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EMIGRATION IN RESPONSE TO RESOURCE AVAILABILITY AS A METHOD  
OF POPULATION REGULATION IN CRAYFISH

*The University of Arizona*

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EMIGRATION IN RESPONSE TO RESOURCE AVAILABILITY  
AS A METHOD OF POPULATION REGULATION IN CRAYFISH

by

John Hotton Menke

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A Dissertation Submitted to the Faculty of the

SCHOOL OF RENEWABLE NATURAL RESOURCES

In Partial Fulfillment of the Requirements  
For the Degree of

DOCTOR OF PHILOSOPHY  
WITH A MAJOR IN FISHERIES SCIENCE

In the Graduate College

THE UNIVERSITY OF ARIZONA

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THE UNIVERSITY OF ARIZONA  
GRADUATE COLLEGE

As members of the Final Examination Committee, we certify that we have read  
the dissertation prepared by John Menke

entitled Emigration in response to resource availability as a method of  
population regulation in crayfish

and recommend that it be accepted as fulfilling the dissertation requirement  
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*John A. Mearns*

#### ACKNOWLEDGMENT

I am indebted to Dr. Jerry C. Tash for his encouragement, leadership, and patience both preceeding and during the course of my research. The frequent discussions on evolutionary biology and population regulation with Dr. Tash, Dr. Matter, and my colleagues Ed Bianchi, Steve Holanov, Tom McMahon, Carl Messik, and Benny Wanjala were indispensable to the choice, design, and execution of this research project.

I thank my committee members: Dr. John Hendrickson, Dr. William Matter, Dr. Jerry Tash, Dr. Donald Thomson, and Chuck Ziebell for their critical review of the contents of this paper. This research project was supported in part by the Arizona Cooperative Fisheries Research Unit, and the Graduate College of The University of Arizona.



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## ABSTRACT

The regulatory emigration hypothesis was tested experimentally using the crayfish Orconectes causeyi Jester. Varying amounts of food and shelter were provided to crayfish in tanks with escape routes. O. causeyi rapidly adjusted its numbers in harmony with available resources through density-dependent emigration. Shelter influenced the distribution and abundance of O. causeyi most. Response to food occurred but was less and took longer than the response to shelter. The small amount of variance between numbers of crayfish that emigrated during both short-term and long-term replicate tests strongly supports the regulatory emigration hypothesis.

## CHAPTER 1

### INTRODUCTION

Many of the recent studies on population regulation in animals were based on the general theory, as expressed by Chitty (1960), that every species has evolved characteristics for regulating its numbers in harmony with available resources. Regulatory mechanisms are mostly unknown but probably vary widely among species. A mechanism that often has been suggested for regulation of numbers in vagile species is the emigration of those individuals in a population that are in excess of the number that would be in harmony with available resources (Chapman 1962, Wynne-Edwards 1962, Lomnicki 1966, Chitty 1967, Taylor and Taylor 1977). I call this mechanism "regulatory emigration;" others (Beckoff 1977, Tamarin 1980) have used the term "dispersal" to refer to essentially the same thing.

Current studies that have considered regulatory emigration as the means of intraspecific regulation have been predominantly field studies of small mammals (Sullivan 1977, Tamarin 1978, Gaines 1979), wherein experimental manipulations were used to obtain the data used to infer factors (especially dispersal) that caused changes in numbers (Krebs 1978). The lack of control of variables in these field studies limits the extent to which they can be used to support the regulatory emigration hypothesis. For example, Sullivan (1977) observed that

island deer mice disperse onto removal grids at a lower rate than on the mainland. However, many factors differed between his test sites (weather, food and shelter availability, and reproductive rate among others) and he was therefore not able to demonstrate a cause-effect relationship between resource availability and dispersal rate; such a relationship must be demonstrated in order to support the regulatory emigration hypothesis.

Field studies are the necessary starting points for all ethological work, but they must be followed by controlled experiments which can isolate variables and test alternative hypotheses (Tamarin 1980). Before clear-cut regulatory emigration can be demonstrated, the design of these experiments must provide organisms with the freedom to leave the test sites in response to variation in specific resources.

To date, few laboratory experiments have been conducted on emigration in response to manipulation of resources. In the few studies which have been done (Streaker 1954, Lomnicki and Slobodkin 1966, Butler 1980), the experimental designs allow for little or no change of resource levels and therefore cannot determine if rates of emigration increase with resource depletion and decrease with resource increases.

The objective of my study was to experimentally test the regulatory emigration hypothesis using the crayfish Orconectes causeyi Jester. Orconectes causeyi was selected because 1) emigration of crayfish in natural habitats has been observed and discussed by numerous



investigators (Tack 1941, Bovbjerg 1959, Abrahamsson 1966, Mobberly and Owens 1966, Momot 1966, Lunt 1967, Hazlett, Ritschhof, and Rubenstein 1974, Berrill 1978, and Saiki and Tash 1979), and 2) the theoretical models of self-regulation of populations by density-dependent emigration (Taylor and Taylor 1977, Lomnicki 1978) appear to be applicable to crayfish.

## CHAPTER 2

### MATERIALS AND METHODS

#### General

Crayfish for experiments were collected by hand and in minnow traps from Parker Canyon Lake, Arizona, on a monthly or bimonthly basis from April 1980 to December 1981. Crayfish were transferred to Tucson in ice chests which were filled with alternating layers of crayfish and aquatic macrophytes (Myriophyllum exalbescens), all overlying a layer of ice. The crayfish, which were delivered to the research area within 4 hr of collection, were always in excellent condition and no mortality of adults was observed.

The crayfish were held in tanks 1.8 m in diameter for at least 30 days prior to use in experiments; no more than 30 crayfish were held in each tank at any time. Each tank was provided with about 20 shelters of various sizes and with dense mats of macrophytes. Crayfish in holding tanks were fed catfish pellets twice a week; the amount added was sufficient to always have an excess of pellets in the tank at any time. Water temperature in the holding tanks was maintained at the level chosen for each experiment by increasing or decreasing the degree of shading in the tanks.

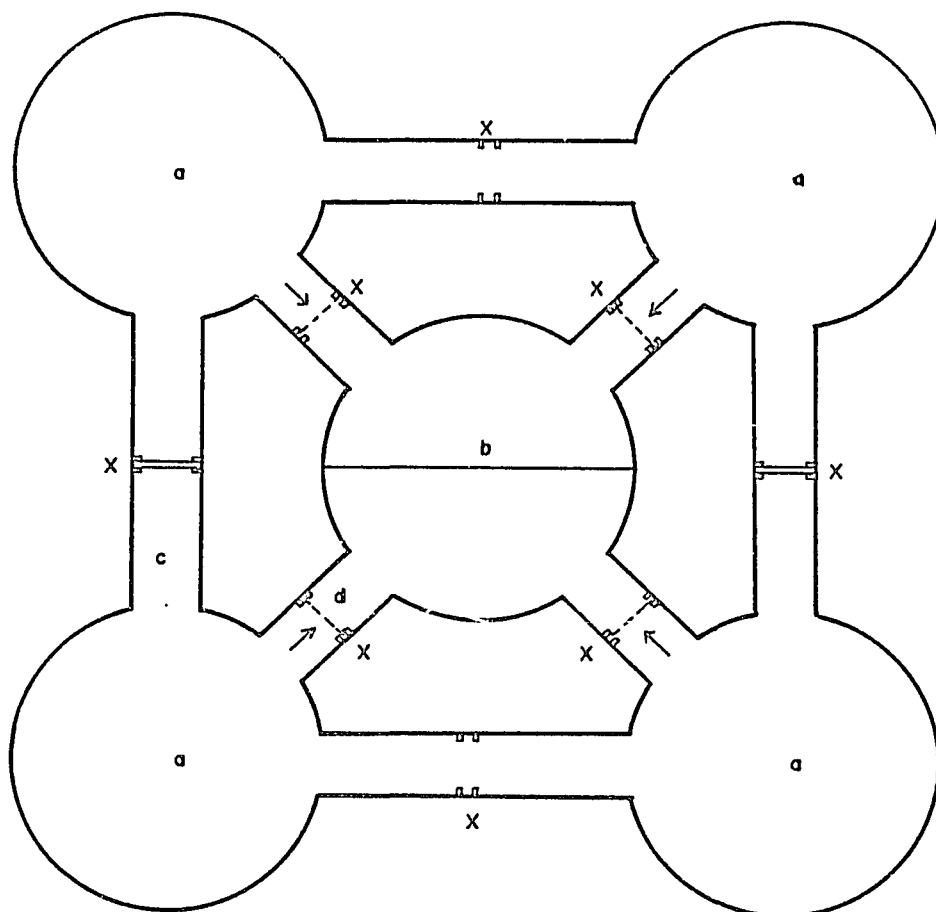
During each collecting trip, observations were made of the various sizes and sexes of crayfish at Parker Canyon Lake and surface

water temperatures (0-5 m) were measured so that experiments could run at normal water temperatures. The crayfish used in the tests were numbered using the Abrahamsson (1965) technique which I modified by substituting lacquer for cauterization. Crayfish were used only once in experiments; ovigerous ("in berry") females were not used. Reproductive males were designated as form I (FI) and non-reproductive as form II (FII) (Stein 1976). Adult crayfish were designated as small if their carapace was 31-40 mm long, medium if 41-50 mm long, and large if 51-60 mm long. Carapace length (CL) equals the distance from the rostral tip to the posteromedian border of the carapace (about half the total length of the crayfish).

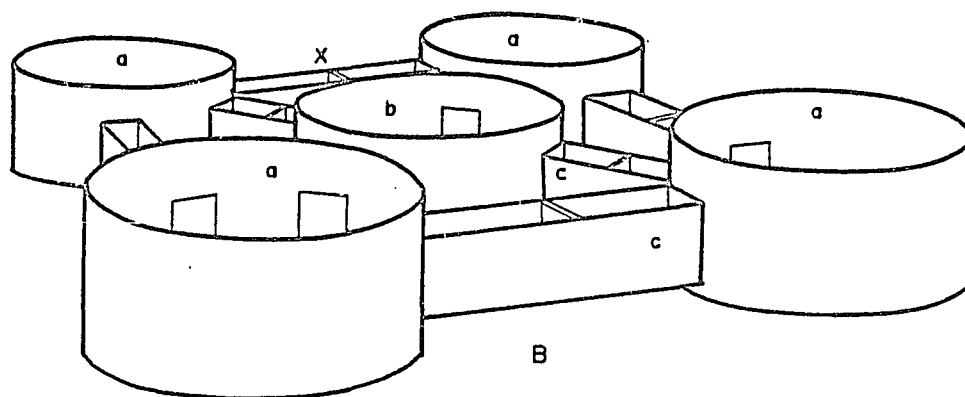
Experiments were carried out in 5 tanks interconnected with troughs; each tank was 1.8 m in diameter, 1.0 m deep, and had a 3.0 m<sup>2</sup> bottom which included half of each attached trough (Figure 1). The outer tanks were lined with 20-mil plastic pool liners and the center tank was coated with blue epoxy paint. Individual experiments were run in either a single peripheral tank or in two interconnected peripheral tanks; the complex permitted simultaneous replicates. Tank water was maintained at temperatures  $\pm 3.0^{\circ}\text{C}$  of the surface water temperatures for the same times of the year in Parker Canyon Lake.

Removable barriers were used in troughs to close off interconnected tanks. Slats for removable barriers were fixed at the midpoint of each trough. Barriers were of two types: 1) complete barriers made of smooth-surfaced wood panels 40 cm high (the smoothness prevented climbing); and 2) one-way barriers made of wood panels 40 cm

Figure 1. Top (A) and oblique (B) views of experimental tanks. (a = peripheral-residential-experimental tanks; b = central-emigration-sink tank; c = 200 cm long x 30 cm wide x 50 cm deep trough connecting two peripheral tanks; d = 100 cm long x 30 cm wide x 50 cm deep trough connecting peripheral and emigration tanks; x = location of slots for insertion of barriers.



A



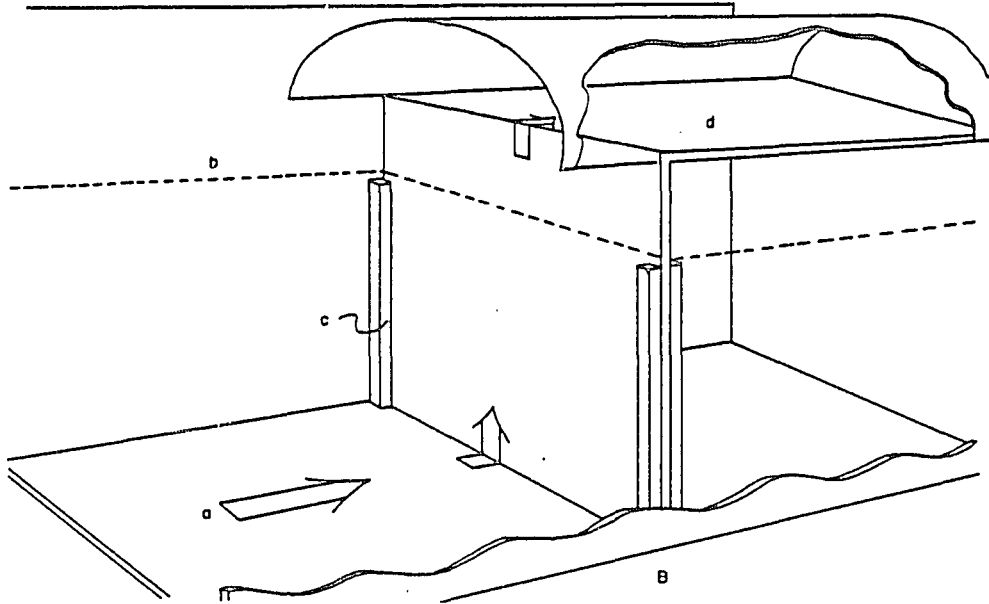
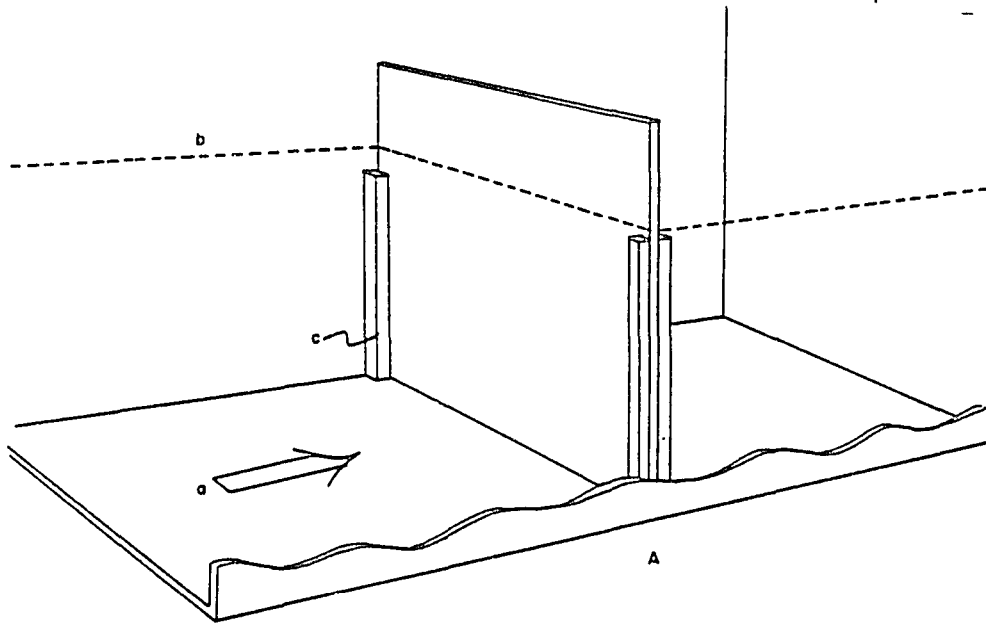
B

high covered with plastic wire mesh (the wire mesh enhanced climbing). One-way barriers had a covered shelf extending 50 cm at a right angle out from the top of the panel (Figure 2). During experiments, water levels in tanks were maintained at 30 cm; at this level, the upper 10 cm of the barriers were out of the water.

The design of the exposed one-way barrier resulted from the need to separate random movements made by residential crayfish during normal exploratory behavior from the non-random movements of emigrating crayfish. During preliminary nocturnal experiments, crayfish moved about randomly, exploring the entire underwater area and readily climbing over all underwater objects, including completely submerged one-way barriers. Crayfish did not readily climb over one-way barriers that had the upper portion exposed above water. During all experiments, one-way barriers were open from each test tank to the central tank.

Three shelter sizes were tested: 1) large ones wherein the height equalled one-half the width; 2) medium ones wherein height equalled one-third width; and 3) small ones wherein the height equalled one-quarter the width. In the final experiments, only the medium-size shelters (selected by all sizes of experimental crayfish) were used as no crayfish selected large shelters and only a few of the smaller crayfish selected the small shelters. All shelters used in the experiment were constructed with a flat tile bottom and a curved plastic roof (both opaque) so that the enclosed space was 20 cm long by 12 cm wide by 4 cm maximum height. One end was fully open and the other end was

Figure 2. Side view of the non-passable barrier (A) and the one-way barrier (B). (a = direction of crayfish movement; b = water level in tank system; c = slot for barrier; d = horizontal shelf). The left end of the trough connects to a peripheral tank and the right end of the trough connects to the central tank.





closed. The roof at the closed end had a 2 cm<sup>2</sup> opening to allow the current created by the movement of the crayfish to flow through the shelter.

Mats of Najas marina and Cynodon dactylon were used as cover. The mats reached from the bottom substrate to the water surface. The mats were sufficiently dense to almost totally mask the substrate covered. In tanks provided with cover, either 12.5% or 50% of the areas of the tanks was covered with mats of macrophytes.

Three types of food were fed to the crayfish: 1) catfish pellets (produced and donated by the Environmental Research Laboratory of Tucson, Arizona); 2) pieces of fresh fish (Tilapia zillii); and 3) aquatic macrophytes, most of which were partially covered with epiphytes. Tanks were cleaned of algae and detritus before the start of each experiment but were never cleaned during experiments.

#### Short-term Experiments

Four experiments lasting from 2-4 days each were run on migration movements of crayfish from environments containing different amounts of food, shelter, and cover. Following the placement of resources in the peripheral tank, crayfish for each experiment were introduced into the peripheral tanks with all exits blocked for a 24-hr acclimation period. After acclimation, a one-way barrier was inserted at dusk between each peripheral tank and the central tank. Locations of crayfish were recorded at 0800 hr, 2000 hr, 2200 hr, and 2400 hr each day for the duration of the experiment.

### Experiment 1

Movements of crayfish were recorded over 3 days in experimental tanks 1) without food, shelters, or cover, and 2) with food, shelters, and cover. Eight replicates were run of each treatment. Food was provided by 2 g of catfish pellets and 10 g of finely-cut fresh fish added daily, cover was provided by aquatic macrophytes spread over 50% of the bottom of each tank, and shelters were provided by evenly spacing 4 medium-size shelters in each tank. These tests were run in each of the 4 single peripheral tanks having complete barriers between them; one 41-50 mm CL FII male crayfish was introduced into each peripheral tank.

### Experiment 2

Movements of crayfish were recorded over 3 days in experimental tanks 1) without food, shelters, or cover, 2) with food only, 3) with shelters only, and 4) with food, cover, and shelters. Four replicates were run of each treatment. Resources were similar in types and amounts to those provided in Experiment 1.

Each test was run in a 2-tank system made up of 2 peripheral tanks without a barrier between them but closed off from the other peripheral tanks. In each test, two 41-50 mm CL crayfish (one FII male and one female) were introduced into a 2-tank system.

### Experiment 3

Movements of crayfish were recorded over 4 days in experimental tanks 1) with shelter only and 2) with both shelter and food. Three

replicates were run in each treatment. Shelters were provided by evenly spacing 6 medium-size shelters in each tank. Food was provided by 16 g of catfish pellets and 40 g of finely-cut fresh fish added daily.

Tests were run in 2-tank systems arranged as described in Experiment 2. In each test, eight 41-50 cm CL FI males were introduced into a 2-tank system.

#### Experiment 4

Movements of crayfish were recorded over 2 days in experimental tanks 1) with food and 2 shelters, 2) with food and 8 shelters, 3) with food, 2 shelters, and a 12.5% macrophyte cover, and 4) with food, 8 shelters, and a 50% macrophyte cover. Four replicates were run of treatments 1 and 2, and 3 replicates each of treatments 3 and 4. Food was provided by 16 g of catfish pellets and 40 g of finely-cut fresh fish added daily. Tests were run in 2-tank systems arranged as described in Experiment 2. In each test, eight 41-50 cm CL FI males were introduced into a 2-tank system.

#### Long-term Experiments

Three experiments, each for different periods of time ranging from 21-37 days, were run on emigration of crayfish from environments with similar levels of food, cover, and shelters but with different temperature regimes. Two replicates were run of each experiment. Experiments were run in 2-tank systems similar to those described above in Experiment 2. Food was provided by 8 g of catfish pellets and 20 g

of finely-cut fish added daily to each system. Cover was provided by aquatic macrophytes spread over 50% of the bottom of each tank and shelters were provided by evenly spacing 4 medium-size shelters under the macrophytes in each tank. Daily temperatures were recorded in each system during tests.

#### Experiment 1

This experiment was run in July and August 1981. In each replicate, two 41-50 mm CL female crayfish were individually numbered and placed in a completely closed system for a 3-day acclimation period. After acclimation, a one-way barrier was placed between each peripheral tank and the central tank. On the third day after acclimation and thereafter on every other day for the following 12 days, one numbered crayfish was added to each system at dusk; female and FI male crayfish (41-50 mm CL) were added alternately.

All macrophyte cover was removed from each system on the night of the 15th day after acclimation. Four of the 8 shelters were removed from each system on the night of the 17th day. Resources were removed very slowly and carefully at night to minimize disturbance of crayfish. Locations of crayfish were recorded each day at 0800 hr, 2000 hr, 2200 hr, and at 2400 hr during each of 21 days, at which time the experiment was ended.

#### Experiment 2

This experiment was run in September and October 1981. In each replicate, two individually numbered female crayfish (one 51-60 cm CL

and one 31-40 mm CL) were placed in a completely closed system for a 3-day acclimation period. After acclimation, a one-way barrier was placed between each peripheral tank and the central tank. On the third day after acclimation and thereafter on every other day (with two exceptions) for the following 25 days, one numbered crayfish was added to each system at dusk; these crayfish were randomly selected from holding tanks containing male and female adults ranging in size from 31-60 mm CL.

All macrophyte cover was removed from each system on the night of the 28th day after acclimation. Four of the 8 shelters were removed from each system on the night of the 31st day. Locations of crayfish were recorded each day at 0800 hr, 2000 hr, 2200 hr, and 2400 hr during each of 37 days, at which time the experiment was terminated.

### Experiment 3

This experiment was run in November and December 1981. In each replicate, 4 individually numbered crayfish (two 41-50 mm CL females and two 41-50 mm CL FI males) were placed into a completely closed system for a 3-day acclimation period. After acclimation, a one-way barrier was placed between each peripheral tank and the central tank. On the 4th day after acclimation and usually thereafter on every other day for the following 14 days, 2 numbered crayfish were added to each system at dusk; these crayfish were randomly selected from holding tanks as described above in Experiment 2.

All macrophyte cover was removed from each system on the night of the 18th day after acclimation. Four of the 8 shelters were removed

on the night of the 21st day. Locations of crayfish were recorded each day at 0800 hr, 2000 hr, 2200 hr, and 2400 hr during each of 32 days, at which time the experiment was terminated.

## CHAPTER 3

### RESULTS

The null hypothesis that "Orconectes causeyi shows the same types of movements in each of several different environments containing varying amounts of food, cover, and shelter" was tested in 4 experiments, each lasting from 2-4 days (designated short-term experiments). Three longer experiments, each lasting a different length of time ranging from 21-37 days, were run to evaluate emigration behavior as it was affected by temporal changes in temperature (designated long-term experiments). Detailed results from these experiments are in Tables 1-11 of the Appendix.

#### Short-term Experiments

##### Experiment 1

One of 8 crayfish emigrated during 72 hr from 8 tanks with an excess of food and shelter in contrast to 8 of 8 leaving within 12 hr from tanks with no food or shelter (R x C test of independence using the G-test,  $p < .005$ ) (Figure 3).

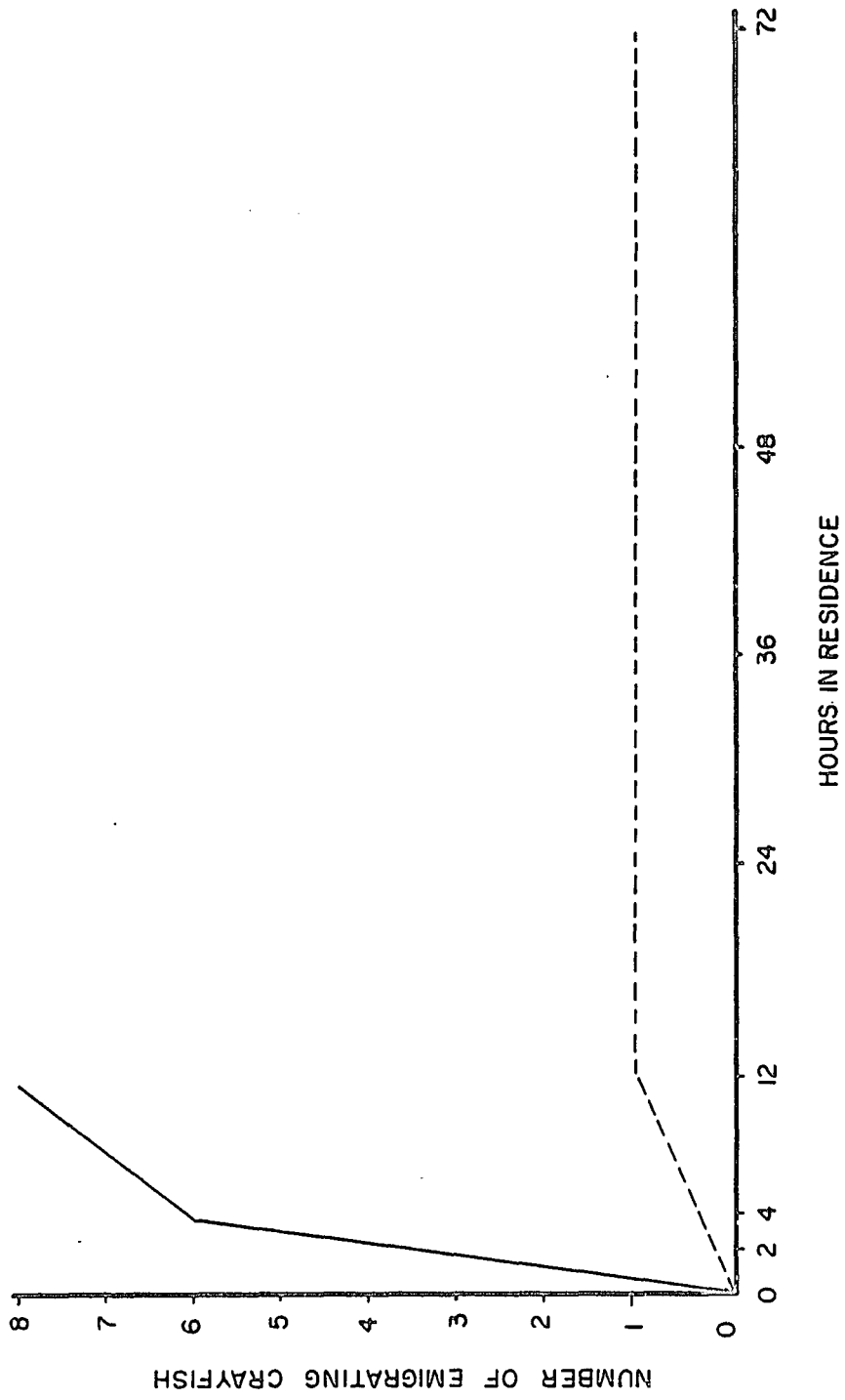
Temperatures in test tanks ranged from 21-22°C during testing.

##### Experiment 2

Eight of 8 crayfish emigrated from 4 tanks without food and shelter and 8 of 8 from tanks with food only (all within 24 hr), in

Figure 3. Cumulative numbers of crayfish emigrating from 8 replicate tanks (1 crayfish per tank) in each of 2 treatments. Treatment 1 - without food or shelter (—————), and treatment 2 - with food and shelter (-----).





contrast to 5 of 8 from tanks with shelter and 0 of 8 from tanks with both food and shelter during 72 hr (R x C test of independence using the G-test,  $p < .005$ ) (Figure 4). Emigrations from tanks with shelter only occurred at a rate of about one every 12 hr. Male and female crayfish showed similar emigration patterns.

Temperatures in test tanks ranged from 22-23°C during testing.

### Experiment 3

Seventeen of 24 crayfish emigrated from three 2-tank systems with shelter only compared to 12 of 24 from tanks with food and shelter during 96 hr (Student's t-test,  $p < .05$ ) (Figure 5).

Temperatures in the test tanks ranged from 12-14°C during testing.

### Experiment 4

Twenty-two of 32 crayfish emigrated from tanks with food and 2 shelters during 48 hr in contrast to 14 of 32 from tanks with food and 8 shelters (Student's t-test,  $p < .01$ ) (Figure 6A).

Thirteen of 24 crayfish emigrated from tanks with food, 2 shelters, and 12.5% cover during 48 hr in contrast to 2 of 24 from tanks with food, 8 shelters, and 50% cover (Student's t-test,  $p < .01$ ) (Figure 6B).

The temperature in all tests ranged from 9-12°C during testing.

Figure 4. Cumulative numbers of crayfish emigrating from 4 replicate tanks (2 crayfish per tank) in each of 4 treatments. Treatment 1 - without food and shelter (—————), treatment 2 - with food only (-----), treatment 3 - with shelters only (-o-o-o-o-o), and treatment 4 - with both food and shelter (-x-x-x-x-x).

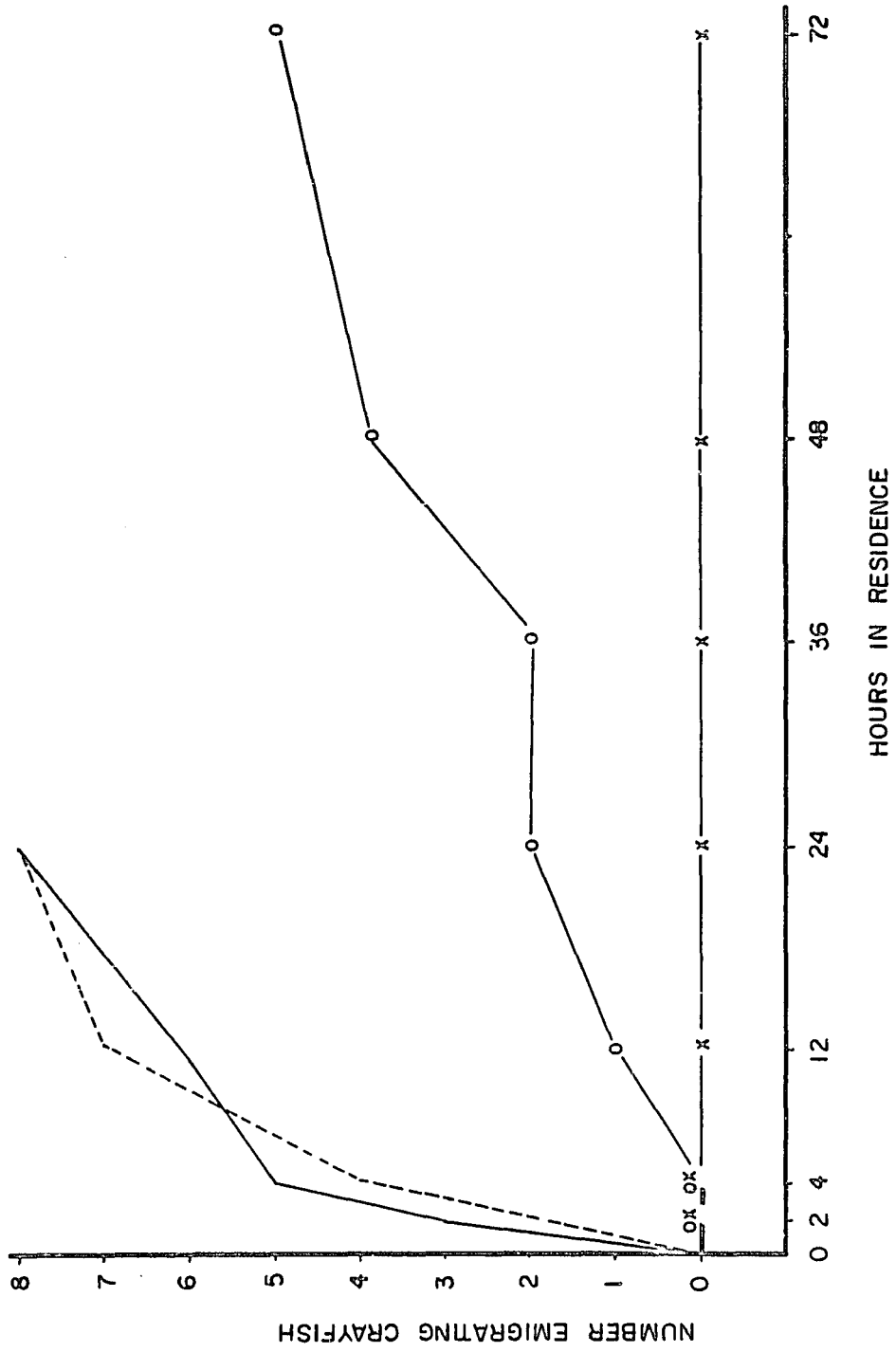


Figure 5. Cumulative mean numbers of crayfish emigrating from 3 replicate tanks (8 crayfish per tank) in each of 2 treatments. Treatment 1 - with shelter only (—————), and treatment 2 - with both food and shelter (-----). Vertical lines indicate 95% confidence limits.

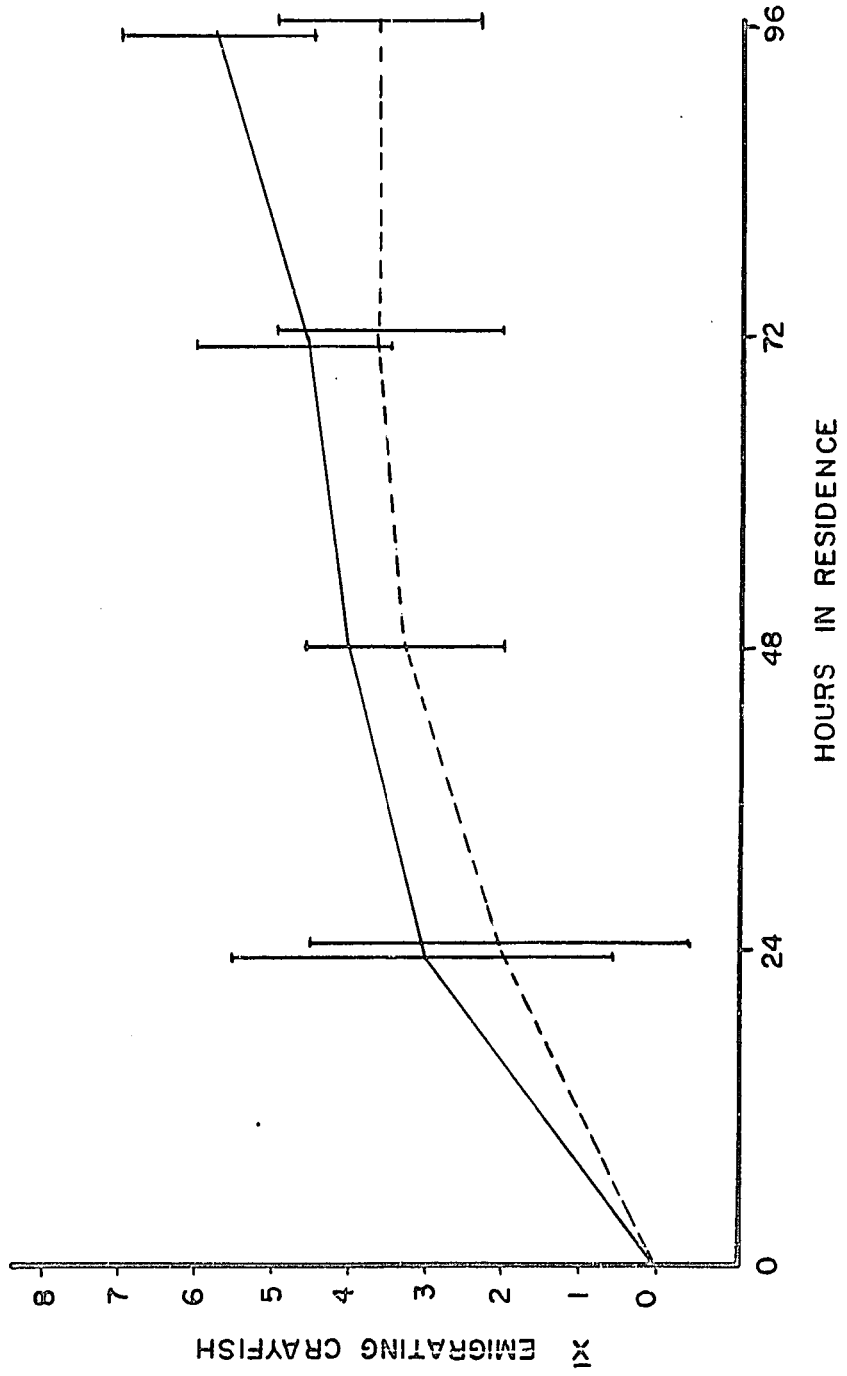
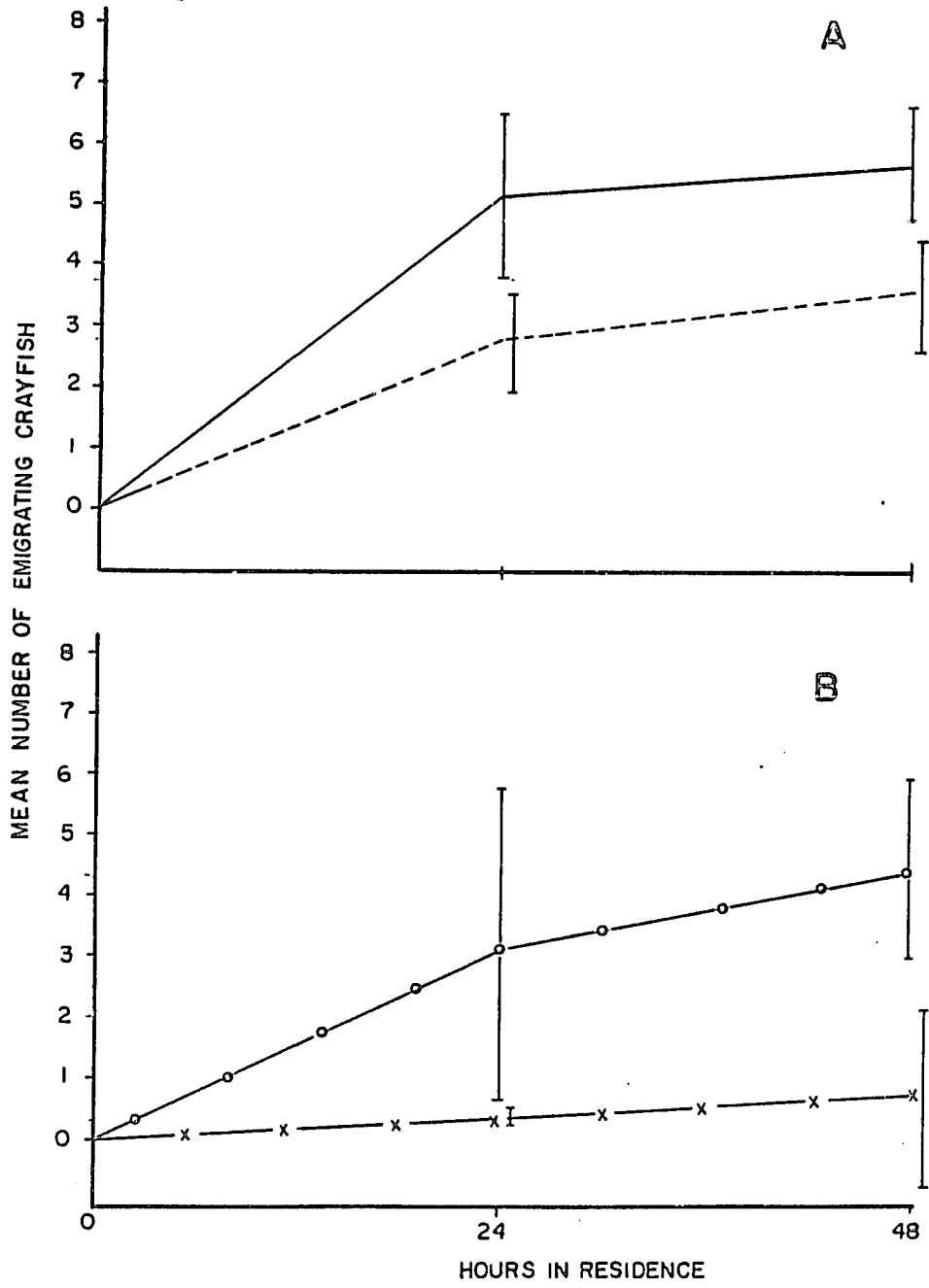


Figure 6. A. Cumulative mean numbers of crayfish emigrating from 4 replicate tanks (8 crayfish per tank) during 2 treatments. Treatment 1 - with food and 2 shelters (—————), and treatment 2 - with food and 8 shelters (-----).

B. Cumulative mean numbers of crayfish emigrating from 3 replicate tanks (8 crayfish per tank) during 2 treatments. Treatment 1 - with food, 2 shelters, and 12.5% cover (-o-o-o-o-o), and treatment 2 - with food, 8 shelters, and 50% cover (-x-x-x-x-x). Vertical lines indicate 95% confidence limits.





## Long-term Experiments

### Treatment 1

This treatment was run in July and August 1981 when water temperatures ranged from 22-25°C.

Resident populations stabilized at 3 crayfish (out of a total of 5 introduced into the tanks) in each of the 2 replicates in 7 days; these population levels remained relatively stable through the 18th day even though 2 more crayfish were added to each replicate (Figure 7, Treatment 1). All individuals introduced after 7 days emigrated within 36 hr while the older residents remained.

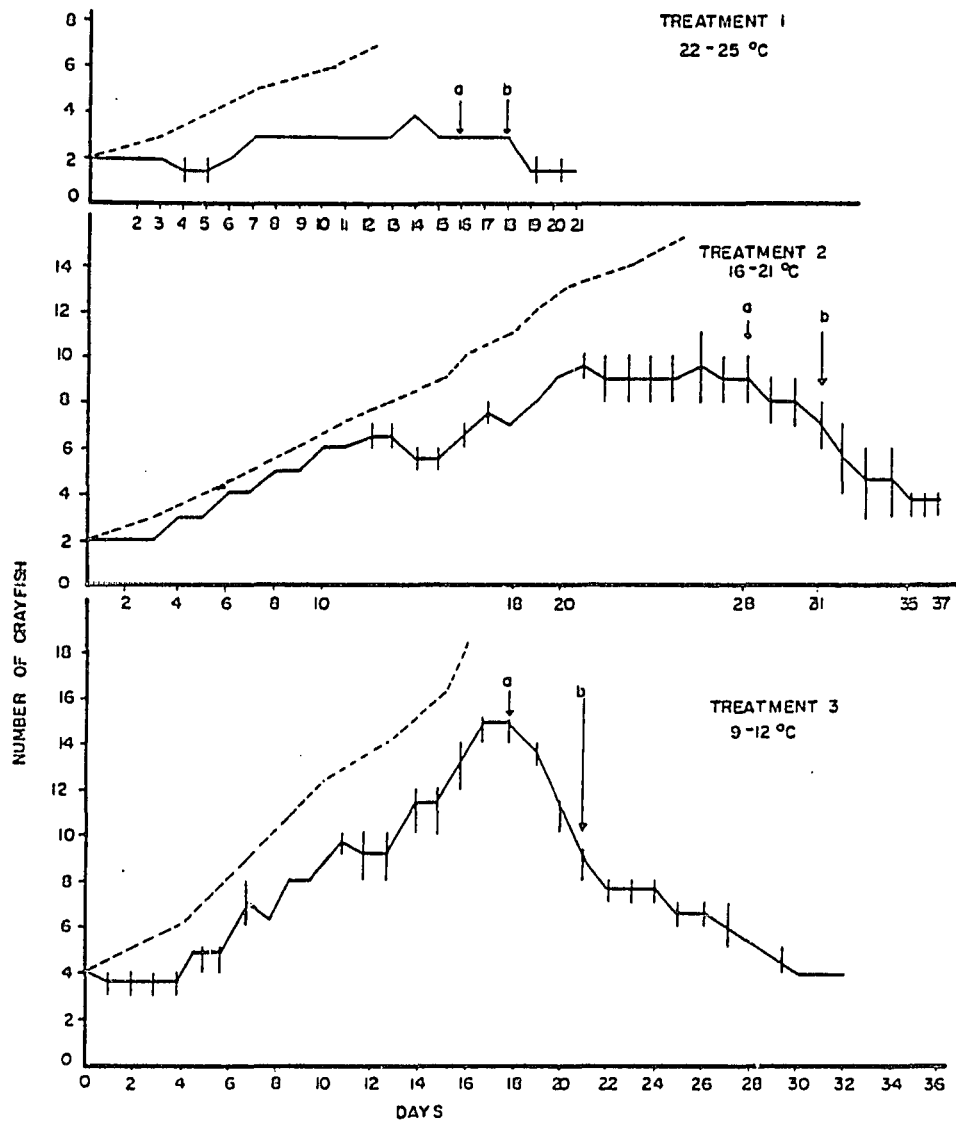
No crayfish emigrated in quick response to the removal of the macrophyte cover, but resident populations dropped from 3 to 2 crayfish in one replicate and from 3 to 1 in the other within 24 hr after 4 of 8 shelters were removed from each on the 18th day; the populations remained at these new levels for the following 48 hr, at which time the experiment was terminated (at 21 days).

### Treatment 2

This treatment was run in September and October 1981 when water temperatures ranged from 16-21°C.

Resident populations stabilized at 8 crayfish in one replicate and 10 in another (out of 13 added to each) in 20 days; these populations remained relatively constant from the 20th through the 28th day despite the addition of 6 more crayfish to each replicate

Figure 7. Cumulative numbers of crayfish added to each of 2 replicate tanks during each of three treatments (-----) and cumulative mean numbers of resident crayfish from 2 replicate tanks during each of 3 treatments (—————). (a = the day that all macrophytes were removed from each tank; b = the day that 4 of 8 shelters were removed from each tank). The vertical lines indicate the range of values between single treatments.



(Figure 7, Treatment 2). Most individuals introduced after the 20th day emigrated within 24 hr while the older residents remained.

Resident populations dropped only slightly after removal of macrophytes on the 28th day but dropped from 6 to 3 crayfish in one replicate and from 8 to 4 in the other after 4 of 8 shelters were removed on the 31st day; the populations remained at these new levels during the following 48 hr, at which time the experiment was terminated (at 37 days).

### Treatment 3

This treatment was run in November and December 1981 when water temperatures ranged from 9-12°C.

The resident populations increased continuously during the 16-day period when 2 crayfish were being added every other day to each of the 2 replicates (Figure 7, Treatment 3). During this time, the populations reached 14 crayfish in one replicate and 15 in the other (out of 18 added in each replicate).

Resident populations dropped from 14 to 8 crayfish in one replicate and from 15 to 9 in the other within 3 days after the removal of macrophytes, and declined to 4 crayfish in each replicate during the 9 days following removal of 4 of 8 shelters in each. The populations remained at 4 each during days 30 and 31, after which the experiment was terminated (at 32 days).

## General Remarks

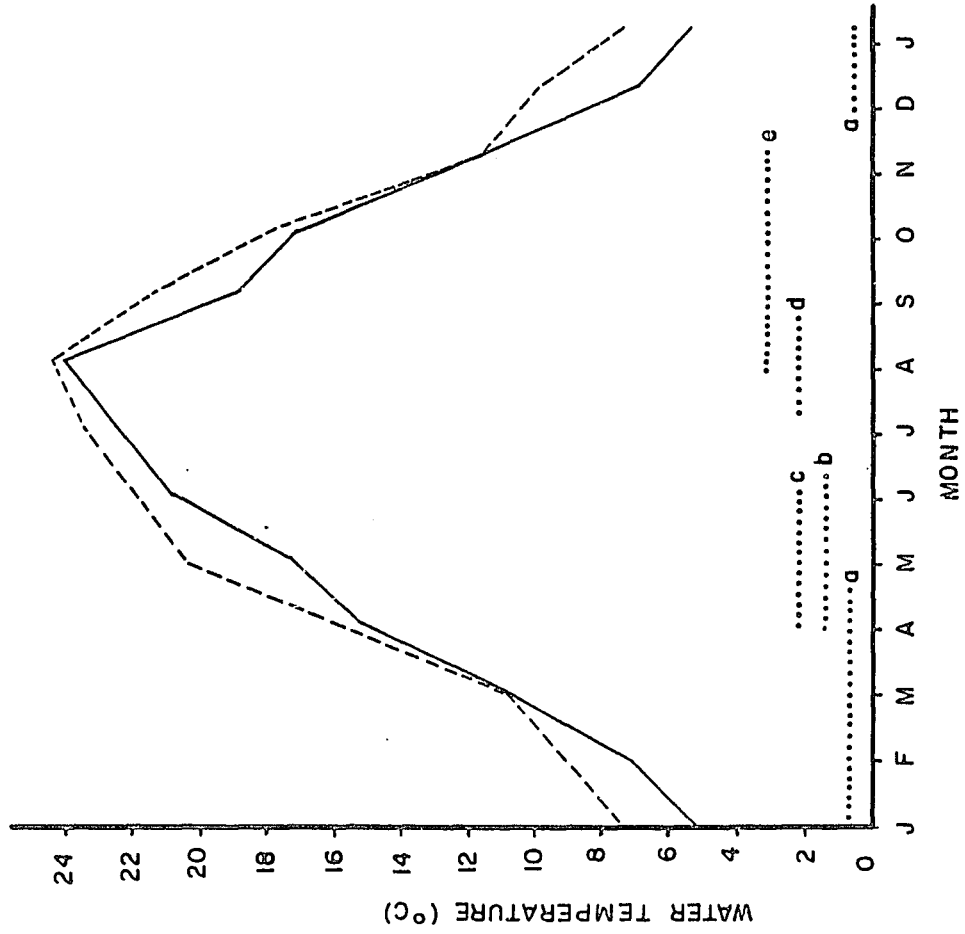
### Seasonal Patterns of Movement

Activity in crayfish slowed as seasonal temperatures dropped despite relatively constant amounts of food, cover, and shelter. Crayfish were always more active at night during July and August than during other times of the year. This was especially true of males, which could always be induced to emigrate by removing shelters. In experiments where water 10°C warmer than in the test tanks was added at night (during October, November, and December), there was increased activity of crayfish that persisted as long as the temperature remained elevated; however, adding warmer water during the day did not increase activity.

Female crayfish became less active after August and almost completely ceased activity by December when they produced their eggs. Females "in berry" remained in shelters from December to March (Figure 8) and used macrophytes to close off the openings of these shelters.

During periods when they are molting (Figure 8), both male and female crayfish remained in shelters or, if no shelter was available, in the densest cover available. After molting, both sexes became much more active; males that molted from FII to FI became very aggressive and attempted copulation with any female crayfish or any smaller male crayfish that they contacted.

Figure 8. Comparison of monthly mean water temperatures in experimental tanks (-----) and in Parker Canyon Lake (————) at 0-5 m. The dotted lines ending in lower case letters show periods during which O. causeyi were: a = female "in berry;" b = adult female molt; c = adult male molt from FI to FII; d = adult male molt from FII to FI; e = reproductive period.



### Daytime Patterns of Movement

Crayfish did not move around during the day unless they were in areas without sufficient cover or shelters to permit them to hide. Even in areas without places to hide, crayfish were usually inactive during the day and remained along wall-floor interfaces. Only a few of the many crayfish placed in test tanks in which there was no food, cover, or shelter emigrated during the day.

### Nighttime Patterns of Movement

Crayfish usually became active at dusk. During the 24-hr acclimation period when the tanks were closed, the crayfish usually moved rapidly along the perimeter walls, attempting to climb wherever possible. When the tanks were opened, crayfish that emigrated usually left within 2 hr after dusk on the first day. Of 25 crayfish observed emigrating during experiments, all climbed the mesh wall, moved across the shelf, and dropped into the water in the central tank without any hesitation or hint of reversal of direction.

Crayfish that became residents moved about experimental tanks throughout the night and, although many climbed the wire mesh of the one-way barrier, most stopped at the air-water interface and returned to the bottom. When food was present, they moved about in a deliberate and slow manner, feeding for at least 2 hr.

### Interactions Between Crayfish

Crayfish, except for FI males, avoided each other during July and August; FI males attempted to mount and copulate when they



encountered female and smaller male individuals. Avoidance reactions occurred when crayfish came into direct contact and consisted of one or both turning away or backing up; larger crayfish usually caused smaller ones to retreat.

In experiments testing shelter dominance, large (51-60 mm CL) ovigerous females displaced all other crayfish. Medium-size (41-50 mm CL) ovigerous females were about equally as dominant as large (51-60 mm CL) FI males, and both of these dominated small (31-40 mm CL) to medium (41-50 mm CL) males and small (31-40 mm CL) ovigerous females (Appendix, Table 12). I never observed cannibalism nor injuries in crayfish as a result of any of these interactions.

#### Use of Shelters and Macrophytic Cover

Crayfish would not hide in cover until shelters became unavailable. Shelters were preferentially used by crayfish in the following order: 1) shelters located under macrophytic cover and positioned near food; 2) shelters under cover but without food; and 3) shelters without cover but with food.

When the number of crayfish in a tank exceeded the number of available shelters, the larger crayfish (either male or female) held the shelters and smaller crayfish hid in or under the macrophytic cover. When experimental tanks were open, there was no multiple-use (more than 1 crayfish per shelter) of shelters; in closed tanks, multiple-use of shelters was common from June to October with as many as 10 various-sized crayfish occupying a single shelter.

The larger crayfish used in tests (51-60 mm CL) often returned to the same shelter that they had occupied during the day, but most crayfish switched shelters. Ovigerous females seldom left shelters.

#### Field Studies in Parker Canyon Lake

I sampled two areas in Parker Canyon Lake in 1981: 1) a littoral area with dense macrophyte cover (Myriophyllum exalbescens); and 2) a littoral area having a substrate and slope similar to the macrophyte area but without macrophytes. During the year, the distribution and abundance of crayfish in these areas varied greatly for the different sizes and sexes of crayfish encountered (Appendix, Table 13).

Females "in berry" stayed in burrows from December to April. During this same period, males were usually in burrows but did move around. Two-year female crayfish (CL  $\geq$  45 mm) were always found in areas of dense macrophyte cover from 0-5 m deep throughout the year. Two-year FI male crayfish (CL  $\geq$  45 mm) usually were found in dense beds of macrophytes from July to April but were seldom in these areas during April to July, the non-reproductive period.

Crayfish smaller than 40 mm CL usually were found in areas without macrophytes from June to October. During this same period, crayfish  $\leq$  14 mm were in water  $\leq$  10 cm with dense beds of macrophytes. Exclusive of small juveniles, most crayfish were found in areas without macrophytes at depths just above the thermocline (usually at about 4 m) from June to September. Crayfish of all sizes were in burrows under dense beds of macrophytes by October.

During the summer months, there were about 25 crayfish burrows per  $m^2$  in areas without macrophyte cover compared to about 5 per  $m^2$  in areas with dense macrophyte cover. Burrows were usually located either below or beside a rock and each was 10-30 cm deep. Burrow diameters were only slightly larger than the carapace width of the crayfish therein. At no time of the year were crayfish found outside of a burrows during daylight hours.

## CHAPTER 4

### DISCUSSION

Crayfish evolved in lotic systems and currently are naturally found over a very broad range (Tack 1941, Hobbs 1942, Berrill 1978). They are relatively large nocturnal invertebrates that are highly vulnerable to predators such as fish, reptiles, birds, and mammals (Magnuson et al. 1975) if shelter is not available during daylight hours (Bovbjerg 1970). In this sense, they are similar to lobsters in that their distribution coincides with the availability of shelter (Cobb 1971, Phillips, Cobb, and George 1980). Individuals of many species of crayfish are rarely seen outside a shelter during the day, even when dense cover in the form of aquatic macrophytes is available (Tack 1941, Pennak 1953, Berrill 1978), and ovigerous crayfish and lobsters may not leave a shelter for many months (Mason 1970, Fast and Momot 1973, Capelli 1980, Cooper and Uzmann 1980).

Shelters suitable for crayfish that occur in streams and rivers are periodically changed by floods which rearrange the sites, destroying some, creating new ones, and, in general, disrupting these resources. Therefore, crayfish must be highly vagile at all life stages and be able to quickly move and locate new habitats that have their required resources. The ability of crayfish (and also many other species) to respond to resource changes by movement is one of

the heuristic bases from which workers on population dynamics in animals derived the hypothesis for regulating populations by emigration.

Lomnicki (1978) proposed a model for population regulation by emigration based on a) the relationship between the movements of individuals with respect to resource availability in spatially and temporally heterogeneous environments (Wiens 1976, Taylor and Taylor 1977), and b) unequal resource partitioning among individuals of a single-species population. His model predicts that unequal resource partitioning, based on a characteristic such as size of organism, results in the emigration of some individuals out of an area so that the number of individuals remaining in the area is adjusted to the amount of available food or other resource so as to provide a higher probability for their long-term survival. In my study, I tested the Lomnicki model and found that the adjustment of the population density of crayfish to resource changes, through emigration, occurred regularly and at a highly significant level.

In the following, I will try to demonstrate the degree to which my results support the general hypothesis of regulatory emigration. More specifically, I will try to use my results for achieving further insights into the population dynamics of O. causeyi and other species of crayfish.

Results from both short and longer-term experiments showed that O. causeyi adjusts its numbers in response to changes in resources. The small amount of variance between numbers of crayfish that emigrated

during short-term replicate tests wherein various levels of resources were used, strongly supports the suggestion that O. causeyi has a genetically fixed characteristic for 1) assessing resource levels in a relatively precise manner, and 2) triggering emigration responses appropriate to resource availability.

O. causeyi did not respond in the same way to every type of resource. In short-term experiments covering only a few days, they always emigrated from areas without shelters and usually remained in areas with shelters, whether food was present or not. Support for the primacy of shelter comes from investigations on both lobsters and crayfish. Scarrett (1968) observed the rapid colonization of an artificial rocky reef by the lobster, Homarus americanus, in a previously barren area. Cobb (1971) studied H. americanus off the coast of Rhode Island and noted that it is distributed in accordance with substrates that afford shelter. Herrnkind (1980) has noted a similar pattern for Panulirus argus as well as for other species of spiny lobsters. Both Flint and Goldman (1973) and Stein and Magnuson (1977) have observed that the structure of the substrate and the presence or absence of predation is central to the distribution of crayfish in a stream or lake. Similarly, Caine (1978) stated that epigeal crayfish of Florida are subjected to intense predation if suitable shelter is not available. In all of my long-term experiments, loss of shelter led to a quick readjustment of numbers to the new level of shelter. In other words, even crayfish which had been residents in an area for weeks emigrated from that area if shelter became no longer available to them

despite the presence of an abundant supply of food. A similar field behavioral pattern has been noted for various species of lobster, such as Panulirus argus, which emigrates from an area when shelter no longer provides adequate protection (Herrnkind 1980).

The absence of food did affect the rate of emigration in my experiments, but its effects were not as immediate as they were for shelter. Crayfish are opportunistic omnivores (Lorman and Magnuson 1978) and, as noted previously, can live for extended periods without food. For example, some crayfish I collected from the field were maintained in the laboratory, without food, for weeks at a time without loss of individuals. Yet growth is critical for young crayfish because it is the difference in size, more than any other single factor, that seems to be the main basis for competitive success in resource partitioning. It would, therefore, be a sound strategy for crayfish to spend as little time as possible at smaller sizes.

In my experiments, all crayfish did not remain in an area with shelter and food under all conditions. The specific reasons for leaving at any given moment were probably various but most ultimately appeared to be dependent on crayfish interactions elicited by unavailability of shelter. The rate of emigrations and the "triggering condition" for any given individual crayfish to remain or emigrate was probably determined primarily by the ability to obtain required shelter. Every crayfish, whether a new immigrant or a long-time resident of an area, will probably improve its survivability by leaving areas where it cannot obtain shelter (Lunt 1967, Christian 1970).

The dominance of larger crayfish over smaller conspecifics (Bovbjerg 1956, Lowe 1956, Camougis and Hichar 1959, Abrahamsson 1966, 1971, Fast and Momot 1973) gives rise to an unequal partitioning of resources among crayfish in a given area (Bovbjerg 1959, Lunt 1967, Mason 1970, Stein 1977, Berrill 1978). Shelters situated under dense macrophytes were usually dominated by larger crayfish. These sites are ideal for maximum fitness as predation is probably low and food availability is high. Abrahamsson and Goldman (1970) have noted this same relationship for the crayfish Pacifastacus lenisculus in Lake Tahoe wherein larger crayfish occupied the best shelter/food sites. Similar observations were made by Fielder (1964) in the spiny lobster Jasus lalandei. I found that smaller crayfish were among the first to emigrate when the number of crayfish approached the number of shelters and all shelters were occupied by larger individuals.

In tanks from which emigration was blocked and in which crayfish exceeded the number of shelters, O. causeyi did share shelters from May through September. Similar behavior has been noted for Orconectes virilis (Bovbjerg and Stephen 1971) and H. americanus (Dunham 1972) under confined conditions. H. americanus is a clawed lobster and like the crayfish, normally occupies shelters singly (Cobb 1971). For species which display overt intraspecific behavior, such as aggressiveness in crayfish, the numbers in excess of a resource (such as shelter) must emigrate, increasing their probability of early death; conversely, dominant crayfish become residents with protection from predation (Bovbjerg 1953, 1956, 1959). Perhaps only in



areas where emigration is impossible do crayfish fail to space themselves with respect to shelter or food. In these circumstances, those that remain in an area without suitable shelters show decreased growth rates, as observed for H. americanus (Aiken and Waddy 1978), and higher predation rates (Caine 1978).

Herrnkind (1980) proposed a model for degree of nomadism for Palinurid lobsters wherein wandering increased as the ratio of food to shelter diverged from unity, but such a model appears to be far too simple to account for patterns of movement in crayfish. Although levels of food and shelter may trigger an emigration response, other factors such as history of the organism (Lomnicki 1966, Aiken 1969) and changes in temperature (Thorp 1978) may alter their level of activity and change their resource assessment values, thereby altering the time when emigration is triggered. For example, in my study, crayfish that had been residents in holding tanks for only a single day were more restless and emigrated more readily (even though both food and shelter were present) than crayfish resident in holding tanks for at least 30 days. I also found that temperature played a major role in crayfish emigration. Temperature affects movement, as it is directly related to metabolic rate and reproduction in invertebrates. I found that the level at which the population size no longer increased was very different at various times of the year and was correlated with water temperature. In November, the number of resident crayfish in a tank during a long-term experiment did not plateau; the number of resident crayfish exceeded by almost 100% the number of available shelters, and many crayfish used macrophyte cover as shelter.

My observations in Parker Canyon Lake were similar to my laboratory results in that they also showed close parallels between temperatures and degree of crayfish movements. During July and August when temperatures were 22-24°C, the largest (45-60 mm CL) crayfish in Parker Canyon Lake were in areas with dense macrophyte cover, whereas smaller (31-44 mm CL) crayfish were in relatively open areas. In November when temperatures had dropped to 8-10°C, virtually all crayfish had moved into the areas of dense macrophyte cover; during this period, crayfish distribution became relatively patchy or coarse-grained (Wiens 1976) rather than the evenly distributed fine-grained pattern that occurred in July and August. Such a summer-winter difference follows somewhat Chapman's (1966) hypothesis which predicts that food-space constraints regulate population size in summer whereas winter spacing is more shelter-related.

A few hypotheses alternate to the one I tested (regulatory emigration) have been suggested for regulating numbers in crayfish. Momot et al. (1978) have described a fecundity-change hypothesis wherein populations of crayfish are self-regulated by density-dependent control of brood stock size in conjunction with changes in growth and mortality. My results contradict this hypothesis in that I found rapid emigration of all sizes of crayfish in response to resource changes; the emigration occurred long before the type of physiological changes caused by inadequate nutrition as suggested by Momot et al. (1978) could have taken place.

Cannibalism by crayfish (Abrahamsson 1966, Lunt 1967) and predation on crayfish by other organisms, such as fish, birds, and mammals (Taub 1972, Rickett 1974, Caine 1978), has been suggested as regulating the populations of crayfish or, at least, helping to control the upper population size. My observations in Parker Canyon Lake seem to refute the suggested regulatory function. The density of O. causeyi at the lake during the period of warmest surface water temperature was lowest in areas most inaccessible to predators (dense macrophyte cover overlying burrows), areas wherein numbers should have been the greatest if predation were regulating. Further, in both my short- and long-term experiments, crayfish density adjusted rapidly and regularly to changes in resources through emigration only; these tanks contained no predators and I never observed cannibalism.

On the other hand, it is very probable that predation is a major destructive factor (in contrast to a regulatory factor) in influencing crayfish population size. Shelter, the most immediately critical resource for crayfish in my experiments, is also probably the predominant habitat character which provides a degree of invulnerability to predation for those crayfish which acquire and hold "prime habitat." The replicability of emigration experiments in both the short- and long-term experiments strongly supports the hypothesis that crayfish populations are regulated in consonance with such critical resources by a behavioral response resulting in emigration of excess individuals. It is these emigrants, not well-provisioned resident crayfish, which are most vulnerable to predators.

Many of the previously cited studies (Abrahamsson 1966, Dean 1969, Fast and Momot 1973, Berrill 1978, Caine 1978) mention that crayfish are often highly vagile and that the distribution of a crayfish population varies greatly both spatially and temporally. Other cited studies (Bovbjerg 1956, Lowe 1956, Lunt 1967, Stein 1977) have focused on differences between crayfish in terms of their ability to obtain required resources and avoid predators. My study links these observations on inter- and intra-specific competition as well as unequal resource partitioning among crayfish with the observed nomadism of individual crayfish and fluidity of crayfish populations.

Emigration is seen as an individual response through which a crayfish can minimize direct competition with conspecifics. The primary resource for which crayfish compete appears to be shelter. Crayfish which are denied access to shelters leave the area rather than risk injury or death by exposure to predators if they fail to emigrate. Crayfish thus do not respond as a population but as individuals to resources or predators, and therefore studies on crayfish populations must focus on the specific characteristics of individuals (size, sex, reproductive state) and on the reactions of these individuals to resources, conspecifics, and predators. Only then can changes in the distribution and abundance of crayfish populations be more clearly explained and possibly predicted.

The incessant search and selection of shelter by crayfish, whereby they can obtain isolation from conspecifics and predators, should be a focus of planning by all people who manage crayfish

populations for food or for sport-fish prey. Crayfish farmers in Louisiana enhance growth and survival of crayfish by providing dense macrophyte cover for crayfish raised in shallow ponds (LaCaze 1976). Commercial crayfish industries in the Pacific coast states rely on natural populations of crayfish. Their resource will be reduced by any factors such as water diversion and siltation that affect food and/or shelter availability. As these resources diminish, crayfish will leave the area and the population size of subsequent year-classes will be smaller. Raising crayfish in intensive culture systems will probably fail as have such systems designed for lobsters because individuals of both groups of organisms are highly agonistic toward conspecifics if denied isolation. To provide adequate isolation under such a system is, at present, prohibitively expensive.

In many managed lake systems, crayfish have been introduced to provide forage food for fish and the reported results of such introductions, which have been very unpredictable, include the gradual loss of aquatic macrophytes, decreased availability of aquatic invertebrates (other than crayfish), predation on game fish eggs, elimination of native species of crayfish, and no observed increase in the growth rate of game fish (Magnuson et al. 1975). The behavior of individual crayfish presumably leads to the selection of habitats that can potentially maximize growth rate and minimize predation. Such habitats have a high food to shelter ratio. The shelters are the limiting factor, and they are usually held by the largest crayfish which are able to utilize the shelters and not be evicted from the area by

larger conspecifics. Smaller crayfish must locate less suitable habitat and they are guided primarily by the availability of shelter. My experimental results indicate that those crayfish that are either unable to locate refuge or are displaced by larger conspecifics, respond behaviorally (increased nomadism) in a manner which makes them highly vulnerable to predators such as bass. These displaced crayfish (usually larger juveniles and small adults) will probably emigrate from the area and may soon be unavailable to bass and other predators if they leave the lake.

A lake with considerable food and shelter per unit area (other factors being equal) will have a greater population of crayfish than will a lake with little food and shelter. In either case, only a small percentage of the crayfish population will be effectively available as forage for fish.

If shelter availability is the primary factor limiting crayfish in most streams and lakes, then management strategy should maximize shelter availability so as to maximize crayfish availability as a forage food for fish. More juvenile crayfish would thus be available each year as the adult population (and therefore reproduction) would be higher per unit area. On the other hand, relatively high shelter availability per unit area may lead to the loss of aquatic macrophytes in the area and thereby expose shelterless and emigrant crayfish to predators. The loss of cover, which may serve as both a source of food and shelter to crayfish, may lead to increased emigration and therefore a decreased availability of food to forage fish.

We are not yet at a point in our understanding of crayfish populations where we can predict with any certainty the outcome of an introduction of crayfish as a forage food in any given lake.

## CHAPTER 5

### SUMMARY

1. O. causeyi rapidly adjusts its numbers in concert with available resources through density-dependent emigration.
2. The adjustment of numbers and resources seems to vary with respect to water temperature and the sex, size, and perhaps with the physiological states of the crayfish.
3. Shelter appears to be the primary resource influencing the distribution and abundance of O. causeyi.
4. Larger crayfish generally dominate shelter use; smaller crayfish are usually the first to emigrate from an area.
5. O. causeyi was never observed to share a shelter in an area which was provided with an emigration route.
6. O. causeyi in areas without shelter remain active during all hours of darkness and are intermittently active during daylight hours; conversely, crayfish with shelter are intermittently active during darkness and are never active during daylight hours.
7. Crayfish were never observed to cannibalize other crayfish when in systems with an open escape route or when shelter and/or cover was readily available to all crayfish in systems not provided with an escape route.



APPENDIX

SUPPLEMENTAL DATA FROM EMIGRATION EXPERIMENTS  
AND FIELD OBSERVATIONS IN PARKER CANYON LAKE

Table 1. Cumulative number of crayfish emigrating from 8 replicate tanks in each of 2 treatments.

HOURS	NUMBER OF CRAYFISH EMIGRATING IN EIGHT REPLICATES			
	CONTROL: NO FOOD OR SHELTER		WITH FOOD AND SHELTER	
	#	%	#	%
0	0	0	0	0
2	3	38	0	0
4	6	75	0	0
12	8	100	1	13
24	8	100	1	13
36	8	100	1	13
48	8	100	1	13
72	8	100	1	13

Table 2. Cumulative number of crayfish emigrating from 4 replicate tanks (2 crayfish per tank) in each of 4 treatments.

NUMBER OF CRAYFISH EMIGRATING IN FOUR REPLICATES												
HOURS	CONTROL:			FOOD			SHELTER			FOOD/SHELTER		
	NO FOOD OR SHELTER											
	♂	♀	%	♂	♀	%	♂	♀	%	♂	♀	%
0	0	0	0	0	0	0	0	0	0	0	0	0
2	1	2	38	1	1	25	0	0	0	0	0	0
4	2	3	63	2	2	50	0	0	0	0	0	0
12	3	3	75	3	4	87	0	1	13	0	0	0
24	4	4	100	4	4	100	0	2	25	0	0	0
36	4	4	100	4	4	100	0	2	25	0	0	0
48	4	4	100	4	4	100	2	2	50	0	0	0
72	4	4	100	4	4	100	2	3	63	0	0	0

Table 3. Maximum hours of residence of crayfish emigrating from 4 replicate tanks (2 crayfish per tank) in each of 4 treatments. (f = food; s = shelter; nf = no food; ns = no shelter).

REPLICATE	MAXIMUM HOURS OF RESIDENCE						
	2	4	12	24	36	48	72
nf/ns							
1	-	♀	♂	-	-	-	-
2	♂	-	-	♀	-	-	-
3	♀	♂	-	-	-	-	-
4	♀	-	-	♂	-	-	-
f/ns							
1	-	♂	♀	-	-	-	-
2	♂	♀	-	-	-	-	-
3	-	-	♀	♂	-	-	-
4	♀	-	♂	-	-	-	-
nf/s							
1	-	-	-	-	-	♂	-
2	-	-	♀	-	-	♂	-
3	-	-	-	♀	-	-	-
4	-	-	-	-	-	-	♀
f/s							
1	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-

Table 4. Cumulative mean number of crayfish emigrating from 3 replicate tanks (8 crayfish per tank) in each of 2 treatments.

HOURS FROM START	NUMBER OF CRAYFISH EMIGRATING IN THREE REPLICATES							
	SHELTER				FOOD AND SHELTER			
	24	48	72	96	24	48	72	96
Replicate								
1	3	4	5	5	1	3	3	3
2	2	4	4	6	3	3	4	4
3	4	4	5	6	2	4	4	4
Total	9	12	14	17	6	10	11	11
Mean	3	4	4.7	5.7	2	3.3	3.7	3.7
%	38	50	59	71	25	41	46	46

Table 5. A. Cumulative mean numbers of crayfish from 4 replicate tanks (8 crayfish per tank) during 2 treatments.  
 B. Cumulative mean numbers of crayfish emigrating from 3 replicate tanks (8 crayfish per tank) during 2 treatments.

# SHELTER/% COVER	NUMBER OF CRAYFISH EMIGRATING							
	A				B			
HOURS FROM START	2/0		8/0		2/12.5		8/50	
	24	48	24	48	24	48	24	48
Replicate								
1	5	6	2	4	4	5	1	1
2	4	5	3	3	2	4	0	0
3	6	6	3	3	3	4	0	1
4	5	5	3	4	-	-	-	-
Total	20	22	11	14	9	13	1	2
Mean	5	5.5	2.7	3.5	3	4.3	0.3	0.7
%	63	69	34	44	34	54	4	9

Table 6. Summary of information on emigration of crayfish from tanks during long-term experiment #1, replicate a (July-August).

	Crayfish						
	1	2	1A	3A	5A	7A	1B
Sex	f	f	m	f	m	f	m
Size	me	me	me	me	me	me	me
# Days From Opening of Escape Route:							
In	0	0	3	5	7	10	12
Out	-	18	4	6	18	11	13
# Resident Days:							
Potential	21	21	17	15	13	10	8
Actual	21	18	1	1	11	1	1
Emigration (# Days):							
Before Resource Removal	-	-	11	9	-	4	2
After Cover Removal	-	-	-	-	-	-	-
After Shelter Removal	-	1	-	-	1	-	-
# Crayfish in Tank When Introduced	0	0	2	2	2	3	3
# Crayfish in Tank at Emigration	-	-	3	3	3	4	4
Did Not Emigrate	X						

Table 7. Summary of information on emigration of crayfish from tanks during long-term experiment #1, replicate b (July-August).

	Crayfish						
	3	4	2A	4A	6A	8A	2B
Sex	f	f	m	f	m	f	m
Size	me	me	me	me	me	me	me
# Days From Opening of Escape Route:							
In	0	0	3	5	7	10	12
Out	-	4	4	-	18	11	14
# Resident Days:							
Potential	21	21	17	16	13	10	8
Actual	21	4	1	16	11	1	2
Emigration (# Days):							
Before Resource Removal	-	11	11	-	-	4	1
After Cover Removal	-	-	-	-	-	-	-
After Shelter Removal	-	-	-	-	1	-	-
# Crayfish in Tank When Introduced	0	0	2	1	2	3	3
# Crayfish in Tank at Emigration	-	3	3	-	3	4	4
Did Not Emigrate	X			X			



Table 8. Summary of information on emigration of crayfish from tanks during long-term experiment #2, replicate a (September-October).

	Crayfish							
	1	2	1A	3A	7A	1B	3B	5B
Sex	f	f	f	f	m	m	m	m
Size	lg	sm	lg	me	lg	me	me	lg
# Days From Opening of Escape Route:								
In	0	0	3	5	7	9	11	13
Out	-	29	32	33	12	13	-	-
# Resident Days:								
Potential	37	27	34	38	30	28	26	24
Actual	37	29	29	28	5	4	26	24
Emigration (# Days):								
Before Resource Removal	-	-	-	-	16	15	-	-
After Cover Removal	-	1	-	-	-	-	-	-
After Shelter Removal	-	-	4	2	-	-	-	-
# Crayfish in Tank When Introduced	0	0	2	3	4	5	6	6
# Crayfish in Tank at Emigration	-	8	6	4	7	6	-	-
Did Not Emigrate	X						X	X

Table 8, Continued.

	Crayfish						
	1C	3C	5C	7C	1D	3D	5D
Sex	f	f	f	m	m	f	m
Size	sm	sm	me	me	lg	me	me
# Days From Opening of Escape Route:							
In	15	16	18	19	20	23	25
Out	31	18	22	32	21	24	26
# Resident Days:							
Potential	22	21	19	18	17	14	12
Actual	16	2	4	13	1	1	1
Emigration (# Days):							
Before Resource Removal	-	10	6	-	7	4	2
After Cover Removal	3	-	-	-	-	-	-
After Shelter Removal	-	-	-	1	-	-	-
# Crayfish in Tank When Introduced	6	7	8	8	9	8	8
# Crayfish in Tank at Emigration	7	8	9	6	10	9	9
Did Not Emigrate							

Table 9. Summary of information on emigration of crayfish from tanks during long-term experiment #2, replicate b (September-October).

	Crayfish							
	3	4	2A	4A	8A	2B	4B	6B
Sex	f	f	f	f	m	m	m	m
Size	lg	sm	lg	me	lg	me	me	lg
# Days From Opening of Escape Route:								
In	0	0	3	5	7	9	11	13
Out	-	31	14	-	14	-	34	14
# Resident Days:								
Potential	37	37	34	32	30	28	26	24
Actual	37	31	11	32	7	28	23	1
Emigration (# Days):								
Before Resource Removal	-	-	14	-	14	-	-	14
After Cover Removal	-	3	-	-	-	-	-	-
After Shelter Removal	-	-	-	-	-	-	4	-
# Crayfish in Tank When Introduced	0	0	2	3	4	5	6	7
# Crayfish in Tank at Emigration	-	9	8	-	8	-	6	8
Did Not Emigrate	X			X		X		

Table 9, Continued.

	2C	4C	6C	Crayfish			
				8C	2D	4D	6D
Sex	f	f	f	m	m	f	m
Size	sm	sm	me	me	lg	me	me
# Days From Opening of Escape Route:							
In	15	16	18	19	20	23	25
Out	27	32	-	33	34	24	29
# Resident Days:							
Potential	22	21	19	18	17	14	12
Actual	12	16	19	14	14	1	4
Emigration (# Days):							
Before Resource Removal	1	-	-	-	-	4	-
After Cover Removal	-	-	-	-	-	-	1
After Shelter Removal	-	1	-	2	4	-	-
# Crayfish in Tank When Introduced	5	6	7	8	9	10	10
# Crayfish in Tank at Emigration	11	8	-	7	6	11	10
Did Not Emigrate			X				

Table 10. Summary of information on emigration of crayfish from tanks during long-term experiment #3, replicate a (November-December).

	Crayfish							
	1A	2A	3A	4A	1C	2C	5C	6C
Sex	m	f	m	f	f	f	m	m
Size	me	me	me	me	sm	sm	sm	sm
# Days From Opening of Escape Route:								
In	0	0	0	0	4	4	6	6
Out	29	8	28	8	21	-	20	20
# Resident Days:								
Potential	32	32	32	32	28	28	26	26
Actual	29	8	28	8	17	28	14	14
Emigration (# Days):								
Before Resource Removal	-	10	-	10	-	-	-	-
After Cover Removal	-	-	-	-	3	-	2	2
After Shelter Removal	8	-	7	-	-	-	-	-
# Crayfish in Tank When Introduced	-	0	0	0	4	4	6	6
# Crayfish in Tank at Emigration	5	8	7	8	13	-	16	16
Did Not Emigrate						X ov		

Table 10, Continued.

	Crayfish									
	1D	2D	1E	2E	1W	2W	5W	6W	1AW	2AW
Sex	f	f	m	m	m	f	m	f	m	f
Size	sm	sm	me	me	lg	lg	me	me	me	me
# Days From Opening of Escape Route:										
In	8	8	10	10	13	13	15	15	16	16
Out	-	22	-	-	21	21	19	17	20	28
# Resident Days:										
Potential	24	24	22	22	19	19	17	17	16	16
Actual	24	14	22	22	8	8	4	2	4	12
Emigration (# Days):										
Before Resource Removal	-	-	-	-	-	-	-	1	-	-
After Cover Removal	-	-	-	-	3	3	1	-	2	-
After Shelter Removal	-	1	-	-	-	-	-	-	-	7
# Crayfish in Tank When Introduced	6	6	8	8	10	10	12	12	14	14
# Crayfish in Tank at Emigration	-	9	-	-	13	13	17	15	16	7
Did Not Emigrate	X ov		X	X						ov

Table 11. Summary of information on emigration of crayfish from tanks during long-term experiment #3, replicate b (November-December).

	Crayfish									
	5A	6A	7A	8A	3C	4C	7C	8C	3D	4D
Sex	m	f	m	f	f	f	m	m	f	f
Size	me	me	me	me	sm	sm	sm	sm	sm	sm
# Days From Opening of Escape Route:										
In	0	0	0	0	4	4	6	6	8	8
Out	11	-	-	1	22	7	21	27	30	12
# Resident Days:										
Potential	32	32	32	32	28	28	26	26	24	24
Actual	11	32	32	1	18	3	15	22	22	4
Emigration (# Days):										
Before Resource Removal	7	-	-	17	-	11	-	-	-	6
After Cover Removal	-	-	-	-	-	-	3	-	-	-
After Shelter Removal	-	-	-	-	1	-	-	6	9	-
# Crayfish in Tank When Introduced	0	0	0	0	4	4	5	5	6	6
# Crayfish in Tank at Emigration	10	-	-	4	9	7	12	6	5	9
Did Not Emigrate		X ov	X						ov	

Table 11, Continued.

	Crayfish							
	3E	4E	3W	4W	7W	8W	3AW	4AW
Sex	m	m	m	f	m	f	m	f
Size	me	me	lg	lg	me	me	me	me
# Days From Opening of Escape Route:								
In	10	10	13	13	15	15	16	16
Out	-	25	-	20	20	19	20	25
# Resident Days:								
Potential	22	22	19	19	17	17	16	16
Actual	22	15	19	7	5	4	4	9
Emigration (# Days):								
Before Resource Removal	-	-	-	-	-	-	-	-
After Cover Removal	-	-	-	2	2	1	2	-
After Shelter Removal	-	4	-	-	-	-	-	4
# Crayfish in Tank When Introduced	8	8	8	8	10	10	12	12
# Crayfish in Tank at Emigration	-	8	-	15	15	16	15	8
Did Not Emigrate	X		X					



Table 12. Relationship of crayfish sex, size, and reproductive state to shelter dominance. All pairings were run in a closed tank containing 2 medium-size shelters. Each replicate contained 4 crayfish, 2 from each category.

REPLICATE NUMBER	NUMBER OF CRAYFISH HOLDING SHELTER					
	♀ Ovig. Large	X ♂ F1 Large	♀ Ovig. Medium	X ♂ F1 Large	♀ Ovig. Medium	X ♂ F1 Medium
1	2	0	1	1	2	0
2	1	1	2	0	1	1
3	2	0	1	1	1	1
4	2	0	0	2	2	0
Total	7	1	4	4	6	2
	♂ F1 Medium	X ♂ F1 Medium	♂ F1 Medium	X ♂ F1 Large	♂ F1 Small	X ♂ F1 Medium
1	1	1	0	2	1	1
2	0	2	0	2	0	2
3	0	2	0	2	1	1
4	1	1	1	1	0	2
Total	2	6	1	7	2	6

Table 13. Relationship of crayfish size to amount of macrophyte cover in areas of high and low macrophyte density at Parker Canyon Lake, Arizona, 1981. All crayfish were caught in minnow traps at night with the exception of supplemental hand collections ( $\frac{1}{2}$  hr per site) in August and October (see asterisk).

PARKER CANYON LAKE, 1981											
	JUNE		JULY		AUGUST		AUGUST*		OCTOBER		
Macrophyte Density	High	Low	High	Low	High	Low	High	Low	High	Low	Low*
Total # Crayfish	34	28	41	47	39	0	36	61	21	0	12
# Crayfish Per Trap	4	5	3	6	3	0	-	-	2	0	-
Tot. #	11	16	27	23	20		17	27	7		5
CL	46	39	48	39	48		43	38	44		40
% CL > 35 mm	100	56	100	83	90		88	74	100		100
% CL > 40 mm	86	38	100	44	85		76	44	71		40
% CL > 45 mm	64	31	74	17	75		47	0	57		20
% CL > 50 mm	36	6	48	9	35		6	0	0		0
% CL > 55 mm	0	0	7	4	0		0	0	0		0
Tot. #	23	12	14	24	19		19	34	15		7
CL	49	35	50	40	48		43	37	46		37
% CL > 35 mm	100	42	100	79	100		84	77	100		86
% CL > 40 mm	96	33	100	46	100		68	27	86		29
% CL > 45 mm	91	11	79	21	90		53	6	60		0
% CL > 50 mm	57	0	64	4	21		16	0	33		0
% CL > 55 mm	21	0	36	0	5		0	0	7		0

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