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Behavioral response of the amphipod Gammarus fasciatus and the isopod Asellus communis to fish (Lepomis macrochirus) and dragon fly (Gomphidae)

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BEHAVIORAL RESPONSE OF THE AMPHIPOD *GAMMARUS FASCIATUS* AND THE ISOPOD *ASELLUS COMMUNIS* TO FISH (*LEPOMIS MACROCHIRUS*) AND DRAGONFLY (GOMPHIDAE) PREDATORS

A Thesis

Presented to

The Faculty of the Department of Biology

The College of William and Mary in Virginia

In Partial fulfillment

Of the Requirements for the Degree of

Master of Arts

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by

Bill D. Saunders

1981

APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of

MASTER OF ARTS

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TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS.. iv

LIST OF FIGURES.. v

ABSTRACT.. vii

INTRODUCTION.. 2

MATERIALS AND METHODS.. 12

RESULTS.. 19

DISCUSSION.. 39

LITERATURE CITED.. 44

VITA.. 49

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LIST OF FIGURES

Figure Page

1a. Typical specimen of the amphipod Gammarus fasciatus.. 8

1b. Typical specimen of the isopod Asellus communis...... 8

2a. Representative dragonfly naiads (Gomphidae) from Lake Matoaka.. 10

2b. Representative bluegill (Lepomis macrochirus) from Lake Matoaka.. 10

3a. Experimental tank showing substrate, artificial shelter, and partition at one end.................... 13

3b. Experimental tank showing natural shelter............ 17

4. Survival of amphipods and isopods in the presence of a fish predator, under varying shelter conditions... 21

5. Survival of amphipods and isopods in the presence of dragonfly predators, under varying shelter conditions... 22

6. Comparison of shelter utilization in May of amphipods and isopods in the absence of predators......... 24

7. Comparison of shelter utilization of amphipods in May and October in the absence of predators.......... 25

8. Comparison of shelter utilization of isopods in May and October in the absence of predators.......... 26

9. Shelter utilization of amphipods in presence of a partitioned bluegill, compared to control............ 28

10. Shelter utilization of isopods in presence of a partitioned bluegill, compared to control............ 29

11. Shelter utilization of amphipods in presence of partitioned dragonflies, compared to control......... 30

12. Shelter utilization of isopods in presence of partitioned dragonflies, compared to control......... 31

LIST OF FIGURES continued

Figure Page

13. Shelter utilization of amphipods in presence of fish water, compared to control...................... 32

14. Shelter utilization of isopods in presence of fish water, compared to control...................... 33

15. Shelter utilization of amphipods in presence of dragonfly water, compared to control................. 35

16. Shelter utilization of isopods in presence of dragonfly water, compared to control................. 36

17. Summary of shelter utilization by amphipods for all experimental treatments.......................... 37

18. Summary of shelter utilization by isopods for all experimental treatments............................. 38

ABSTRACT

Using laboratory experiments, I attempted to determine whether freshwater amphipods (*Gammarus fasciatus*) and isopods (*Asellus communis*) are able to detect predators remotely, i.e. without actual contact by the predator. Predators included both invertebrates (dragonfly naiads, Gomphidae) and vertebrates (bluegill, *Lepomis macrochirus*). Experiments were conducted in 10 liter aquaria, and involved shelter utilization by the prey as the basic index to predator detection. In the presence of a partitioned fish, both amphipods and isopods utilized shelter to a significantly greater extent than did control groups; water in which fish had been maintained also evoked a significant increase in shelter utilization for both groups, which suggests detection via chemical means. Results with dargonfly predators were more equivocal, but also generally support the possibility of remote detection by chemical means. This work also provides general information on shelter utilization and activity rhythms of amphipods and isopods, and on the general nature of the interaction between the predator and prey species.

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INTRODUCTION

Ever since Lotka (1925) and Volterra (1926) proposed formulas to express the relationship between predator and prey populations, a great deal of research has been conducted on the effects of predation, not only on standing crop but also on the structure of whole communities. Aquatic communities, being somewhat more closed and more adaptable to a comparative approach than terrestrial systems, have been studied frequently. Most investigations have dealt with either size-selective predation and its effects on community structure, or behavioral changes associated with predation. My research deals only with the latter aspect. My main interest is in determining whether the common freshwater crustaceans *Asellus communis* (Isopoda) and *Gammarus fasciatus* (Amphipoda) are able to detect vertebrate (fish) and invertebrate (dragonfly naiads) predators remotely, as evidenced by behavioral changes. However, as a general introduction, I present here a brief review of the literature on various aspects of predator-prey interactions, including the relatively few recent papers most directly relevant to my interests.

The size-selective aspect of predation is important because of its effect on species composition and diversity. Brooks and Dodson (1965) showed that through size-selective predation the glut herring (*Alosa aestivalis*) eliminates the large crustacean dominants of the zooplankton which are then replaced by smaller littoral species. Without size-selective predation by *A. aestivalis*, small planktonic herbivores are unable to compete with larger planktonic herbivores who utilize the same small organic particles in their diet. Brooks (1968) also demonstrated that survival time of each instar of a small calanoid copepod preyed upon by _A. aestivalis_ is inversely proportional to its mean body length. Wells (1970) and Warshaw (1972) reported larger planktonic species increased after a die-off of _A. aestivalis_ in a small Connecticut lake and Lake Michigan respectively.

Dodson (1970) demonstrated that one predator population could sustain another as a result of size-selective predation on the prey of both predators. In this study larval salamanders preyed selectively on large zooplankton which allowed the existence of less competitive, smaller zooplankton which supported the larval midge, _Chaoborus_ sp.

Other work (Reif and Tappa, 1966; Sprules, 1972; and von Ende, 1979) has supported the contention of Brooks and Dodson (1965) that the differential predation of an introduced predator can favor the survival of a species whose individuals are smaller than those of the eradicated species. In addition, size-selective predation has been shown to influence polymorphism as it relates to visibility of cladocera (Green, 1967; Zaret, 1969, Zaret, 1972a; Zaret, 1972b; Dodson, 1974; Zaret and Kerfoot, 1975; and O'Brien, _et al_., 1979), sex ratio in prey species when there is sexual dimorphism or behavioral differences between sexes (Maly, 1970), and cost/benefit ratios for the predator (Hartman, 1958; Ware, 1972; Wong and Ward, 1972; Werner, 1974; Werner and Hall, 1974; and Thompson, 1978).

Changes in behavior and distribution of both predator and prey have also been investigated. Several cases of changes in distribution have been documented for vertebrate predators that switch feeding areas when new prey species are sought (Ware, 1971; Oaten and Murdoch, 1975; Murdoch, Avery, and Symth, 1975; Werner and Hall, 1979). Stein and Magnuson (1976) and Stein (1977) showed that in the presence of a smallmouth bass (*Micropterus dolomieui*), crayfish (*Orconectes propinquus*) exhibited what they termed resource depression: selecting rock which provided more shelter over sand substrate and suppressing walking, climbing, and feeding behavior patterns while increasing burrowing and chelae display. This behavior modification was more pronounced in more vulnerable life forms such as females and juveniles. In another study, Sih (1979) demonstrated that mosquito larvae (*Culex quinquefasciatus*), by altering spacing and movement, were able to resist predation. When one to four backswimmers (*Notenecta hoffmanni*) were placed in the experimental tanks, the mosquito larvae reduced movement and congregated at the water surface at the edge of the tank, thus lowering predation significantly. Evasive responses have also been found in mayfly nymphs in the presence of fish predators (Charnov, Orians, and Hyatt, 1976) and by burrowing amphipods in the vicinity of wading birds (Goss-Custard, 1970). Thus, the presence of a predator may differentially influence fundamental prey behavior.

In some cases, sexual behavior is affected by a predator. Farr (1975) showed that guppies (*Poecilia reticulata*) in populations with no predators or only large predators live in dense aggregates along the edge of streams and exhibit a high rate of sexual display. Aggregation aides in protection against large predators as well as in finding mates. However, where the small cyprinodont, *Rivulus hartii*, is the only predator, guppies disperse throughout the stream and sexual display is low. Since *R. hartii* also inhabits the edge of streams, it exerts selective pressure against aggregation and frequent sexual display, thus increasing the difficulty of mate-locating for the guppies. Goss-Custard (1970) and Strong (1972, 1973) showed that the amphipod *Hyalella azteca* reduces the amount of time in amplexus when under heavy predation. When amplexed, the amphipods are more visible and move more slowly, making them more vulnerable to predation.

In recent years other behavioral changes in amphipods related to predation have been reported. Nelson (1979) found that pinfish (*Lagodon rhomboides*) predation may 1) determine the relative abundances in the community of different types of marine amphipod species, 2) determine changes in species diversity, and 3) by an interaction with habitat complexity, determine spatial distribution of amphipod abundance within eelgrass beds. Van Dolah (1978) reported similar results for the amphipod *Gammarus palustris* in regard to habitat complexity when preyed upon by fish, shrimp, and mud crabs. Bethel and Holmes (1977) demonstrated that the amphipods *Gammarus lacustris* and *Hyalella azteca* are increasingly vulnerable to predation due to altered evasive behavior and positive response to light when infected with acanthocephalans. Uninfected amphipods apparently possess the ability to detect predators and respond behaviorally to escape predation.

In all the preceding studies, prey behavioral changes were evoked by the direct presence of the predator. However, only very recently has much work been done on possible chemical communication between a predator and a prey species. Peckarsky (1980) examined the possibility of chemical detection between mayflies and their stonefly predators. *Ephemerella subvaria* and *Stenonema fuscum* avoided the stonefly *Acroneuria lycorias* given only noncontact chemical stimuli. *Ephemerella infrequens* and *Baetis bicaudatus* responded to long-range chemical stimuli from *Megarcys signata* and *Logotus modestus*. However, *Baetis phoebus* and *Heptagenia hebe*, and *Cinygmula* sp. did not respond to stonefly predators given long-range chemical cues alone. These differences among responses of different mayflies were attributed to differential predation pressure or effectiveness of predator evasion tactics. None of the species of mayflies tested responded to the presence of stonefly predators given only visual stimuli.

In a similar study Peckarsky and Dodson (1980) found that stonefly predators *A. lycorias* and *M. signata* depressed prey colonization of and increased prey attrition from experimental cage habitats. The mechanisms causing these effects included feeding, predator avoidance by prey upon contact with foraging predators, and predator avoidance by prey given non-contact stimuli from a restricted predator. The relative importance of these mechanisms varied seasonally.

Other work on chemoreception of predators by prey has dealt mostly with marine organisms. Bullock (1953) and Kohn (1961) examined the chemical detection by gastropod molluscs of predatory starfish and found that gastropod species of *Nassarius* not only could detect predators chemically, but also distinguish between predatory and non-predatory species. In another study Phillips (1978) found that the sea urchin *Strongylocentrotus purpuratus* and the snail *Tegula funebralis* were able to chemically detect the starfish *Pycnopodia helianthoides* and *Pisaster ochraceus* and to distinguish between actively foraging and inactive predators.

In the present study I examine the alteration in shelter utilization of the amphipod *Gammarus fasciatus* and the isopod *Asellus communis* induced by the indirect presence of vertebrate (bluegill, Lepomis macrochirus) and invertebrate (dragonfly naiads, Family Gomphidae) predators. An attempt will be made to answer the following questions: 1) Are isopods and amphipods able to detect predators remotely? 2) If so, how do they detect the predators? and 3) Does response vary with different types of predation tactics? The work also provides information on the importance of shelter to survival of amphipods and isopods and the extent to which such prey may utilize shelter in the absence of predation.

Following is a brief discussion of the biology/ecology of the study organisms. Most of the information on amphipods, isopods and dragonfly naiads is taken from Pennak (1978).

Asellus communis and G. fasciatus (Figs. 1a, 1b) both have approximately one-year life cycles, and breed between February and October. The first five to eight instars are probably immature, but have the general morphological characteristics of adults. The total number of instars may be as high as fifteen to twenty. Populations of both have been recorded as high as several thousand per square meter in some habitats.

Both are commonly found closely associated in the leaf litter of the littoral zone of ponds and streams; however, evidence suggests that they may partition the habitat to some extent with isopods preferring the older, lower leaves and amphipods preferring the newer, upper leaves (Halenda, 1977). Similar results were reported for the isopod A. obtusus and the amphipod Crangonyx gracilis (Martien and Benke, 1977).

For isopods, locomotion is restricted to slow crawling through

Figure 1a. Typical specimen of the amphipod *Gammarus fasciatus* (7-10 mm) from Lake Matoaka.

Figure 1b. Typical specimen of the isopod *Asellus communis* (4-7 mm) from Lake Matoaka.

the leaf litter. Amphipods are also capable of crawling, but their chief means of locomotion is rapid undulatory swimming just above the substrate. Amphipods will swim quickly to a new location and hide in the leaf litter, especially when disturbed.

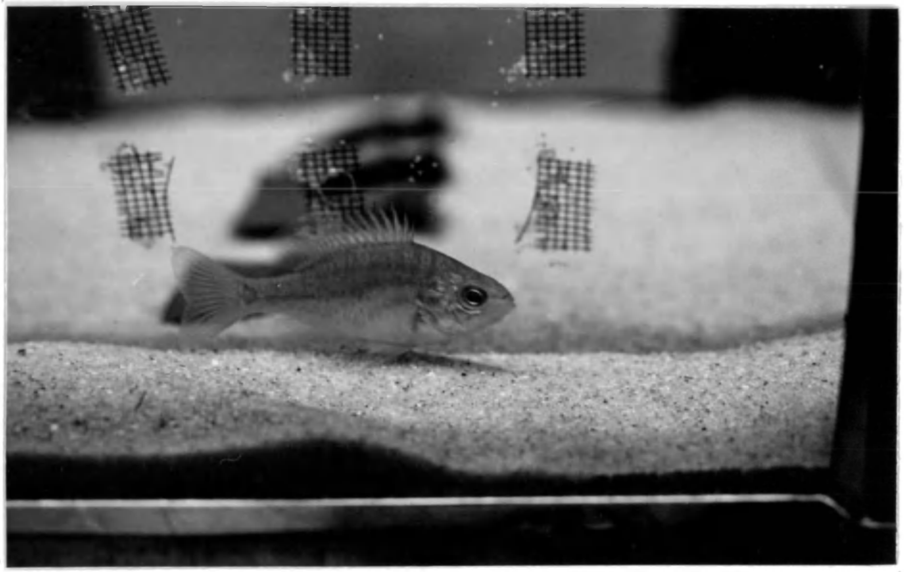
The leaf litter in which both live provides food as well as shelter. Evidence suggests that the fungi and bacteria covering the leaf litter constitute a major part of the diet of both (Marzolf, 1965; Barlocher and Kendrick, 1973; Moore, 1975; Marcus and Willoughby, 1978). Pennak (1978) reports that dead and injured aquatic animals are also consumed on occasion.

Only the nymphal instars of dragonflies (Odonata) (Fig. 2a) are aquatic. Although the complete life histories are lacking for most species, the majority appear to have from 11 to 14 instars with a one year life cycle. Immatures are found climbing or crawling about slowly in dense vegetation or leaf litter or burrowing into the silt bottoms of still waters. All are carnivorous with food consisting chiefly of other aquatic insects, annelids, small crustaceans and mollusks. In the laboratory large dragonfly naiads may be induced to feed on small fish, and under crowded conditions, cannibalism may also occur. In all cases, the prey is seized by an extension and contraction of the modified, scoop-like labium, which, with its two lateral lobes, serves as a clamp to hold the food in position at the mouth where it is crushed by the mandibules.

The bluegill fry (Fig. 2b) is very general in both the array of invertebrate species it consumes and the habitat where it forages, though a vegetated habitat is preferred (Werner and Hall, 1979). The small fry, as used in this study, are found in the shallow edges of

Figure 2a. Representative dragonfly naiads (1.5-3.0 cm) from Lake Matoaka used as predators.

Figure 2b. Representative bluegill *Lepomis macrochirus* (5-8 cm) from Lake Matoaka used as predators.



warmer lakes and streams where they are less susceptible to predation by larger fish species (Eddy and Underhill, 1978).

Preliminary observations confirmed that amphipods, isopods, dragonfly naiads, and small bluegill all occurred together in the littoral zone of Lake Matoaka.

MATERIALS AND METHODS

General preliminary observations on predator-prey interactions among my study organisms were made on six different occasions (four hours total observation time) using the experimental aquaria and artificial shelter described below.

Experiments were conducted between May and November, 1980. *Asellus communis* and *G. fasciatus* were collected from the leaf litter in the littoral zone of Lake Matoaka in Williamsburg, Virginia. They were maintained in fingerbowls (diameter 20 cm) at 18°C with tap water preconditioned in holding tanks for at least 48 hours. Leaf litter from Lake Matoaka was used as both food and shelter in the fingerbowls. Photoperiods were continually adjusted to simulate conditions in the natural environment.

Dragonfly naiads (Gomphidae) and bluegill (*Lepomis macrochirus*) were also collected from Lake Matoaka and used as predators. Dragonflies were maintained in fingerbowls (diameter 20 cm) and fish fry in 30 liter tanks in 18°C preconditioned tap water. Dragonflies were fed isopods, amphipods, and various other small aquatic invertebrates; fish were provided with the same, plus Tetramin.

All experiments were conducted using ten liter tanks (27 x 50 x 30 cm) provided with a sand substrate (particle size = approximately 1.0 mm) mixed with blended leaf litter particles (approximately the same size as sand grains) to provide a uniform food source for the prey (Fig 3a). Preconditioned tap water maintained at 18°C (except

Figure 3a. Experimental tank showing substrate, artificial shelter, and partition at one end.

as noted in experiment 6 and the corresponding control) from holding tanks was used in the experimental tanks. Photoperiod was set to match the natural environment. A transparent plexiglass partition was designed to fit 10 cm from one end of the tank, and was used as necessary to separate predators from prey (Fig. 3a). Twenty-four small holes (diameter 6 mm) in the partition allowed for water exchange. Except for one experiment in which leaf litter was used as a source of shelter, shelter consisted of four 5 cm plastic squares 0.1 mm thick placed equidistantly down the center of the tanks and held in place by a small stone (Fig. 3a).

In all experiments amphipods 7-10 mm and isopods 4-7 mm in length, as measured from the anterior margin of the cephalothorax to posterior margin of the abdomen, were used. Bluegill 5-8 cm standard length and dragonfly naiads 1.5-3.0 cm as measured from anterior margin of head to posterior margin of abdomen were used as predators. Predators were starved 24 hours prior to each experiment.

Isopods and amphipods were placed in tanks at 9:00 a.m. and given 48 hours acclimation period before predators were introduced or data taken. After the acclimation period, six observations were made daily (except as noted) for a period of four to seven days - four during light at 2.5 hour intervals beginning at 9:00 a.m., and two observations in the dark at 9:00 and 11:00 p.m. To minimize disturbance to the animals, night observations were made as quickly as possible by use of a small hand-held light. At each observation, data were taken on the number of isopods and amphipods not under shelters, or on number surviving, as described below.

Each of the following experiments, except as noted, was run using three tanks for each possible combination of prey type (amphipod or isopod) and predator type (fish or dragonfly). Ten prey were placed in each tank. For experiments involving fish, one fish was used per tank; for experiments with dragonflies, three were used per tank.

Experiment 1. Survival as affected by predation - No Shelter. To document that fish and dragonflies prey upon *A. communis* and *G. fasciatus* and to determine the predation rate in the absence of shelter, isopods and amphipods were placed in the experimental tanks with no shelters so that the predators had direct access to them. Numbers surviving at the end of the light period were recorded each day until all animals were eaten. Photoperiod was set at 16L-8D, with the light period beginning at 5:00 a.m.

The next two experiments were designed to see if shelter is utilized and the extent to which it may reduce the predation rate.

Experiment 2. Survival as affected by predation - Artificial Shelter. Isopods and amphipods were placed in tanks with the plastic shelters present (Fig. 3a). After acclimation, the predators were introduced on the same side of the partition and a count was made of the surviving isopods and amphipods at the end of each light period until all were eaten. Counting involved removing the shelters briefly to expose the prey. Predators were partitioned off for the count and returned two hours later after the lights were out. This procedure minimized disturbance effects by providing time for the prey to relocate under shelters before the predators were returned. Photoperiod was set at 16L-8D, with light beginning at 5:00 a.m.

Experiment 3. Survival as affected by predation - Natural Shelter. For a better understanding of how artificial shelters affect survival when compared to a more natural shelter, experiment 2 was repeated substituting leaf litter over the entire sand substrate in place of the four plastic shelters (Fig. 3b). Numbers surviving were counted on alternate days over an eight day period by carefully sorting through the litter. Photoperiod was set at 14L-10D, with the light period beginning at 6:00 a.m.

The remaining experiments were designed to provide information on predator detection by the prey.

Experiment 4. Shelter utilization in the absence of predators. Isopods and amphipods were placed in the experimental tanks with no predators. Numbers of unsheltered animals were recorded for one week. Photoperiod was set at 14L-10D, with the light period beginning at 6:00 a.m.

This experiment was run in May and served as a control for experiment 5. A similar control was run in October for experiment 6, when water temperature was 15°C and photoperiod at 12L-12D with the light beginning at 7:00 a.m.

Experiment 5. Shelter utilization in the presence of a predator restricted from direct access. Procedures were similar to those in experiment 4, except that after the acclimation period, predators were placed behind the partitions. Numbers of unsheltered animals were recorded. This work was completed within two weeks of the corresponding control described in experiment 4. Photoperiod was 14L-10D, with the light beginning at 6:00 a.m.

Experiment 6. Chemical detection of a predator. Tanks were filled with 7.5 liters of water, instead of the usual 10 liters. After the usual acclimation period for the prey, 2.5 liters of water in which

Figure 3b. Experimental tank showing natural shelter.

four fish or twelve dragonfly naiads had been kept starved for 24 hours was added. Thus, any chemicals released by the predators would presumably be the same concentration in the experimental tanks at the onset of the experiment as if one fish or three dragonflies were actually in the 10 liter tanks, as in experiment 5. Assuming any response-inducing chemicals would remain the same concentration or decline in concentration without the actual predator present, and that any response by prey would most likely occur soon after introduction of the new water, observations were made for four days only. Numbers of unsheltered animals were recorded. Water was 15° C, and photoperiod was set at 12L-12D, with lights on at 7:00 a.m. Immediately following this work a corresponding control as described in experiment 4 was completed with the same photoperiod and water temperature.

Data are presented as the average number of unsheltered animals per tank or the average number of animals surviving per tank as determined from 10 animals in each of three tanks for each experiment. The Wilcoxin Matched Pairs Signed Ranks test was employed to test for significant differences between controls and experiments.

RESULTS

From general observations it was determined that bluegill and dragonflies feed on both isopods and amphipods; however, some differences occur in the means by which they capture prey. Bluegill appeared to feed visually by orienting on moving objects on the surface, bottom, or in the water column and then actively pursuing the item, whereas dragonflies sat and waited in ambush on the bottom for the prey item to pass by. At irregular intervals the dragonflies changed their position, but in no way did the change appear to be directed at a particular prey item. Dragonflies were able to get underneath the plastic shelters with the prey, but I was not able to confirm capture of prey under shelters. Bluegill, however, were restricted from sheltered prey.

Bluegill could spot moving prey at the opposite end of the 10 liter tanks and pursuit usually followed. In all instances, even the largest isopod or amphipod was completely taken in the bluegill's mouth. Dragonflies showed no signs of active pursuit, though an occasional lunge accompanied the extention of the labium, and some isopods and amphipods were too large to be taken in one bite. Larger amphipods were able to escape the dragonfly's labium grip at times. Larger isopods however, once clasped by the labium, were not able to escape. Thus, the slow movement typical of isopods drew less attention from the fish but made it more vulnerable to the ambush attack of the dragonflies. Amphipods, in contrast, appeared to be more vulnerable to fish predation, by virtue of their typical rapid movements.

Another important difference between the predators was that bluegill fed only during the light hours. Dragonflies were not so limited. In fact, dragonflies appeared to prey most heavily at night when isopod and amphipod activity was greatest.

Experiments 1-3. Predation rate as affected by variable shelter. Both dragonflies and fish preyed heavily upon isopods and amphipods, but shelter availibility reduced the predation rate (Figs. 4 and 5). Survival increased greatly with natural shelter, probably due to greater shelter surface area afforded by the leaf litter as compared to the plastic squares and possibly due to the greater complexity of the leaf litter resulting from the overlapping and slightly bouyant nature of the leaves.

With leaf litter as shelter, amphipods were more vulnerable to fish predation than were isopods ($P < .05$), whereas isopods were more susceptible than amphipods to dragonfly predation ($P < .05$). Only 5.33 amphipods on average survived to the eighth day as compared to the 7.0 isopods surviving when a fish was the predator. On the other hand, when dragonflies were the predators, only 2.67 isopods survived on average as compared to the 7.67 amphipods.

Furthermore, Figures 4 and 5 suggest that fish exerted a greater predation pressure than did dragonflies on both isopods and amphipods under artificial shelter conditions ($P < .05$). Amphipods and isopods were all eaten by the second and third days respectively with fish as predators. However, some of both survived until the sixth day with dragonfly predators. Although with artificial shelter fish consumed

Figure 4. Survival of amphipods and isopods in the presence of a fish predator, under varying shelter conditions. Difference in numbers surviving under natural shelter between amphipods and isopods is significant (P <.05, Wilcoxin Matched Pairs Signed Ranks test).

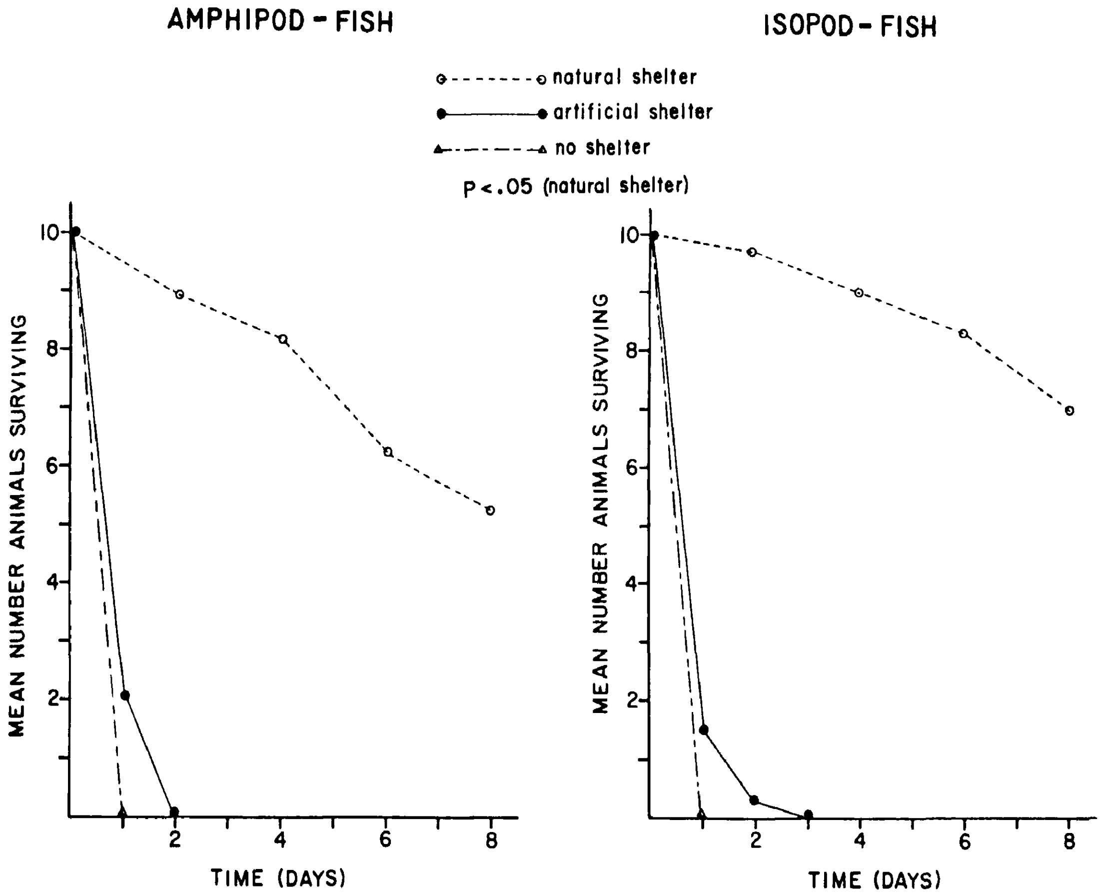
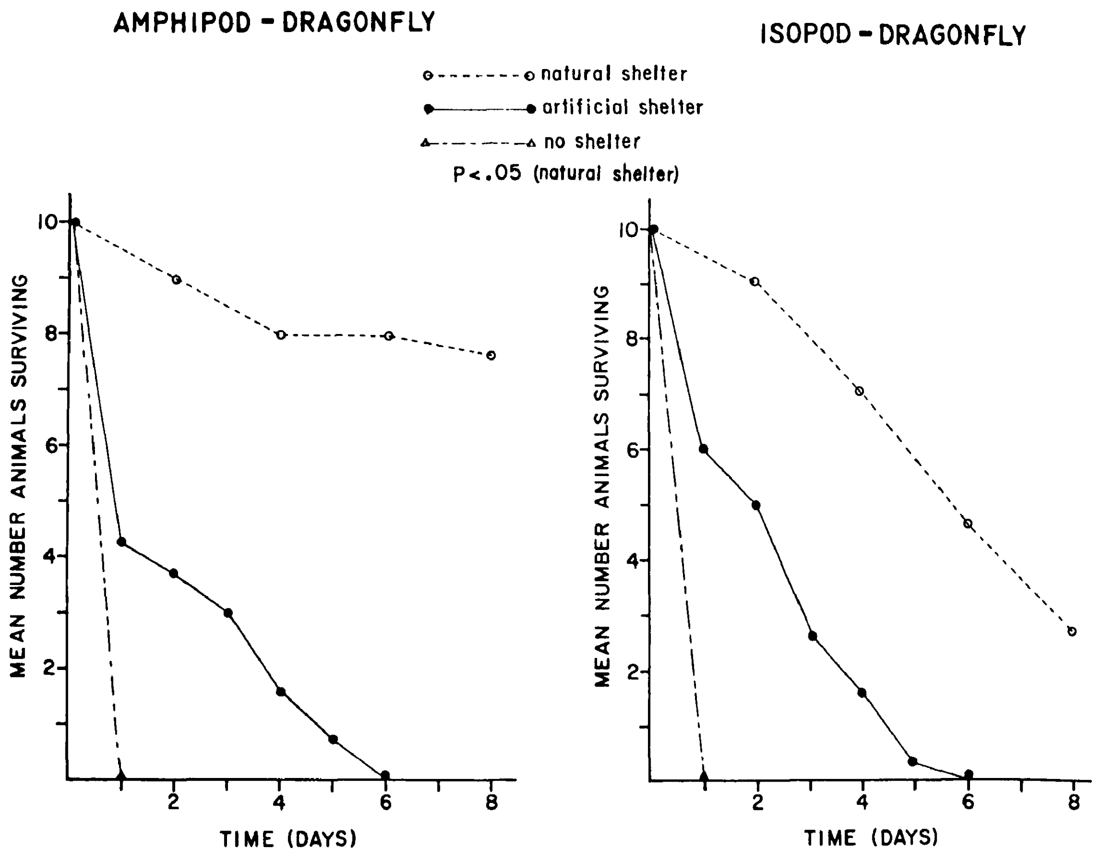

AMPHIPOD - FISH
ISOPOD - FISH
natural shelter
artificial shelter
no shelter
P <.05 (natural shelter)
MEAN NUMBER ANIMALS SURVIVING
10
8
6
4
2
TIME (DAYS)
2
4
6
8

Figure 5. Survival of amphipods and isopods in the presence of dragonfly predators, under varying shelter conditions. Difference in numbers surviving under natural shelter between amphipods and isopods is significant ($P < .05$, Wilcoxin Matched Pairs Signed Ranks test).


AMPHIPOD - DRAGONFLY
ISOPOD - DRAGONFLY
natural shelter
artificial shelter
no shelter
P<.05 (natural shelter)
MEAN NUMBER ANIMALS SURVIVING
10
8
6
4
2
TIME (DAYS)
2
4
6
8

both prey species more quickly than did dragonflies, fish captured more amphipods than isopods ($P < .05$), while dragonflies captured more isopods than amphipods ($P < .05$).

Experiment 4. Shelter utilization in the absence of predators. A distinct circadian rhythm was evident for both isopods and amphipods with increased numbers of animals out from under shelters in the dark hours, though in no instance were all the animals exposed at one time (Fig. 6). Isopods showed a steady decrease in the number unsheltered for the first two days of the observation period, perhaps indicating a longer acclimation period was required. In addition, though both showed an affinity for shelter in the absence of predators, isopods exhibited a significantly greater prederence by virtue of a much stronger tendency to stay sheltered at night ($P = .45$; $P < .01$, night; $P < .025$, day and night combined). Amphipods averaged 5-7 unsheltered at night and 1-2 unsheltered during the day whereas isopods averaged only 1-2 unsheltered at night and 0-1 unsheltered during the day.

Decreased shelter utilization for both isopods and amphipods occurred in early fall ($P < .025$, day; $P < .01$, night; $P < .005$, day and night combined) as revealed by comparing the control from May (14L-10D photoperiod and 18°C water temperature) to the control run in October (12L-12D photoperiod and 15°C water temperature) (Figs. 7,8). As in May, the number of unsheltered amphipods significantly exceeded that of the isopods ($P = .45$, day; $P < .01$, night; $P < .025$, day and night combined) with 6-9 amphipods unsheltered at night and 3-6 in day as compared to 6-7 unsheltered isopods at night and 1-4 in the day in October.

Figure 6. Shelter utilization in May (photoperiod 14L-10D, water temp. 18°C) of amphipods and isopods in the absence of predators. Difference is significant during night only ($P = .45$, day; $P < .01$, night; Wilcoxin Matched Pairs Signed Ranks test). D = day, N = night.

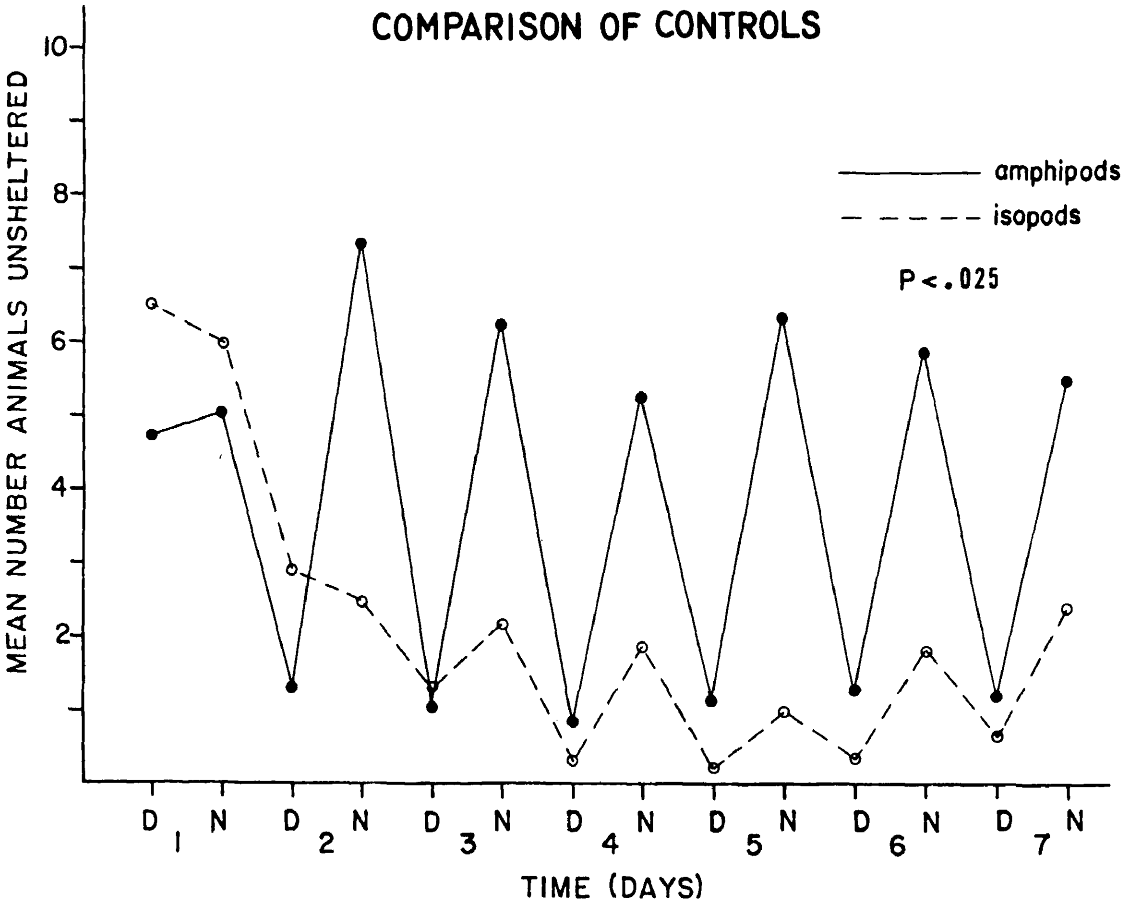

COMPARISON OF CONTROLS
MEAN NUMBER ANIMALS UNSHELTERED
10
8
6
4
2
amphipods
isopods
P<.025
D
N
1
D
N
2
D
N
3
D
N
4
D
N
5
D
N
6
D
N
7
TIME (DAYS)

Figure 7. Shelter utilization of amphipods in May (photoperiod 14L-10D, water temp. 18°C) and in October (photoperiod 12L-12D, water temp. 15°C). Difference is significant during day, night, and both periods combined ($P < .025$, day; $P < .01$, night; $P < .005$, both; Wilcoxin Matched Pairs Signed Ranks test). D = day, N = night.

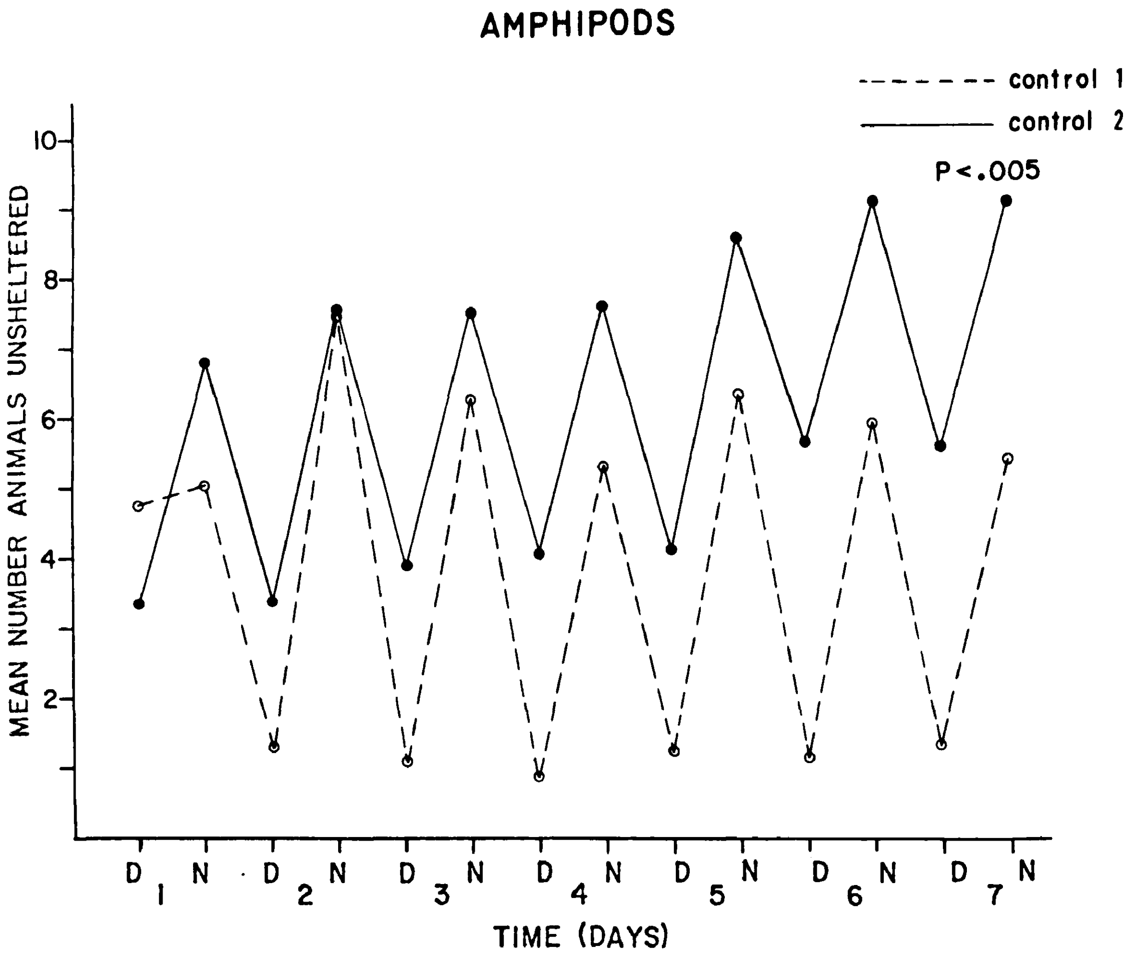
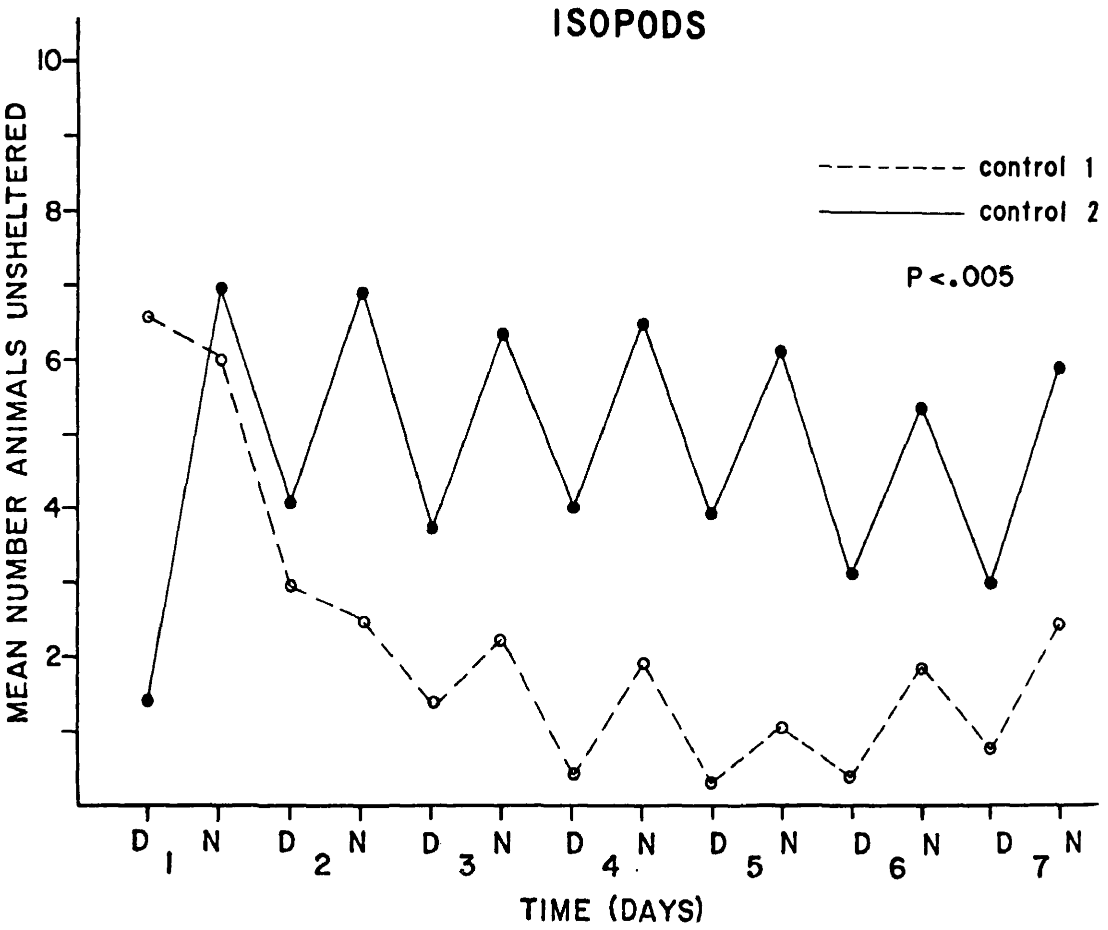

AMPHIPODS
control 1
control 2
P<.005
MEAN NUMBER ANIMALS UNSHELTERED
10
8
6
4
2
D
N
D
N
D
N
D
N
D
N
D
N
D
N
1
2
3
4
5
6
7
TIME (DAYS)

Figure 8. Shelter utilization of isopods in May (photoperiod 14L-10D, water temp. 18°C) and in October (photoperiod 12L-12D, water temp. 15°C). Difference is significant during day, night, and both periods combined ($P < .025$, day; $P < .01$, night; $P < .005$, both; Wilcoxin Matched Pairs Signed Ranks test). D = day, N = night.


ISOPODS
MEAN NUMBER ANIMALS UNSHELTERED
10
8
6
4
2
control 1
control 2
P <.005
D
N
1
2
3
4
5
6
7
TIME (DAYS)

Experiment 5. Shelter utilization in presence of a predator restricted from direct access. Both isopods and amphipods showed a marked increase in shelter utilization in the presence of restricted fish predators ($P < .01$, for both during day; $P < .01$, for both during night; $P < .005$, for both day and night combined) (Figs. 9, 10). During the day with fish present, no isopods or amphipods were ever unsheltered.

With dragonflies, the increase in shelter utilization was less marked. Amphipods showed a consistently lower number unsheltered compared to the control ($P < .01$, day; $P < .01$, night; $P < .005$, day and night combined), but the number unsheltered was significantly higher than when fish were used ($P < .01$, day; $P < .01$, night; $P < .005$, day and night combined) (Figs. 9, 11). The number of unsheltered isopods with dragonflies present (Fig. 12) was significantly lower than the control only during light ($P < .01$). However, during night there was no statistically significant difference ($P = .5$). Also, as with amphipods, the number of unsheltered isopods with dragonflies as predator was significantly higher than with a fish predator ($P < .01$, day; $P < .01$, night; $P < .005$, day and night combined).

Experiment 6. Chemical detection of a predator. When water in which fish were kept was introduced into the tanks (Figs. 13, 14), the number of unsheltered isopods and amphipods was always lower than the number unsheltered in the control tanks in which no fish water was added ($P < .005$; no statistical analysis for day and night separately due to small sample size). In addition, the number of unsheltered isopods and amphipods with fish water was significantly lower than with dragonfly water ($P < .005$).

Figure 9. Shelter utilization of amphipods in presence of a partitioned bluegill, compared to control. Difference is significant during day, night, and both periods combined ($P < .01$, day; $P < .01$, night, $P < .005$, both; Wilcoxin Matched Pairs Signed Ranks test). D = day, N = night.

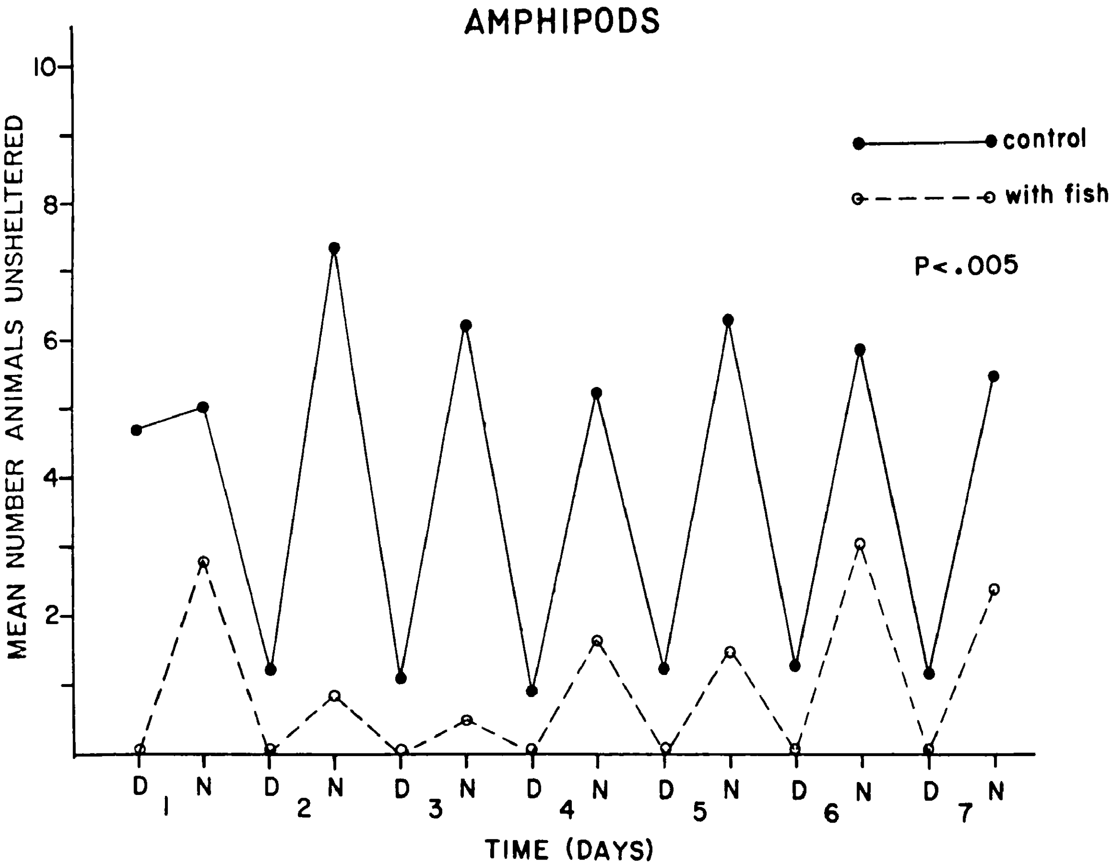

AMPHIPODS
MEAN NUMBER ANIMALS UNSHELTERED
10
8
6
4
2
control
with fish
P<.005
D
N
1
2
3
4
5
6
7
TIME (DAYS)

Figure 10. Shelter utilization of isopods in presence of a partitioned bluegill, compared to control. Difference is significant during day, night, and both periods combined ($P < .01$, day; $P < .01$, night; $P < .005$, both; Wilcoxin Matched Pairs Signed Ranks test). D = day, N = night.

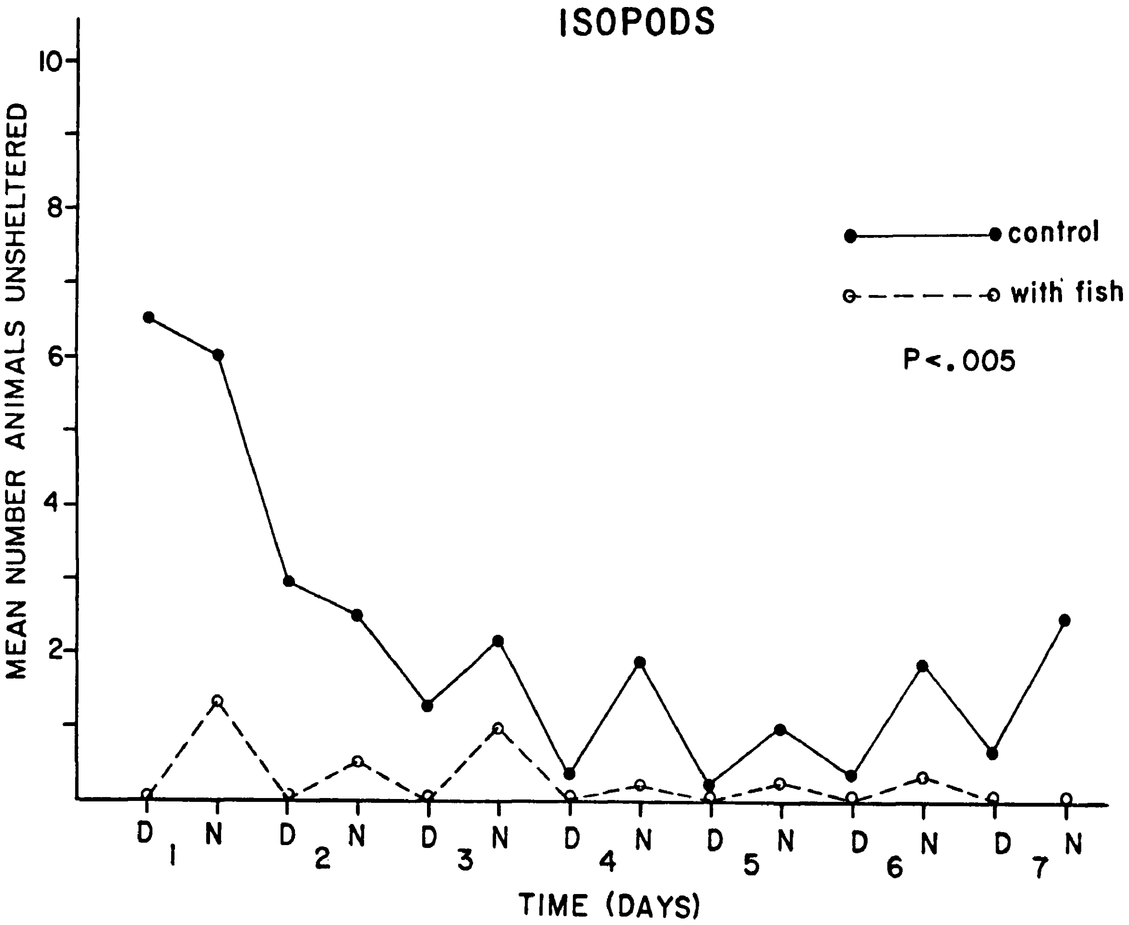

ISOPODS
MEAN NUMBER ANIMALS UNSHELTERED
10
8
6
4
2
control
with fish
P<.005
D
1
N
D
2
N
D
3
N
D
4
N
D
5
N
D
6
N
D
7
N
TIME (DAYS)

Figure 11. Shelter utilization of amphipods in presence of partitioned dragonflies, compared to control. Difference is significant during day, night, and both periods combined ($P < .01$, day; $P < .01$, night; $P < .005$, both; Wilcoxin Matched Pairs Signed Ranks test). D = day, N = night.

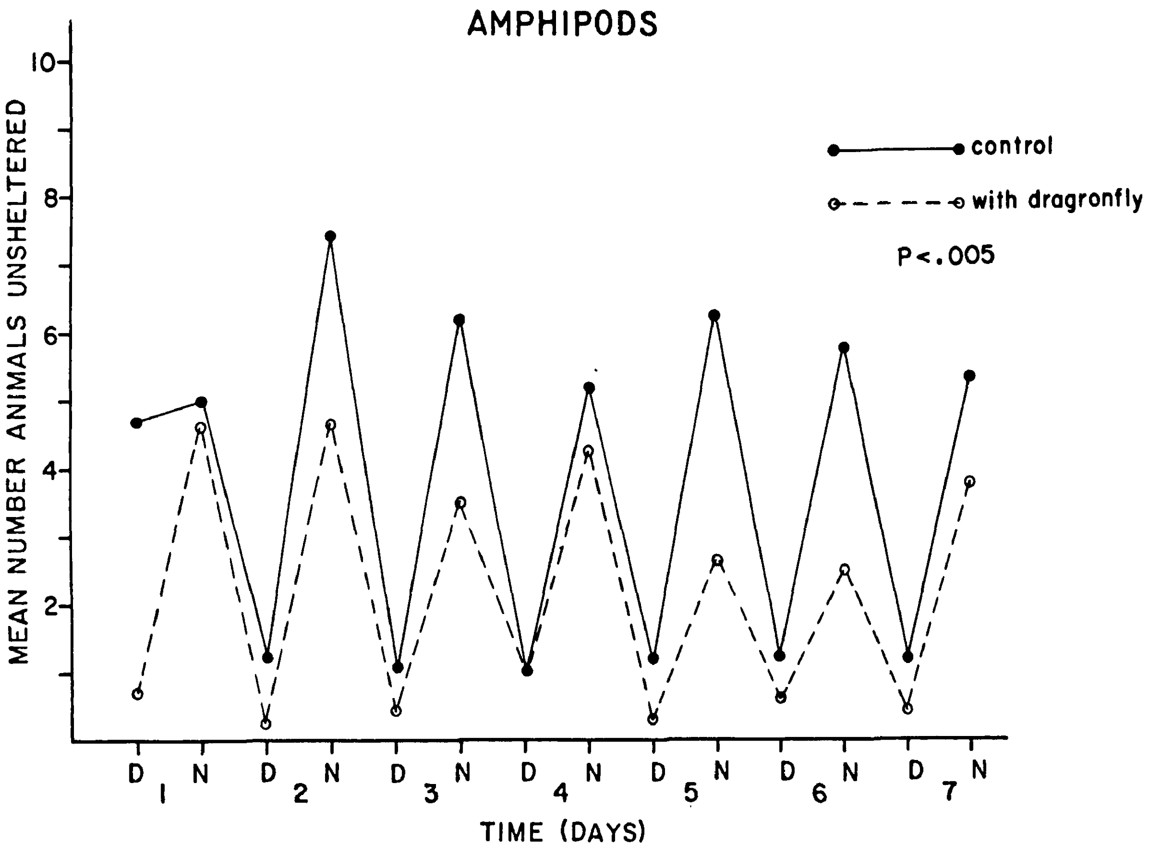

AMPHIPODS
MEAN NUMBER ANIMALS UNSHELTERED
10
8
6
4
2
D
N
D
N
D
N
D
N
D
N
D
N
D
N
1
2
3
4
5
6
7
TIME (DAYS)
control
with dragronfly
P<.005

Figure 12. Shelter utilization of isopods in presence of partitioned dragonflies, compared to control. Difference is significant during the day only ($P < .01$; Wilcoxin Matched Pairs Signed Ranks test). D = day, N = night.

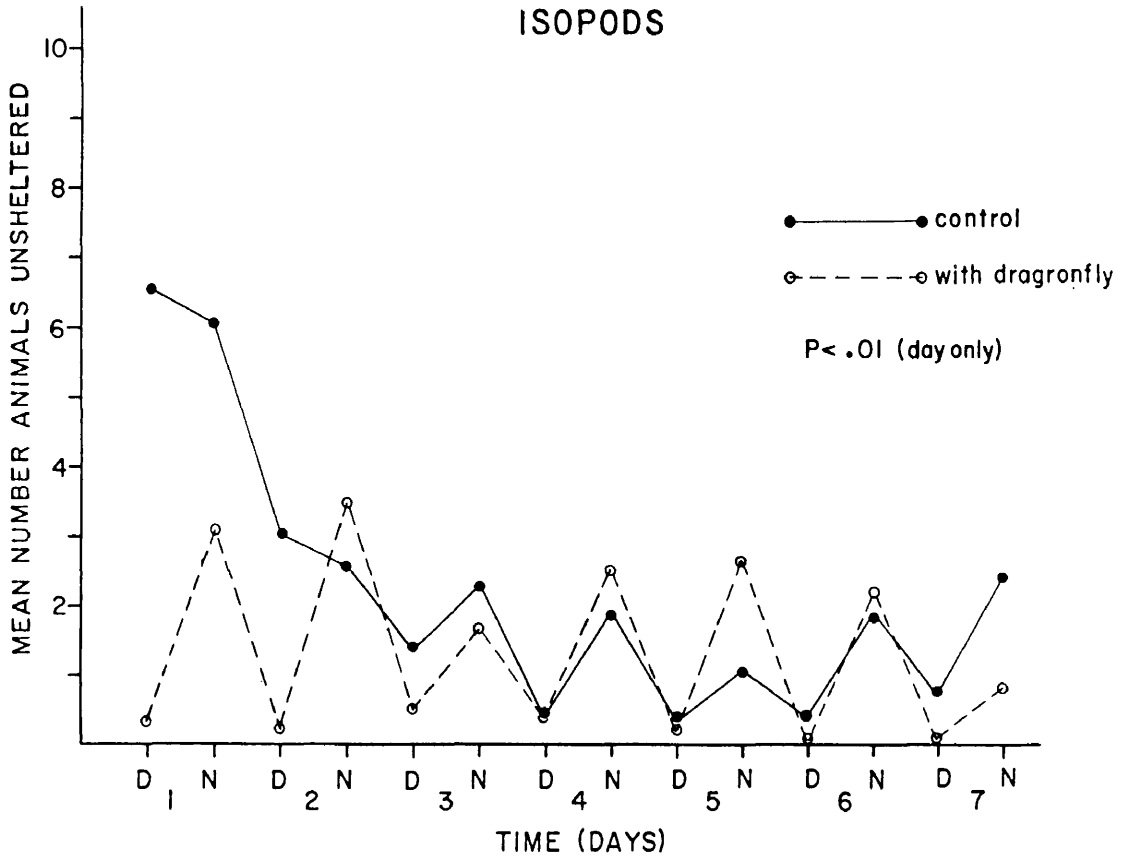

ISOPODS
MEAN NUMBER ANIMALS UNSHELTERED
10
8
6
4
2
control
with dragronfly
P< .01 (day only)
D N D N D N D N D N D N D N
1 2 3 4 5 6 7
TIME (DAYS)

Figure 13. Shelter utilization of amphipods in presence of fish water, compared to control. Difference in shelter utilization is significant ($P < .005$; Wilcoxin Matched Pairs Signed Ranks test). D = day, N = night.

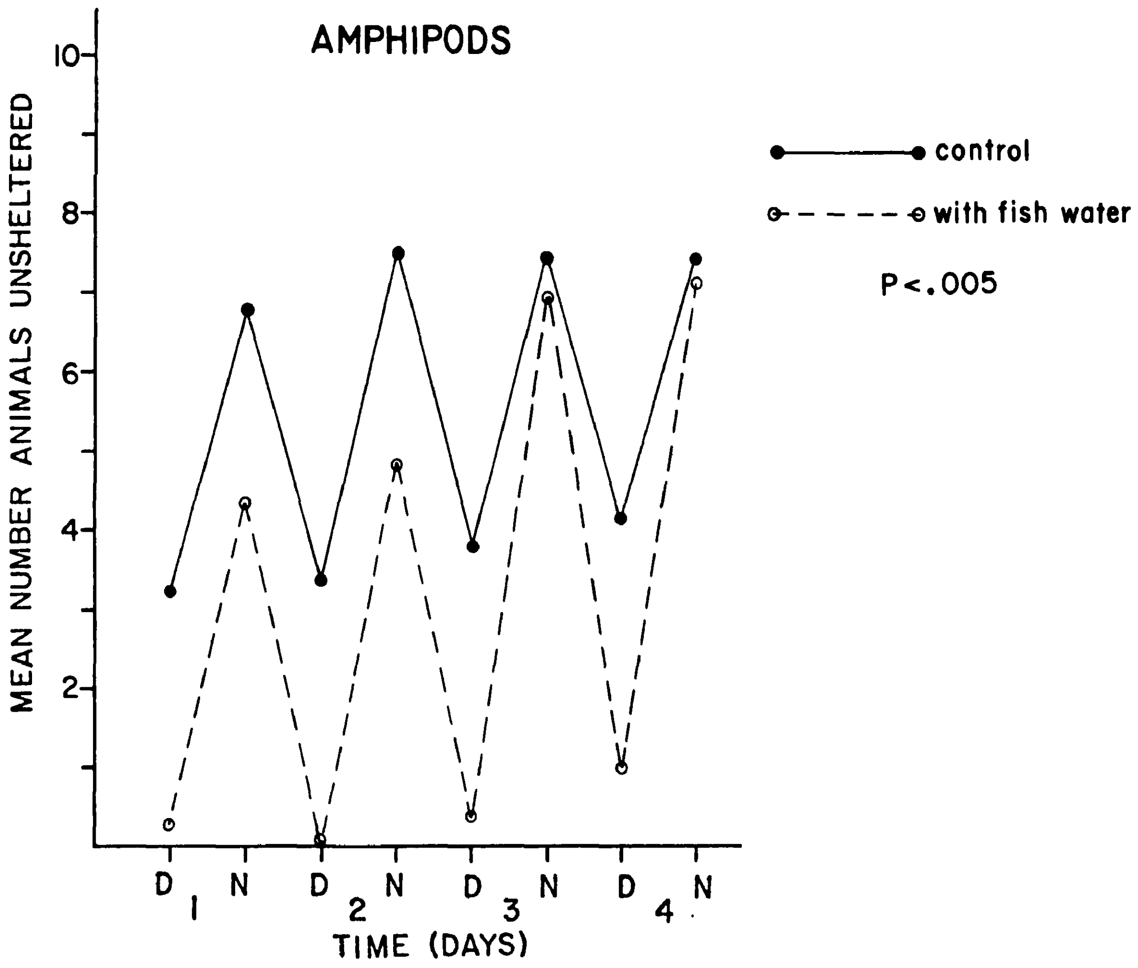
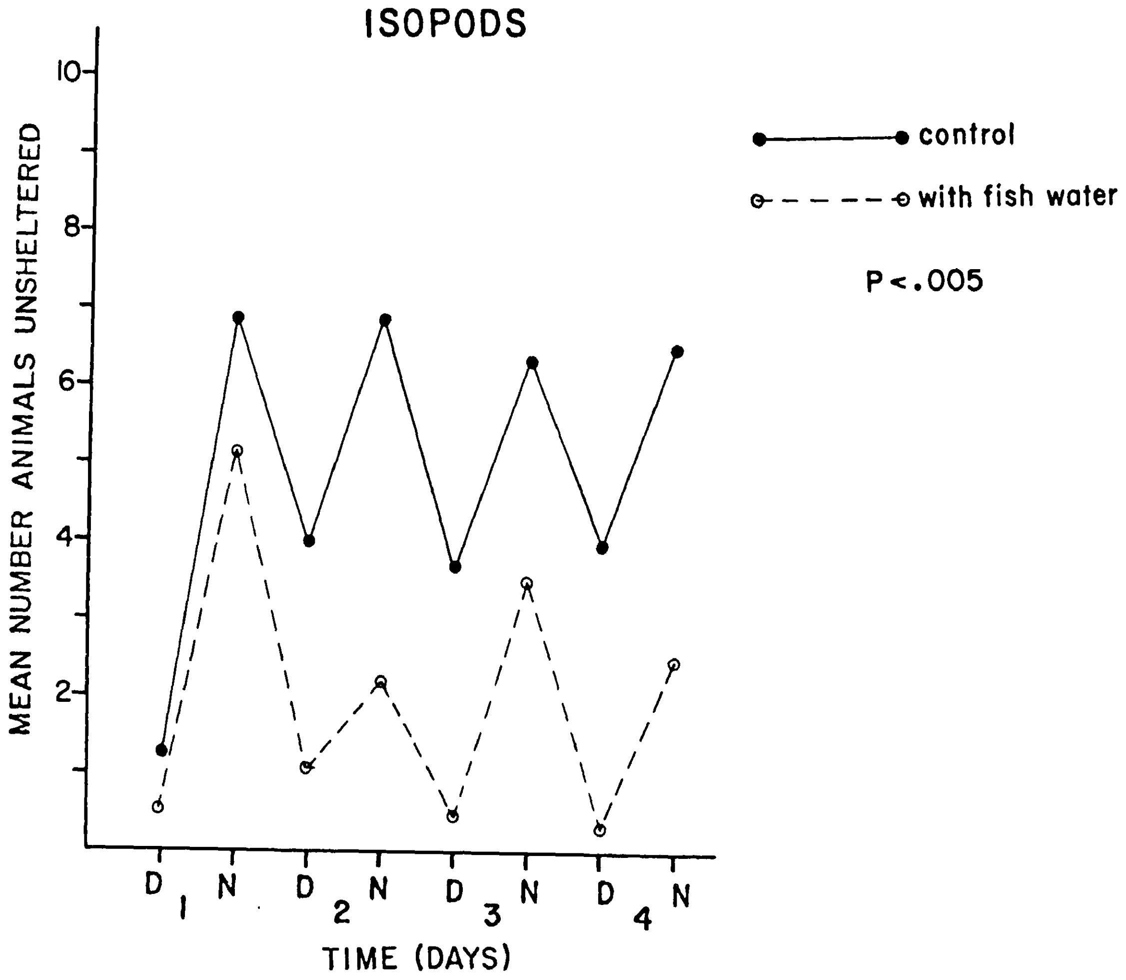

AMPHIPODS
MEAN NUMBER ANIMALS UNSHELTERED
10
8
6
4
2
D
N
D
N
D
N
D
N
1
2
3
4
TIME (DAYS)
control
with fish water
P<.005

Figure 14. Shelter utilization of isopods in presence of fish water, compared to control. Difference in shelter utilization is significant ($P < .005$; Wilcoxin Matched Pairs Signed Ranks test). D = day, N = night.


ISOPODS
MEAN NUMBER ANIMALS UNSHELTERED
10
8
6
4
2
D
1
N
D
2
N
D
3
N
D
4
N
TIME (DAYS)
control
with fish water
P<.005

When comparing control tanks with tanks in which dragonfly water was added, the difference was not as clear as that with fish water (Figs. 15, 16). A significant difference ($P < .05$) was observed for isopods but not amphipods ($P = .25$). However, the data indicated some evidence of chemical detection by the amphipods. Considering only daytime response, the number of unsheltered amphipods was always less with dragonfly water compared to control tanks except during the final light observation (day 4) at which time the number exceeded that of the control slightly.

A summary of isopod and amphipod responses to all treatments is presented in Figures 17 and 18. For ease of comparison, light and dark responses have been separated. Increased activity at night is most noticeable. In addition, the degree to which prey responded to predators or predator water can be seen at a glance. Both prey types increased shelter utilization to a greater extent in response to fish and fish water as compared to dragonflies and dragonfly water respectively.

Figure 15. Shelter utilization of amphipods in presence of dragonfly water, compared to control. Difference in shelter utilization is not significant (P = .25; Wilcoxin Matched Pairs Signed Ranks test). D = day, N = night.

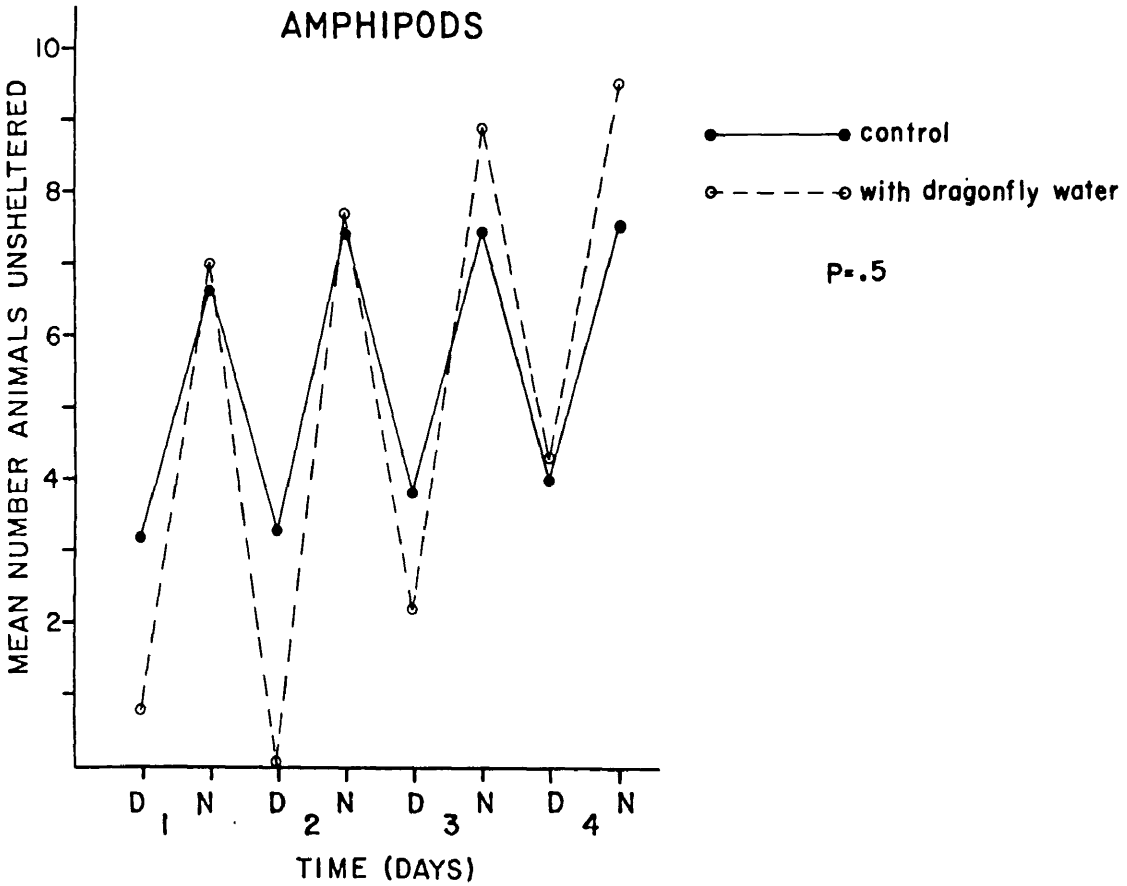

AMPHIPODS
MEAN NUMBER ANIMALS UNSHELTERED
10
8
6
4
2
D
N
D
N
D
N
D
N
1
2
3
4
TIME (DAYS)
control
with dragonfly water
P=.5

Figure 16. Shelter utilization of isopods in presence of dragonfly water, compared to control. Difference in shelter utilization is significant ($P < .05$; Wilcoxin Matched Pairs Signed Ranks test). D = day, N = night.

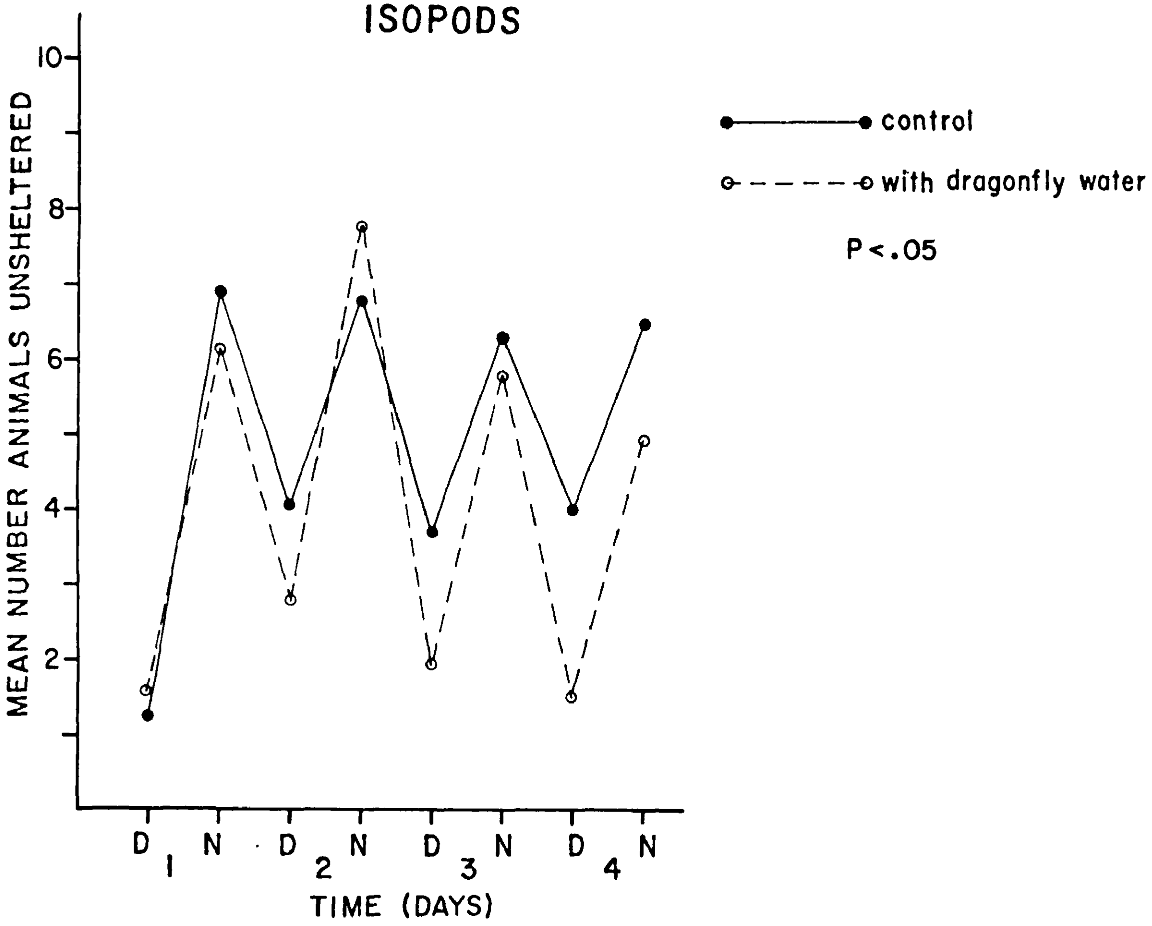

ISOPODS
MEAN NUMBER ANIMALS UNSHELTERED
10
8
6
4
2
D
N
D
N
D
N
D
N
1
2
3
4
TIME (DAYS)
control
with dragonfly water
P<.05

Figure 17. Summary of shelter utilization by amphipods for all experimental treatments. Vertical lines indicate 95% confidence limits.

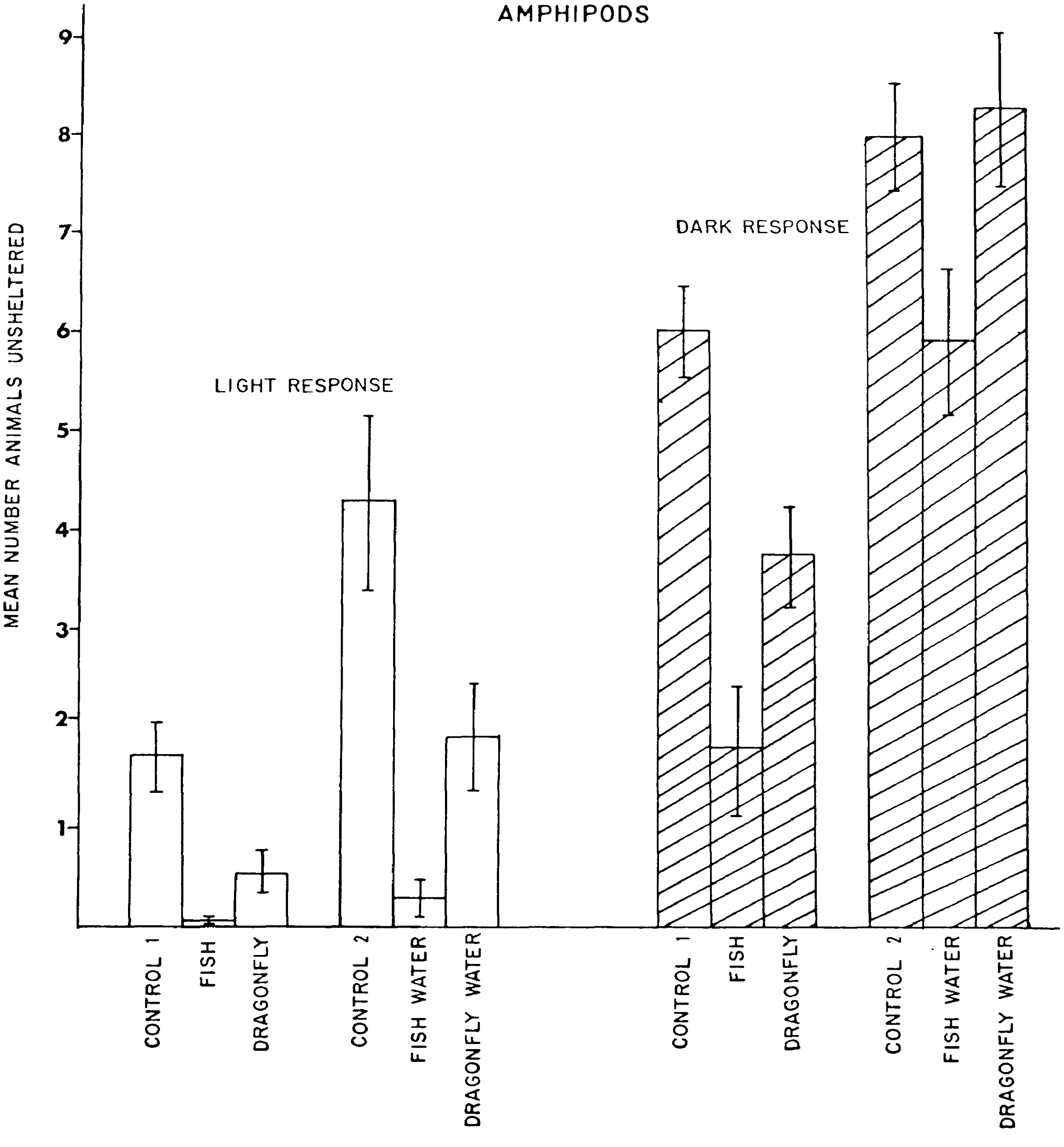
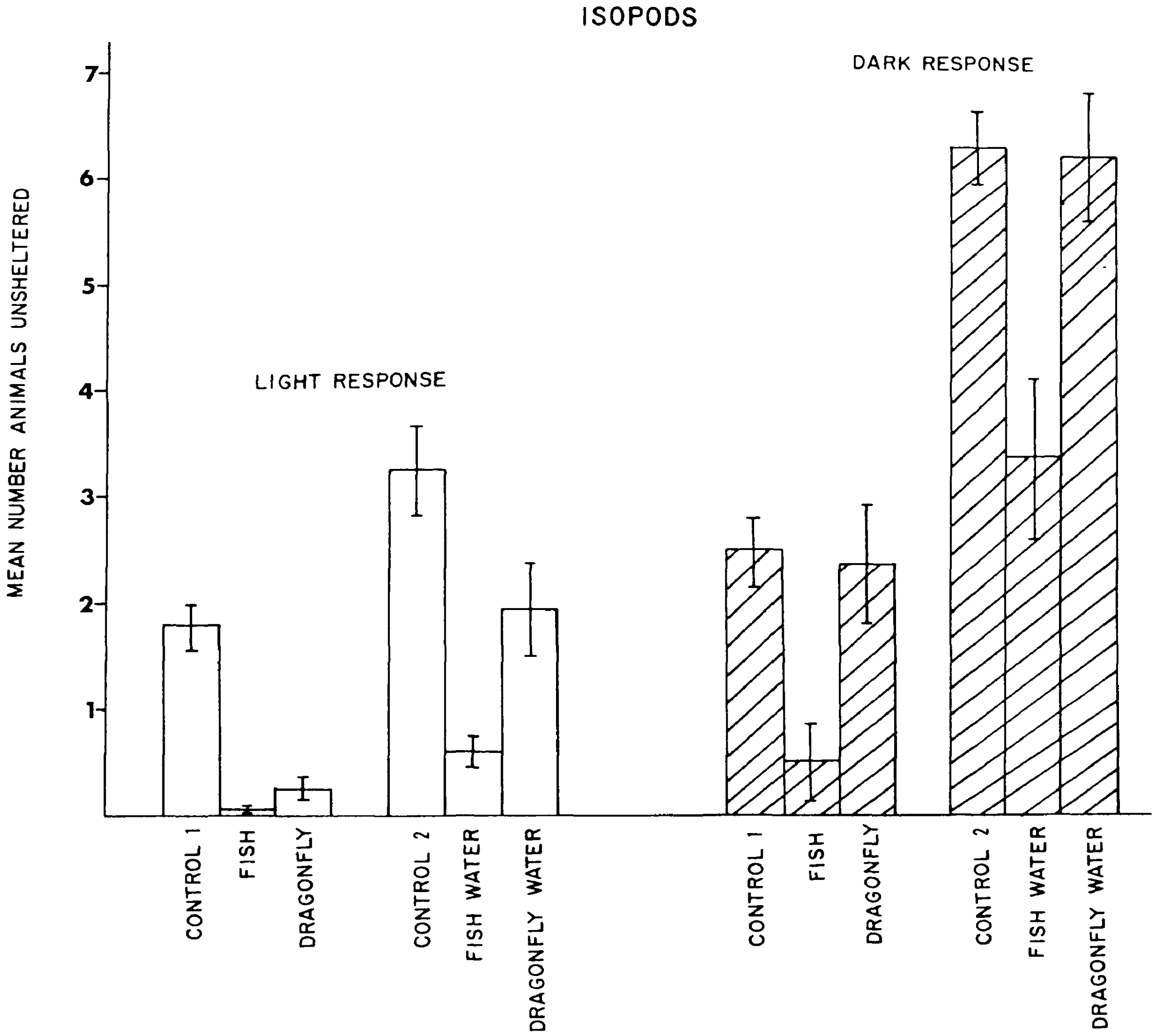

AMPHIPODS
MEAN NUMBER ANIMALS UNSHELTERED
9
8
7
6
5
4
3
2
1
LIGHT RESPONSE
DARK RESPONSE
CONTROL 1
FISH
DRAGONFLY
CONTROL 2
FISH WATER
DRAGONFLY WATER
CONTROL 1
FISH
DRAGONFLY
CONTROL 2
FISH WATER
DRAGONFLY WATER

Figure 18. Summary of shelter utilization by isopods for all experimental treatments. Vertical lines indicate 95% confidence limits.


ISOPODS
MEAN NUMBER ANIMALS UNSHELTERED
7
6
5
4
3
2
1
LIGHT RESPONSE
DARK RESPONSE
CONTROL 1
FISH
DRAGONFLY
CONTROL 2
FISH WATER
DRAGONFLY WATER
CONTROL 1
FISH
DRAGONFLY
CONTROL 2
FISH WATER
DRAGONFLY WATER

DISCUSSION

Both isopods and amphipods spent a great deal of time under shelter, presumably to avoid predators. Since neither amphipods nor isopods are equipped with any defense mechanism other than locomotion to escape predation, this behavior was expected. Both utilized available shelter even in the absence of a predator; at no time were all isopods or amphipods unsheltered. This is probably an innate response, derived from the more or less continuous presence of predators under natural conditions. Even so, both significantly increased shelter utilization when a bluegill was placed behind the partition at one end of the tank. When dragonfly predators were introduced, amphipods again significantly increased shelter utilization during both day and night. Isopods exhibited a significant increase in shelter utilization in response to dragonflies only in the day. In total, these results strongly suggest that both amphipods and isopods are able to detect predators remotely.

Whether or not predators were present, isopods and amphipods both demonstrated a distinct circadian rhythm, with decreased shelter utilization at night. This rhythm may reflect circadian changes in predation pressure in the natural environment since some predators, such as bluegill, do not feed at night.

The decrease in shelter utilization by both isopods and amphipods in October as compared to May also may reflect less predation pressure under natural conditions. By October, bluegill fry usually leave the shallow edges of the lake (pers. obser.) possibly due to their increase in size over the summer and/or to escape cooler water temperatures. In addition, dragonflies may not require as many prey items due to the physiological effect of the cooler water temperature.

Shelter availability makes an obvious difference to prey survival. With no shelter available, neither prey type survived longer than 24 hours with fish or dragonfly predators. With the limited shelter area provided by the plastic squares, survival time of amphipods and isopods was 2 and 3 days respectively with fish and 6 days with dragonflies. With the more extensive shelter provided by leaf litter, survival of some of both surpassed the eight day observation period. In agreement with my findings, Pritchard (1964) and Lawton, _et_ _al_. (1974) reported that dragonflies, under natural conditions, did not eat nearly as much as they did in the laboratory. Also, Benke (1976, 1978) reported that dragonflies have the ability to annihilate their prey under natural conditions, if they are accessible, but suggested that prey are usually saved from annihilation because they can find sufficient refuges in their natural habitat.

Although shelter availability in general increased chances of escaping predation, the differing shelter affinity and locomotive ability of the prey and differing feeding modes of the predators were also factors. Isopods showed a greater affinity for shelter than did amphipods with or without the predators used in this study. Halenda (1977) reported similar findings in that _A_. _communis_ showed a greater preference for shelter over bare sand than did _G_. _fasciatus_, that _Asellus_ _communis_ preferred the deeper leaves whereas _G_. _fasciatus_ preferred the newer, shallower leaves, and that _A. communis_ preferred the darker part of a light gradient while _G. fasciatus_ showed no preference to a gradient.

The greater affinity of isopods for shelter may relate to their inability to swim and maneuver as quickly as amphipods, leaving them more vulnerable to predation. However, if adequate shelter was provided, isopods, due to their greater affinity for shelter, were less susceptible to fish predation than amphipods. In addition, the darker color and slow movement of isopods as compared to that of amphipods presumably camouflages them better in the leaf litter from visually-orienting bluegill predators. However, the slow movement and stronger affinity for shelter which lessened isopods' susceptibility to fish predation left them more vulnerable to the ambush attack of dragonflies also inhabiting the leaf litter. Isopods seldom escaped the lunge of dragonflies, whereas amphipods often escaped capture attempts. Also, unlike isopods, large amphipods sometimes managed to escape from the labium clasp if caught.

The increased shelter utilization by prey in response to a restricted predator raises a basic question as to the means of predator detection by the prey. Predator detection presumably may have been by visual or chemical means, by water movements created by the predator, or by a combination of these.

Although many papers in the literature report evidence of pheromone communication in the Crustacea (Atema and Engstrom, 1971; Dunham, 1978; Katona, 1973; Kittredge and Takahashi, 1972; and Ryan, 1966), only recently has much work been done on chemical communication between a predator and prey in freshwater habitats. Peckarsky (1980) examined the possibility of chemical detection between mayflies and their stonefly predators and found that the avoidance responses appeared to be triggered by a chemical stimulus emanating from the predator.

Results from my study also suggested chemical detection of predators by both prey types. Isopods and amphipods showed a significant increase in shelter utilization when only fish water was introduced, which suggests that visual or vibrational cues are not necessary to induce the response. However, the response of isopods and amphipods to possible chemical cues released by the dragonflies was more equivocal than with fish. Amphipods significantly increased shelter utilization in the presence of restricted dragonflies yet showed no significant response to dragonfly water; isopods exhibited a significant response to restricted dragonflies only during the day, but a significant response to dragonfly water during both day and night. Reasons for the unexpected response of isopods (i.e. an apparently stronger response to dragonfly water than to actual dragonflies) are not clear. Time of year may have been a factor, since the experiments were run during different seasons.

The weaker response of amphipods to dragonfly water as compared to fish water does not eliminate the possibility of chemical detection. Dragonflies, due to their smaller size as compared to fish, may release a lesser amount of the detected chemical. In addition, this chemical may break down in a short period of time, requiring the physical presence of the dragonflies to continually release the chemical in order for concentrations to be maintained at a level detectable by the prey. The difference in the response of amphipods to fish and dragonfly water suggests differential predation pressure or effectiveness of predator evasion tactics, i.e. fish may be a more significant predator for amphipods.

Although chemical detection of predators by isopods and amphipods is probable, visual and vibrational cues may influence shelter utilization as well. However, considering that the acuity of the isopods' and amphipods' compound eyes is somewhat limited, visual cues can probably be eliminated. The importance of possible vibrational cues cannot be clearly determined from my work.

Thus, my data support chemical detection of both predator types by both prey types. The differences in the degree of response shown by isopods and amphipods suggest differential predation pressure and effectiveness of predator-evasion tactics. Bluegill, being a very effective predator, elicited a stronger response from both isopods and amphipods than did dragonflies. As a result of the isopods' greater affinity for shelter, amphipods were more vulnerable to the bluegill predation tactics. However, due to their limited evasive tactics, isopods fell victim to dragonfly predation more often than amphipods, and, in accordance, evidence for chemical detection of dragonflies by isopods appeared stronger.

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