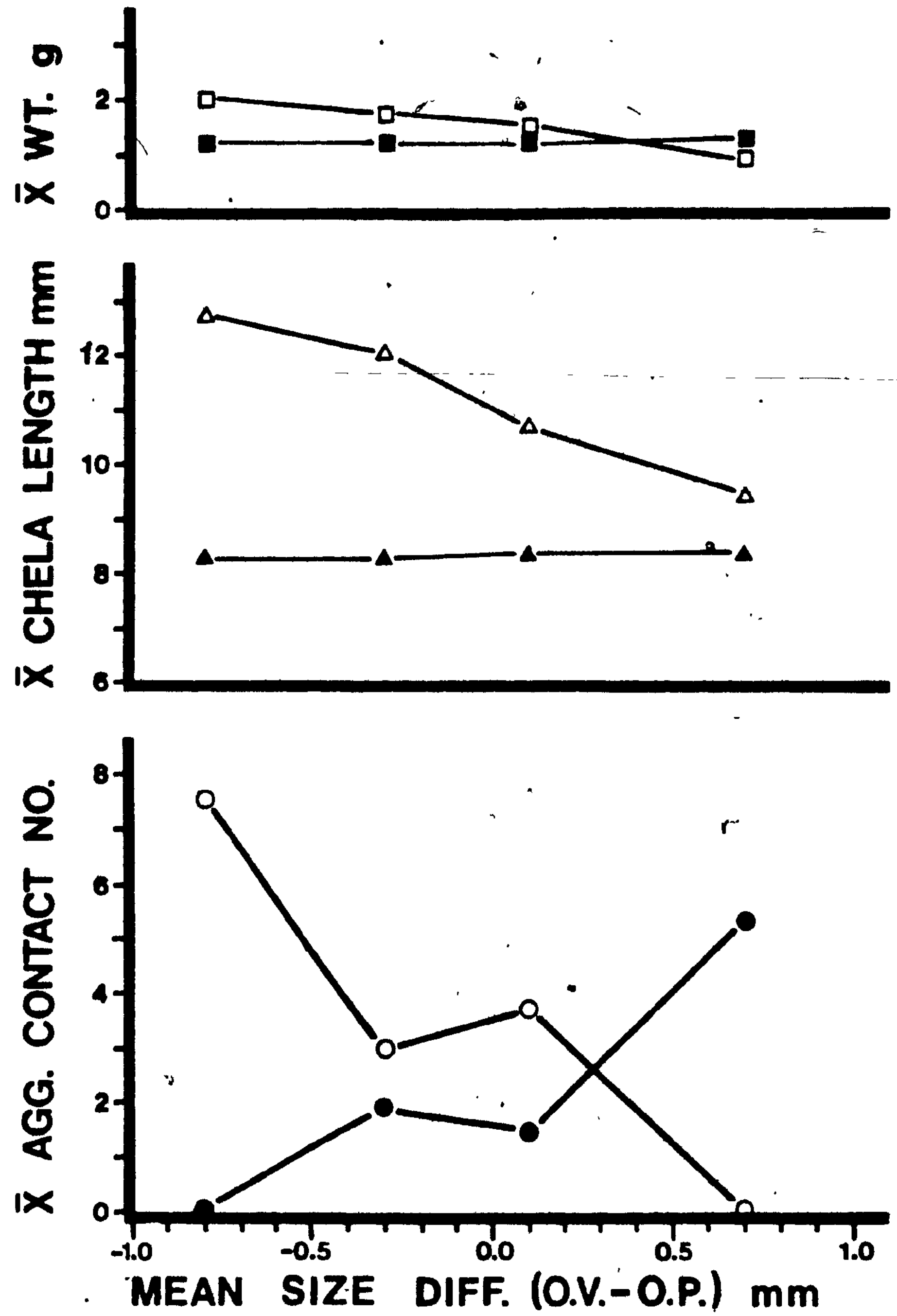

FIG. 16. Differences in number of successful aggression contacts, chela length and weight between crayfish species with decreasing O. propinquus size. Values are means of 2 or 3 experiments. Sizes are areola lengths. Open symbols = O. propinquus; closed symbols = O. virilis.

A. Females; mean O. virilis size is 5.7mm a.l.

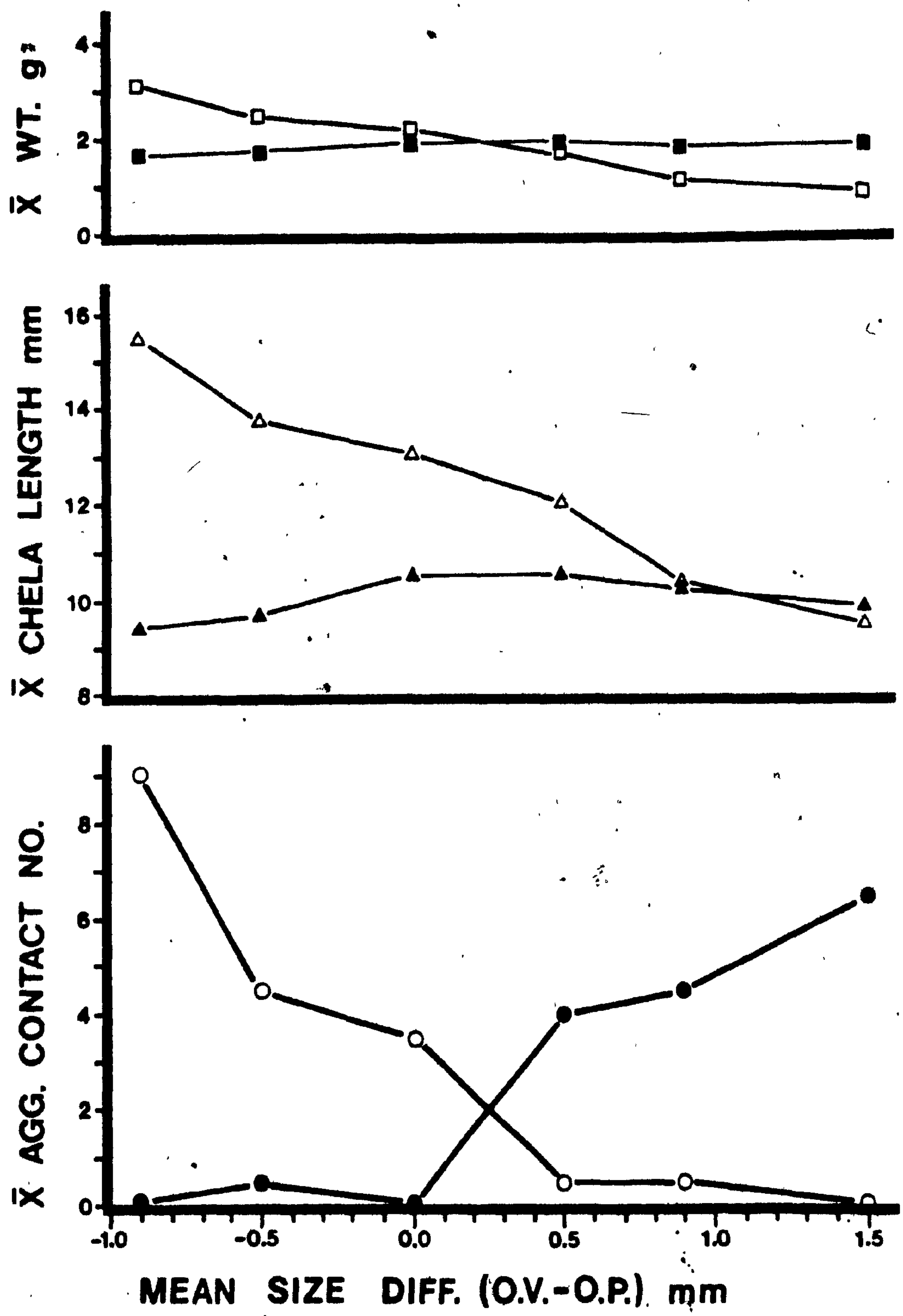

FIG. 16B. Females; mean O. virilis size is 6.5mm a.l.

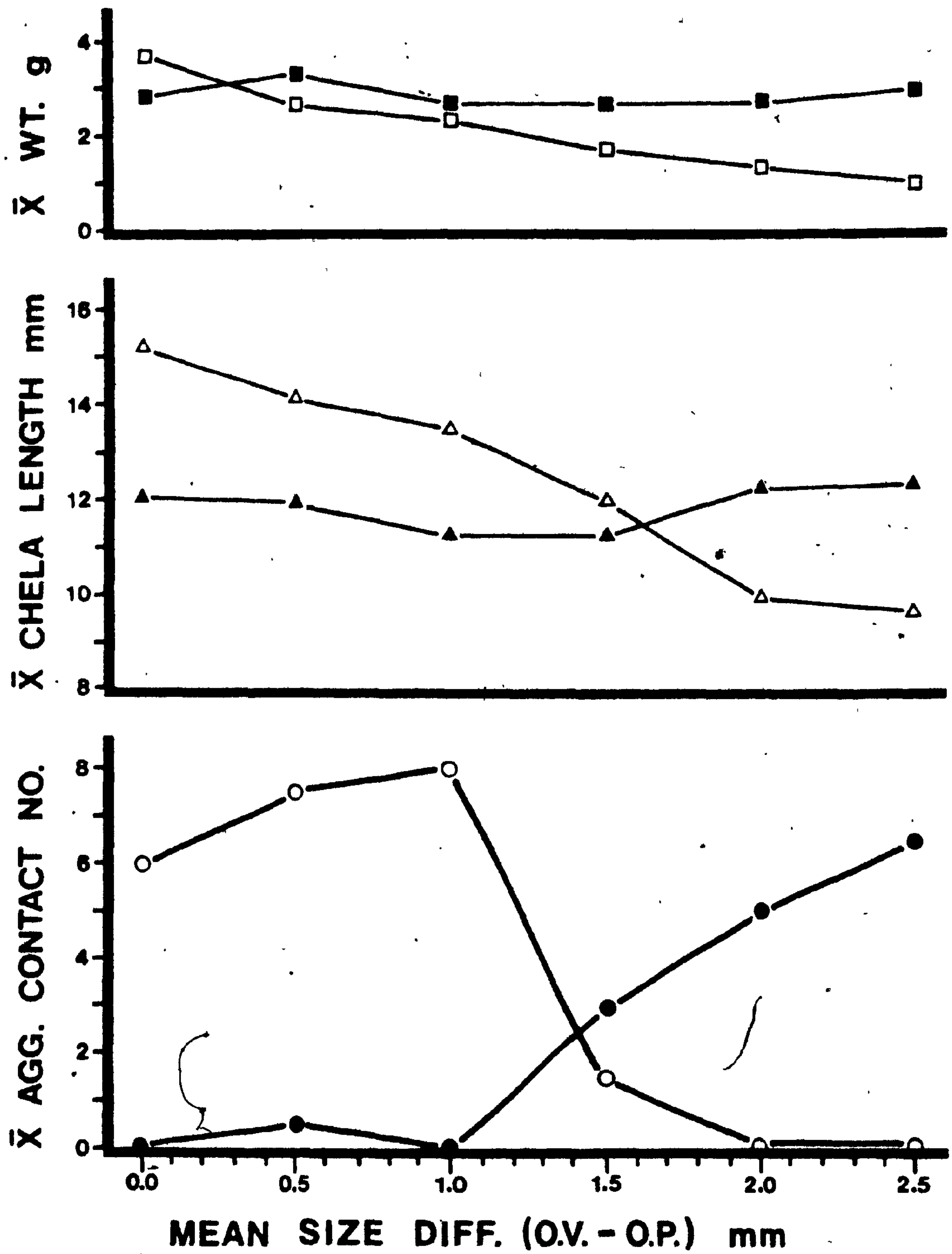

FIG. 16C. Females; mean O. virilis size is 7.5mm a.l.

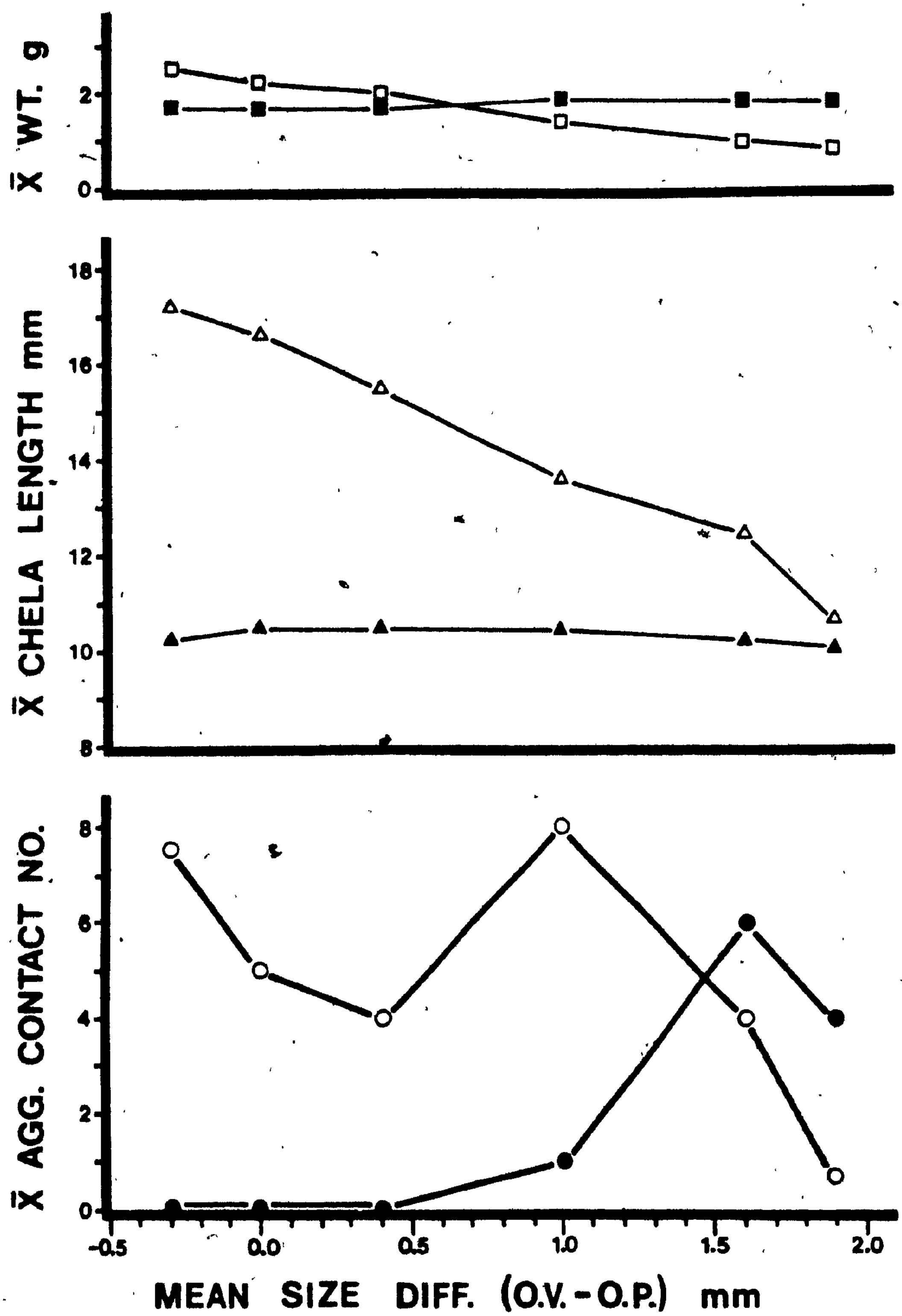

FIG. 16D. Males; mean O. virilis size is 6.6mm a.l.

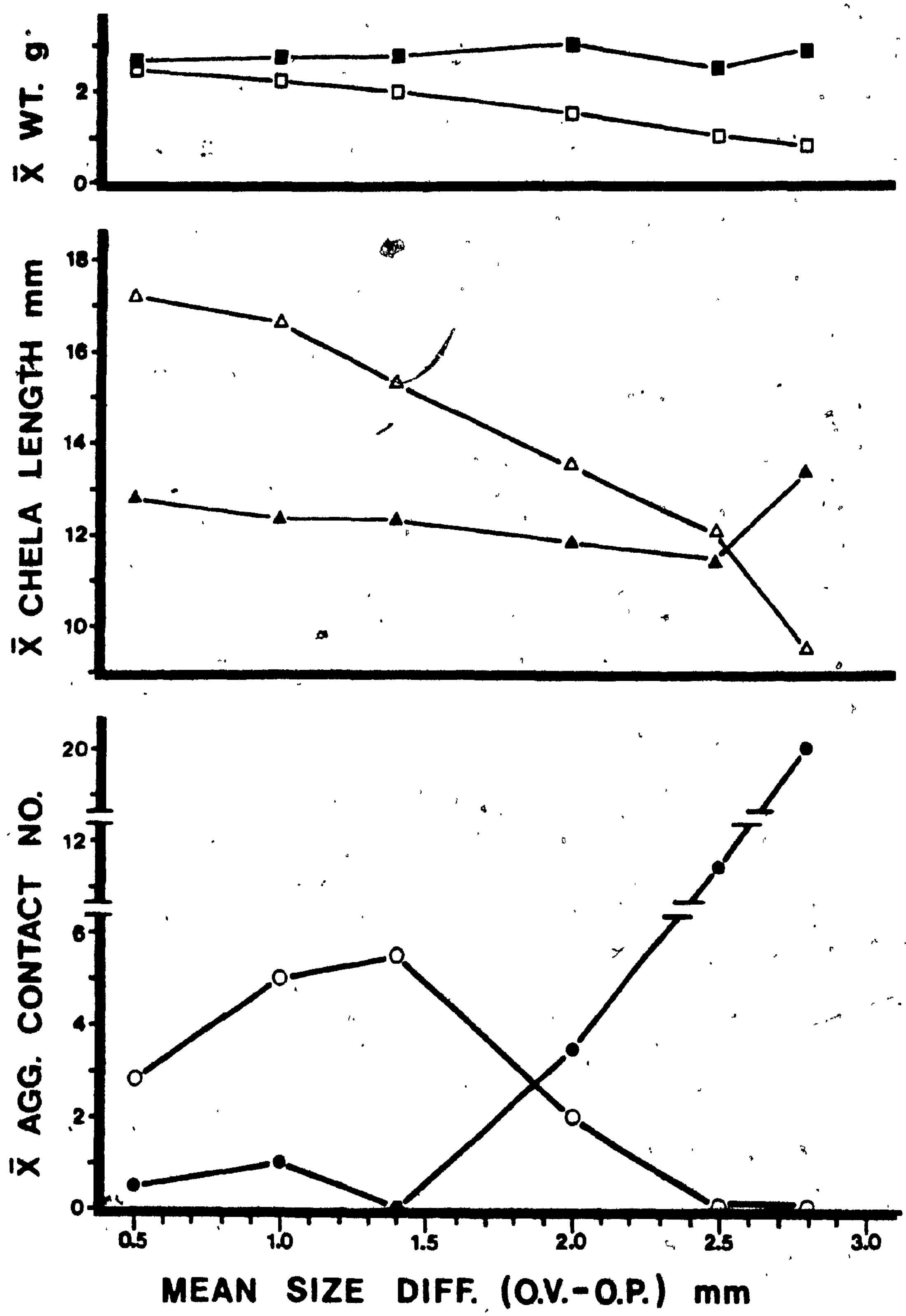

FIG. 16E. Males; mean O. virilis size is 7.5mm a.l.

TABLE 10. Relationship between certain body measurements and the number of successful aggression contacts. (Values in parentheses denote significance levels).

Mean *O. virilis* size (mm)	N	Correlation coefficient Size	Weight	Chela length
Female				
5.1	12	0.827(.001)	0.820(.005)	0.826(.001)
6.5	11	0.900(.001)	0.920(.001)	0.926(.001)
7.6	11	0.872(.001)	0.780(.005)	0.913(.001)
Male				
6.6	14	0.793(.001)	0.643(.025)	0.795(.001)
7.5	11	0.752(.01)	0.803(.005)	0.824(.005)

A high degree of variability was observed between individual aggression levels. To find the size difference at which the two crayfish species were equally aggressive, the mean number of successful aggression contacts for each size pair tested were plotted, and the intersection of the two lines was considered to represent the size difference at which aggression between the two species was equal. From Figures 16A-E and Table 11A, it can be seen that at equal sizes, _O. propinquus_ is always more aggressive than _O. virilis_. When the points of equal aggression are compared, the degree to which _O. propinquus_ can be smaller than _O. virilis_ yet still be equally aggressive is revealed (Table 11B). Female _O. propinquus_ may be 5 to 19% smaller than female _O. virilis_ and be as aggressive, whereas male _O. propinquus_ may be 23 to 25% smaller than male _O. virilis_ and be equally aggressive. This indicates that small male _O. propinquus_ are as aggressive as larger female _O. propinquus_.

Shelter occupation

Crayfish were observed hiding in shelters during the day and leaving their shelters to forage at night. Experiments in which crayfish species were forced to compete against each other for shelter were performed by placing one crayfish from each species in a tank

TABLE 11 A. Differences[a] in weight, chela length, and number of successful aggression contacts at each O. virilis size when both species are of equal size. Values are derived from Figures 16A-E.

Mean O. virilis size (mm)	Mean weight difference (g)	Mean chela length difference (mm)	Mean contact number difference
Female			
5.7	-0.3	-2.7	-1.9
6.5	-0.5	-2.5	-3.5
7.5	-0.8	-3.1	-6.0
Male			
6.6	-0.5	-6.1	-5.0
7.5	-	-	-

B. Differences[a] in weight, chela length, and size at each O. virilis size when the number of successful aggression contacts is equal for both species. Values are derived from Figures 16A-E.

Mean O. virilis size (mm)	Mean weight difference (g)	Mean chela length difference (mm)	Mean size difference (mm)	Percentage that O. p. is smaller than O. v.
Female				
5.7	0.1	-1.9	0.3	5.3
6.5	0.0	-2.0	0.3	4.6
7.5	0.8	-1.0	1.4	18.7
Male				
6.6	0.7	-2.5	1.5	22.7
7.5	1.3	-1.9	1.9	25.3

[a]All differences are O. virilis - O. propinquus

which contained only one shelter. To lessen the probability that chance, and not species interactions, dictated which species occupied the shelter, observations were made on three consecutive days allowing two nights of foraging activity and subsequent occupation of the shelter. The individual that consistantly occupied the shelter should presumably be the more aggressive or defensive of the two. A total of 26 experiments were performed in duplicate or quadruplicate using four size combinations of females and five size combinations of males. The size of O. virilis was kept constant (6.5 mm a.l.) while O. propinquus size was varied. The "winners" of the shelter competition were more accurately determined after one and two days, rather than after 4 hours, and the results show that male and female O. propinquus up to 1.0 mm a.l. smaller (15%) than O. virilis usually occupied the shelter after this period of time (Table 12). Orconectes virilis almost always occupied the shelter after 15 minutes (89%), but after 4 hours, some O. propinquus had pushed O. virilis out of the shelter and had taken up residence themselves (56%). The weights and chela lengths of the crayfish used in these experiments were similar to those used in the aggression studies.

Temperature preference

The temperature preference of adult crayfish is summarized in Figure 17. Most O. propinquus

TABLE 12. Competition for shelter by crayfish of varying size differences with time. Mean *O. virilis* size is 6.5 mm. One crayfish of each species competed for the same shelter.

Mean size difference (*O.v.* - *O.p.*) (mm)		No. of eggs	Species	% occupation after 15 min.	4 hrs.	1 day	2 days
Male	1.9	2	V	100	50	100	100
			P	0	50	0	0
	1.5	4	V	75	50	75	100
			P	25	50	25	0
	1.0	4	V	75	75[a]	25	0
			P	25	50	75	100
	0.5	2	V	100	100	0	0
			P	0	0	100	100
	0.1	2	V	100	50	0	50
			P	0	50	100	50
Female	1.5	4	V	50[b]	100	100	100
			P	25	0	0	0
	1.0	4	V	100	0	0	0
			P	0	100	100	100
	0.5	2	V	100	0	0	0
			P	0	100	100	100
	0.0	2	V	100	0	0	0
			P	0	100	100	100
Mean of all sizes and sexes			V	89	47	33	39
			P	8	56	67	61

[a]V and P in same shelter once.
[b]Shelter unoccupied once.

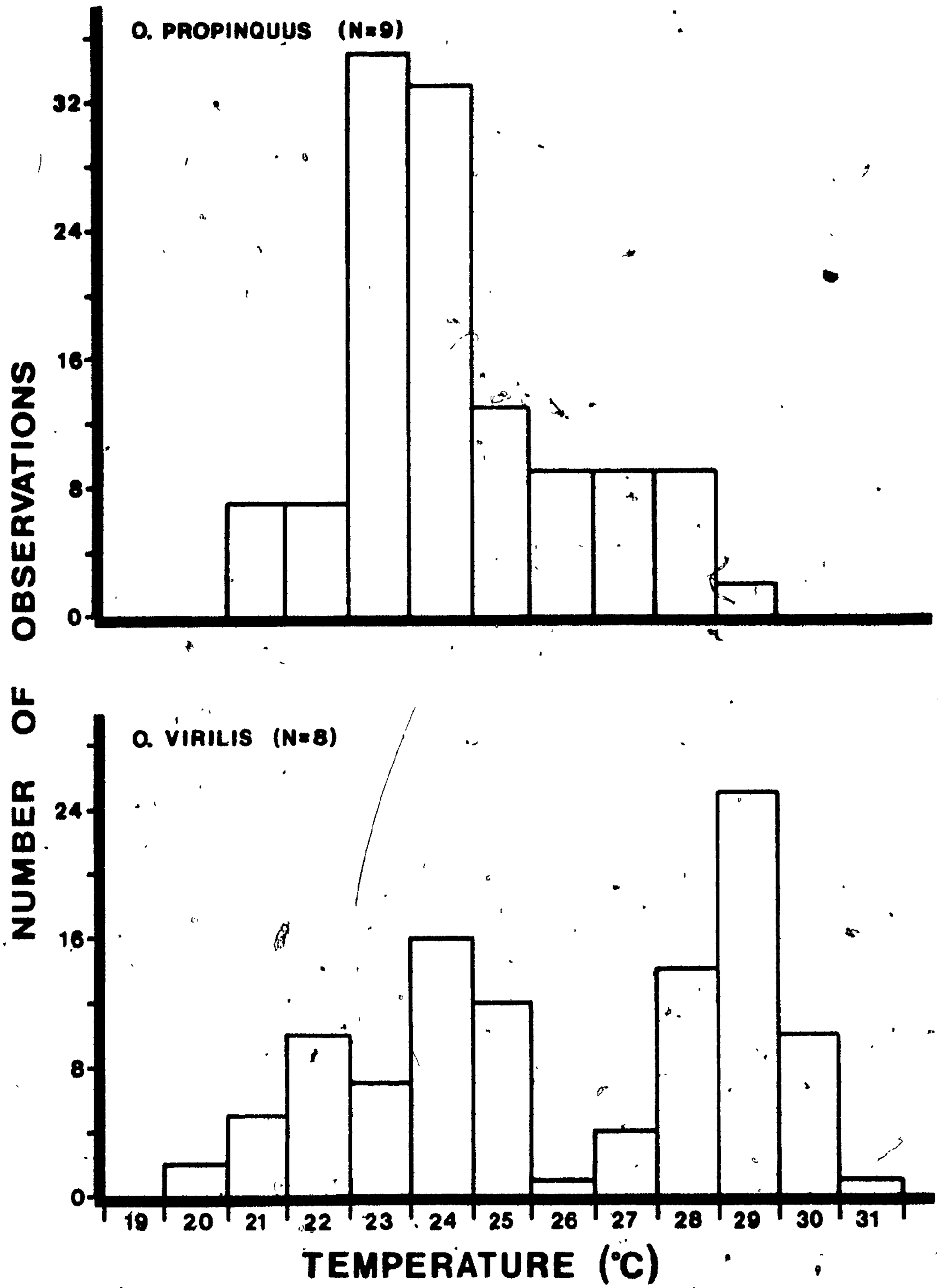

FIG. 17. Temperature preference of adult crayfish. One crayfish was tested per temperature gradient. Observations were made every hour for 7 to 8 hours. The gradient was then reversed and observations repeated.

individuals preferred cooler temperatures (24.4°C ± 0.02 S.E.) than O. virilis, which showed a less pronounced and wider temperature preference (26.0°C ± 0.04 S.E.). Some individual O. virilis tolerated temperatures of 29 and 30°C, whereas O. propinquus did not tolerate these high temperatures. In the field, the highest water temperature just above the substrate, recorded at 0.5 meters from shore was 27°C and at 2.5 meters from shore was 25°C.

Predation by fish

In order to obtain an indication of the crayfish species and the size of individuals preferentially preyed upon by smallmouth bass (Micropterus dolomieui), 20 crayfish of each species were placed in a tank either with rocks for shelter or with no shelter at all, along with the predatory fish. The results, tabulated in Table 13, show that there seems to be no crayfish species preference by the bass, since in both the shelter and no shelter experiments the difference between the number of each species eaten was found to be insignificant using the test for equality of two percentages (Sokal and Rohlf 1969). There was also no significant difference between the total numbers of each species eaten in the experiments with or without shelter. A significantly greater number of female than male O. propinquus were eaten in each experiment (no

TABLE 13. Predation on crayfish by a 16cm smallmouth bass (*Micropterus dolomieui*). Shelter refers to large rocks covering the bottom of the tank.

	Crayfish number in tank					
	O. propinquus			*O. virilis*		
	Males	Females	Total	Males	Females	Total
No shelter:						
Before predation	10	10	20	10	10	20
After 2 wks. of predation	7	2	9	5	6	11
With shelter:						
Before predation	10	10	20	10	10	20
After 2 wks. of predation	9	4	13	5	6	11
After 4 wks. of predation	8	2	10	4	4	8

shelter, t=2.36, P<0.02; shelter, t=2.53, P<0.02), whereas there was no significant difference between the number of male and female O. virilis eaten after two weeks of predation in each experiment.

Table 14 suggests crayfish size selection by the smallmouth bass. The results show that, in the tank with shelter, the same predator consumed larger sized male and female crayfish of each species, as compared to the tank with no shelter. Also, although a smaller size range of O. propinquus than O. virilis was offered to the bass, it is important to note that the largest O. propinquus individuals offered were not eaten, even though they were smaller than the O. virilis individuals that were eaten. This differential consumption may indicate that O. propinquus is more capable of avoiding or protecting itself against fish predation than is O. virilis.

Starvation

Of the four O. virilis that were isolated, one died after one week, and the other three died after 10 to 11 weeks of starvation. Of the four O. propinquus that were isolated, three died after 13 to 14 weeks and the other died after 16 weeks of starvation.

It is obvious that both these species can survive for a considerable amount of time without food.

TABLE 14. Crayfish size selection by the predatory smallmouth bass (*Micropterus dolomieui*). N=10 crayfish of each sex. Values in brackets are means.

	Size range (mm)			
	O. propinquus		*O. virilis*	
	Offered	Eaten	Offered	Eaten
No shelter:				
Males	4.5 - 6.5 (5.6)	4.5 - 4.8 (4.7)	5.0 - 8.8 (7.0)	5.0 - 7.2 (6.5)
Females	3.8 - 7.1 (5.6)	3.8 - 5.6 (4.9)	5.5 - 8.6 (7.0)	5.5 - 7.5 (6.5)
With shelter:				
Males	4.9 - 6.5 (5.4)	5.1 - 5.8 (5.5)	5.4 - 8.8 (7.2)	5.4 - 7.4 (6.5)
Females	4.7 - 7.1 (5.2)	4.7 - 6.6 (5.4)	5.0 - 8.6 (7.0)	5.4 - 8.0 (6.8)

DISCUSSION

This study investigates the natural history of two co-occurring crayfish species of the same genus. A difference in the microdistribution of the two species was discovered and, therefore, both field studies and laboratory experiments were performed in order to determine whether physical factors, biotic factors or both were responsible for the observed distributions.

In answer to the first question posed, "Is the crayfish population under investigation stationary or constantly moving?", the field work did not involve a few, relatively stationary individuals, but rather, concerned a large population of crayfish, as revealed by mark and recapture experiments.

COMPETITION

Momot et al. (1978) state that O. propinquus and O. virilis are often found in the same habitat, "yet little is known about the possible competition between these species."

Both species were found to have similar feeding habits in June and July 1980, when crayfish were most numerous. Filamentous algae was found to be the most common food item. Capelli (1980) also found that O. propinquus fed primarily on filamentous algae (mostly Cladophora). Therefore, even though both species had similar feeding habits, there was probably very little competition for food in the study area since filamentous algae was widespread and extremely abundant during most of the spring, summer and fall.

The fact that there was an ample number of rocks suitable for shelter in the study area, and considering the low density of crayfish (a maximum of 0.7 adults/m^2 and 2.9 young/m^2 compared to 2.5 adults/m^2 and 96.0 young/m^2 observed by Capelli and Magnuson (1975) in a northeastern Wisconsin lake) indicates that there was little or no competition for shelter taking place in the study area. The crayfish population is possibly being kept low by toxic substances in the water or by predation pressure since thre are many different predators present when the young-of-the-year become free-swimming.

NATURAL HISTORY

Seasonal migration

Orconectes propinquus and *O. virilis* were found in nearly equal numbers in the study area, *O. propinquus* being slightly more numerous. The majority of adults of both species were present near the shore between May and August while the young were present between July and November. The decline in numbers of adults and young in the fall suggests that both crayfish species migrate to the deeper waters of the St. Lawrence River to overwinter. This phenomenon has been documented for O. virilis (Momot 1967; Aiken 1968; Momot and Gowing 1972; Fast and Momot 1973) and for O. propinquus (Capelli and Magnuson 1975). Most authors believe this seasonal migration to be associated with gonadal maturation since it follows the molt to maturity in yearlings and the molt to sexual form in adult males (Momot 1967). Fast and Momot (1973) suggest that under crowded conditions, females are forced into deeper waters by more aggressive males, but in the present study, males and females were present in equal numbers at all times, probably because of the low population density in the study area.

In the late summer and fall, adult and young O. virilis declined in number before O. propinquus. This may signify that O. virilis moves to deeper water earlier than O. propinquus, or it may imply that O. virilis has a higher mortality rate due to predation or unsuccessful molting.

Growth

The timing of events in the life cycle of the two crayfish species corresponds with observations made by others (Bovbjerg 1952; Crocker and Barr 1968; Weagle and Ozburn 1972; Capelli and Magnuson 1975; Stein 1977) and is very similar for each species.

The most visible difference between the two species, other than physical appearance, is the growth rate. By October 10, young O. virilis attained a mean size of 6.3 mm a.l. ± 1.0 S.E. (18.9 mm c.l.), while O. propinquus reached 4.7 mm a.l. ± 0.6 S.E. (15.4 mm c.l.). Momot (1967) found that young O. virilis males grew to an average of 20.8 mm c.l. and females 19.2 mm c.l. by late October and early November in a Michigan lake. These values correspond closely to the 18.9 mm c.l. of O. virilis in early October found in the present study. On the other hand, Weagle and Ozburn (1972) have shown that O. virilis young grow to only 14 mm c.l. in their first summer in a N.W. Ontario river. Momot (1978) discovered O. virilis in Ontario lakes to have a faster growth rate, earlier age at maturity, higher mortality rates, lower annual production, and lower mean biomass than in similar Michigan lakes.

The literature clearly demonstrates that there are geographical differences in the growth rate of O. virilis. The same has also been reported for O. propinquus (Van Deventer 1937, as cited by Momot 1967). Orconectes propinquus young have been reported to reach approximately 12-16 mm c.l. by the fall (Stein and Magnuson 1976). This corresponds with the 15.4 mm c.l. mean value found for O. propinquus in the present study.

The large standard errors on the growth curve (Figure 6) for both O. virilis and O. propinquus, and the large size range of age groups in the size-frequency distributions (Figures 7 and 8) show that there are also great differences in the growth rate of individuals of both crayfish species in the same habitat. Pennak (1978) states that for young crayfish, the larger individuals in a single pond or stream may be over twice as long as the smaller ones by autumn. He believes the difference in growth rates to be due mainly to varying activity and amounts of food consumed. Another reason is that young are released at different times due to differences in egg extrusion by individual females (W.T. Momot, pers. comm.).

Momot (1967) chose 37 mm c.l. (13.2 mm a.l.) as the point of separation between two-year-old and three-year-old O. virilis in Michigan. This value corresponds closely with the 12 mm a.l. suggested by the present study using the size-frequency distribution of O. virilis in July (Figure 7). This demonstrates once again, as with the young, that the growth rate of O. virilis in the present study is similar to that in West Lost Lake, Michigan.

Crayfish do not molt over the cold winter months (Aiken 1965; Momot and Gowing 1977a). Cohort analyses (Figures 7 and 8) give further evidence that O. virilis and O. propinquus do not grow between October and April in the area studied and, therefore, do not molt at that time.

Maximum species size

No O. propinquus individuals larger than 8.3 mm a.l. (25.4 mm c.l.) were captured or seen in the two years of sampling the St. Lawrence River at Nun's Island and in one year of sampling the southern shore of the Island of Montreal. This maximum size is much lower than maximum sizes for the species recorded in the literature, as seen in Table 15. Since crayfish may select cooler, deeper waters during the day (Crawshaw 1974), and sampling was only performed in the day, perhaps the larger sized O. propinquus were escaping capture. Therefore, chelae that had been washed-up onto the shore were collected and measured as an alternative sampling method. This method worked well for O. virilis, predicting the size range of living organisms accurately. As for O. propinquus, only three individual chelae were found that may have belonged to crayfish between 8.5 and 10 mm a.l. Since it was not possible to sex the chelae, it is not known whether these three chelae belonged to males or females. If they had belonged to male crayfish, the size range would have been similar to the size range of living organisms found. Admittedly, the method is only an estimate and the sample number of O. propinquus

TABLE 15. Comparison of maximum adult size, minimum female size with eggs, and mean number of eggs per female with literature values. (Sizes are in mm carapace length).

Species	Locality	Max. size	Min. size of females with eggs	Mean number of eggs	Source
O. propinquus	N.E. Wisconsin	-	20	-	Capelli & Magnuson (1975)
	N.E. Wisconsin	-	18.5[a]	-	Stein *et al.* (1977)
	S. Ontario	35	16	-	Berrill (1978)
	N. Indiana	42	19	-	Slack (1955)
	S. Michigan	-	-	(5-250)[b]	Creaser (1934), as cited by Momot *et al.* (1970)
	Central Illinois	40	-	(40-250)[b]	Van Deventer (1937), as cited by Momot *et al.* (1970)
	S. Quebec (Granby)	38.4	-	-	Present study
	S. Quebec	25.4 (8.3 a.l.)	16.7 (5.2 a.l.)	50	Present study
O. virilis	N.W. Ontario	44	25.4	214	Weagle & Ozburn (1972)
	S. Ontario	50	26	-	Berrill (1978)
	N. Michigan	45	24.6	94	Momot (1967)
	N. Michigan	-	-	26-149[c]	Momot & Gowing (1975)
	N. Michigan	-	-	100	Momot *et al.* (1978)
	N. Ontario	-	-	99-150[d]	Momot (1978)
	S.E. Michigan	69	-	-	Hazlett *et al.* (1974)
	S. Quebec	50.2 (18.1 a.l.)	30.1 (10.6 a.l.)	250	Present study

[a]Minimum size at maturity determined by primary sexual characteristics.
[b]Range of egg numbers; no mean was given.
[c]Range of means from 7 lakes over 3 years.
[d]Range of means from 2 lakes over 2 years.

chelae was low. Nevertheless, the data does give additional evidence that, in the study area, O. propinquus does not grow to as large a size as reported in the literature.

More conclusive evidence is made available by cohort analysis (Figure 8) and the fact that O. propinquus survive two to three summers (Stein and Magnuson 1976) with most dying in their second summer (Crocker and Barr 1968). The size-frequency distribution for O. propinquus (Figure 8) clearly shows the complete life span of O. propinquus with the oldest individuals not exceeding the 8.3 mm a.l. maximum size observed.

Since young-of-the-year O. propinquus in the present study have a similar growth rate as other O. propinquus populations, as noted earlier, their rate of growth must decrease after their first summer in relation to other populations. This seems to be what is occurring, as shown by the size-frequency distribution in Figure 8, since the majority of O. propinquus in their second summer have only grown approximately 2 mm a.l. Stein and Magnuson (1976) offer an explanation for the reduced size of O. propinquus. They state that since O. propinquus may be active during the day as well as night, "suppression of diurnal activity of O. propinquus (by predators), especially during midsummer, could result in lower growth rates and fewer offspring."

Reproduction

Reproduction data for both crayfish species are listed in Table 4 and are compared to values found by others in Table 15. The observed minimum female size with eggs and the mean number of eggs correspond with the data in the literature for O. propinquus, but the observed values for O. virilis are slightly higher than the values in the literature. This discrepancy could be due to the small O. virilis sample size and the fact that adult O. virilis prefer large rocks, as observed in the laboratory and in the field, and may have been hiding under large immovable boulders in the area. Since the number of eggs per female is proportional to O. virilis size, as shown in Figure 5A and reported by Weagle and Ozburn (1972), the mean number of eggs per female will depend on the size range of the females under investigation. The mean egg diameter was also found to be proportional to female O. virilis size, as shown in Figure 5B.

Hardiness

The data in Table 2 shows that more appendages are lost by O. virilis (62%) than O. propinquus (44%). Appendages may be lost during aggressive contacts with other crayfish, during molting, or during attacks by predators. Crayfish are especially susceptible to the loss of appendages during the 24 to 36 hours following a molt, when the exoskelton is still soft. The fact that O. virilis loses more appendages than O. propinquus , may suggest that O. virilis molts more often, is weaker, or is more susceptible to predation than O. propinquus.

The greater number of deaths of O. virilis as compared to O. propinquus, observed in the laboratory, provides evidence for the greater hardiness of O. propinquus. During the course of laboratory experiments (excluding predation experiments), 14 O. virilis were found dead, whereas only 4 O. propinquus died in the same experiments. These O. virilis did not die of old age since all O. virilis used in the experiments were one year old or less. The crayfish did not die during molting and newly molted individuals were not used in the experiments. Crayfish did not seem to be killed during fighting with other individuals since no marks indicating this were found on the bodies.

In order to determine whether the crayfish died from starvation, since feeding was reduced or eliminated during some experiments, an experiment was performed to determine how long the two species could survive without food. The results provided additional evidence that O. propinquus is the hardier of the two species since O. propinquus withstood starvation longer than O. virilis. Two of the four O. virilis in the experiment died from causes other than starvation. One died of unknown causes after only one week and the other died while molting. *Orconectes propinquus* individuals also molted, but did so successfully.

More research is needed in order to determine which species has the highest mortality during molting. Observations in the laboratory indicate that *O. virilis* die during molting more frequently than *O. propinquus*. Momot (1967) observed, both in the field and in the laboratory, that *O. virilis* mortality increased following molting, and concluded that these deaths may have been due to physiological and mechanical problems associated with molting as well as to predation and cannibalism. Dye and Jones (1975) consider natural molt mortality, aggressive interactions during molting, and cannibalism of recently molted individuals to be the major sources of young-of-the-year *O. virilis* mortality. The latter two sources of mortality are questionable, since R.V. Bovbjerg (pers. comm.) found that all aggression is inhibited for days before and after molting, and W.T. Momot (pers. comm.) believes that young-of-the-year *O. virilis* are not very cannibalistic, and only eat animals after they have died in molt.

Dominant species

In an extensive field study, Berrill (1978) found that, in five different bodies of water in which *O.*

propinquus and O. virilis were the only crayfish species present, O. propinquus was clearly dominant (more numerous) in at least three of them. In eight other locations where O. propinquus and O. virilis occurred together with other crayfish species, O. propinquus was dominant in at least five of them. Orconectes virilis was found in greater numbers than O. propinquus in only one lake, in which O. rusticus was the dominant species. In the remaining four lakes, either O. propinquus and O. virilis occurred in equal numbers, or the sample size was too small to allow determination of the dominant species.

Capelli and Magnuson (1975) report that in Trout Lake, Wisconsin, O. propinquus is by far the dominant species over O. virilis, even though O. virilis is native to that part of Wisconsin and O. propinquus has invaded within the past 40 years. Orconectes propinquus may also slowly become the dominant species in parts of the St. Lawrence River with suitable substrate. This speculation is based on the field data obtained from the present study. Orconectes virilis has a faster growth rate than O. propinquus, attains a larger size at maturity and produces many more eggs than O. propinquus. This, along with the fact that some female O. virilis survive to produce a second batch of young (Momot 1967; Momot and Gowing 1977c), should allow O. virilis to be present in much greater numbers than O. propinquus. The fact that slightly more O. propinquus were observed, suggests that O. virilis has a much higher mortality rate than O. propinquus.

MICRODISTRUTION IN THE FIELD

The significant difference in microdistribution of two crayfish species within such a short distance (3 meters), as described in the present study (Fig. 10), has not been reported elsewhere. The observation that females with eggs, and young-of-the-year of both species were found mainly in the shallowest water along the shore, has been documented (Momot 1967; Capelli and Magnuson 1975; Momot 1978), but differences in microdistribution of the two species when they occur together has not been documented. The observation that more O. virilis occur closer to the shore than O. propinquus, and more O. propinquus occur farther from the shore than O. virilis during the summer, may only apply in areas where there is a gradient of substrate particle sizes, since different microdistributions were observed in areas with different substrate types than the study area. Regardless of this fact, the observed difference in microdistribution provides an opportunity to study differences in preference and behavior between two crayfish species.

POSSIBLE PHYSICAL FACTORS INFLUENCING MICRODISTRIBUTION

Substrate

Type and size of substrate particles are probably the most important physical factors affecting the wide distribution of O. propinquus and O. virilis in the St. Lawrence River, although current, pollution, and other chemical factors may also be involved. Substrate particle size, also influences microdistribution in the study area, since the number of crayfish along the shore is directly related to the number of large rocks and inversely related to the amount of silt. This is seen for O. propinquus more so than for O. virilis (Fig. 11A).

Although crayfish young may have to filter feed, and adults are probably opportunistic filter feeders (Budd et al. 1978), most adult crayfish are well equipped to strain silt particles from the water to prevent passage into the gill chambers (Hobbs and Hall 1974). Siltation may affect crayfish by filling in the small spaces between rocks that otherwise could be used for shelter.

With distance from shore, the number of O. propinquus is directly related to the number of large rocks, whereas the number of O. virilis is not, since more O. virilis are found near the shore where there are fewer large rocks. Therefore, some factor other than substrate is involved in the microdistribution of

O. virilis. Substrate particle size is unlikely to play an important role in the microdistribution of young-of-the-year crayfish in the study area, since their small size would allow them to find shelter anywhere, even among the small particles near shore.

Laboratory experiments demonstrated that both of the crayfish species preferred large substrate particle sizes, but O. virilis preferred the large sizes more than O. propinquus (Figures 12, 13 and 14). Half of the time, O. propinquus showed a preference for large rocks and half of the time it did not. When both species were placed together in the same tank, the distribution remained the same as that observed for each species separately. This implies that 36 crayfish/m^2 was not enough to cause competition for shelter under laboratory conditions.

When different substrate types (sand, gravel, rock) were used (Fig. 15), O. propinquus again showed less preference for rocks than did O. virilis, whether the species were together or separate. However, when newly captured crayfish of both species were placed toether, 17% more O. propinquus than O. virilis were found on the rock substrate, whereas the reverse was true when each species was separate. This suggests that O. propinquus may have been outcompeting O. virilis for shelter, since at crayfish densities of 33 to 133/m^2, the shelter space must have been near saturation. Bovbjerg (1970a) found in the laboratory that at a density of 44 crayfish/m^2, the shelters in the rock substrate were over-saturated, since O. virilis drove O. immunis from the rock to the less preferred gravel and muck areas. The observed difference between newly captured crayfish and crayfish that had been in captivity several months may be due to O. propinquus becoming acclimated to a predator-free environment.

The laboratory results conflict with field observations, therefore, factors other than substrate particle size may be responsible for the difference in microdistribution between the two crayfish species, away from shore.

Temperature

Since there is an average difference of 2°C between locations where most O. propinquus were found (2.5 meters from shore) and where most O. virilis were found (0.5 meters from shore), temperature preference may be a factor influencing crayfish microdistribution in the study area. In the laboratory, most O. propinquus adults were found to prefer temperatures of 23 to 24°C (Fig. 17). This corresponds with the temperature range of 22 to 25°C which was measured at 2.5 meters from shore on sunny days during July and August.

Orconectes virilis adults were shown to have a wider temperature preference, with some individuals preferring temperatures around 24°C while others preferred 29°C. Crawshaw (1974) found that temperature preference of Orconectes immunis varied greatly even for the same crayfish and that they did not prefer a particular temperature, but avoided temperature extremes. During laboratory experiments, several O. virilis adults were observed at the end of the temperature gradient in 30 to 31°C water. This species may have wandered into even warmer waters, if available. Clearly, O. virilis tolerates higher temperatures than O. propinquus. A preference for high temperature has also been reported for Orconectes obscurus, which has a temperature preference of 30°C (Hall et al. 1978).

The higher temperature preference of O. virilis as compared to O. propinquus may account for the observation that most O. virilis are found within one meter of the shore where the temperature range, in July and August, is 25 to 27°C on sunny days. Fast and Momot (1973) suggest that O. virilis males select shallow water because is is the zone with the highest temperature.

POSSIBLE BIOTIC FACTORS INFLUENCING MICRODISTRIBUTION

Aggression

Large crayfish individuals may dominate smaller individuals of the same species (Bovbjerg 1956), but this rule does not hold for interspecifc interactions. The present study has shown that O. propinquus, the smaller of the two species, has a higher level of aggression than O. virilis (Table 11A). Orconectes propinquus individuals were always more aggressive than O. virilis of the same size, possibly due to the large size of O. propinquus chelae compared to O. virilis chelae (Appendix V). Orconectes propinquus females may be 5 to 19% smaller than O. virilis females and be as aggressive, whereas O. propinquus males may be 23 to 25% smaller than O. virilis males and be equally aggressive (Table 11B). This higher aggression level in male O. propinquus may be due to the increase in chela length difference (O. virilis - O. propinquus) between males and females (Table 11A). The observation that chela length is positively correlated with male dominance has also been reported for O. virilis (Lunt 1967, as cited by Fast and Momot 1973) and for O. propinquus (Stein 1976).

With increasing O. virilis size, more aggression contacts were won by O. propinquus (Table 11A). Also, with increasing O. virilis size, the size difference between O. virilis and O. propinquus had to be greater for both species to have the same aggression level (Table 11B). These observations may indicate that the aggression of O. virilis decreases with age or that the aggression of O. propinquus increases with age.

A high degree of variability was observed among aggression levels of individuals. This variability appears to be normal, since intrinsic differences in aggression levels within similar sized individuals have also been reported for *O. virilis* and *O. immunis* (Bovbjerg 1970a).

Due to the more aggressive nature of *O. propinquus*, it is better able to obtain and defend shelters when competing with *O. virilis*. Laboratory experiments showed that *O. virilis* would almost always occupy shelters immediately upon introduction to the experimental tank but would usually be soon evicted by similar sized or slightly smaller (≤15%) *O. propinquus*.

The observed high aggression level and successful shelter occupation of *O. propinquus*, along with the apparent high mortality of *O. virilis* in relation to *O. propinquus* may explain why *O. propinquus* is dominant over *O. virilis* in many habitats, as observed by Berrill (1978), even though it is the smaller of the two species. In the study area, however, the crayfish densities are too low for exploitative competition for shelter to be taking place. Although *O. propinquus* individuals are more aggressive than similar sized *O. virilis* individuals, the aggression levels of the two species in the field are most probably equal, since *O. virilis* adults are larger than *O. propinquus* adults in nature. This would imply that there is little interference competition taking place in the study area.

Predation

Predation pressure on crayfish in the study area may be considerable, since many known crayfish predators such as: smallmouth bass, brown bullhead catfish, killdeer, ring-billed gull (Crocker and Barr 1968), yellow perch (Stein 1977), and pumpkinseed sunfish (personal observation) were seen in the study area. The mudpuppy (Necturus maculosus) is also a known crayfish predator (Crocker and Barr 1968) and in one study, crayfish were found to make up 38% of their diet (data from A.S. Pearse, as cited by Oliver 1955). Many Necturus ranging in size from 4 to 25 cm were observed under rocks in the study area throughout the summer. Stein (1977) states that sculpins (Cottus spp.) and darters (Etheostoma spp.) may be important predators of young-of-the-year crayfish. These possible predators were also found in abundance, using rocks for shelter. Several young smallmouth bass (Micropterus dolomieui) measuring 4 to 6 cm and some adults measuring 15 to 20 cm were also observed close to the shore.

Momot and Gowing (1977c) state that "fish predation is a common source of stress on crayfish populations," but it rarely has a devastating impact on them. It has been reported that in Nebish Lake, Wisconsin, over 25% of the crayfish mortality is due to fish predation (Stein and Magnuson 1976). Stein (1977) found that O. propinquus contributed 30 to 60% of the diet of smallmouth bass.

The predation rate by fish on crayfish has been found to be inversely related to substrate particle size (Stein and Magnuson 1976), therefore, one would expect that in the presence of fish, crayfish should be found on substrate of larger particle size. In order to determine if predation would alter the microdistribution of adult O. propinquus and adult O. virilis, a smallmouth bass was placed in a large tub with both crayfish species. Before the bass was introduced, crayfish of each species were observed on top of all the different rock sizes. The day after the predator was introduced, no crayfish were seen on top of the substrate and the few individuals remaining on the small rocks had dug themselves in as much as they could. At this time, no crayfish activity could be seen, and after five days no crayfish were observed on the small rocks (Table 9). Some crayfish may have shifted to the larger rocks, although this is difficult to determine since many crayfish were eaten by the bass. Nevertheless, fish predation was shown to drastically alter crayfish distribution. The predation rate may have been more drastic than in nature considering that a large predator was placed in a relatively small area where its only food source was crayfish. Furthermore, the crayfish had very little room in which to move about. Since crayfish have been shown to move great distances (Black 1963; Momot 1966; Hazlett et al. 1974), they would surely have to cross the small rocks at some time. These conditions would not be present in nature since the density of large predaceous fish would be less, the predators would probably have other food sources, and crayfish could perhaps walk about without leaving the shelter of large rocks. Predation experiments of this nature may not reflect natural conditions, but they do make the point that predation, if strong enough, could have a significant effect on the microdistribution of crayfish.

Stein and Magnuson (1976) found that in the presence of a 15-20 cm long smallmouth bass, O. propinquus individuals less than 22.5 mm c.l. (7.5 mm a.l.) modified their substrate preference by moving to larger sized substrate particles. They also decreased their activity, spent less time on top of the substrate and reduced grazing. It was also found that large individuals over 26.5 mm c.l. (9.0 mm a.l.) did not shift their distribution, but their activity was reduced. Field evidence that predation affects crayfish microdistribution has been reported by Stein (1977), who found that the density of crayfish exposed on sand was inversely related to densities of fish in Trout and Allequash lakes, Wisconsin.

The fact that in the laboratory, unlike the field, *O. propinquus* were observed on small rocks and both crayfish species were exposed on top of the substrate, implies that predation does influence crayfish microdistribution in the study area. Predation pressure may explain why more crayfish are found in areas with more large rocks, why most *O. propinquus* are found between two and three meters from shore where there are more large rocks, and why crayfish do not wander about in the open during the day, but it does not explain why most *O. virilis* are found less than two meters from shore where there are fewer large rocks. In fact, one large *O. virilis* was seen in the open, during the day, less than one meter from shore.

The only way predation could be linked to the observed difference in microdistributions in the study area is if *O. virilis* individuals were large enough to avoid predation, while *O. propinquus* individuals were not large enough, at the time when the microdistribution difference was observed. Therefore, a laboratory experiment was performed to determine crayfish species and size preference of smallmouth bass. The results (Table 13) showed that there was no crayfish species preference by the smallmouth bass, since it fed on the smallest individuals of both species. Stein

(1977) found that on a sand substrate, smallmouth bass preyed on O. propinquus in ascending order of size, consuming smallest individuals first, but on larger sized substrate particles, the bass chose larger sized crayfish. The present study also suggests that bass shift their size selection to larger individuals of both crayfish species when adequate shelter is available to the crayfish (Table 14). This may occur because as less crayfish are available, the bass becomes more hungry and will attempt to consume whatever it is able to capture.

The results also show that the smallmouth bass consumed larger sized O. virilis and O. propinquus. This differential consumption implies that O. propinquus is more capable of protecting itself against fish predation than O. virilis, perhaps because of the larger chela size of O. propinquus. Chela size may play a very important role in prey selection by fish since the bass also chose larger sized female O. propinquus than male O. propinquus (males have larger chelae than females, Apendix IV B). Stein (1967, 1977) also found that smallmouth bass consumed female O. propinquus before male O. propinquus because the females have smaller chelae than the males. Therefore, one would expect O. propinquus females to be more cryptic than O. propinquus males, which was determined previously. This statement is also supported by the observation in the field by Stein (1977) that few female O. propinquus were ever found in the open on sand substrate in either Trout or Allequash lakes, Wisconsin.

A differential consumption based on sex of O. virilis was not observed, presumably because in the size range utilized (5-8 mm a.l.), there is a much smaller size difference between male and female chelae of that species than there is for O. propinquus (Appendix V).

Most important and directly related to crayfish microdistribution in the study area is the finding that, in laboratory experiments, the largest O. propinquus eaten by the smallmouth bass in either the shelter or no shelter experiments was 6.6 mm a.l., and the largest O. virilis eaten was 8.0 mm a.l. In the field between July 18 and August 15, when the difference in adult crayfish microdistribution was observed, the size range of adult O. propinquus present was 4.3 to 6.6 mm a.l. with a mean of 5.9 mm a.l., whereas the size range of adult O. virilis present was 7.1 to 16.8 mm a.l. with a mean of 9.8 mm a.l. The laboratory finding suggests that a 16 cm long smallmouth bass, which was representative of the fish in the area, could prey on all O. propinquus present in the field at that time, whereas most O. virilis were already too large to be preyed upon. Therefore, O. virilis could occupy areas with less shelters, as it does in the study area, without being heavily preyed upon, whereas _O. propinquus_ must seek areas with more shelter to avoid predation. One can see, then, that fish predation may indeed influence crayfish microdistribution in the study area.

Since the growth rate of young-of-the-year _O. virilis_ is greater than that of _O. propinquus_, the same differential species selection could be imposed by the smaller predators present such as: young fish, young _Necturus_, sculpins and darters. It is doubtful, though, whether this species selection by predators would influence young-of-the-year microdistribution to the same extent as the adults, since there probably is no preferential substrate for the more heavily preyed upon species to seek, most of the substrate particle sizes being of adequate shelter for the small young-of-the-year crayfish.

SUMMARY

Looking back at the findings of this study, it is obvious that the question, "Is microdistribution of the two crayfish species controlled more by physical conditions or by biotic factors?", has no simple answer. A combination of both physical and biotic factors are probably responsible for the observed microdistributions in the study area, and different factors or combination of factors may be important for different crayfish life stages.

The microdistribution of large adults in their third summer may be influenced solely by temperature. Young adults in their second summer are probably influenced primarily by a combination of substrate particle size and predation, and perhaps secondarily by temperature. Young-of-the-year in their first summer may be influenced by predation or temperature, although this was not proven in the laboratory. Substrate particle size and abundance are the most important factors affecting the number of crayfish present along the shore.

Upon examination of all the different aspects of the life histories of the two crayfish species, certain connections or life history strategies, come to mind. Although purely conjecture, it is possible that both species are doing well (in terms of survival) and are found in equal numbers, in spite of O. propinquus being much smaller than O. virilis, due to the comparable aggression levels of the two populations and due to their different life history strategies, as illustrated in Figure 18.

Crayfish numbers may be low in the study area due to predation pressure or the presence of toxic chemicals in the water (which may also stunt the growth of O. propinquus). If, over the years, crayfish numbers

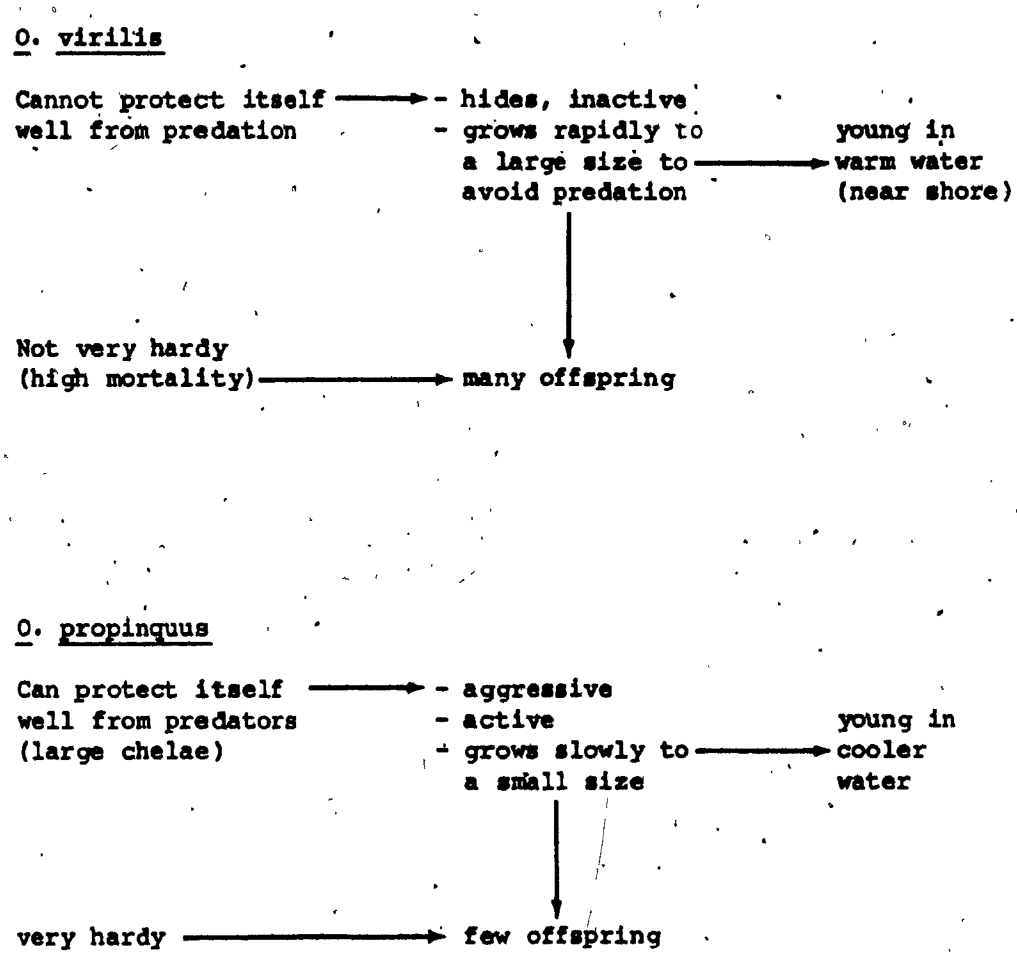

FIG. 18. Possible life history strategies of *O. propinquus* and *O. virilis* in the study area.

were to increase to a point where there was competition for shelter, O. propinquus would probably be the dominant species and coexist with O. virilis because (1) its high aggression level would allow O. propinquus to compete for shelter with O. virilis, and (2) its stunted size would not allow O. propinquus to dislodge O. virilis from the area, which it could possibly accomplish if it grew to its normal size (as recorded in the literature).

CONCLUSIONS

This research was intended to be a broad, general study of two co-occurring crayfish populations and of the possible interactions between them. It has laid the groundwork for future indepth studies concerning crayfish species interactions.

The major findings of this study are as follows:

(1) Crayfish populations are very mobile.

(2) *Orconectes propinquus* and *O. virilis* have similar feeding habits in June and July, feeding primarily on filamentous algae.

(3) Both crayfish species migrate to deeper water in the fall.

(4) *Orconectes virilis* has a faster growth rate than *O. propinquus*, and the growth rate of the latter species decreases markedly after its first summer.

(5) The maximum size attained by *O. propinquus* in the Nun's Island study area is 25.4 mm carapace length, which is much smaller than sizes previously recorded in the literature.

(6) On a gradient of substrate particle sizes, *O. virilis* were found closer to the shore than *O. propinquus*.

(7) *Orconectes virilis* adults tolerate higher water temperatures than *O. propinquus* adults.

(8) Probably due to larger chela size:

(a) *Orconectes propinquus* has a higher level of aggression than *O. virilis*.

(b) *Orconectes propinquus* males are more aggressive than *O. propinquus* females.

(c) *Orconectes propinquus* is better able to obtain and defend shelters than similar sized *O. virilis*.

(d) *Orconectes propinquus* is more capable of protecting itself against fish predation than similar sized *O. virilis*.

(e) *Orconectes propinquus* males are more capable of protecting themselves against fish predation than *O. propinquus* females.

(9) The microdistribution of young adult crayfish in the study area is probably primarily influenced by a combination of substrate particle size and predation pressure, and perhaps secondarily by temperature.

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Appendix I. Comparison of chemical and physical properties among sites along Montreal Island from July to October, 1980.

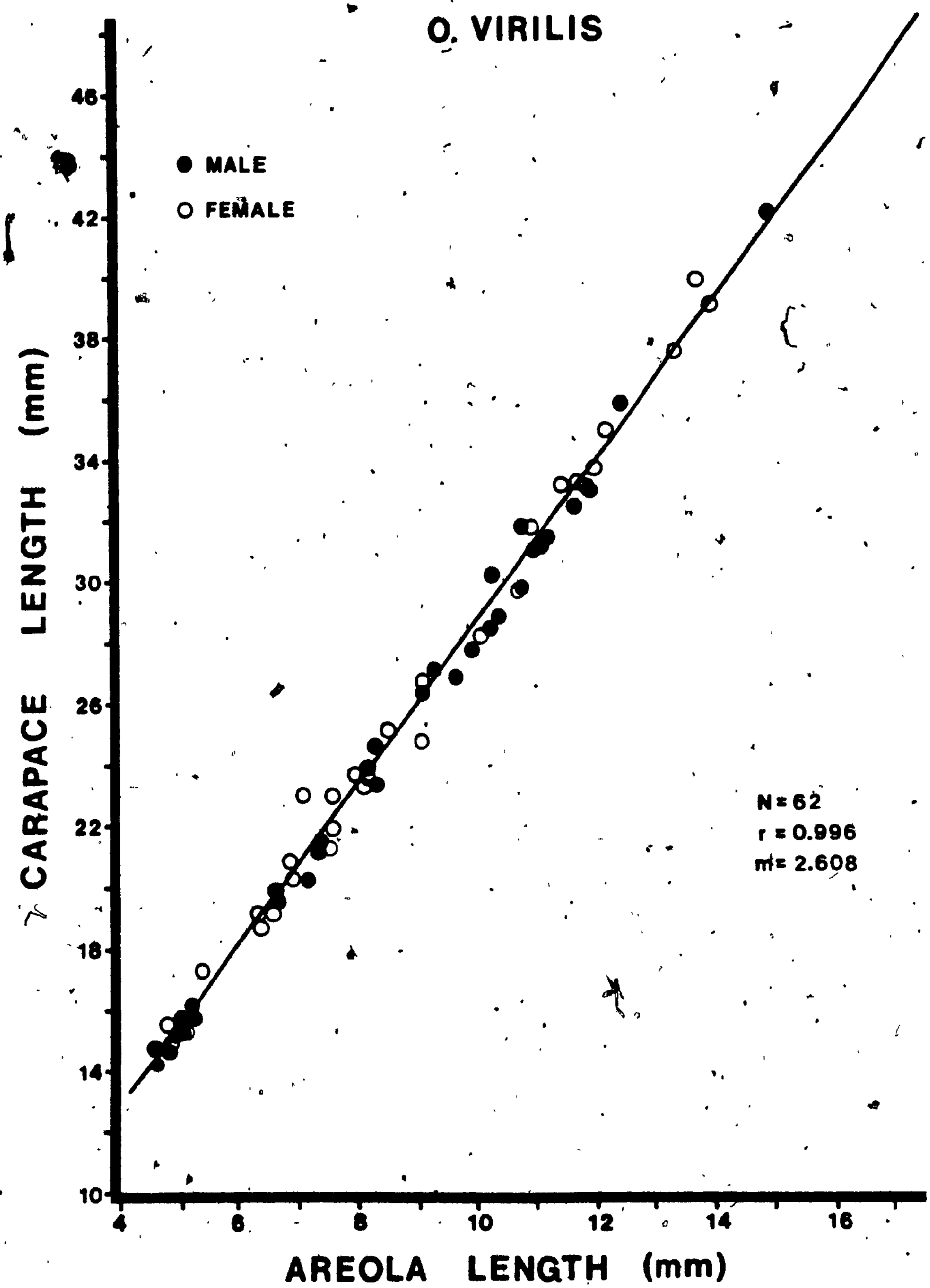
	Mean Values				
	Nun's Island (N=7)	Between Nun's I. and rapids (N=7)[a]	Lachine Rapids (N=1) July	Above rapids (N=6)	Valois Bay, Lake St. Louis (N=6)
$[O_2]$ (mg/l)	9.0	7.6	8.0	9.1	10.5
pH	8.3	7.8	8.5	8.1	8.4
Alkalinity (mg $CaCO_3$/l)	65.7	61.7	75	56.7	64
Calcium (mg $CaCO_3$/l)	72.1	70.0	85	62.5	71
Total hardness (mg $CaCO_3$ & $MgCO_3$/l)	100.0	96.7	115	84.2	85
Color (units of apparent color)	27.9	45.8	100	30.8	68
Turbidity (formazin turbidity units)	9.1	12.8	15	14.2	19.6
Current (m/sec)	0.20	0.02	0.76	0.07	0
Max. temp. (°C)	25	25	-	25	28
Total bacteria (X 10^3/ml)	2.9	14.7	75.0	10.5	5.0
Max. adult crayfish number per day	21	6	0	10	0
Species	<u>O.p.</u> <u>O.v.</u>	<u>O.v.</u>	-	<u>O.p.</u> <u>O.v.</u>	-

[a]Much oil was present.

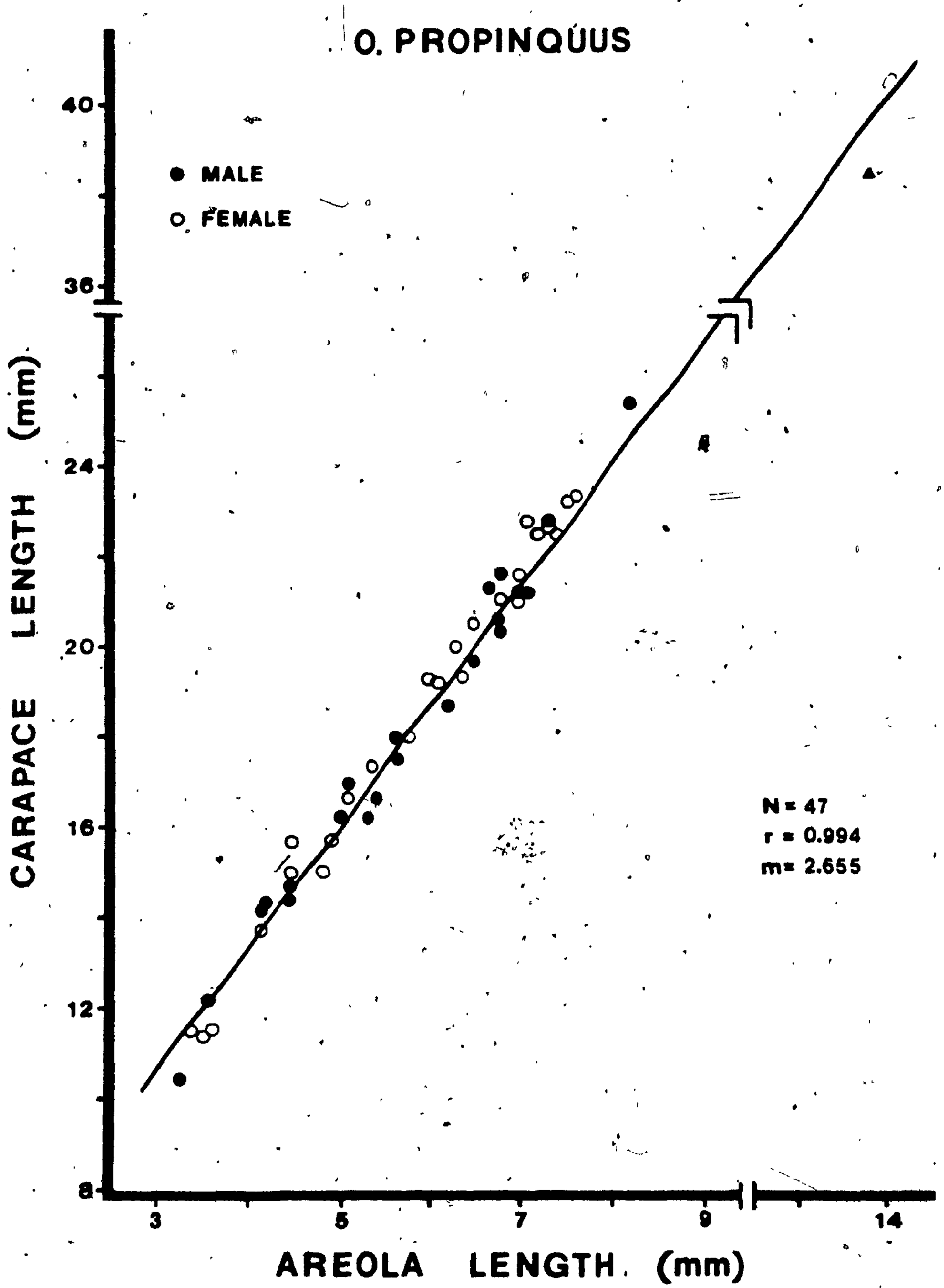
Appendix II. Chemical and physical properties of the water in the study area between June and October, 1980 (Dissolved oxygen determinations were begun in April).

	Mean	Range	N
$[O_2]$ (mg/l)	10.2	8.0 – 14.5	14
pH	8.4	7.8 – 8.9	9
Alkalinity (mg $CaCO_3$/l)	69.0	50 – 85	10
Calcium (mg $CaCO_3$/l)	74.0	55 – 80	10
Total hardness (mg $CaCO_3$ & $MgCO_3$/l)	102.5	80 – 120	10
Color (units of apparent color)	26.0	5 – 45	10
Turbidity (formazin turbidity units)	9.7	2 – 20	10
Current at 2.5 m from shore (m/sec)	0.24	0.15 – 0.30	11

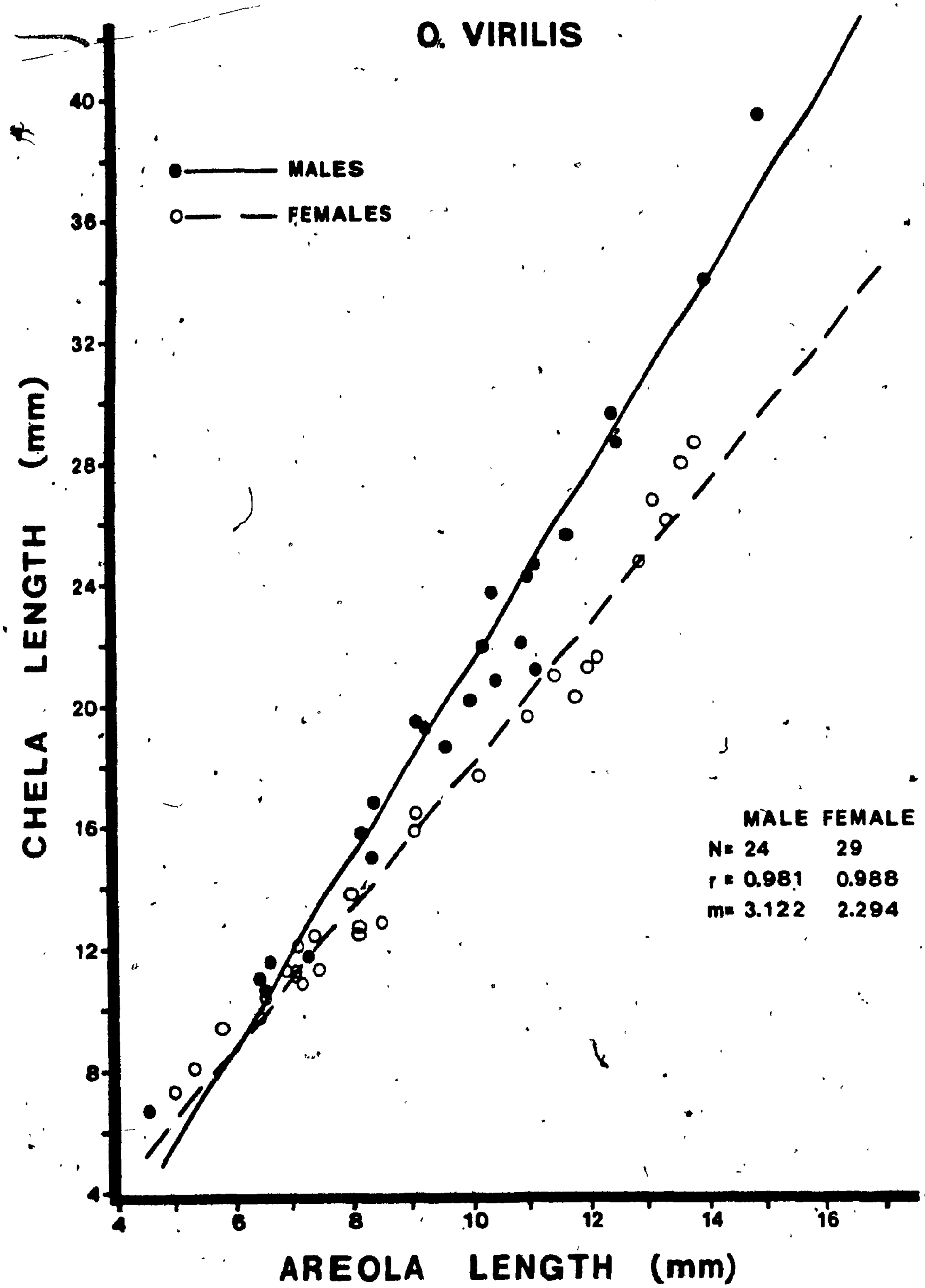
Appendix IIIa. Relationship between areola length and carapace length of Orconectes virilis.



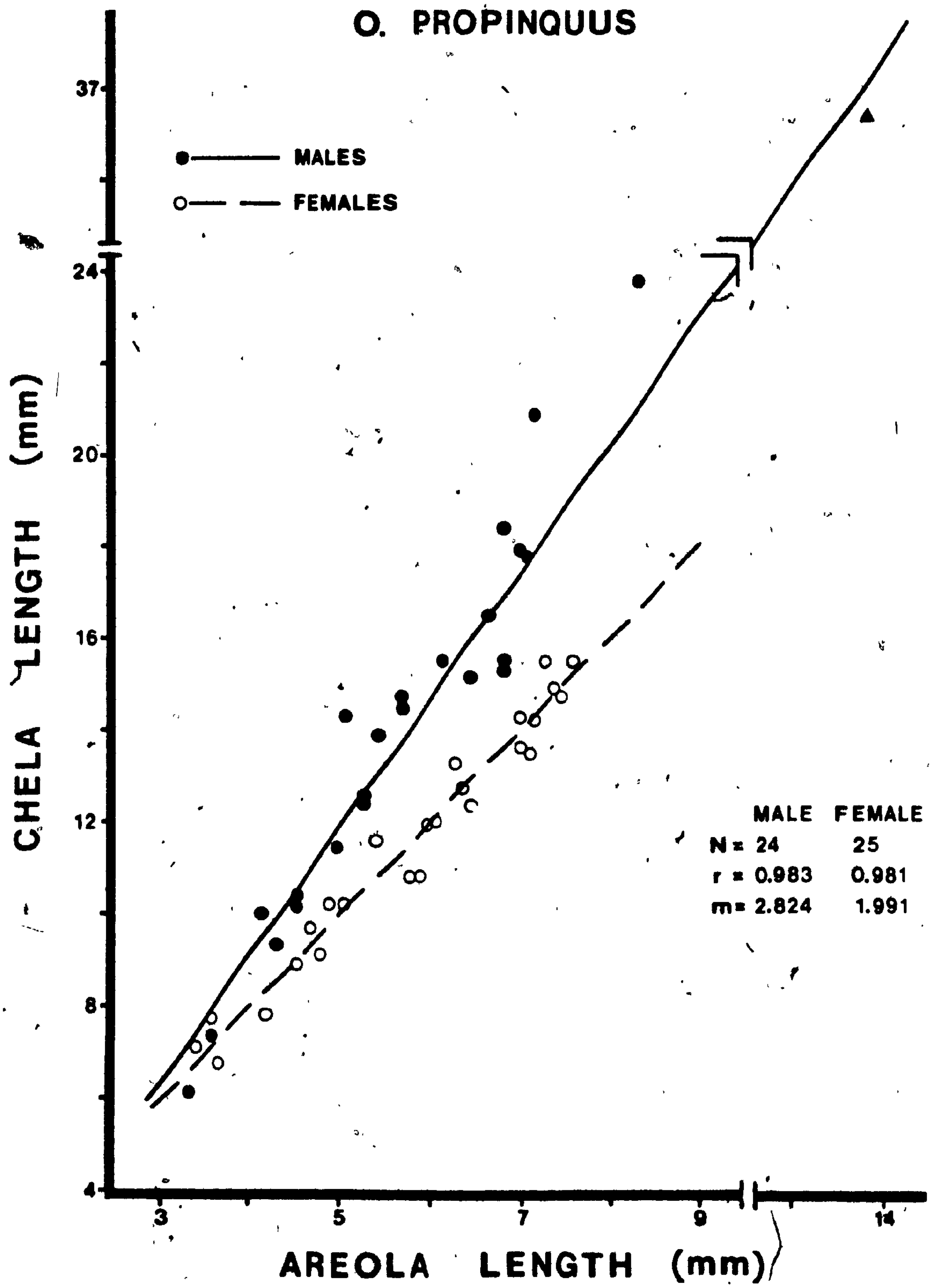
Appendix IIIb. Relationship between areola length and carapace length of <u>Orconectes propinquus</u>. (▲= male caught in <u>Lac Choinière, Granby, Quebec</u>).



Appendix IVa. Relationship between areola length and chela length of Orconectes virilis.



Appendix IVb. Relationship between areola length and chela length of Orconectes propinquus. (▲= male caught in Lac Choinière, Granby, Quebec).



Appendix V. Comparison of O. propinquus and O. virilis chela lengths. The graph was obtained by superimposing the lines in Appendix IVa and IVb on a common scale. (O.P. = O. propinquus; O.V. = O. virilis).