

THE EFFECTS OF CRAYFISH (ORCONECTES RUSTICUS)
ON THE MACROINVERTEBRATE AND ALGAL ASSEMBLAGES
IN A NORTHERN MICHIGAN STREAM

A Thesis

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CHAPTER 1

INTRODUCTION

The rusty crayfish, Orconectes rusticus (Girard), is native to lakes and streams of the lower Midwest (USA) including Indiana, Ohio, Kentucky, and Tennessee (Lorman 1980, also see review by Hobbs and Jass 1988). Within the last 20-30 years, however, this crayfish has invaded or been introduced into lakes and streams of Minnesota (Hobbs and Jass 1988), northern Wisconsin (Capelli 1975, Lorman 1975), and both upper and lower Michigan (Lippson 1976). It also now occurs in parts of the Northeast (USA) (Smith 1981, Hobbs and Jass 1988), southern Ontario (Canada) (Berrill 1978), and areas of New Mexico (USA) (Hobbs and Jass 1988). The broad expansion of the range of O. rusticus probably has been facilitated by anglers who transport the crayfish for use as bait (Berrill 1978, Lorman 1980).

In northern Wisconsin lakes, the effects of omnivory by O. rusticus on both plants and animals of the littoral benthic community have been studied extensively. Experimental analyses have shown that this species can reduce macrophyte species richness (Lodge and Lorman 1987) and abundance (Lorman 1980, Lodge and Lorman 1987, Lodge et al. 1994). By reducing macrophyte abundance, O. rusticus decreases the total surface area available for periphyton colonization and therefore indirectly decreases total periphyton abundance (Lodge et al. 1994). O. rusticus also reduces macroinvertebrate species richness (Lodge et al.

1994) and abundance (Lodge and Lorman 1987, Lodge et al. 1994). Weber and Lodge (1990) found that by affecting local distributions of grazers (snails), O. rusticus indirectly affected the standing crop of periphyton. O. rusticus invasions also have been implicated as the causative factor in the displacement of two congeners (O. propinquus and O. virilis) within northern Wisconsin lakes (Capelli 1982, Lodge et al. 1986, Olsen et al. 1991).

Most studies of stream populations of O. rusticus have focused on its distribution (Lippson 1976, Berrill 1978), production (Momot et al. 1978), diet (Eggleston 1975, True 1990), and breeding periodicity and behavior (Berrill and Arsenault 1982, 1984). Studies of its biotic interactions within streams mostly have addressed the mechanisms (e.g., growth rates, use of shelter, susceptibility to predation) by which O. rusticus displaces congeners (Maude and Williams 1983, Butler and Stein 1985, Mather 1990, True 1990). To my knowledge, no previous studies have addressed the effects of O. rusticus on other components of the stream benthic community.

The ability of other crayfish species to affect stream benthos has been investigated. Huryn and Wallace (1987) studied Cambarus bartonii in a North Carolina stream and found that crayfish feeding and egestion activities increased the conversion rate of coarse particulate organic matter (CPOM) to fine particulate organic matter (FPOM). They speculated that this process would increase the amount of ingestible detritus available to other benthic organisms, and would enhance the rate of mineralization of organic material. Creed (1990) and Hart (1992) demonstrated that O. propinquus grazed upon and thus virtually eliminated the macroalga Cladophora glomerata, thereby reducing the

available refugia and overall densities of Cladophora-associated microtaxa (e.g., Stenonema mayflies). The absence of Cladophora allowed microalgae (e.g., diatoms) and associated micrograzers (e.g., Leucotrichia caddisflies) to colonize the open surfaces. Results of these studies suggest that crayfish can be important components of the stream benthic community by affecting the local abundance and distribution of detritus, algae, and macroinvertebrates.

My study focuses on (1) the role of crayfish in a stream lacking filamentous algal mats (e.g., Cladophora), (2) the direct and indirect effects of crayfish omnivory on multiple trophic levels of stream food webs, and (3) the impact of an introduced or invading species (O. rusticus) on an established ecosystem. Results of this study extend our knowledge of the role of omnivory in aquatic ecosystems, and may be used to make informed predictions of the changes in a stream benthic community following invasion by O. rusticus or ecologically similar species.

CHAPTER 2

OMNIVORY IN A STREAM BENTHIC COMMUNITY: DIRECT AND INDIRECT EFFECTS OF CRAYFISH (ORCONECTES RUSTICUS)

Introduction

Historically, a major focus of ecology has been whether biotic or abiotic factors control food web structure (Andrewartha and Birch 1954). This issue has led to numerous studies exploring abiotic forces such as disturbance (see reviews by Pickett and White 1985, Sousa 1984) and specific biotic interactions such as competition (see reviews by Connell 1983, Schoener 1983) and predation (see review by Sih et al. 1985). Some approaches have combined biotic interactions (e.g., Hairston et al. 1960 which combined competition and predation) or integrated abiotic and biotic processes (e.g., Menge and Sutherland 1976, 1987, Lubchenco 1986).

Menge and Sutherland (1976) proposed a food web model that incorporates biotic interactions (competition and predation) and an abiotic process (disturbance). Unlike other integrating models (e.g., Oksanen et al. 1981) it proposes that omnivory (feeding at more than one trophic level) is prevalent and important in ecosystems (Menge and Sutherland 1987). Omnivory has been shown to be important in several freshwater systems, particularly those containing crayfish. In lakes,

omnivorous crayfish can reduce macrophyte abundance (Lodge and Lorman 1987, Feminella and Resh 1989, Lodge et al. 1994) and species richness (Lodge and Lorman 1987), invertebrate abundance (Lodge and Lorman 1987, Hanson et al. 1990) and species richness (Lodge et al. 1994), and periphyton primary productivity (Flint and Goldman 1975). In streams, crayfish increase leaf processing rates (Huryn and Wallace 1987), decrease periphyton biomass (McCormick 1990), and affect the distribution of macroalgae (Cladophora) and associated macroinvertebrates and epiphytes (Creed 1990, Hart 1992).

To my knowledge, no studies have addressed the impact of crayfish omnivory (both predation and herbivory) on multiple trophic levels of a stream benthic community. My study was designed to (1) assess the types and magnitudes of effects of various densities of crayfish on stream benthos using in-situ enclosures and (2) determine if the experimental results could be used to predict existing conditions within a natural benthic community inhabited by crayfish.

Study Area

This study was conducted in the Middle Branch of the Ontonagon River, which is located in the western half of Michigan's Upper Peninsula (46°N, 89°W). The stream originates as the outflow of Crooked Lake (Gogebic Co., MI), flows northward, and joins other branches to form the Ontonagon River, which empties into Lake Superior. Approximately 36 km downstream of its origin, the river has been impounded to allow diversion of water for electric power generation. Minimum stream discharge is maintained at 1.13 m³/s from June-August and 0.85 m³/s from September-May (Stone and Webster Michigan, Inc. 1987) to

sustain the brook trout (Salvelinus fontinalis) fishery. A substantial falls (Bond Falls) formed by a basalt outcrop occurs 0.5 km downstream of the impoundment. The drainage basin of the Middle Branch covers about 760 km², and the lithology is dominated by sand-gravel or silty clay topsoil underlain by sandstone.

The channel substratum is composed of cobble-on-sand punctuated by bedrock, and wetted and active channel widths average about 16.8 and 26.7 m, respectively. The stream is shallow (about 0.25 m deep on average), has a low gradient (0.4%), and is moderately shaded. Birch (Betula spp.), speckled alder (Alnus rugosa), maple (Acer spp.), poplar (Populus spp.), and eastern hemlock (Tsuga canadensis) dominate the riparian zone vegetation. Brook trout dominated the fish assemblage, but brown trout (Salmo trutta), blacknose dace (Rhinichthys atratulus), longnose dace (R. cataractae), mottled sculpin (Cottus bairdi), and slimy sculpin (C. cognatus) also occurred throughout the stream. Crayfish (Orconectes rusticus) are abundant at the base of Bond Falls, but gradually decline in density with increasing downstream distance.

Study Animal

The rusty crayfish, Orconectes rusticus (Girard), is native to aquatic habitats of the lower Midwest (southern Michigan, Ohio, Indiana, Illinois, Missouri, Kentucky, and Tennessee) (Lorman 1980, see also review by Hobbs and Jass 1988). Within the last 30 years, however, O. rusticus has spread into lakes and streams of Wisconsin (Capelli 1975), northern Michigan (Lippson 1976), southern Ontario (Berrill 1978), and parts of the Northeast (Lorman 1980, Smith 1981). Orconectes rusticus has readily established in these regions, often replacing native

crayfish species, especially orconectid congeners (Berrill 1978, Smith 1981, Capelli 1982, Olsen et al. 1991). In northern Wisconsin, O. rusticus lives to 4 yr (Lorman 1980), with adults ranging in size from 18.5-58.0 mm CL (carapace length) (Lorman 1980, A. Hill, pers. comm.). In rocky or sandy sediments of lakes, adult O. rusticus densities typically range from 1-15/m² (Lorman 1980, Olsen et al. 1991) with a high of 56/m² found in Upper Sugarbush Lake, WI (Lorman 1980). In streams within its native range, O. rusticus densities can range from 2.6-21.2/m² (Momot et al. 1978, Mather 1990). Orconectes rusticus consumes various food resources including detritus (Prins 1968), algae (Eggleston 1975), macrophytes (Prins 1968, Lorman 1980, Lodge 1991), and macroinvertebrates (Lorman 1975, Hill et al. 1993, Lodge et al. 1994). The crayfish uses the chela of its walking legs (pereiopods) to grasp and transfer food items to its mandibles (Holdich and Reeve 1988, Creed 1990, Lodge et al. 1994).

The diet of O. rusticus within the Middle Branch of the Ontonagon River was determined with stomach analysis. Twenty-one crayfish (5 females and 16 males; 24.8-30.1 mm CL) were collected from the stream and frozen at approximately -4°C. Each crayfish stomach subsequently was excised and placed in 10 ml of 90% ethanol. The stomach contents were examined under both a dissecting and a compound microscope for the occurrence of detritus, algae, and macroinvertebrates. Each of these food types was classified as either present or absent within each stomach. Algae (mostly diatoms) and detritus were found in 100% of the stomachs, and macroinvertebrates were found in 76% (16 of 21) of the stomachs. Intact macroinvertebrates in the stomachs included crustaceans (Ostracoda) and chironomid larvae (Diptera). Remnants of

insects (Ephemeroptera, Trichoptera, and Diptera) also were found in the stomachs. Based on these analyses, O. rusticus within the Middle Branch of the Ontonagon River can be considered benthic omnivores.

Methods

Enclosure Experiments

Enclosure Design. Experimental enclosures were constructed from 0.2 m² clear plastic containers (50 x 40 x 20 cm) by replacing the upstream and downstream ends with flexible plastic screening (8 x 14-mm mesh) to allow flow-through. Current velocity within the enclosures was reduced by 60% (from 0.48 to 0.19 m/s), but colonization by algae and movement of most invertebrates and larval fish could occur through the large mesh. Each enclosure was lined with 1 cm of sand on which were placed four rows of seven ovoid, artificial substrata (surface area=130.46 ± 3.81 cm²; $\bar{x} \pm$ S.E.; n=6). The artificial substrata were made of rough, unglazed ceramic that mimicked natural rocks, and were used as the primary sampling unit because of their uniformity in surface area and reproducibility across treatments (Lamberti and Resh 1985).

To indicate the extent of enclosure effects (e.g., Cooper et al. 1990), four sets (four rows of seven) of artificial substrata were placed directly on the streambed within the randomized block design of Experiment I (see below). These substrata were sampled in conjunction with the enclosures (after 30 d and 60 d of colonization) and analyzed for periphyton and macroinvertebrates as described below. I used ANOVA to examine differences between these substrata and substrata sampled from enclosures without crayfish. There were no significant differences in their density of macroinvertebrates ($F=9.503$; $P=.200$) and accrual of

periphyton biomass ($F=0.116$; $P=.756$) and chlorophyll a ($F=0.123$; $P=.749$). Therefore, the enclosures had no significant effects on periphyton and macroinvertebrate colonization rates (Table 1).

Experiment I. Enclosure Experiment I was conducted from June-August 1991 at a site in the Middle Branch of the Ontonagon River that was nearly devoid of crayfish (0.18 ± 0.05 *O. rusticus*/m²; $\bar{x} \pm S.E.$, $n=2$ sampling dates, see below). The experimental site lay within one of the stream reaches (GR4) of the gradient study described below. Twelve experimental enclosures were placed in the stream on 6 June in a randomized block design (3 treatments x 4 blocks) and exposed to colonization by macroinvertebrates and algae for 30 d. On 5 July (day 0 of the experimental period), 8 x 14-mm mesh covers were attached to each enclosure using removable metal clips. *Orconectes rusticus* were collected from an upstream site and added to the enclosures in densities of 0/m² (ZERO; zero crayfish per enclosure), 10/m² (MED; two crayfish per enclosure), or 30/m² (HIGH; six crayfish per enclosure). Both male and female crayfish were employed in ratios (male:female) of 1:1 (MED treatment) and 4:2 (HIGH treatment). Each treatment was replicated four times. Total crayfish biomass in the MED and HIGH treatments was 8.03 ± 0.03 g and 27.13 ± 0.28 g ($\bar{x} \pm S.E.$), respectively. Crayfish used in the experiment were of similar size; each individual was 4.39 ± 0.19 g. On day 0 (just before crayfish were added) and day 30 of the experimental period (4 August), four random substrata from each enclosure were removed and sampled for periphyton chlorophyll a and biomass (two substrata pooled) or macroinvertebrates (two substrata pooled). When sampling for macroinvertebrates, a 50- μ m mesh net was

TABLE 1

COMPARISON OF PERIPHYTON CHLOROPHYLL A, PERIPHYTON BIOMASS, AND MACROINVERTEBRATES ATTACHED TO ARTIFICIAL SUBSTRATA WITHIN EXPERIMENTAL ENCLOSURES (N=4) AND ARTIFICIAL SUBSTRATA PLACED DIRECTLY ON THE STREAMBED (N=4). SUBSTRATA WERE COLONIZED FOR 30 D AND 60 D. DATA PRESENTED ARE MEANS (\pm S.E.)

	Chlorophyll a (mg/m ²)		Biomass (g/m ²)		Macroinvertebrates (no./m ²)	
	30 d	60 d	30 d	60 d	30 d	60 d
Enclosures	5.03 (± 0.38)	8.58 (± 0.72)	3.52 (± 1.15)	8.82 (± 2.63)	6700 (± 2600)	5200 (± 460)
Streambed	4.83 (± 0.38)	9.58 (± 0.42)	2.99 (± 0.53)	5.65 (± 2.37)	11400 (± 4100)	6700 (± 1200)

placed directly downstream of each substratum to collect any dislodged or escaping organisms. Substrata removed on day 0 were replaced with other, non-colonized substrata. These replacement substrata were excluded from the day 30 sampling.

Experiment II. Enclosure Experiment II was conducted from June-August 1992 at the same site as Experiment I. Fifteen experimental enclosures were topped with mesh, placed within the stream in a randomized block design (3 treatments x 5 blocks), and exposed to colonization by macroinvertebrates and algae for 22 days. In contrast to Experiment I, covers were added at the beginning of the colonization period (3 June) to minimize any confounding effects of the simultaneous addition of enclosure covers and crayfish. Orconectes rusticus (males) were collected from upstream and added to the enclosures on 24 July (day 0) in densities of 0/m² (ZERO; zero crayfish per enclosure), 5/m² (LOW; one crayfish per enclosure), or 10/m² (MED; two crayfish per enclosure). Each treatment was replicated five times. Crayfish collected for the experiment were limited to a single sex to reduce any sex-specific variation among treatments. Total crayfish biomass in the LOW and MED treatments was 4.96 ± 0.14 g and 7.4 ± 0.13 g ($\bar{x} \pm S.E.$), respectively. Crayfish used in the experiment were of similar size; each individual was 4.12 ± 0.20 g. On day 0 (just before the crayfish were added) and day 46 of the experimental period (10 August), the enclosures were sampled for periphyton chlorophyll a (two substrata pooled), periphyton biomass (two substrata pooled), and macroinvertebrates (two substrata pooled) as above. Each substratum removed on day 0 was replaced with another, pre-colonized substrata. The number of substrata sampled for

analysis of periphyton differed from Experiment I to accommodate the methodological changes described below. On days 44-46, a total of nine substrata (one to two from each enclosure) were removed randomly from each treatment for estimates of periphyton primary productivity. Primary productivity was estimated by oxygen evolution (Orion Model 840 dissolved oxygen meter) within 2.2-L closed, recirculating Plexiglas[®] chambers (10.2 cm x 30.5 cm) each of which held three of the sampled substrata. Three replicate incubations were conducted for each treatment. Large invertebrates were removed from each substrata before incubation as long as their removal did not disrupt the substrata's periphyton matrix. Because of pump failures, only net community primary productivity was estimated.

During both experiments, the enclosures were monitored every two to three days of the colonization and experimental periods. All debris was cleaned from the enclosure mesh, and any dead or missing crayfish were replaced with another O. rusticus of similar size. Seven (22%) and six (40%) crayfish were replaced in Experiments I and II, respectively.

Gradient Study

To determine if my enclosure results accurately predicted natural stream conditions, I surveyed benthic communities along a natural O. rusticus density gradient in the Middle Branch of the Ontonagon River. Within this gradient, as within the enclosures, crayfish were a top-trophic-level organism because the dominant fish (brook trout) likely do not prey on adult crayfish (sensu Gowing and Momot 1979). I selected four stream reaches (GR1-GR4) with GR1 located 0.7 km downstream of the impoundment, and GR2-GR4 located at successive downstream sites

separated by 0.4-1.6 km (Table 2). Each of the sites had obviously different O. rusticus densities, but similar physical and chemical conditions (Table 2). Crayfish densities at these sites were estimated twice (28 June and 23-28 July 1992) (Table 3) by snorkeling and counting all O. rusticus within replicated (n=4), 0.5-m-wide belt transects aligned perpendicular to stream flow. Average densities at the four sites during 1992 were 0.2, 0.9, 1.8, and 3.1 crayfish/m² (Table 2). As part of another study, crayfish densities at each site were resurveyed in August 1993; these data give some measure of year-to-year variability in crayfish densities (Table 3). At each site, on all sampling dates, O. rusticus was the only crayfish species observed in the stream. In late July 1992 and 1993, I measured various physical, chemical, and biological parameters at each site (Table 2).

During 23-28 July 1992, fifteen rocks were chosen randomly from a 10-m reach of each site for analysis of periphyton chlorophyll a (n=5), periphyton biomass (n=5), and macroinvertebrate abundance and taxa richness (n=5). As in the enclosure experiments, a 50- μ m mesh net was used when sampling macroinvertebrates. An additional nine rocks from each site were selected randomly for estimates of periphyton primary productivity (n=3 per site). Due to pump failure, no productivity estimates were obtained for the medium-density (1.8 crayfish/m²) site.

Laboratory Analyses

Algae. In Experiment I, algae were removed from the substrata with a scalpel and a toothbrush, transferred to water, and filtered onto Whatman GF/F filters (pore size=0.45 μ m). For biomass determination, each filter was dried at 60°C for 24 h, weighed to the nearest 0.1 mg,

TABLE 2

DESCRIPTIVE PARAMETERS FOR STUDY SITES (GR1-GR4) ALONG THE CRAYFISH DENSITY GRADIENT WITHIN THE MIDDLE BRANCH OF THE ONTONAGON RIVER. OUTLET SITE INCLUDED FOR COMPARISONS OF NUTRIENTS AND SUSPENDED BIOMASS WITH DOWNSTREAM SITES

Site	Crayfish (no./m ²)	Dist. from outlet	Canopy (%)	Q (m ³ /s)	Water temp. (°C)	Susp. AFDM (g/L)	Susp. chl. a (µg/L)	TDS (mg/L)	Cond. (µS/cm)	NO ₃ ⁻ (mg/L)	PO ₄ ⁻³ (mg/L)	Ca ⁺⁺ (mg/L)
GR4	0.18 ±0.05	3931	22	1.45	21.0	.03	2.2	60.0	120	0.22	0.01	42
GR3	0.93 ±0.13	2628	27	1.74	22.0	.02	2.1	58.7	117	0.24	0.00	41
GR2	1.80 ±0.31	1075	30	1.35	20.6	.02	2.6	60.0	116	0.26	0.03	42

GRI	3.10	658	47	1.28	18.8	.02	2.1	67.5	134	0.26	0.01	43
	±0.94											

Outlet	-	5	0	1.22	-	.02	2.2	-	-	0.22	0.03	-
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TABLE 3

AVERAGE CRAYFISH DENSITIES (\pm S.E.) AT EACH GRADIENT SITE FOR THREE SAMPLING DATES

Site	June 1992	July 1992	August 1993
GR1	---	3.1 (± 0.9)	4.0 (± 1.5)
GR2	2.6 (± 0.1)	1.1 (± 0.3)	2.3 (± 0.9)
GR3	0.9 (± 0.2)	0.9 (± 0.2)	1.1 (± 0.2)
GR4	0.2 (± 0.1)	0.2 (± 0.1)	0.1 (± 0.0)

combusted at 500°C for 24 h, and then reweighed to estimate ash-free dry mass. For chlorophyll a analysis, each filter was placed in a dark container, frozen, and extracted with 100% methanol for 48 h. Chlorophyll a concentration of the extract was then measured fluorometrically (Sequoia-Turner 450) using the methods of Carpenter et al. (1987). In both Experiment II and in the gradient study, algal biomass was determined as above. Chlorophyll a analysis, however, changed after Experiment I because of concerns regarding the variation in scraping efficiencies (73-95%) and possible limitations of fluorometric analysis (Jacobsen and Rai 1990). To address these concerns, whole substrata (artificial and natural) were frozen, placed in 100% acetone, and extracted for 24 h. The extract was then analyzed spectrophotometrically (Perkin-Elmer Lambda 6) for chlorophyll a using both the trichromatic and acidification methods (APHA, AWWA and WPCF 1985). Phaeophytin generally accounted for only a small proportion of chlorophyll a, so no correction was made. Surface area of artificial substrata and rocks was determined by the foil-wrap method (Lamberti et al. 1991). For periphyton, effective surface area was calculated as 50% of total surface area.

Invertebrates. In the laboratory, invertebrate samples were sorted under a dissecting microscope. All organisms were identified to lowest practicable taxonomic level, classified according to trophic level (detritivore, herbivore, carnivore), and counted for estimates of macroinvertebrate abundance, taxa richness, and trophic composition. Invertebrates were assigned to a trophic level based on their principal food source as listed in Merritt and Cummins (1984). Chironomids were

identified to family level only, and thus were excluded from trophic classification because of the broad range of diets within the family (Berg, in press).

Data Analyses

For Experiments I and II, I used paired t-tests to examine within-treatment changes in algae and invertebrates from the beginning to the end of the experimental period. I also used ANOVA (randomized block design) and Tukey's HSD test to determine differences among treatments at the beginning and again at the end of each experiment. When Bartlett's test for homogeneity of variances detected unequal variance among treatments, data were logarithmically transformed. Means and standard errors presented in the text and figures are non-transformed. All analyses were conducted using Systat version 5.02 (Wilkinson 1990). In 1991, one enclosure was destroyed in a storm; statistical analyses involving missing data in a randomized block design were conducted according to Zar (1984).

In the gradient study, regression analyses were used to examine the relationship between crayfish density (1992 averages) and algal or invertebrate parameters. Data were fitted to a linear model ($\ln y = \ln a + bx$). Similarity in invertebrate taxonomic composition among gradient sites was determined using the SIMI metric (McIntire and Moore 1977, Lamberti et al. 1992). SIMI compares two samples and is calculated as:

$$\text{SIMI} = \frac{\sum_{i=1}^n P_{ih} P_{ik}}{\sqrt{\sum_{i=1}^n P_{ih}^2} \sqrt{\sum_{i=1}^n P_{ik}^2}}$$

where P is the proportion of species i of the entire sample, h is the

first sample, k is the second sample, and n is the number of species. SIMI values range from 0-1.0, with 0 indicating that the samples have no taxa in common, and 1.0 indicating that the samples are identical in both taxonomic composition and relative abundance. Because chironomids were identified to only the family level, they were excluded from the SIMI analysis.

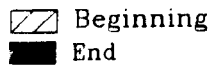
Results

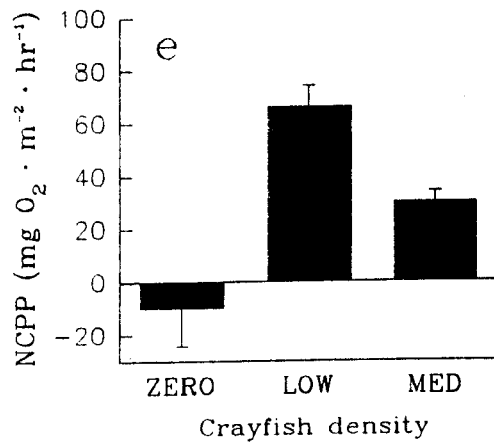
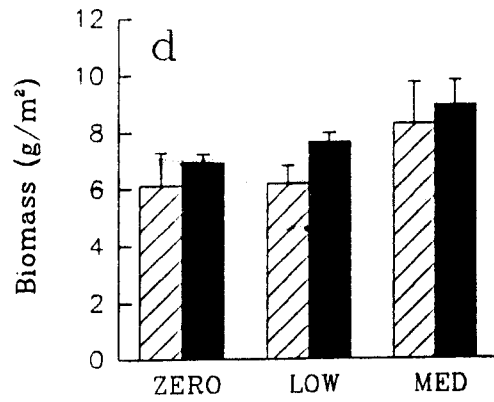
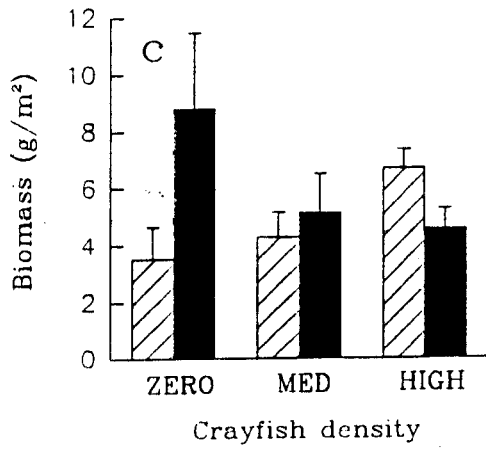
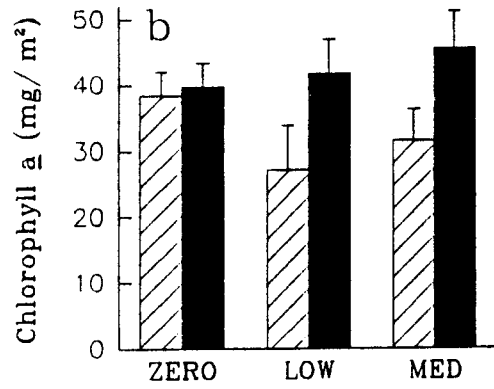
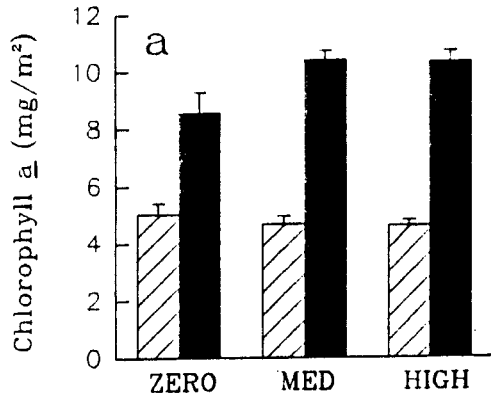
Enclosure Experiments

Algal Response. During Experiment I, chlorophyll a in all treatments increased significantly (Fig. 1a; Table 4) over time. On day 0 of the experiment, there were no significant differences in chlorophyll a among the treatments. On day 30, however, chlorophyll a in the MED and HIGH treatments was significantly higher (by 21%) than in the ZERO treatment (Table 4). Over time, periphyton biomass declined in the HIGH treatment, but did not change significantly in the ZERO and MED treatments (Fig. 1c; Table 4). Periphyton biomass was not significantly different among the treatments on either day 0 or day 30 of the experiment (Table 4).

In Experiment II, chlorophyll a increased significantly over time in both the LOW and MED treatments (by 54% and 30%, respectively), but changed little in the ZERO treatment (Fig. 1b; Table 4). Within-treatment changes in biomass were not significant, but at the end of the experiment (day 46), biomass was significantly greater in the MED treatment than in the ZERO treatment (Fig. 1d; Table 4). Primary productivity was measured only at the conclusion of Experiment II (Fig. 1e). The treatments containing crayfish had significantly higher primary productivity compared to the treatment without crayfish ($P < .01$). Because respiration exceeded production, periphyton on substrata from the ZERO treatment was heterotrophic ($P/R < 1$). Periphyton on substrata

Figure 1. Mean (\pm S.E.) abundances of (a,b) periphyton chlorophyll a and (c,d) biomass within each crayfish treatment at the beginning and end of enclosure Experiments I and II. Mean (\pm S.E.) periphyton net community primary productivity (NCP) within each treatment at the termination of Experiment II (e) also is shown.


 Beginning
 End



Experiment I

Experiment II

TABLE 4

RESULTS OF ANOVA FOR WITHIN-TREATMENT (COMPARING A SINGLE TREATMENT FROM BEGINNING TO END) AND AMONG-TREATMENT (COMPARING ALL THREE TREATMENTS AT BEGINNING OR END) COMPARISON OF PERIPHYTON AND MACROINVERTEBRATE RESPONSE VARIABLES OF ENCLOSURE EXPERIMENTS I AND II. RESULTS OF TUKEY'S HONESTLY SIGNIFICANT DIFFERENCE (HSD) TEST PRESENTED FOR AMONG-TREATMENT COMPARISONS (Z=ZERO; L=LOW; M=MED; H=HIGH).
 NS=P>.05

Comparison	Response variable					
	Chlorophyll a	Periphyton	Invertebrate	Herbivore	Invertebrate	richness
Experiment I:						
Within treatments						
ZERO	P=.013	NS	NS	NS	NS	NS
MED	P=.002	NS	NS	NS	NS	NS
HIGH	P<.001	P=.049	P=.021	NS	NS	P=.008
Among treatments						

Beginning	NS	NS	NS	NS	NS
End	P=.034	NS	P=.003	P=.028	P=.007
HSD	(Z $\overline{M H}$)		(Z $\overline{M H}$)	(Z $\overline{M H}$)	(Z $\overline{M H}$)

Experiment II:

Within treatments

ZERO	NS	NS	NS	P=.006	P=.006
LOW	P=.002	NS	NS	P=.002	P=.018
MED	P=.041	NS	NS	NS	NS

Among treatments

Beginning	NS	NS	NS	NS	NS
End	NS	P=.045	P=.002	P<.001	P=.005
HSD		(Z $\overline{L M}$)	(Z $\overline{L M}$)	(Z L M ^a)	(Z $\overline{L M}$)

^a All three treatments were significantly different from each other.

from the LOW and MED treatments was autotrophic ($P/R > 1$).

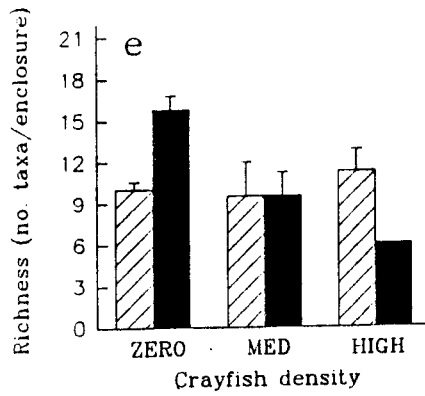
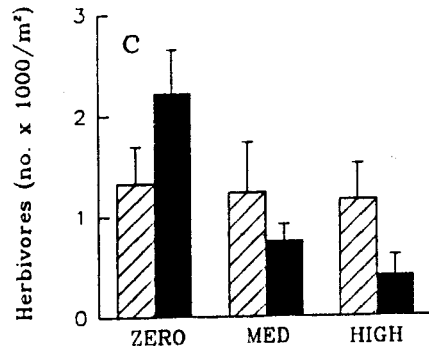
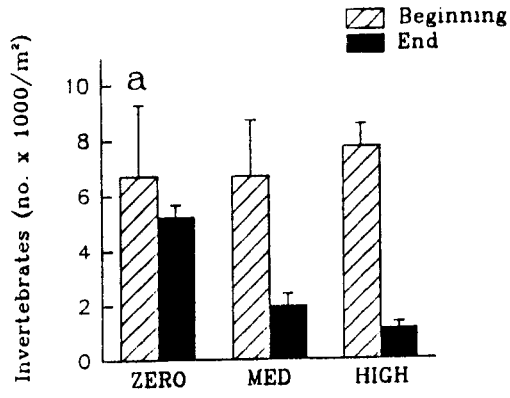
Invertebrate Response. Benthic macroinvertebrates within the experimental enclosures were affected negatively by the presence of crayfish. In the HIGH treatment of Experiment I, there was a significant reduction in invertebrate density and taxa richness over time (Fig. 2a, 2e; Table 4). Likewise, at the end of the experiment (day 30), both the MED and HIGH treatments had significantly fewer invertebrates and taxa than the ZERO treatment (Table 4). Within each treatment, the density of herbivores did not change over the course of the experiment (Fig. 2c; Table 4), but on day 30, the HIGH treatment had significantly fewer herbivores than did the ZERO treatment (Table 4).

In Experiment II, within-treatment changes in invertebrate density were not significant, but at the end of the experiment (day 46), density was significantly lower in the treatments containing crayfish (LOW and MED) than in the treatment without crayfish (Fig. 2b; Table 4). Herbivore density increased significantly in the ZERO and LOW treatments over time (Fig. 2d), and was significantly different among treatments at the end of the experiment (Table 4). Taxa richness increased significantly over time in the ZERO and LOW treatments, but not in the HIGH treatment (Fig. 2f; Table 4). On day 46, invertebrate taxa richness in the MED treatment was significantly lower than taxa richness in the other two treatments (Table 4).

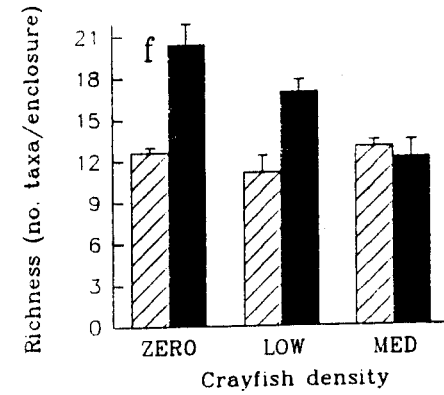
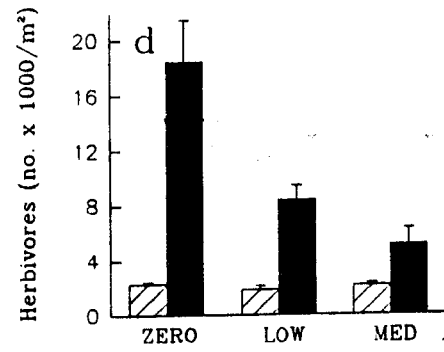
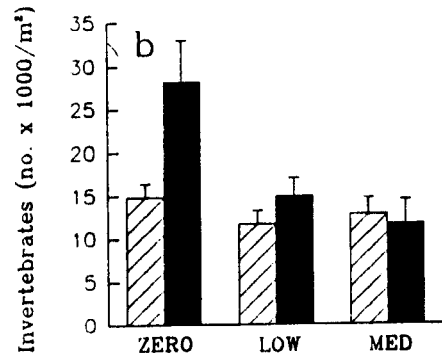
Gradient Study

The periphyton abundance parameters, chlorophyll a and biomass, differed in their relationships with crayfish density. Chlorophyll a tended to increase with increasing crayfish density ($b=0.48$; $R^2=.765$),

Figure 2. Mean (\pm S.E.) (a,b) total macroinvertebrate density, (c,d) herbivore density, and (e,f) taxa richness within each crayfish treatment at the beginning and end of enclosure Experiments I and II.



Experiment I



Experiment II

whereas periphyton biomass showed less change (i.e., lower slope) across the crayfish gradient ($b=.14$; $R^2=.656$) (Fig. 3a, 3c). Chlorophyll a at the highest crayfish density site (3.1 crayfish/m²) was over twice the chlorophyll a at the other three sites. Benthic primary productivity also tended to increase as crayfish became more numerous ($b=.10$; $R^2=.953$) (Fig. 3e). Benthic macroinvertebrate density along the gradient was inversely related to crayfish density ($b=-.66$; $R^2=.931$) (Fig. 3b). Herbivore density ($b=-.47$; $R^2=.873$) and macroinvertebrate taxa richness ($b=-.15$; $R^2=.809$) also tended to decline with increasing crayfish density (Fig. 3d, 3f). Invertebrate densities ranged from 4000-22,000 organisms/m², with chironomid larvae dominating the assemblage.

The regressions were strong as denoted by high R^2 values. Only one regression (macroinvertebrate density vs. crayfish density) was significant, however, likely due to the low degrees of freedom (maximum=2). The degrees of freedom are low because sites (not samples) must be considered the independent variable in the regressions.

SIMI analysis showed that as differences in crayfish densities increased, differences in invertebrate assemblages also increased (Table 5). For example, invertebrate assemblages at sites GR1 (3.1 crayfish/m²) and GR2 (1.8 crayfish/m²) were very similar (SIMI=0.910), whereas assemblages at sites GR1 and GR4 (0.2 crayfish/m²) were more dissimilar (SIMI=0.448).

Figure 3. Regressions of crayfish density along the gradient within the Middle Branch of the Ontonagon River with (a) periphyton chlorophyll a ($R^2=.765$; $P=.125$, $df=2$), (b) macroinvertebrate density ($R^2=.931$; $P=.035$, $df=2$), (c) periphyton biomass ($R^2=.656$; $P=.190$, $df=2$), (d) herbivore density ($R^2=.873$; $P=.066$, $df=2$), (e) gross community primary productivity (GCPP) ($R^2=.953$; $P=.139$, $df=1$), and (f) macroinvertebrate taxa richness ($R^2=.809$; $P=.101$, $df=2$). Data are means (\pm S.E).

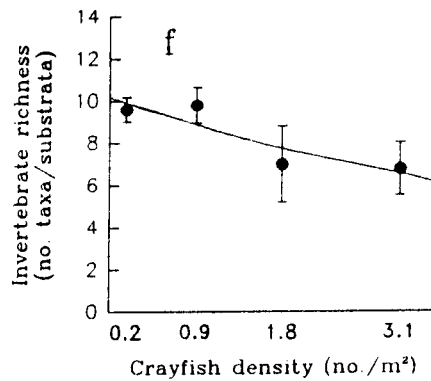
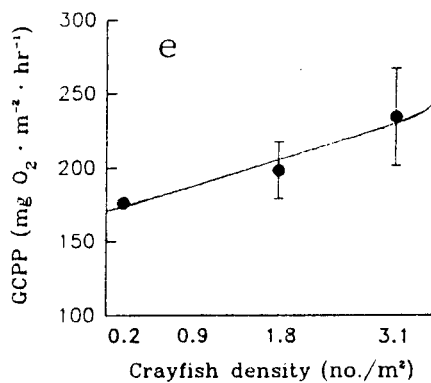
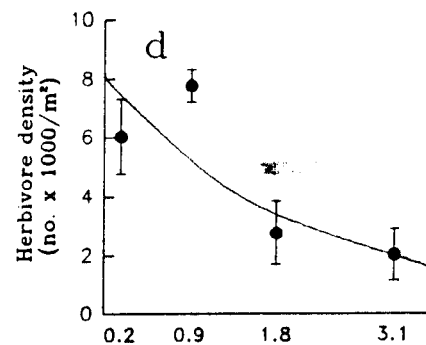
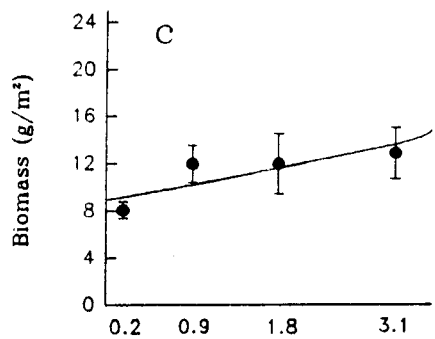
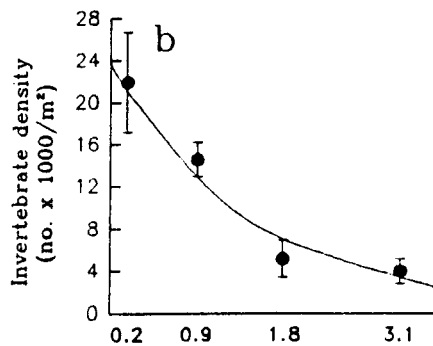
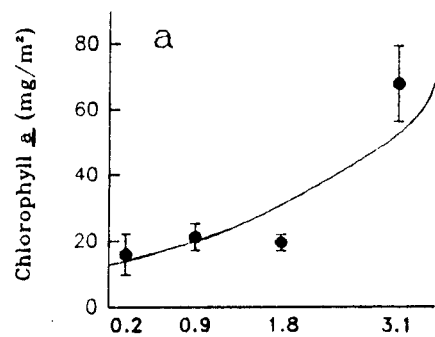


TABLE 5

RESULTS OF SIMI ANALYSES COMPARING MACROINVERTEBRATE ASSEMBLAGES BETWEEN STUDY SITES LOCATED ALONG THE CRAYFISH GRADIENT WITHIN THE MIDDLE BRANCH OF THE ONTONAGON RIVER. SIMI RANGES BETWEEN 0 AND 1; 1 DENOTES COMPLETE SIMILARITY BETWEEN TWO SITES. CRAYFISH DENSITIES ARE AVERAGES FOR 1992

Crayfish (no./m ²)	3.1 (GR1)	1.8 (GR2)	0.9 (GR3)	0.2 (GR4)
3.1 (GR1)	----			
1.8 (GR2)	0.910	----		
0.9 (GR3)	0.757	0.804	----	
3.1 (GR4)	0.448	0.494	0.357	----

Discussion

Interpretation of Results

The in-situ, enclosure experiments, coupled with the study of the natural benthic community along a crayfish gradient, clearly demonstrate that crayfish can substantially affect stream periphyton and benthic macroinvertebrates. In both enclosure experiments, crayfish had a direct negative effect on invertebrates. Periphyton was affected both indirectly and directly; the presence of crayfish increased chlorophyll *a* and primary productivity (indirect effect), and curtailed periphyton biomass accumulation (direct effect).

Crayfish directly reduced invertebrate abundance and taxa richness. My study focused on this outcome, rather than on the precise means by which it occurred. I can hypothesize, however, that invertebrates were reduced through a combination of mechanisms including consumption by crayfish (as indicated by stomach analyses), colonization inhibition or prey escape (Peckarsky and Dodson 1980), and possibly incidental dislodgement by foraging crayfish.

The effects of crayfish on periphyton could have involved any or a combination of three mechanisms: (1) reduction in the abundance of grazing invertebrates; (2) depletion of the periphyton matrix through consumption and dislodgement (Flint and Goldman 1975, Lodge and Lorman 1987); and (3) fertilization of the periphyton standing crop (Flint and Goldman 1975, McCormick 1990). Crayfish reduced macroinvertebrate

abundance, particularly herbivores, thus releasing the algal component of the periphyton matrix from some grazing pressure (see also Power and Matthews 1983, Turner and Mittlebach 1992). This release was manifest in increased chlorophyll a and primary productivity in the presence of crayfish.

Crayfish depleted the periphyton matrix. Quantitative evidence for this comes from the HIGH treatment in which periphyton biomass decreased. Depletion of periphyton by crayfish also may be inferred from the LOW and MED treatments in which there was an increase in chlorophyll a, but no accompanying increase in biomass. The removal of periphyton likely occurred through a combination of consumptive (as indicated by stomach analyses) and non-consumptive (Lodge et al. 1994) foraging behavior. When foraging, crayfish collect periphyton with their pereopods (Holdich and Reeve 1988, Creed 1990). This allows them to remove the loosely adhered components of the periphyton matrix (e.g., detritus, senescent cells, and metaphytic forms), but more tightly adhered material (e.g., adnate algal cells) cannot be removed. This differential removal is common for most grazers of benthic algae (Lamberti et al. 1987, Lowe and Hunter 1988). Depletion of loosely attached material can reduce the average age of algal cells (Gregory 1983), and decrease shading of prostrate cells (Lamberti and Resh 1983). Reductions in the age and shading of the algal cells can increase the chlorophyll/biomass ratio (Hunter 1980) and primary productivity of the periphyton matrix (McIntire 1973, Gregory 1983, Lamberti and Resh 1983). Thus, by foraging on the periphyton matrix, crayfish simultaneously curtailed periphyton biomass accrual, but increased chlorophyll a and primary productivity.

Like all consumers, crayfish increase the rate of nutrient mineralization relative to that occurring through purely decompositional pathways (Hargrave 1970, McNaughton 1985). Excretion of nutrients by crayfish and other benthic invertebrates may fertilize periphyton communities, thus directly contributing to increased primary productivity (Flint and Goldman 1975, McCormick 1990). Although nutrient uptake velocities can be rapid (*sensu* Steinman et al. 1991), crayfish excrement probably contributed little to the periphyton growth given the high dilution and transport rates of streams (Lamberti and Resh 1983)

The effects of crayfish on the stream benthic community were manifest in experiments spanning two years, which suggests that crayfish direct and indirect effects may transcend inherent system variability. There was slight year-to-year variation in the pattern of response within the ZERO treatment and in the magnitude of response within the ZERO and MED treatments. The number of macroinvertebrates that colonized the enclosures also differed. These discrepancies may have been due to natural variation within the system and/or methodological differences between the two experiments (e.g., length of colonization period and length of experiment). Inconsistencies in periphyton chlorophyll a concentrations are readily apparent. Most likely, these discrepancies resulted from a combination of natural variation and imprecision between fluorometric (Experiment I) and spectrophotometric (Experiment II) methods (Holm-Hansen and Riemann 1978, Jacobsen and Rai 1990).

Results from the gradient study were consistent with predictions generated by the in-situ experiments. Therefore, patterns in the

natural stream may be due to mechanisms revealed in my experimental systems. Within the gradient sites containing crayfish, invertebrate abundance and taxa richness generally were lower than within the site without crayfish. Conversely, algal chlorophyll *a* and benthic primary productivity were higher when crayfish were present than when crayfish were absent. These higher values occurred despite increased canopy cover at the higher crayfish sites (Table 2). For streams in general, the patterns of crayfish, macroinvertebrates, and algae that I observed are probably conservative given that stream crayfish can maintain a standing stock biomass of 30.6 g/m² and can reach densities of >21/m².

Factors other than crayfish density also may have contributed to the patterns of invertebrates and periphyton that I observed in the natural stream. Most obvious is the addition of nutrients and suspended biomass from the upstream reservoir, which become diluted or depleted as the water moves downstream (Hynes 1970, Morin and Peters 1988). There were, however, no detectable chemical or seston gradients among the study sites (Table 2). In addition, the invertebrate patterns I observed are contrary to those expected for a lake outlet. A typical lake outlet has its highest invertebrate densities near the outlet (Wotton 1979, Brönmark and Malmqvist 1984, Richardson and Mackay 1991). In my system, the lowest invertebrate densities were at the site closest to the outlet. Lake outlet effects often diminish after a relatively short distance (e.g., 0.5 km; Wotton 1979, Vadeboncoeur 1988); my first gradient site was 0.7 km below the outlet.

Relevance to Food Web Theory

My results suggest that crayfish have substantial effects on the

benthic food web of the Middle Branch of the Ontonagon River. Therefore, my study supports top-down food web models in general (e.g. Hairston et al. 1960, Menge and Sutherland 1976, 1987, Oksanen et al. 1981, Fretwell 1987), and the Menge-Sutherland model (MS) in particular. MS differs from other top-down models by presuming that omnivory is prevalent within food webs (especially by top predators). Omnivory increases connectance among trophic levels; therefore, most trophic levels below the top predator are capable of being predator-limited (Menge and Sutherland 1987, Power 1990). In my system, I found high trophic connectance; crayfish (a top predator) directly affected both invertebrates (primary and secondary consumers) and algae (primary producers).

Other studies of the role of crayfish in benthic food webs have demonstrated similar connectance among trophic levels. Lodge et al. (1994) observed a decline in snail abundance and an increase in periphyton chlorophyll a (attached to plastic strips) within crayfish (Orconectes rusticus) enclosures in a north-temperate lake. Crayfish, however, also reduced macrophyte surface area (which periphyton colonizes). Therefore, total periphyton probably declined within crayfish enclosures. Creed (1990) and Hart (1992) demonstrated that crayfish (Orconectes propinquus) directly reduced the macroalga, Cladophora glomerata, in Augusta Creek, MI, USA. By reducing Cladophora abundance, crayfish allowed microalgae and associated macroinvertebrates to proliferate, thus serving as a "keystone predator" (Hart 1992). Although both stream studies noted that crayfish can directly reduce macroinvertebrates, neither explored the consequences of this direct effect on the benthic food web.

In other top-down models, effects of the top-level organism "cascade" down the food chain, directly affecting prey, but indirectly affecting lower trophic levels (sensu Hairston et al. 1960, Paine 1980, Carpenter et al. 1985). In my study, crayfish did directly reduce their prey (invertebrates), thus indirectly causing an increase in primary producers. These indirect effects, however, were damped by the direct, negative effects of crayfish on primary producers. Thus, the net effect of crayfish on primary producers was less than would have been predicted by a "cascade" model.

A top-level omnivorous organism has produced a trophic "cascade" in other freshwater systems. Carpenter et al. (1987) demonstrated that largemouth bass (Micropterus salmoides) can produce a trophic cascade within north-temperate lakes. Power (1990) demonstrated cascading effects by a top-level omnivore (California roach, Hesperoleucus symmetricus) in a riverine system (South Fork of the Eel River, CA, USA).

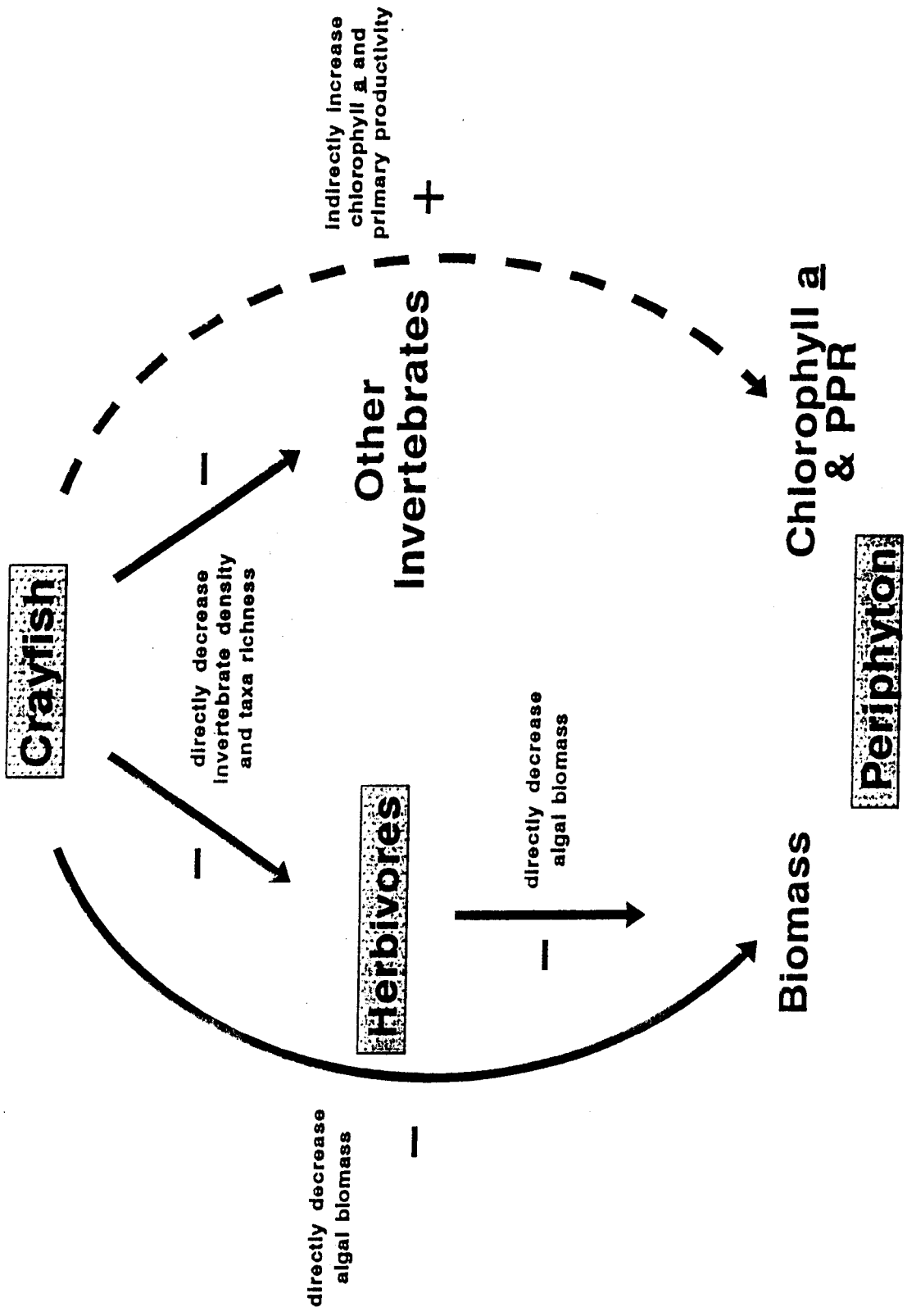
In both of these studies, the importance of omnivory (and subsequent high connectance among trophic levels), may have been underestimated or obscured. Power (1990) acknowledged that roach omnivory affected the Eel River food web in the same way as roach carnivory, yet described the food web as showing "chain-like, rather than web-like dynamics" (Power 1992). By definition, however, omnivory results in a food web, rather than a food chain. Power could be underrating the effects of omnivory by characterizing the food web as a food chain. Carpenter et al. recognize that adult largemouth bass are omnivorous (Carpenter et al. 1987, Hodgson and Kitchell 1987), yet their model incorporates only the effects of adult piscivory (Carpenter et al.

1985). Therefore, Carpenter et al. (1987) probably underestimated the importance of omnivory by not considering the varied diet of their top-level predator. Conversely, Lodge et al. (1994) suggest that omnivory may play a subtle but important role in food webs. If Lodge et al. had not considered the decline in macrophytes from crayfish grazing, they may have concluded that the food web operated through a trophic "cascade". Instead, they concluded that because of omnivory, the food web was more complex and had more interconnections.

Studies examining the effects of omnivorous crayfish on freshwater benthic communities have found that crayfish can affect the abundance, composition, and distribution of species within the community. My study augments this literature by demonstrating the importance of crayfish in streams, especially cool-water streams, in which they are a top-level organism. I conclude that crayfish can have both direct and indirect effects on the benthos (Fig. 4). These effects combine to produce a strong (negative) effect on macroinvertebrates, but a damped effect on algae.

My findings have implications for both applied and theoretical ecology. At the applied level, the crayfish, Orconectes rusticus, is an invading species whose range is expanding. My results suggest that major changes may occur in the stream benthic community upon invasion of this species. At a theoretical level, my results suggest that omnivory can play an important role in structuring freshwater communities. The effects of omnivory, however, may be underestimated or obscured without careful study. By not fully considering the presence and ramifications of omnivory, an important structuring force in food webs is overlooked.

Figure 4. Simplified benthic food web in the Middle Branch of the Ontonagon River, showing direct (solid lines) and indirect (broken lines) effects of crayfish on other food web components. PPR=primary productivity.



CHAPTER 3

CONCLUSIONS

Results from the enclosure experiments and the gradient study demonstrate that the rusty crayfish, Orconectes rusticus, is an important component of the benthic community within the Middle Branch of the Ontonagon River (Michigan, USA). This crayfish directly reduced epilithic periphyton biomass and macroinvertebrate density, and indirectly increased epilithic periphyton chlorophyll a and primary productivity. These impacts are comparable to those exerted by O. rusticus on lake littoral communities in northern Wisconsin; crayfish directly reduced snail densities, which led to enhanced benthic periphyton biomass (Weber and Lodge 1990) and enhanced epiphytic periphyton chlorophyll a (Lodge et al. 1994). My results extend the information generated from other stream crayfish studies (Creed 1990, Hart 1992), which have shown that a congeneric crayfish (Orconectes propinquus) can have direct negative effects on the abundance of benthic macroalgae (e.g., Cladophora). By harvesting macroalgae, crayfish indirectly reduced the local abundance of microalgae and macroinvertebrates that are associated with macroalgae.

My findings suggest that stream benthic communities are altered by the invasion or introduction of O. rusticus. Results from the enclosure experiments and the gradient study indicated that O. rusticus in densities of 5/m² and 3/m², respectively, affected both periphyton and

macroinvertebrates. In streams within its native range (e.g., Ohio), O. rusticus can reach densities of 21/m² (Momot et al. 1978). If this crayfish is able to obtain similar densities in streams it invades or in which it is introduced, I would expect even greater responses in periphyton and macroinvertebrates than those observed in this study. Its introduction in streams also may indirectly affect the resident fishes that rely on macroinvertebrates and algae for food (e.g., trout, minnows). By feeding on the benthos, O. rusticus may reduce the amount of food available to fish, thus affecting fish growth or survival. This process may have important ramifications for streams such as the Middle Branch of the Ontonagon River that support a sport fishery.

I expect O. rusticus to have a greater effect on stream benthic communities than either O. propinquus or O. virilis, two closely related congeners of O. rusticus that currently inhabit streams of northern Wisconsin and Michigan. O. virilis is the native orconectid, and O. propinquus was introduced about 60 years ago (Capelli and Munjal 1982). O. rusticus has a higher feeding rate than the other two species (Olsen et al. 1991), and thus likely would consume more benthic organisms than its congeners. Also, because of its large size (DiDonato and Lodge 1993, Olsen et al. 1991) and aggressiveness (Garvey et al. 1994), adult O. rusticus are less susceptible to predation by fish (e.g., bass) than either adult O. propinquus or O. virilis (Garvey et al. 1994). Therefore, in streams with fish that prey on adult crayfish, predation may be less effective in regulating populations of O. rusticus than in regulating populations of O. virilis and O. propinquus.

Results of this study also indicate that omnivory (defined as feeding at more than one trophic level; Pimm and Lawton 1978) by

crayfish is an important process in the Middle Branch of the Ontonagon River. This supports the Menge-Sutherland model that proposes that food webs are controlled from the top down, and presumes that omnivory is prevalent in aquatic ecosystems (Menge and Sutherland 1987). The importance of omnivory in aquatic food webs, however, may be underestimated (see Lodge et al. 1994). This is especially true in food web studies that examine the effects of a poly-trophic organism, but only focus on (1) a particular component (e.g., detritivory, herbivory, or predation) of its omnivory (e.g., Power 1990), or (2) the effects of a poly-trophic predator (e.g., bass) on a single trophic level (e.g., Carpenter et al. 1987). Failure to consider omnivory in its entirety may result in underestimation of an important structuring process in aquatic ecosystems.

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APPENDIX A: SUPPLEMENTARY DATA

APPENDIX A.1

STREAMS IN NORTHERN WISCONSIN AND THE UPPER PENINSULA OF MICHIGAN SURVEYED FOR O. RUSTICUS IN JUNE/JULY 1991
AND LOCATION OF SAMPLING SITES

Stream	County and state	Sampling site	Sampling method	<u>O. rusticus</u> (no./m ²)
Allequash Creek	Vilas Co., WI	75 m upstream of Trout Lake	Snorkeling and counting within 0.25/m ² quadrats	2.2
Mann Creek	Vilas Co., WI	Downstream of Mann Pond	Single mark/recapture	4.2
			Visual survey	0
			of 75 m	

Stevenson Creek	Vilas Co, WI	50 m upstream of Trout Lake	Visual survey of 20 m	0
Tamarack River	Ontonagon Co., MI	Downstream of Old U.S. 2	2 traps/site	0
		Upstream of Old U.S. 2/downstream of Tamarack Lake	Visual survey of 100 m	0
Trout River	Vilas Co., WI	50 m downstream of Trout Lake	Visual survey of 50 m	0
Wisconsin River	Oneida Co. WI	Roadside park, highway 70, Eagle River	Visual survey of 20 m	8

APPENDIX A.2

ADDITIONAL DESCRIPTIVE PARAMETERS FOR STUDY SITES (GR1-GR4) ALONG THE CRAYFISH GRADIENT WITHIN THE MIDDLE BRANCH OF THE ONTONAGON RIVER. DATA FOR WATER DEPTH, CHANNEL WIDTH, AND ROCK SIZE (MEASURED AS ROCK DIAMETER) ARE MEANS (\pm S.E.)

Site	Water depth (m)	Channel width		Gradient (%)	Rock size (cm)
		Wetted (m)	Active (m)		
GR4	0.2 (± 0.02)	18.0 (± 2.2)	23.9 (± 2.8)	2.1	10.0 (± 0.5)
GR3	0.2 (± 0.02)	17.7 (± 1.4)	34.7 (± 2.9)	1.1	7.7 (± 0.4)
GR2	0.3 (± 0.01)	15.9 (± 0.5)	19.8 (± 1.2)	0.25	5.4 (± 0.4)
GR1	0.2 (± 0.01)	15.8 (± 0.3)	28.7 (± 2.5)	0.45	7.2 (± 0.5)

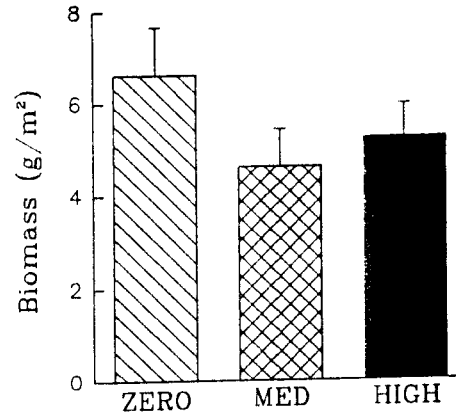
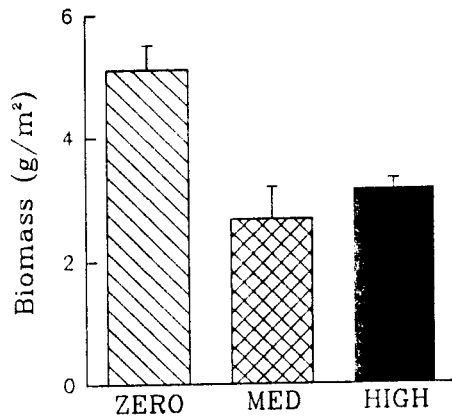
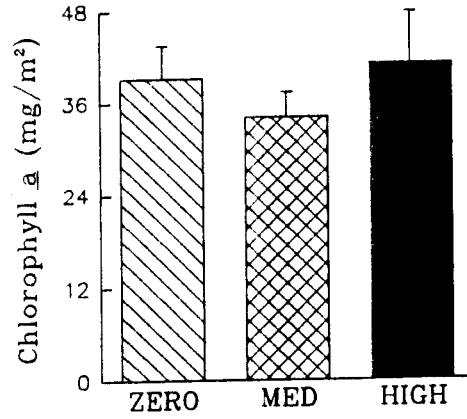
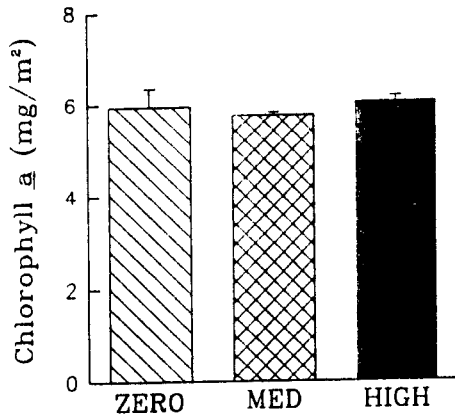
APPENDIX A.3

COMPARISON OF PERIPHYTON CHLOROPHYLL a, PERIPHYTON BIOMASS, MACROINVERTEBRATE DENSITY, AND MACROINVERTEBRATE TAXA RICHNESS ON ARTIFICIAL SUBSTRATA WITHIN EXPERIMENTAL ENCLOSURES (N=5) AND NATURAL SUBSTRATA (ROCKS; N=5) SAMPLED FROM THE STREAMBED. ARTIFICIAL SUBSTRATA WERE COLONIZED FOR 22 D. NATURAL SUBSTRATA WERE COLONIZED FOR AN UNDETERMINED PERIOD. DATA PRESENTED ARE MEANS (\pm S.E.)

Substrata	Chlorophyll <u>a</u> (mg/m ²)	Biomass (g/m ²)	Macroinvertebrates (no./m ²)	Macroinvertebrate taxa richness (no. taxa/enclosure)
Artificial	38.4 (\pm 3.6)	6.1 (\pm 1.2)	14878 (\pm 1513)	12.6 (\pm 0.4)
Natural	15.9 (\pm 6.2)	8.1 (\pm 0.7)	21891 (\pm 4764)	9.6 (\pm 1.3)

APPENDIX A.4

PERIPHYTON CHLOROPHYLL a AND BIOMASS AT THE MIDPOINT OF EXPERIMENT I (DAY 16) and EXPERIMENT II (DAY 21). DATA ARE MEANS (\pm S.E.)



Experiment I

Experiment II

APPENDIX A.5

ESTIMATES OF NET COMMUNITY PRIMARY PRODUCTIVITY (NCPP), COMMUNITY RESPIRATION (CR), AND GROSS COMMUNITY PRIMARY PRODUCTIVITY (GCPP) AT THE END OF EXPERIMENT I. A SINGLE INCUBATION OF THREE SUBSTRATA WAS CONDUCTED FOR EACH TREATMENT. SUBSTRATA WERE INCUBATED WITHIN A PLEXIGLAS® CHAMBER AS DESCRIBED BY FULLER AND BUCHER (1991)

Treatment	NCPP (mg O ₂ ·m ⁻² ·hr ⁻¹)	CR (mg O ₂ ·m ⁻² ·hr ⁻¹)	GCPP (mg O ₂ ·m ⁻² ·hr ⁻¹)
ZERO	131.9	33.9	165.8
MED	118.6	34.8	153.4
HIGH	180.6	30.1	210.7

APPENDIX A.6

MACROINVERTEBRATE TAXA SAMPLED FROM THE MIDDLE BRANCH OF THE ONTONAGON RIVER IN EXPERIMENT I, EXPERIMENT II, AND IN THE GRADIENT STUDY. AN "X" INDICATES THAT A TAXON WAS PRESENT

Taxon	Experiment I	Experiment II	Gradient Study
Hydroida			
Hydridae			
<u>Hydra</u> spp.	X	X	
Nematoda	X	X	X
Gastropoda	X	X	
Ancylidae	X	X	X
Lymnaeidae	X	X	
Physidae			
<u>Physa</u> spp.	X	X	
Planorbidae		X	
Pelecypoda	X	X	
Oligochaeta	X	X	X
Hydracarina	X	X	X
Ostracoda	X	X	
Collembola	X		

Ephemeroptera	X	X	X
Siphonuridae			
<u>Ameletus</u> spp.	X		
Baetidae	X	X	X
<u>Baetis</u> spp.	X	X	X
<u>Pseudocloeon</u> spp.		X	
Heptageniidae	X	X	X
<u>Epeorus</u> spp.		X	
<u>Leucrocuta</u> spp.	X	X	X
<u>Stenonema</u> spp.		X	
Ephemerellidae		X	X
<u>Attenella</u> spp.		X	
<u>Serratella</u> spp.	X	X	X
Tricorythidae			
<u>Tricorythodes</u> spp.	X	X	
Caenidae	X		X
<u>Caenis</u> spp.	X	X	X
Leptophlebiidae	X	X	
<u>Paraleptophlebia</u> spp.		X	
Plecoptera		X	X

Peltoperlidae	X		X
Perlidae	X		
<u>Acroneuria</u> spp.		X	X
<u>Beloneuria</u> spp.		X	X
Trichoptera	X	X	X
Psychomyiidae	X	X	X
Polycentropodidae	X		
Hydropsychidae	X	X	X
<u>Hydropsyche</u> spp.	X	X	X
Rhyacophilidae	X		
Glossosomatidae			
<u>Glossosoma</u> spp.	X	X	X
Hydroptilidae	X	X	
<u>Hydroptila</u> spp.		X	
<u>Leucotrichia</u> spp.	X	X	X
<u>Neotrichia</u> spp.			X
Brachycentridae			
<u>Brachycentrus</u> spp.		X	
Lepidostomatidae			
<u>Lepidostoma</u> spp.	X	X	

Limnephilidae	X		
<u>Neophylax</u> spp.			X
Helicopsychidae			
<u>Helicopsyche</u> spp.	X	X	
Leptoceridae	X		X
<u>Ceraclea</u> spp.		X	
<u>Oecetis</u> spp.	X	X	
<u>Setodes</u> spp.	X	X	
Coleoptera	X		
Psephenidae		X	
Elmidae	X	X	
<u>Optioservus</u> spp.			X
<u>Stenelmis</u> spp.	X		
Diptera	X		
Tipulidae	X	X	X
<u>Antocha</u> spp.	X	X	X
Ceratopogonidae	X	X	
Simuliidae	X	X	X
Chironomidae	X	X	X
Athericidae			

<u>Atherix variegata</u>		X	
Empididae	X		
<u>Hemerodromia</u> spp.		X	X
Ephydriidae		X	

APPENDIX A.7

DENSITIES (NO./M²) OF MACROINVERTEBRATE TAXA SAMPLED FROM EACH GRADIENT SITE WITHIN THE MIDDLE BRANCH OF THE ONTONAGON RIVER. DATA ARE MEANS (N=5)

Taxon	GR1	GR2	GR3	GR4
Nematoda	--	--	--	16.4
Ancylidae	--	--	15.6	--
Oligochaeta	20.8	--	--	--
Hydracarina	45.9	39.1	57.1	113.3
Ephemeroptera				
Baetidae				
<u>Baetis</u> spp.	626.3	678.7	1673.2	966.0
Unidentified	100.5	360.1	764.1	861.3
Heptageniidae				
<u>Leucrocuta</u> spp.	143.7	12.4	103.3	--
Unidentified	184.0	259.2	446.1	311.1
Ephemerellidae				
<u>Serratella</u> spp.	--	--	20.8	--
Unidentified	41.8	80.0	1428.6	132.7
Caenidae				

<u>Caenis</u> spp.	---	--	67.1	--
Unidentified	--	--	41.5	--
Unidentified	528.9	859.0	1092.4	383.7
Plecoptera				
Peltoperlidae				
<u>Acroneuria</u> spp.	--	13.3	43.1	35.9
<u>Beloneuria</u> spp.	--	--	62.7	39.0
Unidentified	20.8	--	--	--
Unidentified	208.0	12.4	--	113.3
Trichoptera				
Psychomyiidae	118.7	27.9	211.6	175.3
Hydropsychidae				
<u>Hydropsyche</u> spp.	--	64.8	263.3	--
Unidentified	45.9	111.7	307.3	19.5
Glossosomatidae				
<u>Glossosoma</u> spp.	187.2	304.7	1821.5	239.0
Hydroptilidae				
<u>Leucotrichia</u> spp.	25.1	176.8	--	2296.1
<u>Neotrichia</u> spp.	--	--	--	16.4
Limnephilidae				

<u>Neophylax</u> spp.	100.5	13.3	--	--
Leptoceridae	--	--	--	19.4
Unidentified	17.6	14.6	85.3	116.9
Coleoptera				
Elmidae				
<u>Optioservus</u> spp.	--	--	--	19.4
Diptera				
Tipulidae				
<u>Antocha</u> spp.	20.9	13.3	42.5	659.9
Unidentified	105.1	114.8	114.3	1404.2
Simuliidae	--	--	58.0	--
Chironomidae	1408.6	1962.4	5754.5	13266.9
Empididae				
<u>Hemerodromia</u> spp.	--	--	20.8	--

THE EFFECTS OF CRAYFISH (ORCONECTES RUSTICUS)
ON THE MACROINVERTEBRATE AND ALGAL ASSEMBLAGES
IN A NORTHERN MICHIGAN STREAM

Abstract

by

Patrice Marie Charlebois

The rusty crayfish, Orconectes rusticus, has invaded streams of northern Wisconsin and Michigan, but its effects on benthos in these streams are unknown. In the Ontonagon River (Michigan), crayfish effects on periphyton and macroinvertebrates were examined within experimental crayfish enclosures and along a natural crayfish density gradient that occurs over 3 km of the stream. In enclosures, crayfish directly reduced herbivore densities by 55-82% and total macroinvertebrates by 47-79%. Crayfish indirectly increased chlorophyll a by 21-54% and enhanced primary productivity by two orders of magnitude. By removing herbivores and loosely attached periphyton, crayfish may have allowed adnate algal cells to flourish. Similar relationships among densities of crayfish, macroinvertebrates, and algae were observed along the natural gradient. Therefore, O. rusticus directly or indirectly affected at least two trophic levels of the stream benthic food web. These results indicate that rusty crayfish can exert strong effects on the benthic systems of streams that they invade.