FEEDING AND ACTIVITY OF THE CRAYFISH ORCONECTES RUSTICUS IN A NORTHERN WISCONSIN LAKE

by

James Garfield Lorman

A thesis submitted in partial fulfillment of the
requirements for the degree of
MASTER OF SCIENCE
(Zoology)
at the
UNIVERSITY OF WISCONSIN-MADISON

1975

To P3
+2

ABSTRACT

FEEDING AND ACTIVITY OF THE CRAYFISH ORCONECTES RUSTICUS IN A NORTHERN WISCONSIN LAKE

James Garfield Lorman

Under the supervision of Professor John J. Magnuson

Populations of the crayfish *Orconectes rusticus* were sampled in Lower Sugarbush Lake, Vilas County, Wisconsin, on a day-night and a diel basis to evaluate patterns of feeding activity and to provide information for a long-term study of the importance of this recently-introduced species in structuring aquatic communities of northern Wisconsin.

Counts and size measurements of exposed (active) and hidden (inactive) crayfish collected within sampling rings at two depths (1 and 3 m) during the afternoon and again after dark revealed an increase in the number of crayfish exposed at night. However, more adult males were found exposed than hidden during both day and night, and small crayfish were more nocturnal than large ones. Crayfish did not appear to migrate into shallow water at night, but a higher percentage of animals were found exposed at night at 1 m than at 3 m.

Stomach fullness of crayfish collected in the field over three 24-hr periods was measured to determine patterns of feeding activity. Fullness was expressed as a proportion of the maximum stomach capacity for a crayfish of a given carapace length, determined by feeding experimental animals *ad libitum*. Results of diel collections revealed increased feeding at night, but patterns of feeding reflected differences in crayfish size and sex, and climatic (photoperiod and temperature) conditions.

Males collected in June showed little variation in stomach fullness throughout 24-hr sampling; females showed greater variation in fullness both in respect to time of day and to crayfish size. Animals collected while exposed in October and November had fuller stomachs than animals collected while hidden; this difference was largest at night in October, and was larger for females than males. Crayfish apparently confined all feeding activity to the night in November.

Stomach analysis of crayfish collected in 24phr samples revealed a wide range of food items. Males were more carnivorous than females, and large crayfish more herbivorous than small ones. Mayfly nymphs were more common in crayfish stomachs in November than in October and June.

Differences in feeding activity patterns probably reflect different foraging strategies and may be mediated by differential responsiveness to zeitgebers. Quantitative analysis of these differences would require measurements of feeding and digestion rates, length of feeding bouts and of intervals between bouts, and consumption of different food items. Calculations of energy flow and analysis of functional relationships from these measurements allow evaluation of the role of crayfish in structuring aquatic communities.

ACKNOWLEDGMENTS

I wish to thank my major professor, John Magnuson, for his advice, support, and encouragement throughout the course of this study. I also would like to thank: members of my committee, John Magnuson, Jim Kitchell, Tim Moermond, and Warren Porter, for their helpful criticisms; Keith Nelson, Tim Evans, Pat Marinac, and Steve Lozano, for assistance in collecting data; Mr. and Mrs. Jack Wenzlick, for providing access to Lower Sugarbush Lake; Mike Murphy and Bill Albright, for technical assistance; and Joey Meyer, for drawing final fugures. Special thanks to Roy Stein, who provided intellectual stimulus and helped in every phase of my study.

This research was supported form grants to John Magnuson from the National Science Foundation (GB-40697) and the Wisconsin Department of Natural Resources (Federal Aid in Fish Restoration Act, D.J. Project F-83-R).

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Background

Orconectes rusticus (Girard) is distributed form southern Michigan and northeastern Ohio southward and westward through Indiana, Illinois, Kentucky, and Tennessee to parts of Missouri, Alabama, and Virginia (Crocker and Barr 1968). *O. rusticus* was recorded in Lake Superior (Bundy 1882) and in Racine, Sauk, and Rock Counties in Wisconsin (reported in Creaser 1932). Creaser (1932), however, did not find *O. rusticus* in extensive sampling throughout Wisconsin, and felt that these earlier records refer to aberrant forms of *O. propinquus*. In the past few years, we have observed several occurrences of *O. rusticus* in northern Wisconsin (Capelli 1975, Table 1), and it is likely that these occurrences represent recent introductions by fishermen bringing crayfish as bait from other states. Populations of *O. rusticus* have also become established in several Ontario lakes, where summer vacationers from midwestern states are common (Crocker and Barr 1968).

The dense populations of *O. rusticus* in several northern Wisconsin lakes (see Table 1) have in recent years supported some commercial harvesting and have also led to numerous complaints by lake residents. In at least six lakes with *O. rusticus* (Long Lake, Chippewa County; Sugarbush, Island, and Presque Isle Lakes, Vilas County; Crescent and Big Bearskin Lakes, Oneida County), residents and commercial crayfishermen have noticed an increase in the number of crayfish within the last 10-15 years, coincident with a dramatic decline in the abundance of aquatic macrophytes. Many residents claim that crayfish have destroyed fish spawning beds and are a nuisance to swimmers. Although a change in

Table 1. Confirmed occurrences of *O. rusticus* in northern Wisconsin and estimates of density and biomass of adults in the littoral zone of three lakes based on unpublished data from Trout Lake Biological Station, University of Wisconsin. Date of first confirmation is given. Where quantitative sampling was done, sampling date is shown in parentheses. Density estimates are based on counts from 10 tosses of 0.25, 0.5, or 1.0 m^2 sampling rings at 1-2 m water depth. Dry weight estimates are measurements directly from animals collected in the ring, or are conversions from carapace length measurements based on a length-weight curve.

County	Lake or river	Date	Density (Number/m^2)	Dry weight (g/m^2)
Vilas	Lower Sugarbush	1973		
		(August 1974)	2	4
	Middle and Upper Sugarbush	1974		
	Alder	1975		
	Wild Rice	1975		
	Spider	1972		
	Clear	1975		
	Rest	1975		
	Manitowish River	1975		
	Presque Isle	1975		
	Sparkling	1975		
	Anne	1975		
	Island	1975		
	Big	1975		
	Boulder	1975		
Forest	Franklin	1972		
	Butternut	1972		
Oneida	Big Bearskin	1974		
		(June 1975)	4	10
	Crescent	1970		
Chippewa	Long	1973		
		(August 1974)	3	10
	Pine	1974		

crayfish species prior to the numerical increase can not be confirmed in most of these lakes, the increase in crayfish abundance in Presque Isle Lake has been attributed to invasion by O. rusticus into water formerly occupied only by O. virilis (Sam Readel, Amherst, Wisconsin, personal communication).

Study objectives

Casual observations, conversations with lake residents, previous literature on crayfish (for example, Langlois 1935, Abrahamsson 1966, Dean 1969, Rickett 1974) and quantitative measures of density and biomass (Table 1) suggest that the introduction of O. rusticus can result in significant changes in the structure of some aquatic communities. The present study was undertaken as part of a long-term project to evaluate both the descriptive and the functional aspects of these changes.

These two aspects, descriptive and functional, represent two approaches to determining the importance of a species in structuring a community (Dayton 1975). The descriptive, or numerical, approach attempts to define the relative importance of a species based upon quantitative measures such as abundance, biomass, and productivity. The functional, or mechanistic, approach considers how a species may influence community structure in ways that can not be explained only in terms of the species' numerical importance. This latter approach usually involves experimental manipulations of species composition, and may lead to new interpretations of the manner in which communities are structured (for example, Connell 1961, Brooks and Dodson 1965, Paine 1966, 1969, Dayton 1975).

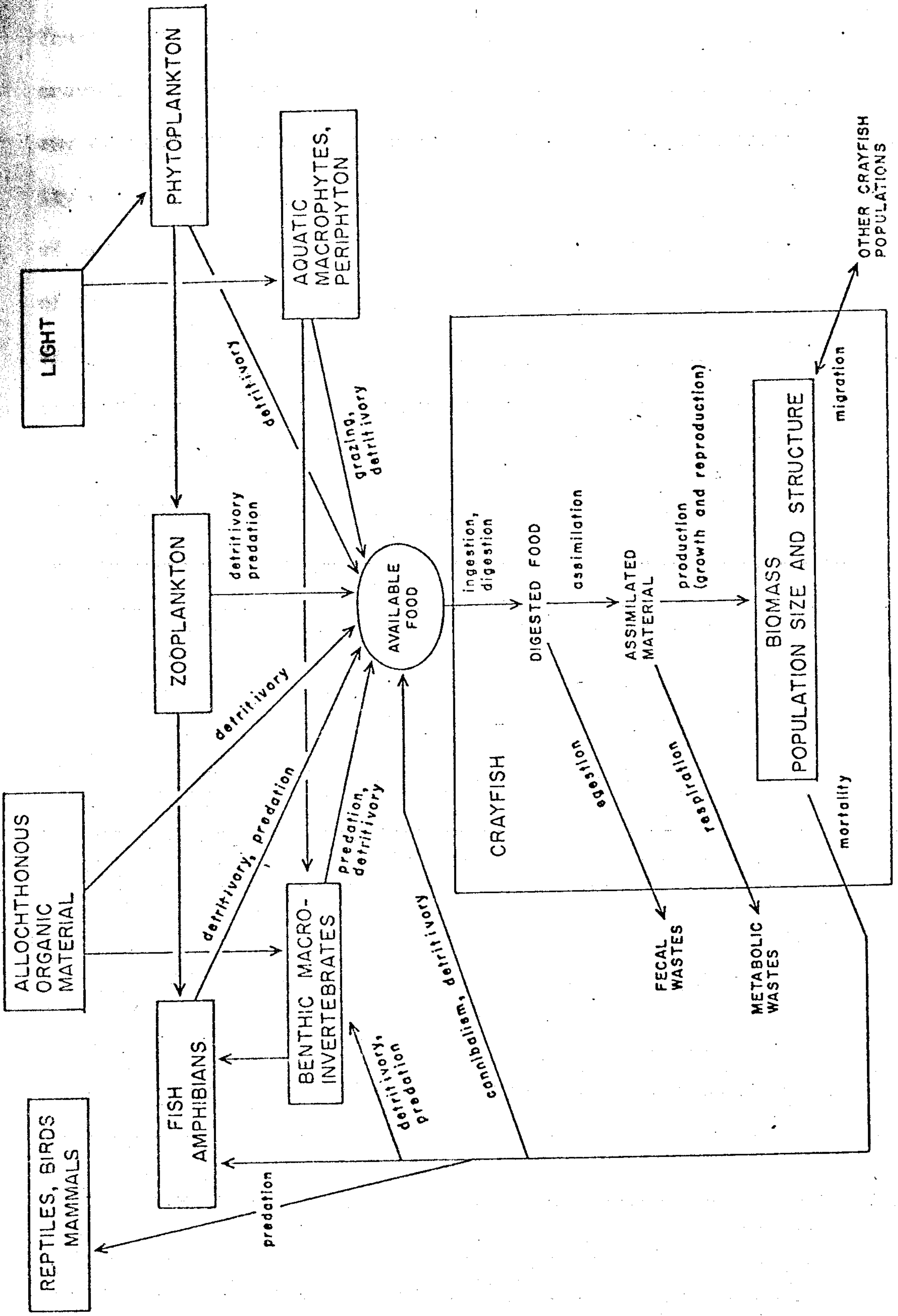
The long-term goal of our crayfish study is to apply both of these approaches to the following questions in regard to aquatic systems recently colonized by O. rusticus:

1. Through what mechanisms do crayfish structure aquatic communities, and what is the nature and extent of the structural changes that occur as a result of the operation of these mechanisms?

2. What factors determine the extent to which the above mechanisms operate in a given system, and what is the quantitative relationship between these factors and the resulting changes in community structure?

A simplified compartmentalization of the lake ecosystem provides a basis for relating the descriptive and functional aspects of control of community structure by crayfish (Figure 1). Crayfish are food generalists, their food type and particle size relatively unrestricted by morphology (Caine 1975). Stomach analysis and direct field observation have revealed that crayfish graze on vascular hydrophytes and algae (Viosca 1931, Martin and Uhler 1939, Tack 1941, Norton 1942, Sakowicz and Kompowski 1962, Mason 1963, Kossakowski 1964, Abrahamsson 1966, Minshall 1967, Prins 1968, Dean 1969, Capelli 1975), feed on detritus from both aquatic and terrestrial sources (Creaser 1934, Tack 1941, Norton 1942, Mason 1963, Abrahamsson 1966, Minshall 1967, Prins 1968, Dean 1969, Capelli 1975), and prey on zooplankton (Tack 1941, Norton 1942, Mason 1963, Abrahamsson 1966, Minshall 1967, Prins 1968), benthic invertebrates (Creaser 1934, Norton 1942, Mason 1963, Kossakowski 1964, Minshall 1967, Prins 1968, Dean 1969, Capelli 1975), and fish (Tack 1941, Minckley and Craddock 1961, Sakowicz and Komposwski 1962, Dean 1969).

Figure 1. A simplified compartmentalization of the lake ecosystem emphasizing the relationship of crayfish to energy flow. Arrows represent the direction of energy flow between various compartments and within the crayfish population.


LIGHT
PHYTOPLANKTON
AQUATIC MACROPHYTES, PERIPHYTON
ZOOPLANKTON
ALLOCHTHONOUS ORGANIC MATERIAL
FISH AMPHIBIANS
BENTHIC MACRO-INVERTEBRATES
REPTILES, BIRDS MAMMALS
detritivory
grazing, detritivory
detritivory predation
detritivory
detritivory, predation
predation, detritivory
detritivory, predation
cannibalism, detritivory
predation
AVAILABLE FOOD
CRAYFISH
ingestion, digestion
DIGESTED FOOD
assimilation
ASSIMILATED MATERIAL
production (growth and reproduction)
BIOMASS POPULATION SIZE AND STRUCTURE
migration
OTHER CRAYFISH POPULATIONS
egestion
respiration
mortality
FECAL WASTES
METABOLIC WASTES

Thus, a large number of direct functional relationships exist between crayfish and various components of the community. The importance of any one of these relationships in structuring a specific aquatic community depends upon the descriptive nature of the relationship (the amount of actual energy flow), which in turn depends upon possible switching of food items by crayfish as various items become more or less available, and upon the biomass of the crayfish population. The latter is determined by the total amount of food available, the ability of the crayfish to exploit this food, by the gross production efficiency of the crayfish (assimilation efficiency + growth and reproduction efficiency), and by losses due to mortality and net outward migration. Energy losses due to mortality flow through detrital pathways or through invertebrate (Dye 1974) or aquatic vertebrate (Mason 1963, Crocker and Barr 1968) predators, or are converted directly back to crayfish biomass through cannibalism and detritivory by the crayfish population itself (Mason 1963, Momot 1967a).

Both descriptive and functional approaches are needed to answer the questions posed above. The specific objectives of the research presented in this paper are concerned with the nature and extent of crayfish exploitation of available food. Specific objectives listed below help evaluate the potential importance of the various functional relationships through which crayfish may structure a community, as well as provide a data base for further quantitative measures of energy flow within the ecosystem:

1. Evaluate diel and seasonal patterns of feeding activity from differences in the quantity of food present in crayfish stomachs and

differences in crayfish behavior.

2. Examine stomach contents of O. rusticus to determine the relative importance of various food items in the diet of crayfish of different sexes and sizes at different times of the year.

3. Provide quantitative data on the quantity of food present in crayfish stomachs for calculations of feeding rates and energy flow.

METHODS

Study area

All sampling was in Lower Sugarbush Lake, Vilas County, a mesotrophic drainage lake (surface area 73 ha, maximum depth 12 m), where residents have considered the abundant *O. rusticus* population to be a problem for over a decade (Black *et al*. 1963). Two stations were chosen for sampling: station 1 is located along the northern shoreline approximately 300 m east of the outlet to Sugarbush Creek; station 2 is along the extreme northeastern shoreline. *Scirpus* is common vegetation at both stations in water less than 1 m, with *Nuphar* abundant in 1-1.5 m water at station 1, and *Potamogeton angustifolius*, *P. amplifolius*, *Vallisneria americana*, and *Myriophyllum exalbescens* common in 1-2 m water at both stations. Substrate in both areas consists of fine sand, with abundant rocks in station 2.

Day-night ring sampling

We sampled crayfish at two depths during the day and at night to monitor diel changes in activity and depth distribution. We used 0.5 or 1.0 m^2 metal sampling rings to obtain random samples of crayfish (Capelli 1975, Stein 1975). Rings tossed in the air along a given depth contour sank to the lake bottom and SCUBA divers collected all crayfish within the ring. Night samples were made with the aid of underwater flashlights. Sampling was done on three dates in 1974, at station 1 on 2 August and 4 September and station 2 on 23 August. Ten ring tosses were made at each of two depths (approximately 1 and 3 m) during the afternoon (1400-1600 CST) and soon after dusk (1900-2230 CST).

Crayfish that were exposed (most of body visible) and hidden (most of body under cover of sand, rocks, aquatic vegetation, detritus, etc.) were collected separately, sexed, and their carapace lengths measured to the nearest 0.1 mm with vernier calipers.

Because sample sizes were small, sampling dates were combined for analysis of results. Three-way contingency tables were computed using factors of carapace length (<20.0, 20.0-29.9, 30.0-39.9, >40.0 mm), location (hidden and exposed), depth (1 and 3 m), and time of day (day and night). I tested the null hypothesis of independence between each pair of factors and the null hypothesis of lack of interaction among each three-way combination of factors. In addition, I made pair-wise tests of independence and a three-way test of interaction among factors of sex (male and female adults), time, and location. The latter tests were made for adults only, since young-of-year crayfish were not sexed. The G-statistic (which has a distribution approximating X^2) was used to test significance since it is more easily computed than X^2 and usually produces more exact results (Sokal and Rohlf 1969).

Diel collections

Three 24-hr field collections were made to quantify diel changes in the weight of crayfish stomach contents and to determine the importance of different food types in the crayfish diet. Sampling conditions for the 24-hr collections are given in Table 2. Collections were made by hand using SCUBA in 1-3 meters of water, and a maximum collecting time was established of 30 minutes per sample. In June, we attempted to collect equal numbers of male and female adults but did not collect

Table 2. Sampling information for three diel collections in Lower Sugarbush Lake, Vilas County, Wisconsin, during 1974. All times are CST. Temperatures are approximate surface water averages during each 24-hr period. Number per sample represents the goal that was set prior to each collection rather than the actual numbers caught.

Date and time	Station	Sample interval	Number/ sample	Temp.	Sunrise	Sunset
26 June (0700) to 27 June (0500)	1	2 hr	10♂, 10♀	20°C	0409	1955
4 Oct (1500) to 5 Oct (1100)	2	4 hr	10 exposed, 10 hidden	11°C	0603	1733
15 Nov (1500) to 16 Nov (1100)	2	4 hr	10 exposed, 10 hidden	4°C	0654	1702

animals with respect to location (hidden or exposed). Results from day-night ring sampling and informal behavioral observations suggested that differences in location may be important in evaluating feeding activity, and that the "random" hand collections used in diel sampling provide a potential bias since percentages of hidden and exposed crayfish collected may not be representative of the percentages in the actual population. In October and November, therefore, hidden and exposed adults were collected by different divers and analyzed separately. October and November collections were made at station 2 because crayfish were found to be more abundant than at station 1, making collections more efficient.

Crayfish were frozen on dry ice in the field immediately after each sampling period (except in November, when air temperatures were low enough to freeze crayfish within a few minutes) and stored frozen in the laboratory. Individuals were thawed prior to dissection, and the sex, carapace length, and molt condition (hard or soft exoskeleton) were recorded. Intact stomachs were removed, the contents emptied into a large watch glass, and any sand separated from the food material by rinsing with distilled water and decanting. Contents were then examined under a dissecting microscope, and the presence of recognizable food items recorded. Stomach contents and crayfish were dried separately at 70-80° C to constant weight and weighed to the nearest 0.1 mg (stomach contents) or 10 mg (crayfish).

Stomach fullness for each crayfish was calculated as:

$$P = (Sact/Smax),$$

where P= proportion fullness, Sact= actual dry weight of stomach contents, and Smax= maximum stomach capacity for a crayfish with a given carapace length. This allowed direct comparisons of the amount of food in stomachs of animals of different sizes, eliminating size-related differences in weight of food expressed as a percentage of body weight. Carapace length is thought to be a better measure for estimating relative stomach capacity than body weight, since the latter is greatly influenced by variations due to missing and regenerating appendages and to sexual dimorphism in chelae size.

To determine Smax, five size groups of O. rusticus (Table 3) were placed into five separate flow-thru aquaria (water from Trout Lake, maintained at 22.5 ± 0.5° C), starved for 48 hours, then allowed to feed on frozen brine shrimp ad libitum for 1 hour. Previous observations indicated that 1 hour was sufficient for crayfish to feed to satiation. Crayfish were then frozen and their stomachs later dissected as described above for animals collected in the field. No significant difference existed between weights of stomach contents of male and female crayfish, so the maximum stomach contents (g dry wt) from each group was used to calculate a regression of log weight vs. log carapace length. The resulting equation was used to calculate Smax.

Twelve molting crayfish with soft exoskeletons were found in June. All had empty stomachs and were excluded from further data analysis since the behavior of crayfish is markedly different during ecdysis (Norton 1942, Bovbjerg 1953). Frequency histograms of proportion stomach fullness were made for each of the 12 sampling times in June. Separate histograms were made for hidden and exposed crayfish for each of the six sampling times in October and November. Means and 95% confidence limits

Table 3. Size groupings of *O. rusticus* used in *ad libitum* feeding experiment for determination of maximum stomach capacity.

Carapace length (mm)				
Mean	Range	Males	Females	Total
45.1	44.5-45.5	4	1	5
34.9	34.5-35.5	5	0	5
25.2	24.6-25.9	5	5	10
14.3	13.3-15.8	2	2	4
11.6	10.2-12.9	2	2	4
Total		18	10	28

were calculated for the data in each histogram. Stomach fullness and number of crayfish with empty vs. not empty stomachs ("stomach emptiness") were treated as dependent variables and were tabulated for each date according to factors of time of day, sex, carapace length, and location (in October and November). Each of these factors was tested for significant effects on stomach fullness using the Kruskal-Wallis one-way analysis of variance (Siegal 1965). Two- and three-way interactions were tested using nonparametric analysis of variance (Wilson 1956). For the above tests, I used NPAR, a statistical computer program developed at Michigan State University and provided by the Social Science Data and Program Library Service, University of Wisconsin-Madison. Tests for significance of the above factors on stomach emptiness were made using the G-statistic calculated from three-way contingency tables. In calculations of G-values, day sample times were combined and night sample times combined. Thus, only two levels of time (day and night) were used in tests on stomach emptiness. For analysis of variance tests, sample times were kept separate (12 levels of time in June, 6 in October and November).

During stomach analysis, counts were made of whole animals found in each stomach. Animal parts were identified as completely as was practical. For presentation of results, food types were classified into categories of plant material, insect order (Ephemeroptera, Plecoptera, Odonata, Tricoptera, Coleoptera, Diptera), crustacean order (Cladocera, Copepoda, Ostracoda, Amphipoda, Decapoda), molluscan class (Gastropoda, Pelecypoda), fish parts, and unidentifiable animal material. Frequency of occurrence (percentage of stomachs containing a given item on each date excluding empty stomachs) was calculated for each of these categories and for an additional category consisting of all animal material. I used three-way contingency tables to test the significance of sampling date, crayfish size, and sex on the presence of the four most abundant food categories (plant material, animal material, Diptera, and Ephemeroptera).

RESULTS

Day-night ring sampling

Numbers of crayfish at 1 and 3 m depths did not differ between day and night, among different sized crayfish, nor between hidden and exposed animals (Table 4). A higher percentage of crayfish at 1 and 3 m were exposed at night than during the day, and this day-night difference was greater at 1 m than at 3 m (Table 5). This three-way interaction was statistically significant (Table 4).

A higher percentage of small crayfish (<20.0 mm) were hidden than observed for larger crayfish (Table 6). However, the percentages of hidden crayfish in the smaller two size groups are lower at night and higher during day than in larger animals. In addition, crayfish less than 20 mm comprised a much higher percentage (60%) of the total number of crayfish found during the day than they did at night (39%); the reverse was true for crayfish in the 30-40 mm size class (6% during the day, 26% at night). Statistical results are summarized in Table 4.

In adults, a significant interaction existed among factors of sex, location, and time of day ($G = 10.300$, $p < 0.01$). The percentage of adult males exposed changed very little at the two sampling times; more were exposed than hidden at both times (Table 7). The percentage of females exposed, however, changed from 10% during the day to 75% at night.

Ad libitum feeding and diel collections

The regression of log weight stomach contents vs. log carapace length calculated from *ad libitum* feeding provided a good fit in relation

Table 4. Summary of results from two-way independence and three-way interaction tests among factors of size (four categories of carapace length), time (day or night), depth (1 or 3 m), and location (hidden or exposed). G-values based on contingency tests using combined data from day-night sampling on three dates. Total n=94. (** prob < 0.01, * prob < 0.05)

Hypothesis tested	G	df
Depth x time independence	0.152	1
Depth x size independence	2.762	3
Depth x location independence	0.006	1
Location x time independence	18.232**	1
Location x size independence	28.472**	3
Size x time independence	12.450**	3
T x L x D interaction	7.540**	1
T x S x L interaction	16.590**	10
T x S x D interaction	4.868	3
S x L x D interaction	1.780	3

Table 5. Percentage of crayfish hidden and exposed at two depths during day and night sampling. Numbers of crayfish in each cell are shown in parentheses.

	Depth					
	1 meter		3 meter		Total	
Location	Time		Time		Time	
	Day	Night	Day	Night	Day	Night
Hidden	90 (17)	13 (2)	67 (24)	42 (10)	75 (41)	31 (12)
Exposed	10 (2)	87 (13)	33 (12)	58 (14)	25 (14)	69 (27)

Table 6. Percentage of crayfish of four size classes hidden and exposed during day and night sampling. Number of crayfish in each cell is shown in parentheses.

Size	Location	Time		
		Day	Night	Total
20 mm	hidden	97 (32)	47 (7)	81 (39)
	exposed	3 (1)	53 (8)	19 (9)
	total	100 (33)	100 (15)	100 (48)
20-30 mm	hidden	56 (9)	0 (0)	30 (9)
	exposed	44 (7)	100 (14)	70 (21)
	total	100 (16)	100 (14)	100 (30)
30-40 mm	hidden	0 (0)	50 (5)	38 (5)
	exposed	100 (3)	50 (5)	62 (8)
	total	100 (3)	100 (10)	100 (13)
40 mm	hidden	0 (0)	0 (0)	0 (0)
	exposed	100 (3)	0 (0)	100 (3)
	total	100 (3)	0 (0)	100 (3)

Table 7. Percentages of male and female adults exposed and hidden during day and night sampling. Number of crayfish in each cell is shown in parentheses.

Location	Sex			
	Males		Females	
	Day	Night	Day	Night
Hidden	40 (8)	36 (5)	90 (18)	25 (6)
Exposed	60 (12)	64 (9)	10 (2)	75 (18)
Total	100 (20)	100 (14)	100 (20)	100 (24)

to maximum weights of stomach contents of animals collected from field collections (Figure 2).

Food was present in most crayfish at all times but general trends in stomach fullness are evident. Stomachs were fuller at night on all dates, and exposed animals collected in October and November tended to have fuller stomachs than hidden animals (Figure 3).

Trends are more visible in graphs of mean stomach fullness and percentage of animals with empty stomachs (Figures 4 and 5). Although crayfish were observed feeding during the day in June, stomach contents indicated maximum feeding activity at night (Figure 4). Stomachs contained significantly more food late in the night (2300-0300) than early in the night (1900-2100). Except during early morning hours when all stomachs sampled contained food, 4-16% of stomachs were empty. An increase in fullness after dawn (0700-1100) may represent a second peak in feeding, but it is not statistically significant.

Exposed crayfish in October showed a pattern similar to crayfish collected in June (Figure 5). Fullness increased after dark, although the rise was not as marked as that in June. In October, none of those exposed at night had empty stomachs. Hidden crayfish had opposite trends, a decrease in fullness and an increase in percentage empty occurred at dusk. The difference between exposed and hidden crayfish in proportion fullness and percentage crayfish with empty stomachs was largest after dusk.

In November, feeding was apparently limited to the night, as no animals were exposed during day. For both hidden and exposed animals, fullness increased and percentage empty decreased during the night.

Figure 2. Weight of stomach contents vs. carapace length for crayfish collected in the field during three diel collections (n=501) and for crayfish fed *ad libitum* in the laboratory (n=28). Regression representing maximum stomach capacity calculated from *ad libitum* data (r^2=0.996).

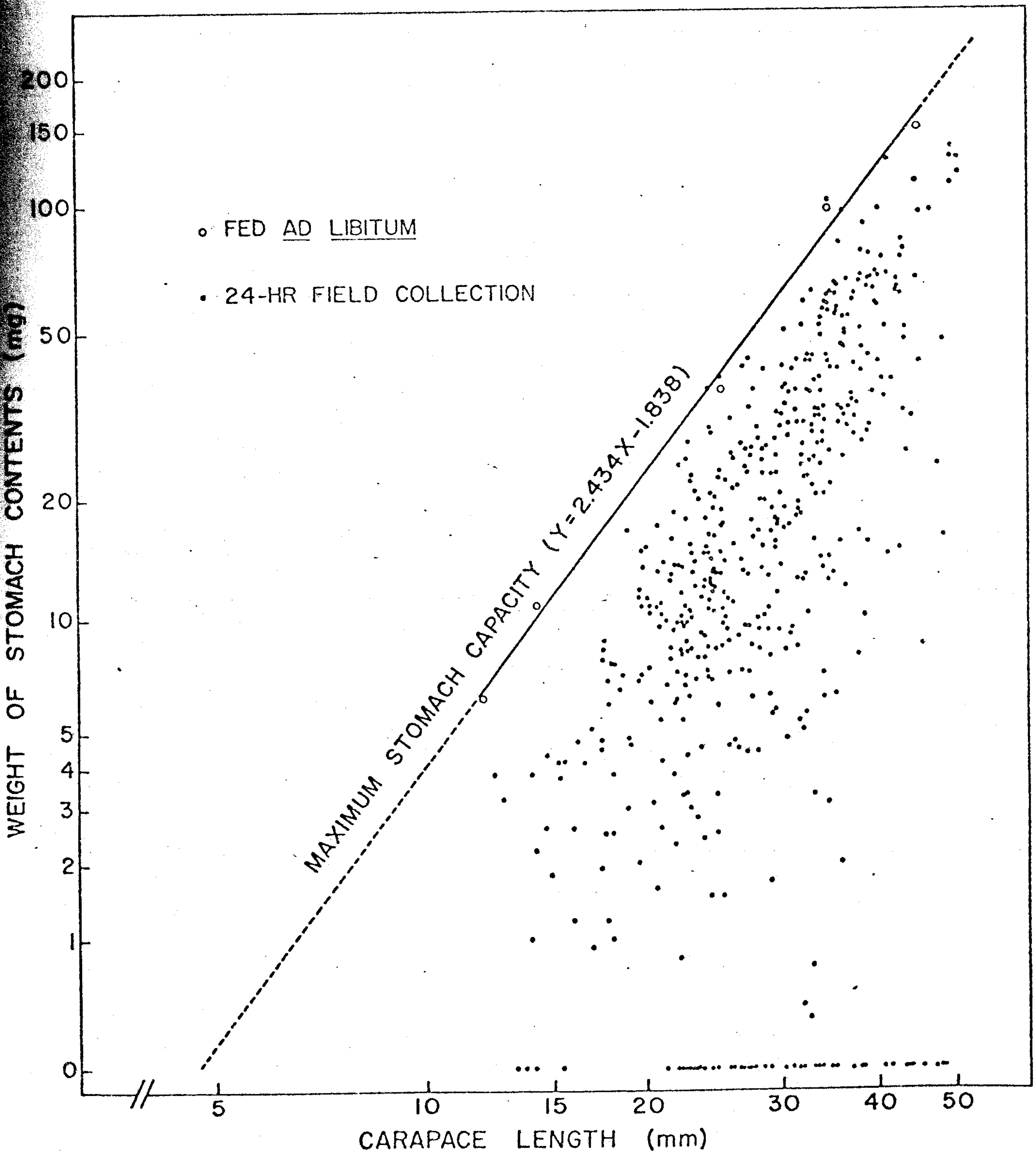

o FED AD LIBITUM
• 24-HR FIELD COLLECTION
MAXIMUM STOMACH CAPACITY (Y=2.434X-1.838)
WEIGHT OF STOMACH CONTENTS (mg)
200
150
100
50
20
10
5
4
3
2
1
0
5
10
15
20
30
40
50
CARAPACE LENGTH (mm)

Figure 3. Frequency histograms of stomach fullness for 12 sampling times in June (a) and for hidden (——) and exposed (---) crayfish from 6 sampling times in October and November (b).

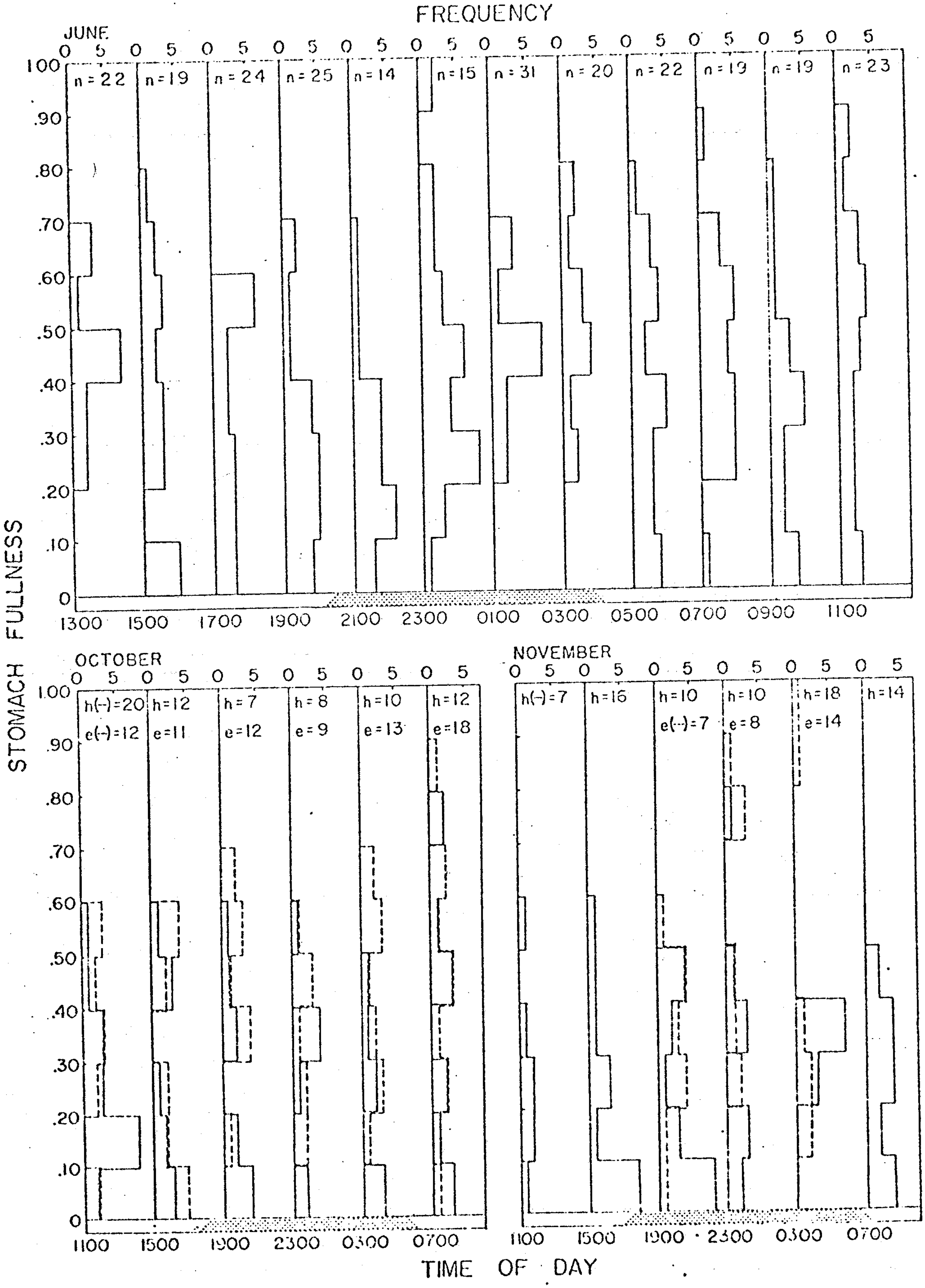

FREQUENCY
JUNE
0 5 0 5 0 5 0 5 0 5 0 5 0 5 0 5 0 5 0 5 0 5 0 5
n = 22
n = 19
n = 24
n = 25
n = 14
n = 15
n = 31
n = 20
n = 22
n = 19
n = 19
n = 23
1.00
.90
.80
.70
.60
.50
.40
.30
.20
.10
0
1300
1500
1700
1900
2100
2300
0100
0300
0500
0700
0900
1100
STOMACH FULLNESS
OCTOBER
0 5 0 5 0 5 0 5 0 5 0 5
h(-)=20
e(-)=12
h=12
e=11
h=7
e=12
h=8
e=9
h=10
e=13
h=12
e=18
1100
1500
1900
2300
0300
0700
NOVEMBER
0 5 0 5 0 5 0 5 0 5 0 5
h(-)=7
h=16
h=10
e(-)=7
h=10
e=8
h=18
e=14
h=14
1100
1500
1900
2300
0300
0700
TIME OF DAY

Figure 4. Mean stomach fullness (a) and percentage empty (b) vs. time for June collection. Vertical bars are 95% confidence intervals.

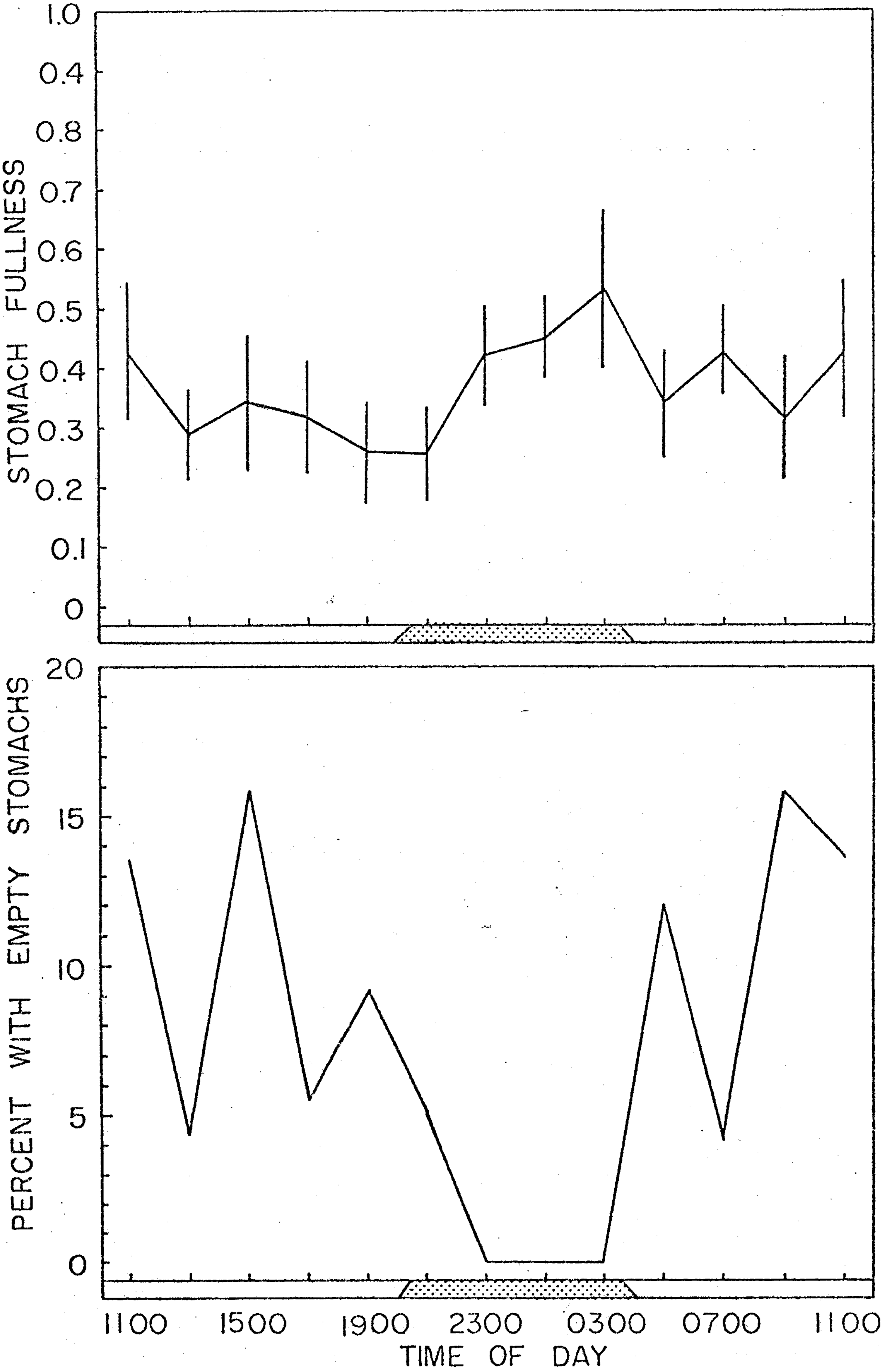
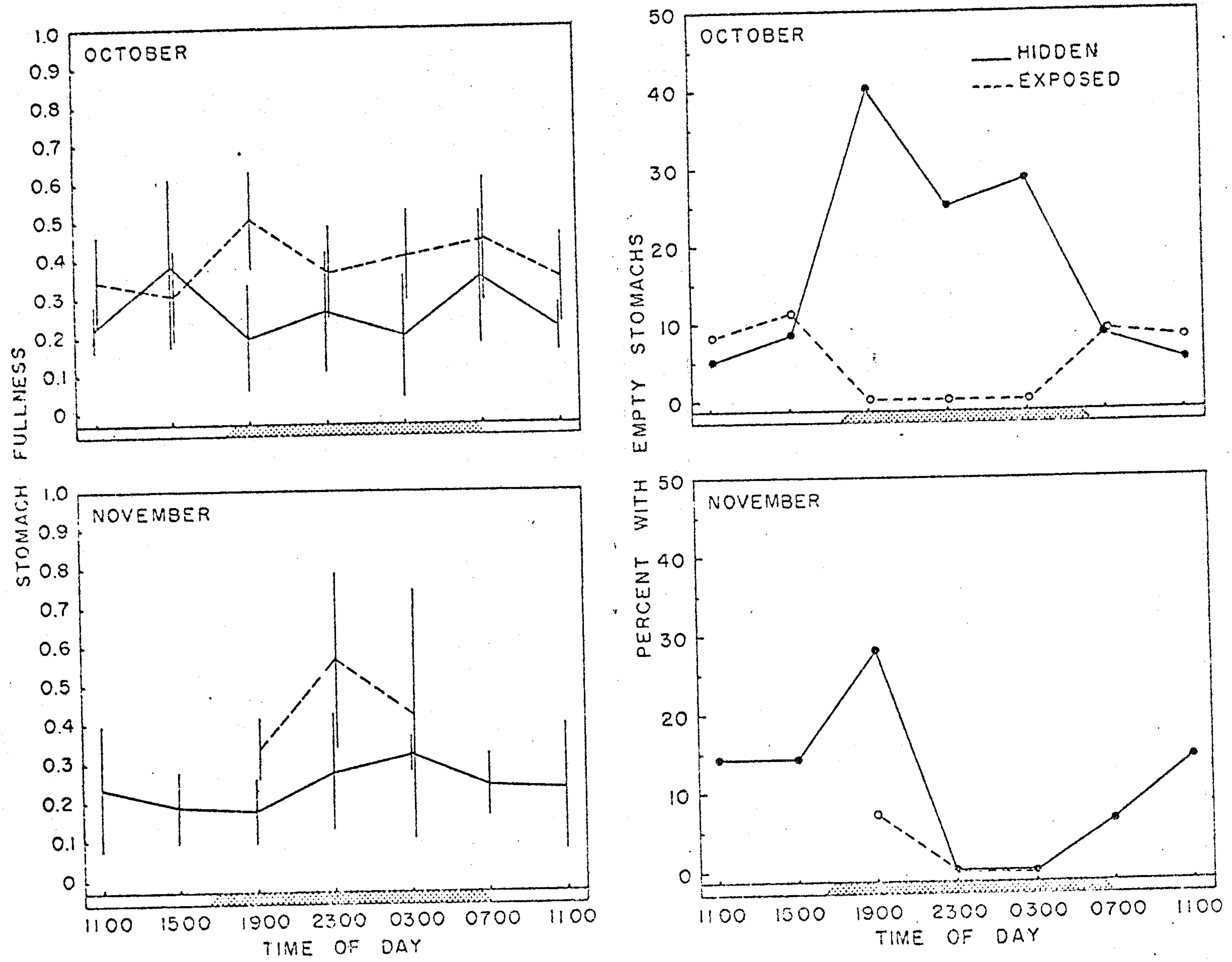

1.0
0.4
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
STOMACH FULLNESS
20
15
10
5
0
PERCENT WITH EMPTY STOMACHS
1100
1500
1900
2300
0300
0700
1100
TIME OF DAY

Figure 5. Mean stomach fullness (a) and percentage empty (b) for October and November collections. Vertical bars are 95% confidence intervals.


OCTOBER
NOVEMBER
OCTOBER
HIDDEN
EXPOSED
NOVEMBER
STOMACH FULLNESS
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
PERCENT WITH EMPTY STOMACHS
50
40
30
20
10
0
1100
1500
1900
2300
0300
0700
1100
TIME OF DAY

Hidden crayfish showed a gradual decrease in fullness and an increase in percentage empty during the day.

Mean fullness and percentage empty are summarized for factors of sex, size, date, and location in Table 8, and results of statistical analysis of time, sex, size, and location are in Table 9. Main effects of time and crayfish size on both proportion fullness and stomach emptiness were significant in June. In addition, there was a significant interaction effect on proportion fullness among factors of time, size, and sex (Figure 6; to clarify relationships, successive 2-hr samples are averaged and the smallest and largest size categories, which had small sample sizes, are not shown). Stomach fullness of males changed little throughout the 24-hr collecting period and did not differ greatly between different size groups; feeding appeared to peak at night in females, but this peak was most pronounced in the 30-40 mm size category.

Location had a significant effect on stomach fullness in October and November and on emptiness in October. Interactions were significant in October for time, location, and emptiness (Figure 5a) and for time, location, sex, and fullness (Figure 7). Females exhibited greater variation in fullness through time than did males. Hidden females showed a significant increase in stomach fullness at 0700, while fullness of hidden males decreased.

Stomach analysis

The most common food, plant material, occurred in more than 90% of animals sampled in each month (Table 10). Terrestrial leaf fragments and unrecognizable vascular tissue comprised the bulk of the plant mat-

Table 8. Mean fullness and percentage of animals with empty stomachs for crayfish of different sex and size on three diel collection dates. Hidden and exposed animals are considered separately in October and November.

	June			October						November					
				Hidden			Exposed			Hidden			Exposed		
Sex	Mean fullness	% empty	n	Mean fullness	% empty	n	Mean fullness	% empty	n	Mean fullness	% empty	n	Mean fullness	% empty	n
Males	0.38	8.0	100	0.25	9.4	32	0.39	5.3	38	0.21	15.9	44	0.39	8.3	12
Females	0.36	6.5	153	0.29	21.6	37	0.39	5.4	37	0.26	6.5	31	0.43	0.0	17
Size (mm)															
20.0	0.42	0.0	2	0.28	8.2	11	0.51	0.0	4	0.24	6.5	31	0.62	0.0	3
20-30	0.30	7.0	57	0.27	13.0	54	0.39	6.7	60	0.23	15.0	40	0.40	4.0	25
30-40	0.40	4.0	150	0.27	50.0	4	0.36	0.0	10	0.14	25.0	4	-	-	0
40	0.35	18.2	44	-	-	0	0.47	0.0	1	-	-	0	0.34	0.0	1
Total	0.37	7.1	253	0.27	15.9	69	0.39	5.3	75	0.23	12.0	75	0.42	3.5	29

Table 9. Summary of results of testing factors of time (sampling hour for proportion fullness tests, day-night for emptiness tests), sex (male or female), size (four size groups of carapace length), and location (hidden or exposed) on dependent variables of proportion stomach fullness and percentage empty. Main effects on proportion fullness were tested using Kruskal-Wallis one-way analysis of variance, interaction terms using a 2- and 3-way nonparametric analysis of variance. All effects on emptiness were tested using G-values. (** prob < 0.01, * prob < 0.05)

	June				October				November			
	Proportion fullness		Emptiness		Proportion fullness		Emptiness		Proportion fullness		Emptiness	
Main effects	H	df	G	df	H	df	G	df	H	df	G	df
Time	31.057**	11	7.932**	1	4.926	5	1.038	1	9.308	5	0.094	1
Sex	0.567	1	0.200	1	0.013	1	1.596	1	2.866	1	3.282	1
Size	8.909*	3	8.764**	3	0.693	3	0.624	3	2.748	3	1.714	3
Location	-		-		12.911**	1	4.458*	1	11.718**	1	2.014	1
Interaction effects	X^2	df	G	df	X^2	df	G	df	X^2	df	G	df
TS	21.972	33	3.624	3	5.223	15	7.802	3	7.801	15	1.106	3
TG	3.775	11	1.540	1	3.846	5	1.336	1	4.041	5	1.624	1
TL	-		-		7.107	5	11.274**	1	3.100	5	-	
LG	-		-		0.975	1	0.400	1	0.002	1	0.400	1
LS	-		-		0.319	3	4.128	1	0.000	3	0.480	1
GS	7.454	3	1.914	3	3.288	3	0.586	3	3.243	3	4.676	3
TLG	-		-		17.553**	5	-		7.333	5	-	
TLS	-		-		17.742	15	-		6.885	15	-	
TSG	61.056**	33	-		14.649	15	-		20.132	15	-	
SLG	-		-		4.556	3	-		2.587	3	-	

Figure 6. Relation of stomach fullness to time of day in male and female crayfish of different sizes collected in June diel sampling. Horizontal lines represent averages of successive 2-hr sampling times. Solid line 20-30 mm carapace length; dashed line 30-40 mm carapace length. Sample sizes are given for each line.

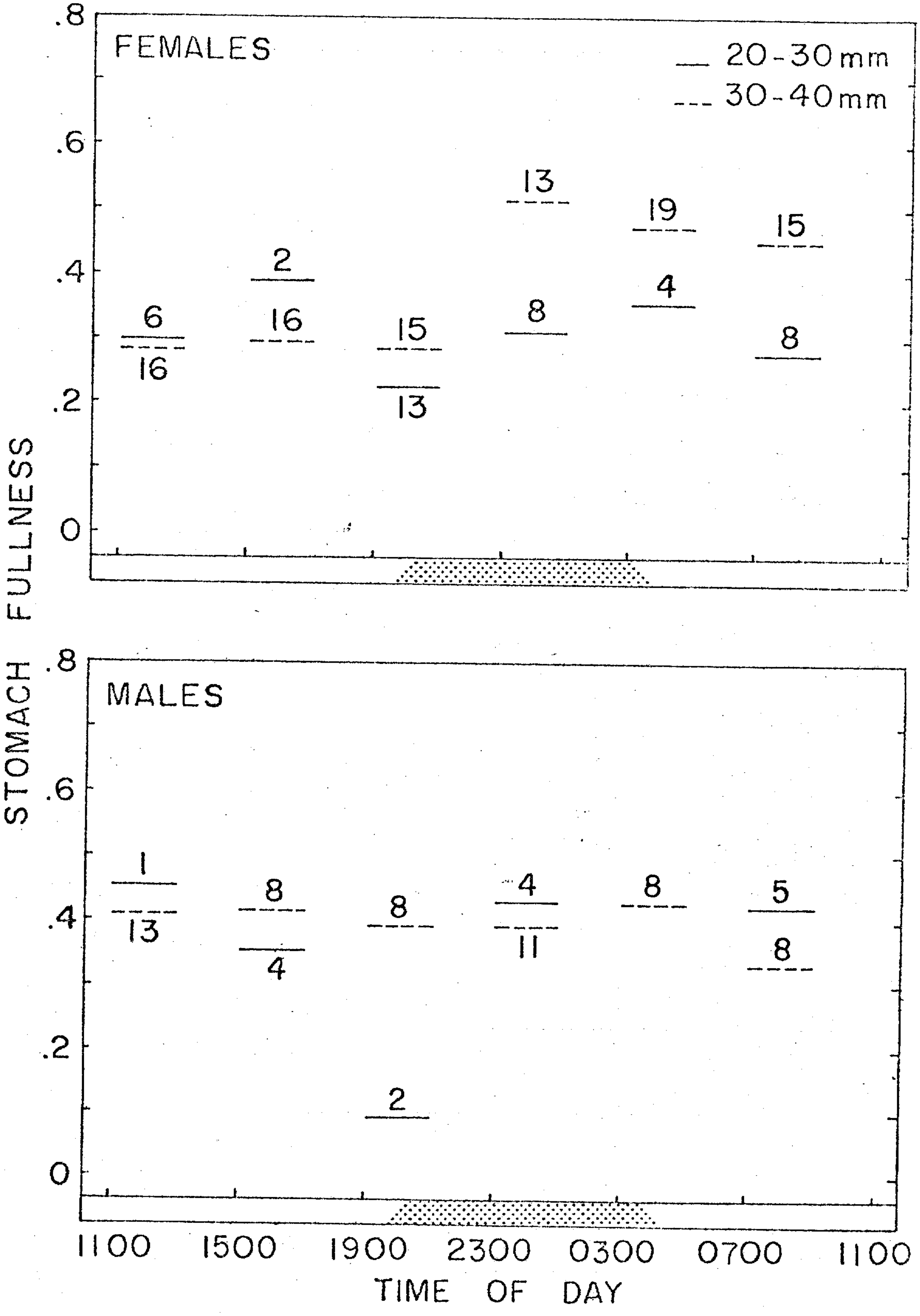

FEMALES
— 20-30mm
--- 30-40mm
.8
.6
.4
.2
0
6
16
2
16
15
13
13
8
19
4
15
8
MALES
.8
.6
.4
.2
0
1
13
8
4
8
2
4
11
8
5
8
STOMACH FULLNESS
1100
1500
1900
2300
0300
0700
1100
TIME OF DAY

Figure 7. Relation of stomach fullness to time of day in male and female crayfish found hidden and exposed during October diel sampling. Vertical lines represent 95% confidence intervals.

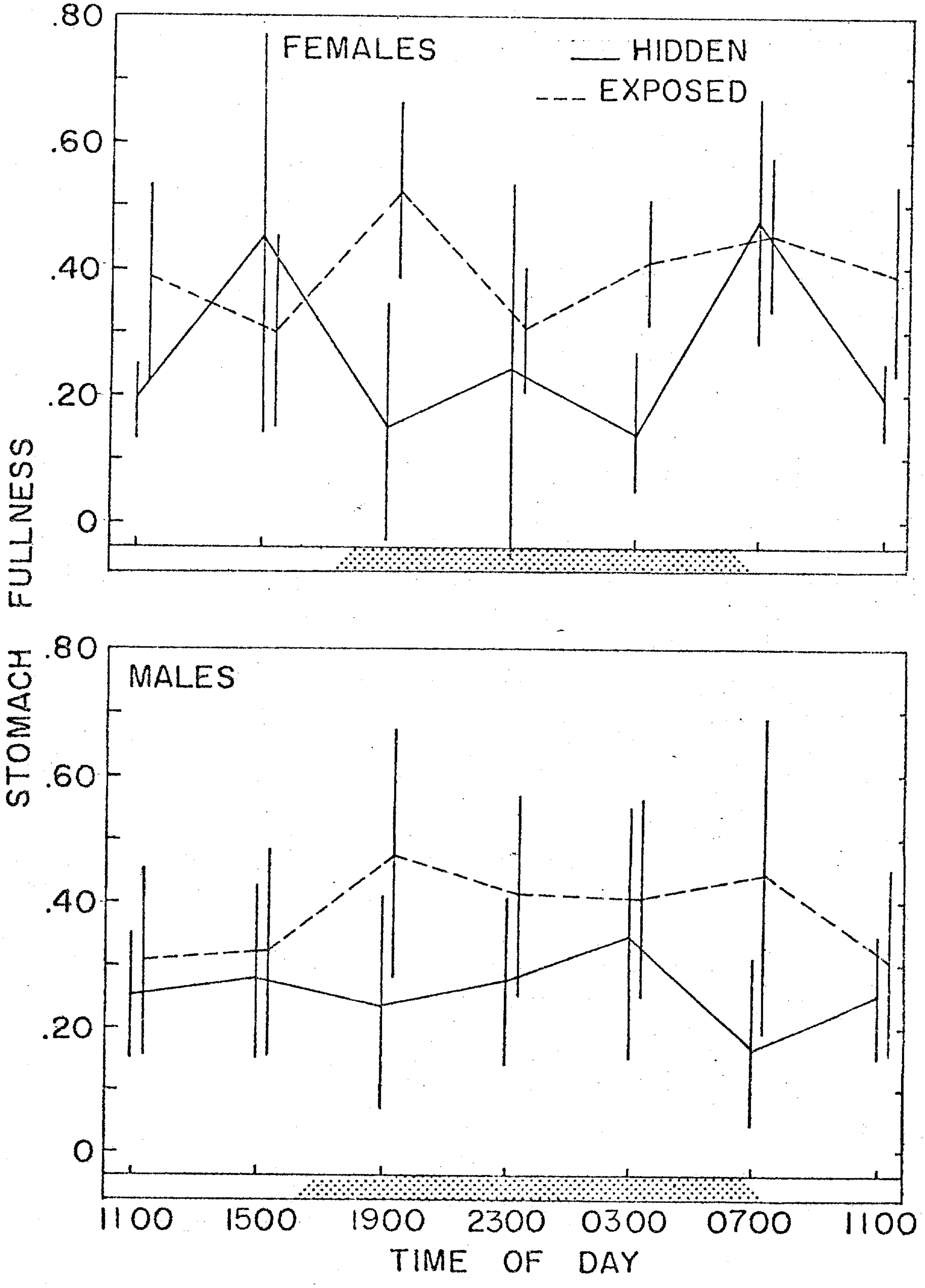

.80
.60
.40
.20
0
FEMALES
HIDDEN
EXPOSED
STOMACH FULLNESS
.80
.60
.40
.20
0
MALES
1100
1500
1900
2300
0300
0700
1100
TIME OF DAY

Table 10. Frequency of occurrence of each food category in crayfish stomachs from three collection dates.

Food type	Date			
	June n=237	October n=128	November n=94	Total n=459
Plant material	99.6	93.0	90.4	95.9
Animal material	77.2	81.3	83.0	79.5
unid. animal material	11.0	19.5	7.5	12.6
Insecta				
Ephemeroptera	45.2	49.2	67.0	50.8
Plecoptera	3.0	0.0	0.0	1.5
Odonata	0.4	2.3	0.0	0.9
Tricoptera	9.3	3.1	3.2	6.3
Coleoptera	0.0	0.0	2.1	0.4
Diptera	11.8	8.6	9.6	10.5
unid. insect	0.4	0.0	0.0	0.2
Crustacea				
Cladocera	0.4	3.1	18.1	4.8
Copepoda	0.0	2.3	9.6	2.6
Ostracoda	6.8	2.3	3.2	4.8
Amphipoda	3.4	0.0	10.6	3.9
Decapoda	6.8	7.8	3.2	6.3
unid. crustacean	4.6	4.7	3.2	4.4
Mollusca				
Gastropoda	3.4	1.6	0.0	2.2
Pelecypoda	0.8	0.8	0.0	0.7
unid. mollusca	2.1	0.0	0.0	1.1
Fish	1.7	1.6	0.0	1.3

erial, but filamentous green algae (Nitella) and fragments of vascular hydrophytes could be recognized in a few cases.

Animal material was present in 80% of the crayfish. Ephemeropterans were by far the most important animal food (frequency of occurrence, 51%); the genus Ephemera was the most common mayfly but Hexagenia, Stenonoma, and Caenis were also present. Dipterans (Chironomidae) were the second most common animal food (10%). Other recognizable animal foods included plecopterans (1.5%), odonates (0.9%), tricopterans (Oecetis, 6.3%), coleopterans (0.4%), cladocerans (4.8%), copepods (2.6%), ostracods (4.8%), amphipods (3.9%), decapods (crayfish, 6.3%), gastropods (2.2%), pelecypods (0.7%), and fish (scales and bones of Percidae, 1.3%).

Size, sex, and date had significant effects on food composition (Table 11). The percentage containing plant material increased significantly with size of crayfish for all dates combined but not for individual dates (Figure 8).

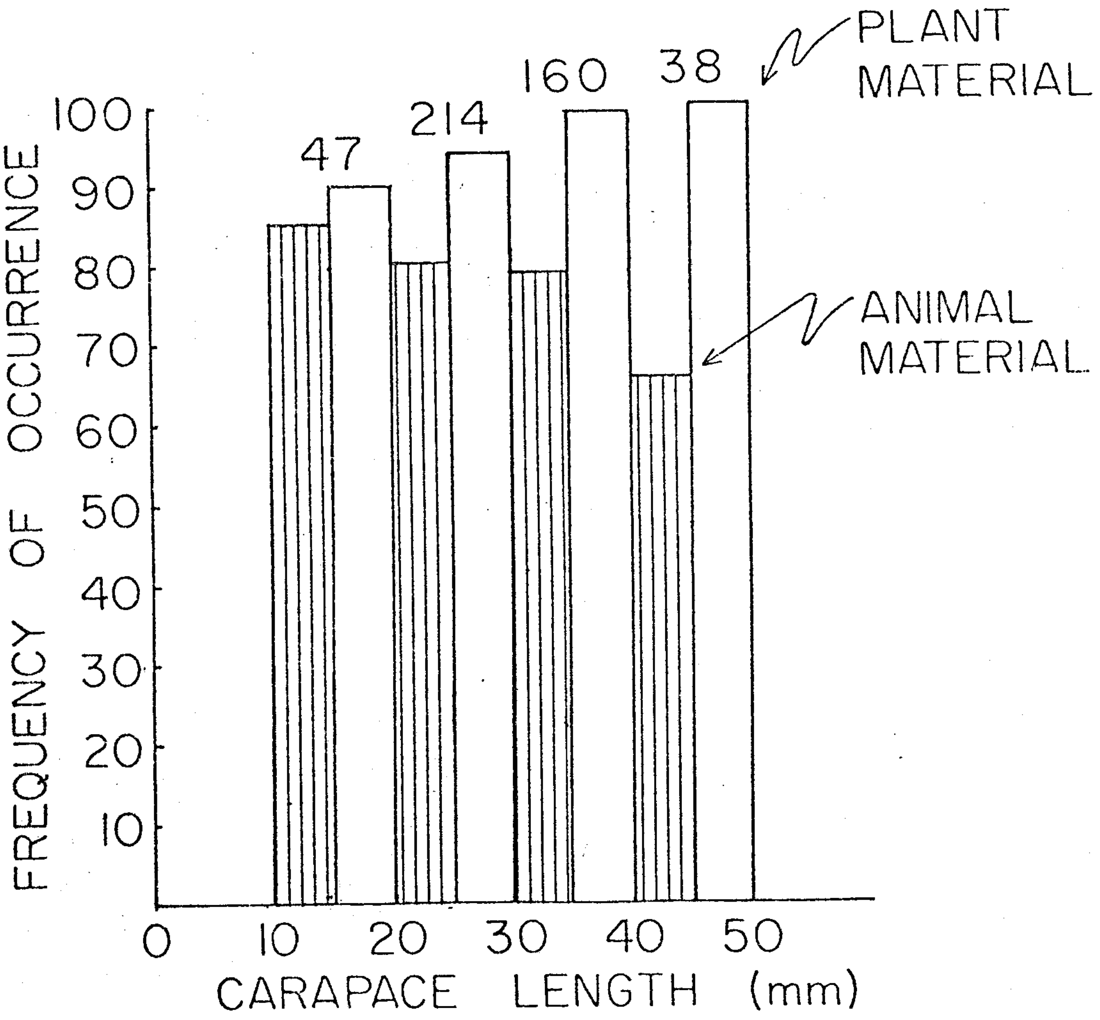
Since the average size of crayfish collected in June was greater than those collected in October and November (see values for n in each of the four size classes in Table 8), I tested the effect of size X date interaction on the presence of plant material. Because the interaction G-value was negative, it was necessary to perform an alternative set of partitions (Sokal and Rohlf 1969). This analysis (Kullback 1959) revealed that the effects of date on the presence of plant material (Table 11), can be explained solely on the basis of differences in size on the three dates. Size differences also appeared related to the percentage of stomachs containing animal material (Figure 8), but this trend was not significant.

Table 11. Summary of statistics for effects of sex, size, and date on presence of plant material, animal material, Ephemeroptera, and Diptera in crayfish stomachs. (**prob < 0.01, *prob < 0.05)

Food type	Date							
	June		October		November		Combined	
Effect	G	df	G	df	G	df	G	df
Plant material								
Sex	1.014	1	3.152	1	3.478	1	0.050	1
Size	2.972	3	1.454	3	1.542	3	12.400**	3
Date	-		-		-		20.808[1]	2
Animal material								
Sex	1.998	1	5.260*	1	0.207	1	4.638*	1
Size	3.450	3	3.136	3	4.150	3	5.322	2
Date	-		-		-		1.716	2
Ephemeroptera								
Sex	0.148	1	5.320*	1	0.006	1	1.485	1
Size	0.968	3	3.820	3	2.870	3	2.952	3
Date	-		-		-		13.274**	2
Diptera								
Sex	0.002	1	0.906	1	0.990	1	0.556	1
Size	4.962	3	2.967	3	1.987	3	0.830	3
Date	-		-		-		1.032	2

[1] This is significant at the 0.01 level; however, effects can be explained solely on the basis of differences in size on the three dates (see text).

Figure 8. Percentage of crayfish stomachs of four size groups containing plant and animal material. Numbers over bars indicate sample size.


PLANT MATERIAL
ANIMAL MATERIAL
47
214
160
38
FREQUENCY OF OCCURRENCE
100
90
80
70
60
50
40
30
20
10
0
10
20
30
40
50
CARAPACE LENGTH (mm)

The frequency of occurrence of animal material was significantly higher in males than in females in October (89% and 73%, respectively) and for all dates combined (84% and 76%). In October, the presence of mayflies differed significantly between males and females. Mayflies were present in 59% of the males in October but only 39% of the females. The percentage of animals containing mayflies differed significantly on the three sampling dates. Percentages for June, October, and November were 45, 49, and 67, respectively. The percentage of crayfish containing dipterans did not differ significantly with either size, sex, or date.

DISCUSSION

The concept of feeding strategy has recently been developed as a characteristic subject to optimization through natural selection (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971). Although sometimes simply defined as the choice of taking or ignoring a particular food item encountered (Pulliam 1974), feeding strategy also includes aspects of the relation of feeding rate to food density (Holling 1961), timing of feeding activity, and extent of foraging range (Schoener 1971). Below, I discuss my results as they relate to three key aspects of foraging strategy: diet, foraging period, and foraging space.

Diet

Stomach analyses showed that O. rusticus consumes a wide range of food types, a result consistent with other crayfish studies (Creaser 1934, Tack 1941, Norton 1942, Mason 1963, Abrahamsson 1966, Minshall 1967, Prins 1968, Dean 1969, Capelli 1975). Although crayfish can therefore be considered food generalists (Schoener 1971), feeding does involve some degree of food selection (Mason 1963, Alan Covich, Washington University, personal communication). Males of O. rusticus eat more animal material than females; large crayfish eat more plant material than small ones (Table 11, Figure 8). The shift from an animal to a plant diet as crayfish grow larger has been reported previously (Creaser 1934, Mason 1963, Abrahamsson 1966). The decrease in percent occurrence of animal food with increase in crayfish size seen in O. rusticus (Figure 8) was not significant, but the use of presence-absence indices of feeding activity reduces the validity of testing such differences.

Differences in crayfish diets could result from variation in costs involved in securing different food items. For example, small crayfish might be more efficient than large crayfish as predators on small active prey (Abrahamsson 1966). Differences in energetic requirements could explain dietary shifts: an increase in herbivory in larger animals could result from a reduction in protein requirements or a need to generalize the diet in order to meet increased energy requirements (Schoener 1971).

Explanations of sex- and size-related differences in crayfish require nutritional as well as energetic (caloric) information. Addition of vegetable matter to the diet of brown shrimp (<u>Penaeus aztecus</u>) increased protein level and decreased vegetable matter in food (Venkataramiah <u>et al</u>. 1975).

Differences in percent occurrence of mayflies in stomachs on the three dates (Table 10) may reflect changes in prey abundance or changes in feeding strategy due to climatic (temperature and photoperiod) differences. Peterson grab samples taken on dates of diel collections contained approximately equal numbers of mayfly nymphs in October and November, but samples were not taken in June. Climatic changes could affect feeding strategy by affecting energy requirements, efficiency of prey capture, and activity patterns of both crayfish and prey.

Variation in diet probably reflects different optimal foraging strategies associated with sex, size, and climate differences. However, explanation of these differences requires more detailed information on nutritional and energetic requirements of crayfish, and costs and gains of food items, and the relation of diet to food availability.

Foraging period

Field measurements of activity

Most studies on crayfish activity have been conducted under controlled laboratory conditions (Roberts 1944, Rice and Armitage 1974, Crawshaw 1974, Page and Larimer 1975, Capelli 1975); few have quantified activity patterns under natural conditions. Tack (1941) studied relative day and night activity of O. immunis in the field by comparing day and night trap catches and by counting numbers of crayfish seen active in a marked area during the day and at dusk. The validity of the two methods used to quantify activity in my study requires some discussion:

1. Day-night ring tosses. Activity in crayfish is associated with movement outside of cover (Tack 1941, Penn 1943, Roberts 1944). My observations on O. rusticus during day and night indicate that exposed animals are active, either feeding, moving slowly along the bottom using periopods in apparent search for food material, or stopping for short periods of grooming. During the mating season (fall, winter, and spring), some exposed animals can be observed copulating. Crayfish found under cover appear inactive, usually in a crouched position with appendages drawn close to the body. Location can therefore be used as a measure of general activity; but without measurements of feeding rate and percentage of time spent feeding in exposed animals, it only provides an indirect measure of feeding activity.

2. Diel collection. Stomach fullness depends not only upon feeding rate, but also upon digestion rate and length of time since last feeding. Without knowledge of these additional parameters, stomach fullness provides only a general measure of feeding activity and not a specific

measure of feeding rate.

Patterns of feeding activity

Diel differences in percentage animals exposed and in stomach fullness indicate that most activity in O. rusticus occurs at night, although the extent of nocturnal behavior varies with crayfish sex and size, and with differences in climate (temperature and length of day). Crayfish have been considered primarily nocturnal (Girard 1852, Huxley 1880, Ortmann 1906, Chidester 1908, 1912, Tack 1941, Roberts 1944, Crawshaw 1974, Capelli 1975), although diurnal activity has been reported in O. propinquus (Van Deventer 1937, Capelli 1975) and O. immunis (Tack 1941).

Crayfish feeding behavior can be viewed as successive periods of activity (crayfish exposed) and rest (crayfish hidden). Some of the variation in stomach fullness is associated with differences in sex and size (Table 9); however, a large proportion of the variation can only be explained by individual differences in patterns of activity and rest.

Photoperiod is an important factor controlling activity in crayfish under laboratory conditions (Roberts 1944, Rice and Armitage 1974, Crawshaw 1974, Page and Larimer 1972, 1975). Reduced light intensity at dusk is the most important stimulus for onset of activity in crayfish (Roberts 1944, Page and Larimer 1972, 1975), as well as in other decapods (Hagerman 1970, Honegger 1973, Lehmann et al. 1974). Variations in feeding patterns due to differences in crayfish sex or size, or due to seasonal changes probably reflect differential responses to zeitgebers. Small crayfish and females appear to respond to light-dark changes to a greater degree than large males. Since susceptibility and responsiveness to fish predation increases with decreasing crayfish size (Stein 1975), nocturnal behavior in small crayfish may be related to reduced fish predation at night.

Crayfish responsiveness to photoperiod appears to exhibit seasonal differences. Stomach fullness of hidden crayfish remains fairly constant throughout the night in October, but exhibits a gradual increase in November (Figure 5). This difference may be caused by a delay in the onset of feeding by a higher percentage of the population in October than in November. Further support for this is provided by differences in percentage of hidden animals with empty stomachs on the two dates (Figure 5). A high percentage of stomachs are empty throughout the night in October, but no stomachs are empty after the first night sample in November. Feeding in November is more synchronized than in June or October, occurring over a relatively short period at night. Seasonal change in the number of activity periods occurs in shrimp (Crangon vulgaris, Hagerman 1970) and in many other animals (Schoener 1971).

Patterns of feeding activity in crayfish can be explained at least partly in terms of energy requirements. Metabolism is higher in male than in female crayfish (Rice and Armitage 1974); thus, males may need to feed during the day to meet higher energy requirements. Similarly, reduced energy requirements at lower temperature could explain the lack of diurnal feeding in November.

Foraging space

Little quantitative information is available on the foraging range of crayfish. Crayfish are reported to migrate to shallow water during the night to feed (Crocker and Barr 1968). O. rusticus did not appear to exhibit this behavior, but more crayfish were exposed in shallow water than in deeper water at night (Tables 4 and 5). In addition, more small crayfish were found during the day than at night, and more large crayfish were found at night. Unless samples were size-biased due to reduced visibility at night, which I believe is unlikely, this suggests that crayfish migrate into deeper or shallower water than that sampled. Migrations could be related to changes in temperature with depth. When provided with a temperature gradient, O. immunis selects lower temperatures during the day than at night; daily movement into deeper, cooler waters may reduce predation and lower energy expenditure during periods of inactivity (Crawshaw 1974).

Vertebrate predators typically have larger home ranges than herbivores (Schoener 1971). Since stomach analyses indicate that male and small crayfish use predator tactics more often than do female and large crayfish, home ranges might be expected to be larger in the former. Baited traps catch a higher percentage of male and large crayfish than are present in the population (Capelli 1975, Lorman, unpublished data). This could reflect a wider foraging range for these animals than for females and small crayfish. However, my own observations on behavior of crayfish in the vicinity of baited traps suggest that aggressiveness also affects which crayfish are caught. Aggressiveness is influenced by sex and size of crayfish, males being dominant over females and large individuals over small individuals (Bovbjerg 1956, Stein 1975).

Evidence suggests that foraging crayfish differ in their use of space; however, a complete analysis of how these differences reflect maximization of fitness requires a knowledge of the temporo-spatial availability of food items (Schoener 1971).

Conclusions

As food generalists, crayfish directly interact with many other components of the community and possess a variety of mechanisms with which they can potentially structure the community (Figure 1). As detritivores crayfish affect energy flow through detrital pathways in two ways: (1) Detritus assimilated by crayfish is converted to a form readily available to other components of the community (e.g., fish predators). (2) Detrital particles ingested but not assimilated are reduced in size, thereby increasing the surface area available for colonization by decomposing micro-organisms. As herbivores, crayfish reduce the abundance of aquatic macrophytes, affecting members of the community that utilize macrophytes for shelter or food and changing the qualitative or quantitative nature of primary production. As carnivores, crayfish influence other community members through predation or competition.

The ability to feed on a wide variety of food types allows crayfish to be opportunistic, changing strategies to optimize foraging according to specific conditions. Since feeding patterns determine the qualitative and quantitative nature of exploitation of available food by the crayfish population, it is of interest to know how specific aspects of foraging strategy change in response to such factors as food availability, energy requirements, and predation pressure. Possible responses include changes in diet (type and breadth of food items), feeding period (length of feeding bouts and of intervals between bouts, timing of bouts in relation to photoperiod, and degree of synchrony of bouts among members of the population), and foraging space (extent of foraging movements).

Patterns observed in the diet and timing of feeding activity of *O. rusticus* reflect differences in responses between (1) male and female crayfish, (2) crayfish of different sizes, and (3) crayfish feeding under different climatic (temperature and photoperiod) conditions. Patterns also appear to have highly individualistic components, since behavior is not highly synchronized even among crayfish of the same size and sex. This lack of synchronization may itself be an adaptive strategy; the distribution of activity bouts throughout the day may increase the efficiency of exploiting food resources by reducing the number of crayfish feeding at any one time.

Foraging strategy is one aspect of feeding behavior; a second is energy flow, including quantitative measures of daily ration, assimilation efficiency, etc. If digestion rates are known, measures of proportion fullness over 24-hr periods from this study can be used to calculate daily ration (Bajkov 1935, Darnell and Meierotto 1962, Keast and Welsh 1967, Lawton 1971). Measurements of digestion and feeding rates, lengths of feeding bouts and of intervals between bouts, and consumption of different food items provide information necessary for quantitative analysis of both foraging strategy and energy flow. Such an analysis is necessary to evaluate the role of crayfish in structuring aquatic communities.

BIBLIOGRAPHY

Abrahamsson, S.A.A. 1966. Dynamics of an isolated population of the crayfish *Astacus astacus*. Oikos 17(1): 96-107.

Bajkov, A.D. 1935. How to estimate the daily food consumption of fish under natural conditions. Trans. Amer. Fish. Soc. 65: 288-289.

Black, J.J., L.M. Andrews, and C.W. Threinen. 1963. Surface water resouces of Vilas County, Lake and Stream Classification Project, Wis. Cons. Dept., Madison, Wis.

Bovbjerg, R.V. 1953. Dominance order in the crayfish *Orconectes virilis*. Physiol. Zool. 26: 173-178.

____________. 1956. Some factors affecting aggressive behavior in crayfish. Physiol. Zool. 29: 127-136.

Brooks, J.L. and S.I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150: 28-35.

Bundy, W.F. 1882. A list of the crustacea of Wisconsin with notes on some new or little known species. Trans. Wis. Acad. Sci. 5: 177-184.

Caine, E.A. 1975. Feeding and masticatory structures of six species of crayfish genus *Procambarus* (Decapoda: Astacidae). Forma et Functio 8: 49-66.

Capelli, G. 1975. Distribution, life history, and ecology of crayfish in nothern Wisconsin, with emphasis on *Orconectes propinquus* (Girard). PhD Thesis, Univ. Wisconsin-Madison. 214 p.

Chidester, F.E. 1908. Notes on the daily life and food of *Cambarus bartonius bartoni*. Amer. Natur. 42: 710-716.

____________. 1912. The biology of the crayfish. Amer. Natur. 46: 279-293.

Connell, J.H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42: 710-723.

Crawshaw, L.I. 1974. Temperature selection and activity in the crayfish, *Orconectes immunis*. J. comp. Physiol. 95: 315-322.

Creaser, E.P. 1932. The decapod crustaceans of Wisconsin. Trans. Wis. Acad. Sci., Arts, and Letters. 27: 321-338.

____________. 1934. A biological survey of the Raquette watershed. V. The larger crustacea of the Raquette watershed. Suppl. to 23rd Ann. Rep. N.Y. Cons. Dept., Biol. Surv., 8: 158-163.

Crocker, D.W. and D.W. Barr. 1968. Handbook of the crayfish of Ontario. Univ. of Toronto Press, Toronto. 158 p.

Darnell, R.M. and R.R. Meierotto. 1962. Determination of feeding chronology in fishes. Trans. Amer. Fish. Soc. 91: 313-320.

Dayton, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. 45: 137-159.

Dean, J. L. 1969. Biology of the crayfish *Orconectes causeyi* and its use for control of aquatic weeds in trout lakes. Tech. Papers, Bur. Sport Fish. and Wildl. No 24, 15 p.

Dye, L. 1974. An investigation of the genus *Aeshna* as a predator on young-of-year *Orconectes virilis*. Titles and abstr. presented at 22nd Annual Meeting of the Midwest Benthological Society, National Environ. Res. Center, Cincennati, Ohio.

Emlen, J.M. 1966. The role of time and energy in food preferences. Am. Nat. 100: 611-617.

Girard, C. 1852. A revision of the North American Astaci, with observations on their habits and geographical distribution. Proc. Acad. Nat. Sci. Philadelphia 6: 87-91.

Hagerman, L. 1970. Locomotory activity patterns of *Crangon vulgaris* (Fabricius) (Crustacea, Natantia). Ophelia 8: 255-266.

Holling, C.S. 1961. Principles of insect predation. Annu. Rev. Entom. 6: 163-182.

Honegger, H.W. 1973. Rhythmic activity responses of the fiddler crab *Uca crenulata* to artificial tides and artificial light. Mar. Biol. 21: 196-202.

Huxley, T.H. 1880. The crayfish. An introduction to the study of zoology. Inter. Sci. Ser. 28. D. Appleton, New York. 371 p.

Keast, A. and L. Welsh. 1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. J. Fish. Res. Bd. Can. 25(6): 1133-1144.

Kossakowski, J. 1964. Coexistence of *Astacus astacus* L. and *Astacus leptodactylus* Esch. in Loby Lake. Roczniki Nauk Rolniczych, Warsaw, 84, series B, 2: 431-455. *In* Polish Ecol. Biblio. for 1964, Polish Academy of Sciences, Institute of Ecology, March, 1968.

Kullback, S. 1959. Information theory and statistics. Wiley, New York. 395 p.

Langlois, T.H. 1935. Notes on the habits of the crayfish, Cambarus rusticus Girard in fish ponds in Ohio. Trans. Amer. Fish. Soc. 65: 189-192.

Lawton, J.H. 1971. Ecological energetics studies on larvae of the damselfly Pyrrhosoma nymphula (Sulzer) (Odonata: Zygoptera). J. Anim. Ecol. 40: 385-423.

Lehmann, U., D. Neumann, and H. Kaiser. 1974. [Tidal and spontaneous activity patterns in fiddler crabs. I. A new approach to a quantitative analysis of locomotor rhythms.] J. comp. Physiol. 91: 187-221.

MacArthur, R.H. and E.R. Pianka. 1966. On optimal use of a patchy environment. Am. Nat. 100: 603-609.

Martin, A.C. and F.M. Uhler. 1939. Food of game ducks in the United States and Canada. U.S.D.A. Tech. Bull. No. 634: 139-140.

Mason, J.C. 1963. Life history and production of the crayfish, Pacifasticus leniusculus trowbridgii (Stimpson) in a small woodland stream. Masters thesis, Oregon State Univ., Corvallis. 204 p.

Minckley, W.L. and J.E. Craddock. 1961. Active predation of crayfishes on fishes. Prog. Fish. Cult. 23(3): 120-123.

Minshall, G.W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrood community. Ecology 48: 139-149.

Momot, W.T. 1967a. Population dynamics and productivity of the crayfish, Orconectes virilis in a marl lake. Amer. Midl. Nat. 78: 55-81.

__________. 1967b. Effects of brook trout predation on a crayfish population. Trans. Am. Fish. Soc. 96: 202-209.

Norton, E.M. 1942. The food of the crayfish at Reelfoot Lake. Rep. Reelfoot Lake Biol. Stn. 6: 51-54.

Ortmann, A.E. 1906. The crayfishes of the State of Pennsylvania. Mem. Carneg. Mus. 2: 343-533.

Paine, R.T. 1966. Food web complexity and species diversity. Am. Nat. 100: 65-75.

__________. 1969. A note on trophic complexity and community stability. Am. Nat. 103: 91-93.

Page, T.L. and J.L. Larimer. 1972. Entrainment of the circadian locomotor activity rhythm in crayfish. J. comp. Physiol. 78: 107-120.

__________. 1975. Neural control of circadian rhythmicity in the crayfish I. The locomotor activity rhythm. J. comp. Physiol. 97: 59-80.

Penn, G.H. 1943. A study of the life history of the Louisiana redcrawfish, Cambarus clarki Girard. Ecology 24: 1-18.

Pulliam, H.R. 1974. On the theory of optimal diets. Am. Nat. 108: 59-74.

Prins, R. 1968. Comparative ecology of the crayfishes Orconectes rusticus and Cambarus tenebrosus in Doe Run, Meade County, Kentucky. Int. Rev. Ges. Hydrobiol. 53(5): 667-714.

Rice, R.R. and K.B. Armitage. 1974. The effect of photoperiod on oxygen consumption of the crayfish Orconectes nais (Faxon). Comp. Biochem. Physiol. 47(1A): 261-270.

Rickett, J.D. 1974. Trophic relationships involving crayfish of the genus Orconectes in experimental ponds. Prog. Fish. Cult. 36(4): 207-211.

Roberts, T.W. 1944. Light, eyestalk chemical, and certain other factors as regulators of community activity for the crayfish Cambarus virilis, Hagen. Ecol. Monogr. 14: 360-392.

Sakowicz, S. and A. Kompowski. 1962. Fish eggs as food of Orconectes limosus Raf. Inst. Inland Water Fish., Olsztyn, Poland. Biol. Abstr. 45(2) Abstr. No. 5006. 1964.

Schoener, T.W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369-404.

Siegal, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York. 312 p.

Sokal, R.R. and F.S. Rohlf. 1969. Biometry, the principles and practices of statistics in biological research. W.H. Freeman, San Francisco. 776 p.

Stein, R.A. 1975. Selective predation, optimal foraging, and resource depression within the predator-prey interaction between fish and crayfish. PhD Thesis, Univ. Wisconsin-Madison. 194 p.

Tack, P.I. 1941. The life history and ecology of the crayfish Cambarus immunis. Am. Midl. Nat. 25: 420-466.

Van Deventer, W.C. 1937. Studies on the biology of the crayfish, Cambarus propinquus. Ill. Biol. Monogr. 15(3): 67 p.

Venkataramiah, A., G.J. Lakshmi, and G. Gunter. 1975. Effect of protein level and vegetable matter on growth and food conversion efficiency of brown shrimp. Aquaculture 6: 115-125.

Viosca, P., Jr. 1931. The bullhead, *Ameiurus melas catulus*, as a dominant in small ponds. Copeia 1931(1): 17-19.

Wilson, K.V. 1956. A distribution-free test of analysis of variance hypotheses. Psych. Bull. 55(1): 96-101.

Approved

John J. Magnuson

John J. Magnuson, Professor

December 20, 1975

Date