Hydrobiologia **462:** 131–144, 2001.

A comparison of the trophic ecology of the crayfishes (*Orconectes nais* (Faxon) and *Orconectes neglectus* (Faxon)) and the central stoneroller minnow (*Campostoma anomalum* (Rafinesque)): omnivory in a tallgrass prairie stream

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Received 21 September 2000; in revised form 26 June 2001; accepted 5 August 2001

Key words: food webs, herbivory, omnivory, stable isotopes, gut analysis

Abstract

Omnivorous fish, such as the central stoneroller minnow (*Campostoma anomalum* (Rafinesque)), and crayfish often play important roles in the trophic dynamics of streams. The trophic role of these two omnivores has not been compared within a system even though they both consume algae, detritus and invertebrates and often co-occur in streams in the Midwestern United States. Natural abundance of ^{15}N and ^{13}C isotopes and a whole stream ^{15}N-labeled ammonium chloride release were used to compare the trophic ecology of the central stoneroller minnow (*Campostoma anomalum* (Rafinesque)) and two species of crayfish (*Orconectes neglectus* (Faxon) and *Orconectes nais* (Faxon)) in a tallgrass prairie stream. The δ^{15}N and δ^{13}C values of *Orconectes* spp. were more similar to coarse benthic organic matter (CBOM) and filamentous green algae than to invertebrates, fine benthic organic matter (FBOM), and periphyton. Values for δ^{15}N and δ^{13}C in *C. anomalum* were more similar to grazer and collector invertebrates and filamentous green algae than to FBOM and periphyton. Results from a ^{15}N tracer release also indicated a portion of algae and/or invertebrates were a component of nitrogen assimilated in *Orconectes* spp. and *C. anomalum* diets. Gut contents of *C. anomalum* were also analyzed. In contrast to stable isotope data, amorphous detritus was a significant component of *C. anomalum* guts, followed by diatoms and filamentous green algae. A significant percentage of invertebrate material was found in *C. anomalum* guts sampled in the spring. Experiments were conducted in artificial streams to determine if *Orconectes* spp. and *C. anomalum* could reduce epilithic algal biomass in small streams. Algal biomass on clay tile substrata was decreased relative to controls in artificial stream channels containing *O. neglectus* (3.4 fold, p=0.0002), *C. anomalum* (2.1 fold, p=0.0012), and both species combined (3.0 fold, p=0.0003). Results indicate that *Orconectes* spp. are functioning more as algal and detrital processors than as predators in Kings Creek. Isotope and gut content data show that *C. anomalum* includes invertebrates as well as algae and detritus in its diet. Both species have the potential to affect algal biomass and are important omnivores in the stream food web.

Introduction

The central stoneroller minnow (*Campostoma anomalum* (Rafinesque)) and two species of crayfish, *Orconectes nais* (Faxon) and *Orconectes neglectus* (Faxon), co-occur in Kings Creek, a tallgrass prairie stream located within Konza Prairie Biological Station (KPBS), Kansas. Both crayfish and *C. anomalum* are important components of nitrogen cycling through the food web in Kings Creek (Dodds et al., 2000). These

omnivorous organisms are known to ingest detritus, algae, and macroinvertebrates. However, we know of no published studies on the detailed feeding ecology of both crayfish and *C. anomalum* within a system. This subject was addressed in the present study.

C. anomalum is a widespread and abundant cyprinid fish species in eastern and central North America. They can consume up to 27% of their body weight in benthic algae per day (Fowler & Taber, 1985), significantly decrease algal biomass (Power et al., 1985; Stewart, 1987; Power et al., 1988; Gelwick & Matthews, 1992), reduce algal spatial and temporal heterogeneity (Gelwick & Matthews, 1997), and affect algal community composition (Power & Matthews, 1983; Power et al., 1988).

Crayfish are found in many freshwater benthic habitats and often comprise a significant component of invertebrate biomass in lakes and streams (Vannote, 1963; Mason, 1974; Momot et al., 1978, Rabeni et al., 1995). Crayfish also can be important consumers of algae (Whiteledge & Rabeni, 1997) and can affect benthic algal communities of aquatic systems through both direct and indirect trophic interactions. Crayfish grazing can decrease the biomass of *Cladophora* (Hart, 1992; Creed, 1994) and diatom abundance (Keller & Ruman, 1998) in streams, and can decrease algal biomass in artificial pools (McCormick, 1990). However, they have also been shown to have positive effects on benthic algal communities (i.e. increases in periphyton biomass or periphyton chlorophyll *a* per unit area) in both lentic and lotic systems (Lodge et al., 1994; Charlebois & Lamberti, 1996; Nystrom et al., 1999).

Benthic algal production is an important carbon (C) source in upland prairie reaches and can equal particulate allochthonous C inputs in the downstream gallery forest reaches of Kings Creek (Tate, 1990; Dodds et al., 1996). Both crayfish and *C. anomalum* have the potential to impact algal communities in Kings Creek. However, few comparative data on the feeding ecology of crayfish and *C. anomalum* are available from tallgrass prairie streams. Our main objectives were: (i) to compare the importance and feeding ecology of algal food sources to *C. anomalum*, *O. nais* and *O. neglectus* in a tallgrass prairie stream using stable isotopes and gut analyses, and (ii) to determine if crayfish and *C. anomalum* could affect periphyton biomass in small streams, using experiments in artificial stream channels.

We used natural abundance of carbon and nitrogen isotopes (^{13}C and ^{15}N) and an in-stream ^{15}N-labeled ammonium chloride release to assess the trophic position of crayfish and *C. anomalum*, and to determine likely food sources important for tissue production in Kings Creek. Measurements of stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) yield a time-integrated assessment of resource use and can indicate broad categories of food sources, which are important for tissue production (Peterson & Fry, 1987; Gearing, 1991; Vander Zanden & Rassmussen, 1999). The concentrations of ^{13}C and ^{15}N in consumer body tissue are often slightly higher than those concentrations found in their food sources because the lighter isotopes (^{12}C and ^{14}N) are preferentially used by enzymes associated with assimilation, respiration and excretion. The fractionation of N is greater and more consistent than that of C (Peterson & Fry, 1987; Focken & Becker, 1998). An average fractionation of 0.2–1‰ is found for $\delta^{13}C$ values of consumer tissue relative to their food source (DeNiro & Epstein, 1978; Peterson & Fry, 1987) and an average of 3.2 to 3.4‰ for $\delta^{15}N$ consumer tissue (DeNiro & Epstein, 1981; Peterson & Fry, 1987; Vander Zanden & Rassmussen, 1999) relative to the isotopic ratio of their food source.

Examination of gut contents also can be helpful in determining resource use by an animal; such data indicate actual food sources ingested at a particular moment in time, but not assimilation. Gut contents of *C. anomalum* were examined to compare food sources ingested with those indicated to be important for tissue production from stable isotope data. In addition, a series of experiments in artificial stream channels were conducted to confirm the ability of natural densities of *Orconectes* spp. and *C. anomalum* to control algal biomass.

Materials and methods

Site description

Kings Creek drains approximately 1059 ha of KPBS, a tallgrass prairie preserve located near Manhattan, Kansas. Riparian vegetation of the upland reaches of Kings Creek consists of grasses and shrubs and the stream channel receives high irradiance (Watershed N20B, N4D and N2B, Fig. 1). In contrast, lower reaches (Nature Trail Area in Watershed AL, Fig. 1) are in an oak gallery forest and receive less irradiance. Primary production by algae in Kings Creek can account for 83% of the C input in upstream reaches and 24% in gallery forest reaches in some years (Gurtz et

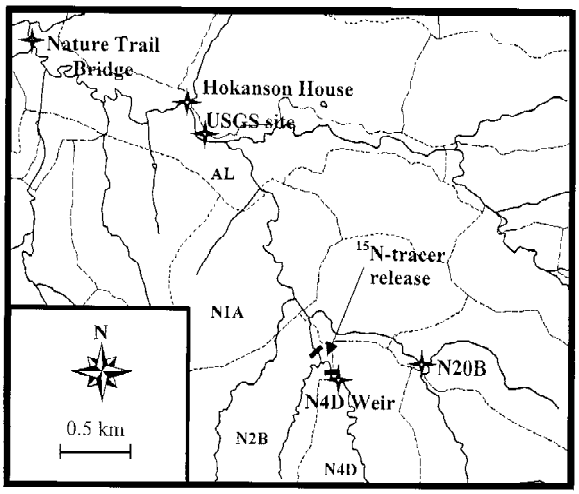

Figure 1. Kings Creek drainage basin located within Konza Prairie Biological Station. Solid lines indicate the stream channel. Dotted lines designate watershed boundaries. Natural abundance samples for ^{15}N and ^{13}C were taken from each starred site. The ^{15}N ammonium release took place between the two solid lines in watershed N4D

al., 1988; Dodds et al., 1996). Detailed site descriptions of KPBS stream hydrology, geochemistry and ecology have been published (Gray et al., 1998; Gray & Dodds, 1998).

C. anomalum is one of the most common and abundant fish species in Kings Creek (Gray & Dodds, 1998). Densities ranged from 0.16 to 1.6 ind m^{-2} in 1999 (Evans-White, 2000). *Orconectes* spp. densities ranged from 0.12 to 8.5 ind m^{-2} in that same year. Biomass of *C. anomalum* and *Orconectes* spp. estimated in 1998 in conjunction with the ^{15}N-labeled ammonium chloride release were 0.01 and 0.13 g dry mass (D.M.) m^{-2}, respectively, (Dodds et al., 2000). Average annual biomass of *C. anomalum* and *Orconectes* spp. in 1999 were 0.20 and 0.54 g AFDM m^{-2}, respectively (Evans-White, 2000).

Natural abundance of ^{13}C and ^{15}N

Samples of algae, detritus, invertebrates and fishes were collected for stable isotope analysis from Kings Creek on 17 June, 7 July, 26 July, 1 December 1995, and 20 February, 14 June, 18 June 1996 to (i) determine which food resources are important to *Orconectes* spp. and *C. anomalum* in Kings Creek, and (ii) to compare *Orconectes* spp. and *C. anomalum* $\delta^{13}C$ and $\delta^{15}N$ measurements with those of other consumers in the system. Samples were collected from a variety of sites including headwater and lower reaches of Kings Creek that are separated by approximately 2–3 km (Fig. 1).

Periphyton and diatom samples were obtained by scraping several rocks with apparently healthy pigmented mats with a knife blade at each site on each date. Aquatic insects and other small invertebrates were collected with hand nets (0.25-mm mesh) or by hand picking from stream substrata. Macroinvertebrates sampled included *Physa* sp., *Stenonema femoratum*, Baetidae, Corixidae, Chironomidae, *Chemautopsyche* sp., *Hydropsyche* sp., *Tipula* sp., *Polycentropus* sp., *Perlesta placida*, Dytiscidae and a Zygoptera nymph. Seines (6-mm mesh) and hand nets were used to capture a range of sizes of *Orconectes* spp. (17.5–42.5 mm carapace length (C.L.), *C. anomalum* (40–90 mm total length (T.L.)), southern redbelly dace (*Phoxinus erythrogaster*) (30–70 mm T.L.), orangethroat darters (*Etheostoma spectabile*) (23–50 mm T.L.) and creek chubs (*Semotilus atromaculatus*) (40–100 mm T.L.). Living filamentous algae (*Cladophora*, *Spirogyra*, *Oedogonia*, *Ulothrix*) and macrophytes (*Veronica* sp.) were collected by hand from the stream bottom. Sample sizes for biota and detritus ranged from 1 to 6 within a sampling period (Tables 1, 2 and 3).

Benthic detritus was collected by scooping shallow benthic surface accumulations. The material then was separated into coarse benthic organic matter (CBOM, >1 mm) and fine benthic organic matter (FBOM, 0.071–1.0 mm) fractions by elutriation through standard sieves. CBOM was mostly leaf litter. Small wood pieces composed $<5\%$ of the allochthonous CBOM analyzed. Large pieces of wood were rare and not retained for further analysis.

All samples were placed in plastic bags and frozen until sorted and identified in the laboratory. *Orconectes* spp. and fish muscle tissue were removed to insure that body lipid content would not influence ^{13}C measurements (Focken & Becker, 1998) and the remaining carcasses discarded. After this initial processing, all samples were dried at 60°C for 96 h, ground to a fine powder, and stored in plastic vials. Samples with carbonates present (e.g. limestone fragments in periphyton scrapings) were split into two subsamples. The subsample for ^{13}C analysis was treated with dilute HCl to remove carbonates. After bubbling ceased, the sample was treated with dilute NaOH to neutralize excess acid and dried. The subsample for ^{15}N analysis was not treated.

Mass spectrometry was performed with a Europa Scientific 20/20 stable isotope analyzer attached to

Table 1. Mean, standard error, and sample size ($X \pm 1$ SE (N)) of δ^{15}N values for algae, detritus, *Orconectes* spp., and fishes on each date. Filamentous greens include several genera of filamentous green algae combined

	June/July–1995	December–1995	February–1996	June–1996
Periphyton	5.0 ± 1.81 (4)	–	–	–
Filamentous greens	2.1 (1)	–	–	–
Spirogyra sp.	–	10.0 ± 0.69 (3)	5.9 ± 0.51 (3)	2.9 ± 0.20 (3)
Ulothrix sp.	–	4.3 ± 0.29 (3)	–	–
Cladophora sp.	–	5.3 ± 0.14 (3)	2.8 ± 0.38 (3)	2.2 ± 0.47 (3)
Oedegonium sp.	–	–	–	4.0 ± 0.16 (3)
Diatoms	–	6.3 ± 0.82 (3)	6.1 ± 0.24 (3)	4.9 ± 0.24(3)
FBOM	4.3 ± 1.41 (4)	6.2 ± 0.27 (3)	–	2.7 ± 0.12 (3)
CBOM	3.0 ± 1.44 (3)	4.0 ± 0.05 (3)	–	1.1 ± 0.19 (5)
Veronica sp.	4.5 (1)	5.3 ± 0.58 (3)	–	–
O. nais	5.5 ± 0.65 (4)	–	–	7.5 ± 0.18 (2)
O. neglectus	–	7.4 ± 0.27 (3)	–	7.2 ± 0.32 (3)
E. spectabile	8.2 ± 0.50 (3)	12.0 ± 0.07 (3)	–	–
P. erythrogaster	7.7 ± 2.03 (2)	10.7 ± 0.17 (3)	–	8.7 ± 0.41 (6)
C. anomalum	9.3 (1)	12.1 (1)	10.8 ± 0.35 (3)	8.9 ± 0.98 (6)
S. atromaculatus	11.4 (1)	10.6 ± 1.06 (3)–62.6 ± 2.45 (2)		

a Europa automated N and C analyzer in the Kansas State University Department of Agronomy. Citrus leaves were used as the reference standard for ^{15}N determinations. Mean standard error of duplicate citrus leave standards was 0.27‰. For the ^{13}C analysis, pure cane sugar that had been standardized against NBS19 limestone served as the reference standard (duplicate standard error (S.E.)=0.29‰). Stable isotope ratios are reported in the standard notation:

$$\delta X = [R_{\text{sample}}/R_{\text{standard}}) - 1 \times 1000,$$

where X is ^{13}C or ^{15}N and R is ^{13}C/^{12}C or ^{15}N/^{14}N, respectively. Values are expressed on a per mil (‰) basis.

Gut content analysis

C. anomalum, *P. erythrogaster* and *E. spectabile* were collected for gut content analyses to determine how gut contents would compare to the food sources suggested to be important by stable isotopes. Fishes were seined on 14 June and 18 June 1996, 8 July and 7 August 1998, and on 25 March 1999 and frozen for later analysis. Fishes sampled in 1996 were taken directly from sites where stable isotope samples were taken (Watershed N20B, N4D, and the Nature Trail area (NT), Fig. 1)). Samples from 1998 were taken from the stream reach where the ^{15}N ammonium tracer release took place (Watershed N4D). All samples collected in 1999 were collected from the NT area and were representative of previous stable isotope collection sites. Foreguts from fishes collected in 1996 and the first quarter of the gut of fishes from 1998 were suspended in distilled water, filtered through a Millipore HA filter (0.45 μm), and examined microscopically (400× = total magnification) (Gray & Ward, 1979). The percentage area on the filter of each food type relative to all food types present was quantified for 20–25 fields of view. Foreguts of *C. anomalum* collected in 1999 were analyzed on a slide microscopically (400× = total magnification). The percentage area of each food type in 10 random fields of view was digitally analyzed using Scion Image software. These were done in conjunction with another study and, therefore, methodology was slightly different than for the 1998 and 1996 samples, but the methods compared favorably (Evans-White, 2000). *C. anomalum* and southern redbelly dace gut contents taken from site N4D in 1996 were pooled according to size category of each fish species and one filter was examined for each size category (40–50 mm and 60–70 mm T.L.).

$^{15}NH_4$ tracer release

Isotope data for *C. anomalum* and *Orconectes* spp. collected during a ^{15}N-labeled ammonium chloride release into Kings Creek were analyzed to (i) determine

Table 2. Mean, standard error, and sample size ($X \pm 1$ SE (N)) of δ^{13}C values for algae, detritus,*Orconectes*spp., and fishes on each date

	June/July–1995	December–1995	February–1996	June–1996
Periphyton	-11.0 ± 1.54 (4)	–	–	–
Spirogyra sp.	–	-31.7 ± 1.69 (3)	-36.0 ± 1.35 (3)	-18.3 ± 0.24 (3)
Ulothrix sp.	–	-36.5 ± 0.32 (3)	–	–
Cladophora sp.	–	-30.0 ± 0.77 (3)	-37.2 ± 1.25 (3)	–
Oedegonium sp.	–	–	–	-27.5 ± 0.06 (3)
Diatoms	–	-18.3 ± 3.09 (3)	-9.3 ± 0.13 (3)	-18.9 ± 0.32 (3)
FBOM	-13.2 ± 1.94 (4)	-21.2 ± 2.91 (3)	–	-17.9 ± 0.11 (3)
CBOM	-25.9 ± 0.65 (3)	-28.3 ± 0.19 (3)	–	-27.9 (1)
O. nais	-26.7 ± 0.55 (3)	–	–	-26.6 ± 0.14 (3)
O. neglectus	–	-25.5 ± 0.84 (3)	–	-26.8 ± 0.16 (3)
E. spectabile	-28.7 ± 0.51 (2)	-27.3 ± 0.72 (3)	–	–
P. erythrogaster	-24.4 (1)	-28.4 ± 0.10 (3)	–	-27.7 ± 0.30 (6)
C. anomalum	-32.7 (1)	-26.5 (1)	-29.3 ± 0.18 (3)	-29.2 ± 0.58 (6)
S. atromaculatus	-25.6 (1)	-27.3 ± 2.20 (3)	–	-25.0 ± 0.13 (3)

important nitrogen food sources for *Orconectes* sp. and *C. anomalum*, and (ii) compare those food sources to ones indicated by natural abundance ^{13}C and ^{15}N data obtained in 1995 and 1996. A 210 m intermittent prairie stream reach was used for the ammonium release (Fig. 1). This reach dried the previous summer and resumed flow over the winter. *Orconectes* spp. and *C. anomalum* re-colonized the reach within 14 days after the start of the ammonium release (7 April 1998) from either upstream or downstream reaches with permanent flowing water. A solution of 0.23 mm NH_4^+ enriched to 10 mol% ^{15}N was released at an average rate of 2.2 ml min^{-1}and raised background ammonium concentrations by less than 1% over a period of 35 days. Samples of *Orconectes* spp., *C. anomalum* and various food sources (leaves, epilithon, FBOM, macroinvertebrates) were collected for mass spectrometer analysis from various sites above (i.e. a control site for determination of natural abundance of ^{15}N) and below the release station approximately every 7 days for the duration of the release and for several days after it was terminated. Generally, only one sample was taken from each site on each date. Refer to Dodds et al. (2000) for a more detailed site and sampling description. All invertebrates and fishes sampled were placed in containers for 24 h to allow them to clear their guts before they were sacrificed for analysis. Sampled *Orconectes* spp. were divided into 3 size classes for δ^{15}N analysis: 10–19, 20–29 and $>$29 mm (C.L.). *C. anomalum* were also divided into 3 size classes for δ^{15}N analysis: 41–50, 51–60 and 61–70 mm total length (T.L.). Whole organisms were oven dried (50°C) for 48 hrs and ground to a fine powder. Whole organisms could be used for these measurements, but not the natural abundance determination of C described above, because body parts with slow turnover do not confound N analysis as is the case with lipids and C isotope determination.

Experiments in artificial channels

A set of two experiments in outdoor artificial stream channels were conducted to (i) test the ability of natural densities of *Orconectes* spp., *C. anomalum*, or both grazers combined to decrease algal biomass on cobble substrata relative to controls with no large grazer, and (ii) test grazer effects on clay tiles relative to controls with no large grazers. In both experiments, 3 replicates of each treatment (*C. anomalum*, *O. neglectus*, both, or neither) were randomly assigned to 12 channels. We used a size structure of *Orconectes* spp. and *C. anomalum* in the channels comparable to that occurring in Kings Creek and densities that fell within the range that had been observed in the past in Kings Creek (Loring, 1987; Fritz & Tripe, unpublished data). Total biomass of *O. neglectus* and *C. anomalum* stocked into stream channels was calculated using length–dry-weight relationships established in conjunction with the ammonium release in 1998.

Outdoor artificial streams were composed of plastic channels that were 3 m long, 7.6 cm wide and

Table 3. Mean, standard error, and sample size (X ± 1 SE (N)) of δ^{15}N and δ^{13}C for macroinvertebrates excluding *Orconectes* on each date

	δ^{15}N June/July–1995	δ^{15}N December–1995	δ^{13}C December–1995
Physa sp.	–	7.0 (1)	−29.6 (1)
Stenonema femoratum	4.2 ± 0.98 (3)	5.5 ± 0.11 (2)	−30.9 ± 0.52 (2)
Baetidae	5.4 ± 0.38 (3)	6.3 (1)	−32.8 (1)
Chironomidae	4.6 ± 1.59 (2)	–	–
Tanypodinae	–	8.6 (1)	–
Orthocladiinae	5.5 ± (2)	5.8 (1)	−34.5 (1)
Cheumatopsyche sp.	–	6.8 (1)	−32.1 (1)
Hydropsyche sp.	–	6.6 ± 0.19 (2)	−32.1 (1)
Tipula sp.	–	6.3 (1)	−26.2 (1)
Polycentropus sp.	–	9.2 (1)	–
Perlesta placida	5.6 ± 0.60 (4)	–	–
Dytiscidae adults	7.8 (1)	–	–
Zygoptera nymph	7.6 (1)	–	–
Corixidae	5.4 (1)	–	–

5.7 cm deep. Each channel had an area of 0.23 m^2 and was covered with 6 mm mesh hardware cloth to prevent animals from escaping and to protect them from predation. All stream channels had a continuous supply of flowing spring water, which averaged ∼15 °C (Edler & Dodds, 1992). The water from this spring was generally low in inorganic nitrogen and phosphorus (Edler & Dodds, 1992; Eichem et al., 1993), and similar chemically to stream water chemistry (Dodds et al., 1996). Prior to experiments, flat rocks of native limestone were taken from Kings Creek and all visible invertebrates were removed. The rocks were then distributed evenly within artificial stream channels, and algae were allowed to grow with minimal grazing pressure for 4–10 days before each experiment. After 10 days incubation time in the first experiment, the artificial stream channels became inundated with diatom mats and filamentous green algae; shorter algal development times were used in the following experiment.

The first experiment, conducted from 16 to 30 June 1995, was designed to test for effects of *O. neglectus*, *C. anomalum*, or both species combined, on epilithic algae. Treatments with no *O. neglectus* or *C. anomalum* were included as controls. *O. neglectus* ranging from 11–25 mm (C.L.) were stocked at a density of 43 ind m^{-2} (13.4 g m^{-2}). This was within the range of estimated densities of both species of *Orconectes* combined in Kings Creek (Loring, 1987). *C. anomalum* (35–60 mm T.L.) were stocked at approximately 9 ind m^{-2} (0.7 g m^{-2}) which was also within the range of observed densities in Kings Creek (Fritz & Tripe, unpublished data).

The second experiment was conducted from 21 June to 5 July 1996 to determine if *O. neglectus* and *C. anomalum* would have the same effect on algal biomass growing on clay tiles as they had on cobble substrata. Except for the density of *C. anomalum* stocked, treatments were similar to the first experiment. *C. anomalum* (50–70 mm T.L.) were stocked at 18 ind m^{-2} (7.2 g m^{-2}) and *O. neglectus* (17.5–30 mm C.L.) was stocked at 43 ind m^{-2} (29.9 g m^{-2}). Cobble or clay substrate samples were taken from a 10 cm length of each stream channel on the initial day, and approximately every 7 days thereafter, for the duration of the experiment. All rocks and tiles were stored in a freezer at −4 °C prior to chlorophyll *a* (chl*a*) analysis.

Periphyton on rocks was scraped off by hand to increase exposure of the periphyton biomass to the acetone solution. Chl*a* was extracted by completely submerging and soaking rocks and tiles in a 9:1 acetone:water solution for 24 h at 4 °C in the dark. Following extraction, the solvent was centrifuged to remove particulates. Remaining periphytic material did not appear green, therefore, the acetone extraction procedure was assumed to be complete. Chl *a* in extracts was determined by a fluorometric method with a specific lamp/filter combination that prevents

interference by other chlorophylls and phaeophytin (Welschmeyer, 1994). The fluorometer was calibrated using standard chl *a* concentrations quantified by the spectrophotometric chl *a* method (APHA, 1992) to provide results consistent with spectrophotometric chlorophyll determination. To obtain total areas of rocks, images of their top surfaces were taken with a computer color scanner and surface area calculated with Sigma Scan software. Artificial clay tiles with a known surface area of 0.006 m^2 were used in the second experiment.

Data analysis

A 2-factor ANOVA was used to analyze natural abundance data with taxon or organic matter category and date as factors and δ^{15}N and δ^{13}C as dependent variables. Data were split into the sampling periods found in Table 1 and *S. atromaculatus* δ^{15}N values from June 1996 were not included in the analysis because of their particularly high enrichment . A Fischer's protected LSD multiple comparison test was used to compare means after ANOVA. In the summer of 1996, a 1-factor ANOVA was used to test for a significant difference in δ^{15}N and δ^{13}C between sites. This was the only sampling season when enough samples were taken from each site to test for a site effect. A linear regression was used to determine if a correlation existed between total length and δ^{15}N and δ^{13}C values taken in 1995 and 1996 when possible. A linear regression also was used to test for a correlation between total length and δ^{15}N of *C. anomalum* on the 35th day of the ^{15}N-labeled ammonium release because only one sample per total length category was available. When no significant length relationship was found, all the *C. anomalum* samples for this date were combined and a 1-factor ANOVA was used to test for significant differences between *C. anomalum* and the three different length categories of *Orconectes* spp.. Tukey's HSD multiple comparison test was used to test for differences among *C. anomalum* and *Orconectes* length categories. A 2-factor ANOVA was used to test for significant effects on chl *a* in each of the channel experiments with crayfish and *C. anomalum* as factors. Fischer's protected LSD multiple comparison tests were used to test for significant differences among means following ANOVA.

Results

Natural abundance of ^{13}C and ^{15}N

The mean and standard error of δ^{15}N and δ^{13}C for each taxon and category of organic matter sampled on each date and sampling period are shown in Tables 1, 2 and 3. No significant differences in δ^{15}N or δ^{13}C within organic matter categories were found among the different sites sampled in the summer of 1996. In addition, no significant correlations were found between the ratio of either element and *Orconectes* spp. or *C. anomalum* length. Therefore, all data for each taxon or organic matter category collected during each sampling period were combined for further analysis. A significant interaction between taxon or the type of organic matter and the sampling period collected (June/July–1995, December–1995, February–1996, and June–1996) was found for δ^{15}N (p=0.0001, F=104.9) and δ^{13}C (p=0.0001, F=12.1) values. Multiple comparison tests revealed that all of the statistically significant variation in δ^{13}C values by date occurred in algae (*Spirogyra*, *Cladophora*, and diatoms) and FBOM ($p<0.05$). No consistent trend was observed in the significant differences in these groups. The ^{15}N values of algae (*Spirogyra*, *Cladophora*, and diatoms), FBOM, CBOM, *P. erythrogaster* and *E. spectabile* were also sometimes dependent upon sampling date ($p<0.05$). *Spirogyra*, diatoms FBOM, and *E. spectabile* were more enriched in winter sampling periods.

C. anomalum were always more enriched in ^{15}N and less enriched in ^{13}C than *Orconectes* spp.. The *C. anomalum* δ^{15}N value was 4.3‰ more enriched than periphyton in the summer of 1995 and 2.1‰ more enriched than *Spirogyra* in December 1995 (Table 1). In 1996, *C. anomalum* δ^{15}N values were 4.7‰ more enriched than diatoms in February and 4‰ more enriched than diatoms in June 1996. These specific algae were the primary producers most enriched with heavy isotopes in each season and the only ones that fell close to 3.4‰ (the expected ^{15}N enrichment of a consumer relative to its food source) of *C. anomalum*. *C. anomalum* ^{13}C values were never closer than 1-2‰ to values from any algal sample (Table 2). Macroinvertebrate δ^{15}N values were generally 3–3.4‰ lower than *C. anomalum* in the summer and winter of 1995 (Tables 1 and 3). In addition, macroinvertebrate δ^{13}C values were more similar to the *C. anomalum* value than algae was in December 1995 (Tables 2 and 3). *C. anomalum* had higher values for δ^{15}N than or-

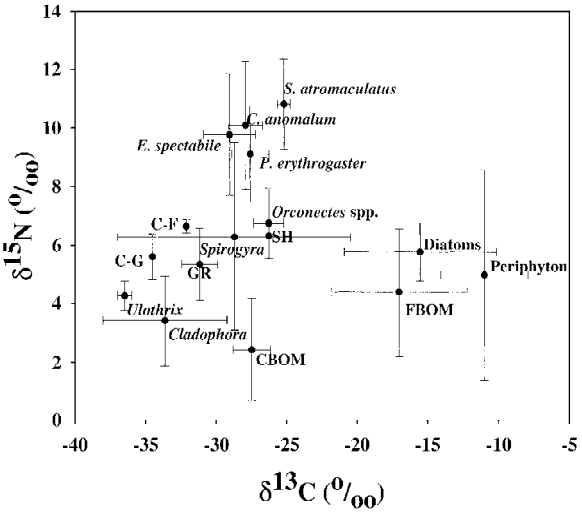

Figure 2. Natural abundance δ^{15}N and δ^{13}C values for all animals and food sources from all sampling dates and sites in 1995 and 1996. Mean and standard error is given for each sample. Abbreviations were used for invertebrate functional feeding groups, C-F=Collector-filterer, C-G=Collector-gatherer, GR=Grazer, SH=Shredder.

angethroat darters (*Etheostoma spectabile* (Agassiz)), which actively pursue invertebrate prey, in June/July and December 1995 (Table 1). Stable isotope values associated with *C. anomalum* clustered with those of other fishes in the system that are known to ingest invertebrates (i.e. *P. erythrogaster* and *E. spectabile*) (Fig. 2).

In all seasons sampled, δ^{15}N values for *Orconectes* spp. suggested algae and CBOM were more likely to serve as a food source than FBOM and macroinvertebrates given the expected 3.4‰ trophic enrichment (Table 1). *Orconectes* spp. δ^{13}C values were also very similar to algae (i.e. *Oedogonium* sp., Table2) and CBOM (Table 2 and Fig. 2). *Orconectes* spp. δ^{15}N values clustered more closely to algae, FBOM and CBOM than those of *C. anomalum* (Fig. 2).

Gut content analysis

C. anomalum gut contents generally included a large proportion of amorphous detritus relative to algae (Table 4). All individuals sampled in June 1996 were taken from the same sites and dates that isotope data were collected. Only individuals from site N20B in June 1996 and the Nature Trail site in March 1999 had a majority of their gut contents composed of algae. Macroinvertebrates were found only in the March 1999 gut samples and consisted mainly of chironomids with a few small Heptageniidae larvae.

Adult *P. erythrogaster* gut contents also contained amorphous detritus and algae. In addition, they had a greater percentage of their gut contents made up of algae at the N4D site in 1996 than did *C. anomalum*. However, no statistics were done given that each size group was made up of only one composite sample. Young-of-the-year southern redbelly dace and an adult orangethroat darter contained only chironomid larvae.

$^{15}NH_4$ tracer release

Orconectes spp. and *C. anomalum* were consistently sampled from a pool site 70 m below the $^{15}NH_4$ tracer release point. δ^{15}N values for crayfish and *C. anomalum* from that site on the final day (i.e. day 35) of the release are presented in Figure 3. A trend in increasing *C. anomalum* δ^{15}N values with increasing total length of the size class was observed but was not statistically significant. Therefore, all size categories were combined and compared to *Orconectes* spp. values. Significant differences were found among the δ^{15}N values of the different size categories of *Orconectes* spp. and *C. anomalum* (p=0.0006, F=28.48, Figure 3). *Orconectes* spp. less than 20 mm (C.L.) and *C. anomalum* δ^{15}N values were not significantly different ($p>0.05$). Both labeled between FBOM and filamentous green algae, indicating they assimilated some material that was more enriched than leaves and the bulk FBOM samples. The δ^{15}N values of adult *Orconectes* spp. (>20 mm C.L.) were significantly lower than those of *Orconectes* spp. less than 20 mm C.L. and all *C. anomalum* ($p<0.05$). Larger *Orconectes* spp. were more closely labeled to leaves than were the smaller *Orconectes*.

Experiments in artificial channels

There was a marginally significant difference among treatments (p=0.085, F=3.2) in the change of chl *a* on cobbles in the first experiment from the initial to the final chl *a* measurement after 2 weeks (Fig. 4). *O. neglectus* treatments resulted in the dominant primary effect in this analysis (p=0.024, F=7.7). In the second (clay tile) experiment, the standing stock chl *a* (p=0.0006, F=18.3) and the change of chl *a* on tiles from the initial to the final day of the experiment (p=0.001, F=15.2, Figure 5) were significantly different among treatments. A significant interaction also was observed in the standing stock chl *a* (p=0.006, F=13.6) and in the change in chl *a* (p=0.008, F=12.1).

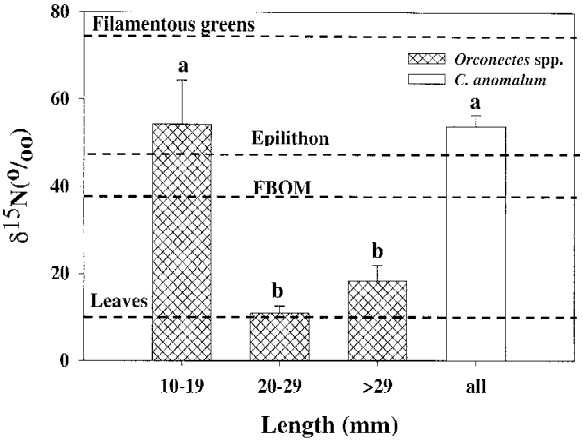

Figure 3. *C. anomalum* and *Orconectes* spp. δ^{15}N values from a site 70 m downstream of the ^{15}N-ammonium release point on day 35 of the release. Bars represent δ^{15}N values of *C. anomalum* and three carapace length categories of *Orconectes* spp. Dashed lines represent δ^{15}N values of possible food sources. Different letters indicate significant differences among groups ($p<0.05$).

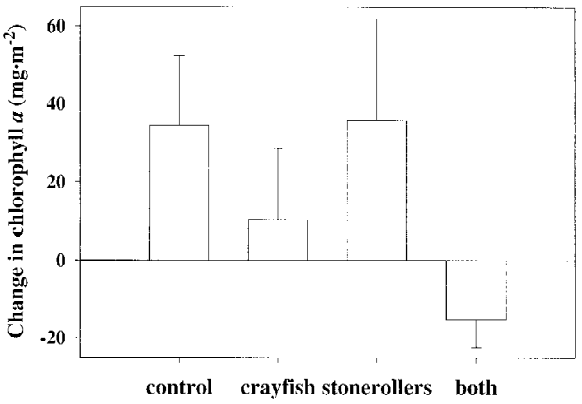

Figure 4. Mean change and standard error of chlorophyll *a* biomass on rocks in each treatment in artificial stream channels from 16 to 30 June 1995 with *O. neglectus* and *C. anomalum* present. Control = neither *O. neglectus* nor *C. anomalum* present; *O. neglectus* = 43 ind m^{-2}; *C. anomalum* = 9 ind m^{-2}; both = 43 *O. neglectus* m^{-2} and 9 *C. anomalum* m^{-2}.

On average, the *O. neglectus* treatment had 3.4 times less, the *C. anomalum* treatment had 2.1 times less, and the combined *O. neglectus* and *C. anomalum* treatment had 3 times less chl *a* on clay tiles than the control treatment (p=0.0003). Mean change in epilithic chl *a* was positive in each treatment. However, *O. neglectus* (p=0.0003), *C. anomalum* (p=0.002), and combined treatments (p=0.0005) had a smaller increase in chl *a* than the control treatments. *O. neglectus* and *C. anomalum* treatment means were not significantly different from each other ($p>0.05$).

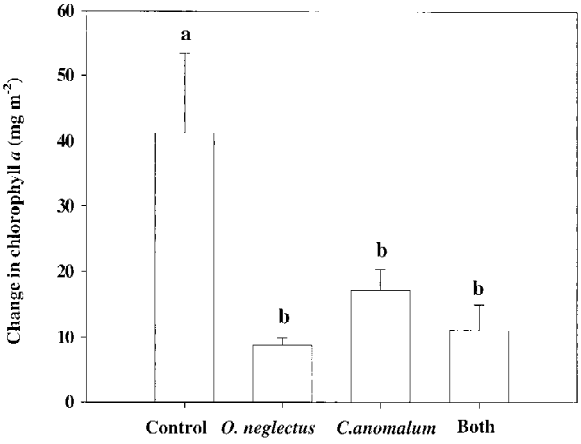

Figure 5. Mean change and standard error of chlorophyll *a* biomass on clay tiles in each treatment in artificial stream channels from 16 to 30 June 1995 with *O. neglectus* and *C. anomalum* present. Control = neither *O. neglectus* nor *C. anomalum* present; *O. neglectus* = 43 ind m^{-2}; *C. anomalum* = 18 ind m^{-2}; both = 43 *O. neglectus* m^{-2} and 18 *C. anomalum* m^{-2}. Different letters indicate significant differences among groups ($p<0.05$).

Discussion

The trophic ecology of crayfish and *C. anomalum* has not, to our knowledge, been compared within the same stream system, even though both animals potentially consume similar components of the benthos, including algae, fine benthic organic material, and invertebrates (Kraatz, 1923; Fowler & Taber, 1985; Whitledge & Rabeni, 1997). We used four different methodologies including natural abundance of ^{15}N and ^{13}C, a whole stream ^{15}N labeled ammonium chloride release, gut content analysis (*C. anomalum* only), and grazing experiments in artificial streams to compare the feeding ecology of these omnivores within the same system and to determine the importance of algal food sources to each animal.

Crayfish clustered more closely to detrital and algal food sources than did *C. anomalum* when stable isotope values from all sites and all seasons were combined (Fig. 2). This trend was clear even though stable isotope ratios of C and N in algae and detritus often differed depending on sampling dates. Thus, closer inspection of the C and N natural abundance can be fruitful. McLeod & Barton (1998) found that stream periphyton ^{15}N and δ^{13}C are strongly influenced by factors influencing metabolic activity such as light and temperature. Therefore, it is important that stable isotope ratios of *C. anomalum* and *Orconectes* spp. were compared to algal food sources within these dates as well as across dates and to utilize other methods

Table 4. Mean percent composition by area of various food types for *C. anomalum*, *P. erythrogaster*, and *E. spectabile* from various dates and sites along Kings Creek. ∗=represents a sample where one filter was examined and fish gut contents were pooled; NT=gallery forest site; N20B=prairie site in watershed N20B; N4D=prairie site in watershed N4D

Taxa	Sample size	Total Length (mm)	Sample Site	Sample Date	Detritus (%)	Filamentous green algae (%)	Diatoms (%)	Animal (%)
C. anomalum	3	55–65	N20B	Jun-96	20	75	5	0
	1	60	NT	Jun-96	90	0	10	0
	3∗	60–70	N4D	Jun-96	90	0	10	0
	4∗	40–50	N4D	Jun-96	90	0	10	0
	1	44–60	N4D	Jul-98	95	0	5	0
	1	41–71	N4D	Aug-98	65	0	34	0
	7	40–62	NT	Mar-99	37	3	43	17
P. erythrogaster	5∗	15–20	N20B	Jun-98	0	0	0	100
	2∗	35–45	N4D	Jun-96	50	0	50	0
	5∗	55–60	N4D	Jun-96	60	10	30	0
E. spectabile	1	–	N4D	Jun-96	0	0	0	100

such as gut content analysis to confirm food sources suggested by natural abundance values.

C. anomalum ^{15}N and ^{13}C values indicate that they could be depending both on algae and macroinvertebrates for nourishment in Kings Creek. Diatoms generally were more abundant in *C. anomalum* gut contents than filamentous green algae, which is consistent with previous gut content studies (Kraatz, 1923; Fowler & Tabor, 1985; Burkhead, 1989). *C. anomalum* were slightly more than 3.4‰ enriched in ^{15}N than diatoms in all of the sampling periods they were both collected (Table 1). However, corresponding diatom δ^{13}C values were 8‰, 20‰ and 10.3‰ more enriched than *C. anomalum* in those same sampling periods. A similar result was observed with periphyton in the summer of 1995. This may indicate that *C. anomalum* are assimilating only certain portions of the diatom or periphyton mat, which we were unable to detect with our broad sampling method.

Both gut content analysis and stable isotope data indicate that *C. anomalum* is somewhat dependent upon macroinvertebrates for nourishment. Macroinvertebrates fall within the expected enrichment range for both elements in seasons where both *C. anomalum* and macroinvertebrates were sampled (Tables 1, 2 and 3). In addition, *C. anomalum* stable isotope ratios cluster with predatory fish in the system (Fig. 2). Macroinvertebrates were only found in the gut contents of *C. anomalum* in March 1999 and it is possible that their ingestion is seasonal. The majority of macroinvertebrates found in guts were chironomid larvae. These and other types of benthic invertebrates have been found in the guts of *C. anomalum* in other studies as well (Kraatz, 1923; Burkhead, 1980) and could be incidentally or purposefully ingested by foraging *C. anomalum*. There have been reports of fisherman in Tennessee successfully angling for *Campostoma* using worms (Burkhead, 1980). Invertebrates are easily digested and could contribute significantly to tissue production even though they make up a moderate percentage of the gut contents when compared with algae and detritus. Ingestion of invertebrates may explain the incongruent relationship between *C. anomalum* and algal food sources when both C and N elements were considered.

Amorphous detritus often made up the majority of the material in *C. anomalum* guts. Large amounts of amorphous detritus have been reported in *C. anomalum* guts in previous studies (Kraatz, 1923; Fowler & Tabor, 1985; Burkhead, 1989). However, stable isotope ratios do not directly indicate that FBOM is an important food source for tissue production and the role of detritus in *C. anomalum* diets is undetermined. FBOM may be incidentally ingested and hold little nutritional value for *C. anomalum* or it may play a significant role in their diet. Ahlgren (1990) found that

although detritus would not support growth (i.e. tissue production) in the white sucker (*Catostomus commersoni*) it was digestible, and may provide energy at times when high protein food sources are not abundant. If detritus is important in maintaining weight but not supporting growth during periods when other food sources are low, its importance to *C. anomalum* diets may not be revealed with stable isotope analysis. We also assumed that the FBOM sampled for stable isotopes is similar to the amorphous detritus consumed by *C. anomalum.* In reality, however, they may be selectively ingesting or assimilating more nutritious portions of fine detritus that had different isotopic signatures than the bulk samples.

Orconectes spp. were always less enriched in ^{15}N and more enriched in ^{13}C than *C. anomalum* in natural abundance samples. Crayfish are well-known consumers of leaf litter (Huryn & Wallace, 1987; Whiteledge & Rabeni, 1997) and this may deplete *Orconectes* spp. δ^{15}N values and enrich their δ^{13}C values relative to *C. anomalum*. In addition, *Orconectes* spp. must not be consuming a significant portion of animal material relative to other items in their diet because they had δ^{15}N values similar to grazing, collecting, and shredding macroinvertebrates and appear to be on a similar trophic level. Therefore, combined δ^{15}N and δ^{13}C data indicate that *Orconectes* spp. are more likely behaving as algal and detrital processors than predators in Kings Creek (Fig. 2). Crayfish are also important consumers of detritus and algae in other systems (Huryn & Wallace, 1987; Creed, 1994; Whitledge & Rabeni, 1997). We found no significant trophic differences between *O. nais* and *O. neglectus*: more study is required to demonstrate how these crayfish partition the environment.

Data from the ^{15}N-labeled ammonium release do not contradict any of the conclusions drawn from natural abundance data. If *Orconectes* spp. and *C. anomalum* are more than 4‰ more labeled than a possible food source, they must be deriving some nourishment from a more highly labeled food source. Therefore, we can use these data to determine what food sources might be important to both animals. In contrast to the natural abundance data where no relationship was found between *Orconectes* spp. carapace length and the ratios of either element, smaller individuals (<20 mm C.L.) were more enriched in ^{15}N than larger individuals (>20 mm C.L.) at the end of this study. It is possible that the smaller individuals may have been more dependent on highly labeled food sources such as algae or invertebrates than the larger individuals. Larger *Orconectes* spp. δ^{15}N values were more similar to those of leaves and FBOM than algae and macroinvertebrates. This type of diet shift has also been observed in a stable isotope study of *Orconectes virilus* in oligotrophic lakes (France, 1996). In this study, smaller crayfish (<21 mm C.L.) relied more upon epilithic algae than terrestrial detritus food sources, and larger crayfish (>28 mm C.L.) relied more upon terrestrial detritus than epilithic algal food sources. However, differences in δ^{15}N values could also be due to factors such as differing colonization times, N turnover rates, and growth rates. For example, the larger *Orconectes* spp. sampled may have moved into the study reach at a later date than the smaller ones and, therefore, could not take up as much of the ^{15}N label. In addition, smaller *Orconectes* spp. may also be growing faster and acquiring the label at a greater rate than larger ones.

The δ ^{15}N values of *C. anomalum* were similar to those of the smaller *Orconectes* spp. (<19 mm C.L.) with tracer addition, which indicates that they may be relying on similar food resources. Data suggest that *C. anomalum* were feeding upon a more isotopically enriched food source than FBOM such as filamentous green algae or macroinvertebrates, or that they were selectively assimilating a portion of the FBOM that was more highly labeled than our bulk FBOM samples. A trend (though not significant) toward increasing δ^{15}N values with increasing size was observed for *C. anomalum*. Again, this could result from differential feeding, differential colonization times, or differential growth rates and this relationship was not observed in the 1995–1996 natural abundance stable isotope sampling period.

Orconectes spp. and *C. anomalum* did not colonize our site until 14 days after the initiation of the release and neither animal reached isotopic steady state before the release was terminated (i.e. isotope levels were higher on day 35 than on day 28). In addition, immigration and emigration of animal populations in the study reach was possible. A 1.5 m high waterfall approximately 10 m above the site reach impeded movement of existing animal populations from within the study reach upstream. Just downstream of the pool where *Orconectes* spp. and *C. anomalum* samples were collected was another waterfall (0.67 m) that may also have impeded upstream movement of populations from downstream. However, fishes and crayfishes from outside the study reach could have been continuously colonizing from upstream reaches throughout the experiment. Regardless of possible movements of

fishes and crayfishes in and out of the study reach and the fact that neither *Orconectes* spp. nor *C. anomalum* had reached isotopic steady state, both animals and food sources were labeled well above any background samples ever taken in Kings Creek, and were more labeled than some of their potential food sources.

Our final objective was to determine if *Orconectes* spp. and *C. anomalum* alter algal biomass in small streams with grazing experiments in artificial stream channels. The experiments in artificial stream channels confirmed that *O. neglectus* could reduce algal biomass on both cobble and tile substrata relative to exclusion treatments. *C. anomalum* treatments showed no decline in algal biomass on cobble. However, there was a significant decrease in algal biomass accrual observed on clay tiles. The artificial stream channels were shallow and similar to riffle habitat. Cobble substrata were used in the first channel experiment. *C. anomalum* were able to take cover under these cobbles and were observed doing so. In the clay tile experiments, *C. anomalum* were forced out of hiding and were observed grazing in the channels. This may account for the observed decrease in algal biomass in the second, but not the first channel experiment.

Compared to *C. anomalum*, *O. neglectus* treatments had a greater decline in algal biomass relative to control treatments in the experiment where clay tiles were used. This is likely due to differences in animal biomass among treatments. However, *Orconectes* spp. were purposefully stocked at a higher density because their density and biomass are often greater than *C. anomalum* in Kings Creek. It is also possible that *C. anomalum* feeding behaviors were altered because of the small size of the channel. *C. anomalum* normally feed in schools (Matthews et al., 1987). The effect of *C. anomalum* on algal biomass in deeper habitats, such as pools, could have been underestimated by the channel experiments if small school size or the dimension of the channel inhibited their grazing behavior. Feeding behavior of *O. neglectus* could also have been altered by the small size and nature of the channel.

A significant and interesting interaction effect was observed in the channel experiment utilizing clay tiles. This interaction was primarily due to the fact that the *O. neglectus* treatment had less algal biomass and a smaller increase in algal biomass over time than treatments containing a combination of *O. neglectus* and*C. anomalum*. This indicates that *O. neglectus* grazing may have been inhibited by the presence of *C. anomalum*. Vaughn et al. (1983) found that crayfish secondary production was lower in the presence of *C. anomalum* than when no *C. anomalum* were present in artificial pool experiments. They noted that crayfish spent significantly less time feeding during the day in the presence of than in the absence of these fish.

Both *Orconectes* spp. and *C. anomalum* use algal and detrital food sources in Kings Creek. In addition, *C. anomalum* natural abundance ^{15}N values indicated that they might be obtaining a significant amount of nourishment from macroinvertebrates. Macroinvertebrates appear to contribute less significantly to *Orconectes* spp. tissue production than other food sources in this system. *C. anomalum* gut contents also contained a large amount of amorphous detritus relative to algae on many sampling occasions. The role of detritus and macroinvertebrates relative to algae in the diet of *C. anomalum* and *Orconectes* spp. in this system needs further study. *O. neglectus* and *C. anomalum* are both able to inhibit epilithic algal biomass accumulation. It is possible that *Orconectes* spp., because they are often present at higher densities and biomass, have a more significant effect on benthic algal biomass than *C. anomalum* in this stream.

Both of these omnivores become large enough that they are unlikely to be preyed upon by any other stream organisms in Kings Creek. They consume many of the same food resources as smaller macroinvertebrates found in the stream. Given the substantial biomass of *Orconectes* spp. and *C. anomalum* in Kings Creek, we hypothesize that they are significant competitors for food with many organisms. They should also tend to shorten the food web in streams where large aquatic predators are absent (i.e. sunfishes, catfishes, etc.) because they are less vulnerable to smaller aquatic predators (i.e. darters and invertivorous minnows) than other herbivorous and detritivorous organisms (i.e. insect macroinvertebrates) that inhabit stream systems.

Acknowledgements

This research was supported by a U.S. NSF grant to Konza Long Term Ecological Research (BSR-9011662), including a Research Experience for Undergraduate supplements for MAE, and NSF funding for the LINX project through the Ecosystems program. D. Gudder provided technical assistance and reviewed the manuscript. B. Culbertson provided technical assistance in the stream channel experiments. Konza Prairie Biological Station is owned by the Nature Conservancy and managed by the Division of Biology at

Kansas State University. This is contribution 98-266-J from the Kansas Agricultural Experiment Station.

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