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Ecosystem significance of crayfishes and stonerollers in a prairie stream: functional differences between co-occurring omnivores

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Abstract. The ecosystem significance of crayfishes (*Orconectes nais* (Faxon) and *O. neglectus* (Faxon)) and central stoneroller minnows (*Campostoma anomalum* (Rafinesque)), was examined in a tallgrass prairie stream by estimating the trophic basis of production and consumption for each species. Annual ash-free dry mass production and production to biomass ratios of *C. anomalum* (260 mg m^{-2} y^{-1}, 1.3) were lower than that of *O. nais* (719 mg m^{-2} y^{-1}, 2.4) and *O. neglectus* (508 mg m^{-2} y^{-1}, 2.1). Gut content analysis revealed no significant differences in the percentages of the various food items ingested by *O. nais* and *O. neglectus*, indicating they were functionally similar with respect to the types of organic matter processed in this system. We found a significant difference among seasons in the % of invertebrates in *C. anomalum* guts ($p = 0.0001$) and the % of algae in *Orconectes* spp. guts ($p = 0.005$), indicating the importance of measuring resource use throughout the growing season. Leaves contributed most to *Orconectes* spp. annual production (45%) followed by animal matter (30%), algae (19%), and amorphous detritus (6%). Algae contributed most to *C. anomalum* production (47%) followed by amorphous detritus (30%), animal matter (21%), and leaves (2%). *Orconectes* spp. consumed more leaf litter, filamentous green algae, and macroinvertebrates than *C. anomalum*, whereas *C. anomalum* consumed more diatoms. Crayfish and central stonerollers are both omnivores that function as important consumers and processors of algae and detritus in this tallgrass prairie stream, but each focuses on slightly different types of similar resources.

Key words: *Orconectes*, central stonerollers, omnivory, growth rate, secondary production, gut contents.

Crayfish and central stonerollers (*Campostoma anomalum* (Rafinesque)) are widespread and abundant benthic omnivores in North American streams (Momot 1984, Matthews et al. 1987). These organisms often co-occur in midwestern streams in the United States and are thought to consume similar food resources. However, few comparative data exist on the functional role of these 2 omnivores within the same stream system.

Crayfish can play important roles in structuring benthic macroinvertebrate and algal communities (Creed 1994, Charlebois and Lamberti 1996, Parkyn et al. 1997) as well as in organic matter processing and energy flow (Huryn and Wallace 1987, Whitledge and Rabeni 1997). An examination of the trophic basis of production of crayfish in a Missouri stream indicated that animal (29–51%) and detrital (32–56%) material contributed the most to secondary production, followed by algae (14–18%) (Whitledge and Rabeni 1997). In addition, Whitledge and Rabeni (1997) found crayfish were important consumers of animal matter, detritus, and algae when compared to other invertebrates in this system. Similar information on the role of *C. anomalum* in organic matter processing and energy flow is lacking, even though these fish can be extremely abundant in small and medium-sized streams and sometimes dominate the fish community both numerically and in terms of biomass (Schmulbach 1953, Lennon and Parker 1960, Beets 1979, Matthews et al. 1987).

Studies of *C. anomalum* have focused primarily on its ability to structure benthic algal communities and to reduce algal biomass in prairie and Ozark mountain streams (Power et al. 1985, 1988, Gelwick and Matthews 1992, 1997, but see Vaughn et al. 1993). In addition to algae, *C. anomalum* also ingests animal matter and a signif-

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icant amount of detritus (Kraatz 1923, Fowler and Taber 1985, Burkhead 1980). However, the relative importance of these food sources to *C. anomalum* production is not known. In addition, few investigators have measured *C. anomalum* growth rates (Schmulbach 1953, Lotrich 1973) or secondary production (Lotrich 1973) in a way that can be compared among streams and among different components of stream communities (e.g., macroinvertebrates).

Recent investigations in a prairie stream provided comparative data for the roles of crayfish and *C. anomalum* in material processing. Dodds et al. (2000) quantified N cycling in Kings Creek, a tallgrass prairie stream located on Konza Prairie Biological Station (KPBS), and found that crayfish (*Orconectes* spp.) played a more significant role than other stream macroinvertebrates and *C. anomalum* in algal and detrital N processing. However, this experiment spanned only 2 mo of the growing season (April and May). In a related study, natural abundance isotope data (^{15}N and ^{13}C) collected over many seasons from the same stream suggested that crayfishes might be more dependent than *C. anomalum* upon algal and detrital resources for growth (Evans-White et al. 2001).

The objective of our study was to compare the ecosystem significance of *Orconectes* spp. and *C. anomalum* in Kings Creek by estimating the trophic basis of their production and comparing consumption of food resources. We addressed 2 component objectives: 1) to estimate *Orconectes* spp. and *C. anomalum* biomass, growth, and production in Kings Creek over 1 growing season, and 2) to determine food sources used by each omnivore in Kings Creek by examining gut contents of *Orconectes* spp. and *C. anomalum*. We predicted that algal and detrital food sources would be more important to the production of crayfish than *C. anomalum* given previous evidence from natural abundance δ^{15}N and δ^{13}C studies. In addition, we predicted crayfishes, because of their apparently higher biomass in this stream, would be more significant than *C. anomalum* as processors of algae and detritus.

Methods

Study area

Kings Creek drains ~1059 ha of KPBS, a tallgrass prairie preserve located in the Flint Hills region of northeastern Kansas (Fig. 1). The availability of detrital and algal resources to consumers in Kings Creek depends upon the composition of the riparian vegetation, which has 3 distinct zones. Grasses and forbs dominate the riparian zones of headwater channels (Gurtz et al. 1988). Shading of the stream corridor in headwater reaches ranges from 0 to 10%. Grasses, forbs, shrubs, and small trees become dominant in the middle reaches (stream order 3), and gallery forest is prominent along higher-order (4–5) reaches. Shading of the stream corridor in the gallery forest ranges from 50 to 100% (Gurtz et al. 1988). Allochthonous detritus becomes a more important C source than algal production with increased canopy cover (Tate 1990, Dodds et al. 1996). Study sites were located in gallery forest (lower reaches) and prairie parts of the watershed (middle and upper reaches).

Biomass estimates

Sampling dates for *Orconectes* spp. were 26 March, 9 June, 15 July, 21 August, and 15 October 1999. *Campostoma anomalum* were sampled on 26 March, 14 July, and 15 October 1999. Each sample site consisted of 2 riffle–pool complexes and ranged in length from 40 to 90 m. Representative sites were selected and sampled in each of the upper, middle, and lower reaches of Kings Creek. These sites were within 250 m upstream or downstream of sites where animals were sampled for gut contents (Fig. 1). *Orconectes* spp. and *C. anomalum* were sampled from different sites within the upper, middle, and lower reaches. *Campostoma anomalum* populations were sampled during the daytime, whereas *Orconectes* spp. samples were sampled after sunset, except those taken on 26 March 1999, which were taken during daylight hours. The March *Orconectes* spp. samples were low and skewed towards small individuals. Often, larger individuals were seen hiding in holes within clay banks and could not be sampled efficiently. Therefore, all subsequent sampling took place at night when crayfish ventured out of their hiding places and were more easily captured. An additional nocturnal *Orconectes* spp. population estimate was taken in April 2000 to compare to values from March 1999.

Sample sites were either blocked on the upstream and downstream end by seines or by the

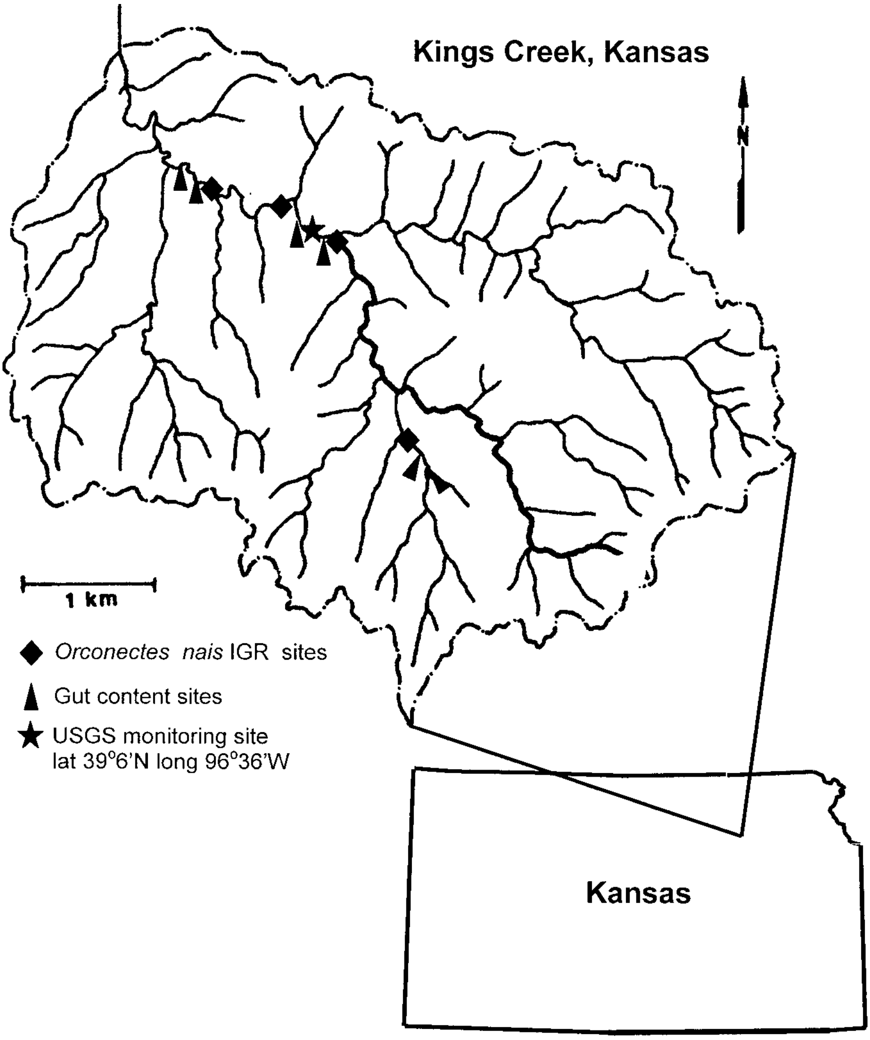

FIG. 1. Study sites in Kings Creek watershed, located within the Konza Prairie Biological Station. The tops of triangular symbols point to gut content sample sites. IGR = instantaneous growth rate. Gallery forest is predominantly located downstream of the US Geological Survey (USGS) monitoring site.

presence of dry or shallow (<2.5 cm deep) riffles. Populations were sampled using repeated passes (3–5) moving upstream within the reach with either a Coffelt backpack electroshocker (*C. anomalum*) or a seine (5 mm mesh) (*Orconectes* spp.). Crayfish populations were sampled by kick-seining riffle and pool habitats. The seine was emptied after kick-seining each riffle habitat and several times throughout a pool habitat during each pass. In pool sites >2 m in width, seine hauls were made by working the seine in partial circles with a person on one side of the stream standing still and the person on the opposite side of the seine working through the thalweg and then to the opposite bank. An additional person was positioned in front of the seine to kick and disturb substrate. In this way, both deep and shallow shore areas were sampled. Individuals collected during each pass were counted, measured, and then released downstream. *Orconectes* spp. carapace length (CL = tip of rostrum to posteromedian margin of carapace) and *C. anomalum* total length (TL = tip of nose to tip of longest caudal fin ray) were measured to the nearest 0.1 mm and 1 mm, respectively. *Orconectes* spp. sex and species were

TABLE 1. Linear regression equations and statistics estimated for the relationship between length and mass for *Campostoma anomalum, Orconectes nais,* and *O. neglectus.* All regressions were significant at $p < 0.001$. y = ln ash-free dry mass (g); x = ln (total length for fish or carapace length for crayfish in mm); *n* = sample size.

Species/sex	Regression equation	r^2	*n*
C. anomalum	$y = 3.204x - 14.07$	0.94	56
O. nais (male)	$y = 3.273x - 10.81$	0.94	70
O. nais (female)	$y = 3.273x - 10.65$	0.92	50
O. neglectus (male)	$y = 3.244x - 10.66$	0.94	39
O. neglectus (female)	$y = 3.046x - 10.03$	0.93	57

also recorded. Length of each macrohabitat (i.e., riffle, pool) within a reach was measured, width was measured at 3 places (~0.25, 0.50, and 0.75 times the total length of each macrohabitat), and area was calculated.

The Leslie depletion method was used to estimate the population size of *Orconectes* spp. and *C. anomalum* at each site (Ricker 1975). Density and biomass were estimated for each 5-mm size class using population estimates and species-specific length–mass relationships (see below), respectively. Values for each size class were summed to obtain total density and biomass for each site. ANOVA and a Tukey's multiple comparison test (HSD) were used to determine if there were seasonal differences in the biomass of each species ($\alpha = 0.05$).

Length–mass relationships

Orconectes spp. and *C. anomalum* were collected throughout 1999 for population estimates and gut content analysis, and used to establish length–mass relationships. Approximately equal numbers of individuals were used from each season sampled. *Orconectes nais* (12.3–44.9 mm CL, *n* = 120), *O. neglectus* (11.7–38.7 mm CL, *n* = 96), and *C. anomalum* (32–109 mm TL, *n* = 56) were dried (60°C) for at least 48 h, desiccated for an additional 24 h, and weighed on a Mettler AE260 microbalance (to nearest 0.1 mg). Samples were then ashed in a muffle furnace (550°C for at least 2 h) and reweighed to determine ash-free dry mass (AFDM). Crayfish incorporated into length–mass relationships had all appendages intact. Contents of the foregut were removed in some individuals; however, empty foregut tissue remained with each individual processed for length–mass relationships.

Linear regressions between ln-transformed length and ln-transformed AFDM were calculated for *C. anomalum* and for both male and female *O. nais* and *O. neglectus* (Table 1). ANCOVA was used to test for significant differences between the sexes of each species of crayfish. Sex and species-specific relationships were used to calculate biomass for *Orconectes* spp. (Table 1), even though no significant sex-specific differences were found (*O. nais*: $p = 0.998$, *O. neglectus*: $p = 0.257$). A relationship based on both male and female individuals was used to estimate *C. anomalum* biomass because it was often difficult to determine the sex of individuals in field collections.

Instantaneous growth rates

Temperature-specific instantaneous growth rates (IGR) were derived for 2 size classes of *O. nais* (≤25 mm and >25 mm CL), and a predictive model was developed to apply to each sampling interval. In July 1999, individuals were placed in flow-through plastic containers at 4 pool sites chosen based only on stream water temperature. No other abiotic variables were measured, but sites differed in canopy cover and the amount of groundwater input. Average temperatures for these sites in July were 14, 18.5, 19.5 and 24°C. Either 2 individuals (≤25 mm CL) or 1 individual (>25 mm CL) were placed in each plastic container (30.5 × 16.5 × 11.5 cm), which had two 10 × 5 cm and two 20 × 5 cm windows covered with 5-mm mesh metal screen. All containers were initially filled with ~300 g wet mass of pebbles (<1 cm diameter), ~1400 g of periphyton-covered cobbles (>1 cm diameter), and ~30 g of conditioned leaf litter from Kings Creek. Chambers were placed in the field 1 wk prior to the addition of crayfish to allow for colonization by invertebrates. A total of 6 *O. nais* ≤25 mm CL (13.8–23.3 mm CL) and 5 *O. nais* >25 mm (29.3–42.1 mm CL) were placed in chambers at each site. Temperature data loggers were also placed at each site and set to record stream temperature every 15 min for the duration of the growth study (July to September 2000). Food resources were provided in excess to minimize food limitation of growth. Periphyton and its associated macroinvertebrate communities were replenished in chambers when <50% of cobbles had thick growths of periphyton representative of the stream. Conditioned leaves were replenished when their total wet mass fell below ~15 g per container. Macroinvertebrates were observed on the cobbles within containers throughout the experiments.

CL was measured every other day throughout the duration of the experiment. Individuals were followed through one complete molting cycle and the average stream temperature during which every individual in a size category molted was taken at each site. On average, individuals >25 mm CL took >2.5 times longer than individuals ≤25 mm CL to complete a molting cycle. Therefore, average stream temperature does not correspond between the 2 size categories even though they were placed at the same location starting on the same date. CL at the beginning and end of each molt cycle was converted to AFDM using the species-specific length–mass equations. Daily IGR values were calculated using the following equation:

$$\mathrm{IGR} = \frac{\ln(W_{t+\Delta t}/W_t)}{\Delta t} \qquad (1)$$

where W_t is the AFDM of an individual at the beginning of a molt cycle, $W_{t+\Delta t}$ is the AFDM of an individual at the end of the molt cycle, and Δt is the length (in days) of the molting cycle (see Benke 1996). Linear regression was used to model relationships between average temperature and IGR.

IGRs of *C. anomalum* were estimated using the Peterson method (Ricker 1971). *Campostoma anomalum* scales, from the area above the lateral line and just behind the opercle (Jearld 1983), were taken from a subset of the population used for length–mass regressions and gut content samples. These scales were used to determine age classes in March, July, and October 1999. In March, individuals with no observed annulus were assumed to be age-1 and those with an annulus were assumed to be age-2. An age-length key was used to extrapolate ages to fish not directly aged (Ricker 1975). The mean length of each age class was converted to a mean AFDM (g), which was used to determine the IGR using equation 1.

Age-0 *C. anomalum* were not observed in the field until July. Therefore, the initial mass and hatching time of age-0 individuals was not known for the 26 March to 13 July 1999 sampling increment. Post yolk-sac larval length of *C. anomalum* ranges from 9 to 13 mm TL (Auer 1982), so an average initial length of 11 mm was used to calculate IGRs for age-0 *C. anomalum* during that sampling increment. The peak hatch period for *C. anomalum* was assumed to occur on 20 April 1999 because peak spawning time has been documented in mid-April in Illinois streams (Burkhead 1980), and eggs take from 69 to 93 h to hatch at 17 to 23°C, respectively (Auer 1982).

Production

Orconectes spp. and *C. anomalum* production were calculated separately for each 5-mm size class in each sampling increment:

$$P = G\bar{B} \qquad (2)$$

where $\bar{B}$ is the mean biomass of a 5-mm size class over 2 consecutive sampling periods and G is the IGR for the average size or age of individuals in that size class (Benke 1996). An average growth rate of 0.003/d was used for large *Orconectes* spp. >25 mm CL because no significant relationship was found between temperature and IGR.

Gut content analysis

Sites representative of upper, middle, and lower reaches were usually sampled each month for gut content analysis of *C. anomalum* and *Orconectes* spp. (Fig. 1). However, the middle reaches were dry in March and October 1999, so gut contents for each species were only analyzed from a lower and an upper site (Fig. 1). Gut contents of *Orconectes* spp. and *C. anomalum* were analyzed from the same sites in all 3 mo. Additional *Orconectes* spp. gut contents were examined from the April 2000 biomass samples and combined with the March 1999 gut content data to increase sample size for spring. Sample size in each season ranged from 7 to 22 for each *Orconectes* spp. (12–38.7 mm CL) and 12 to 26 for *C. anomalum* (30–93 mm TL). *Orconectes* spp. and *C. anomalum* were collected with a seine and backpack electroshocker and immediately placed in bags of crushed ice and water. Animals were frozen (−4°C) upon returning to the lab. The presence of food sources (e.g., leaves, filamentous green algae, and diatoms) was also noted at 5 random points along 5 randomly placed horizontal transects at each site to estimate the relative availability of different food sources. In the laboratory, foregut contents of each species were removed and placed in formalin (2.5% by volume) until contents could be quantified and identified. *Campostoma anomalum* foreguts included the gut from the mouth to the first bend in the intestinal tract.

Campostoma anomalum gut contents contained very fine materials that were quantified microscopically at 400× total magnification. Areas of various food types were digitally analyzed using Scion Image software for 10 haphazardly chosen fields of view for most gut samples. Additional samples were analyzed using an ocular grid for 20 haphazardly chosen fields of view for each individual specimen. Gut contents were placed in the following categories: terrestrial vascular plant fragments, amorphous detritus (i.e., complex aggregates of amorphous material), diatoms, filamentous green algae, cyanobacteria, and animal matter. When diatoms were found dispersed throughout amorphous material, the whole field was classified as diatom.

Some *Orconectes* spp. food items were relatively large. To quantify both fine and coarse particles, the relative percentages of each food type were determined by a combination of mass and area. *Orconectes* spp. gut contents were separated into 2 size categories (<500 μm and ≥500 μm) using a sieve. Food sources <500 μm were analyzed under a microscope as described above for *C. anomalum* guts. Food items >500 μm were identified and sorted using a dissecting microscope. Each food source (animal matter, terrestrial vascular plant detritus, filamentous green algae, and particles <500 μm) was then dried (60°C, 24 h) and ashed (550°C, 5 h) to determine AFDM. The proportion (based on area) of each food type in the <500 μm fraction was multiplied by the mass (AFDM) of all <500 μm food material combined to determine the relative mass of each food type.

A 1-way ANOVA was used to determine if there were seasonal differences in the % of each food type in gut contents of *C. anomalum* and *Orconectes* spp. Separate ANOVAs were run for each food type within each species. Multiple comparisons among seasons were made using Tukey's (HSD) test ($\alpha = 0.05$). Percentage data were arcsine transformed before performing statistical analyses.

Ecological efficiencies and consumption estimates

An average of the mean % of each food type ingested in the spring, summer, and autumn months was used to estimate the annual trophic basis of production for each species. Assimilation efficiencies (AEs) for most of the resources were taken from Evans-White (2000). In Evans-White (2000), AE was calculated using ash as an indigenous marker (Conover 1966) and was defined as the amount of organic matter removed by the gut as a % of that ingested. AEs used in estimates for *Orconectes* spp. were 42%, 53%, and 15% for leaves, filamentous green algae, and diatoms, respectively (Evans-White 2000). For *C. anomalum*, AE values of 41% and 18% were used for filamentous green algae and diatoms, respectively (Evans-White 2000). An AE value of 10% was used for amorphous detritus for *Orconectes* spp. and for leaves and amorphous detritus for *C. anomalum* (Benke and Wallace 1980). An AE of 70% for animal matter was used for both *C. anomalum* and *Orconectes* spp. based on Benke and Wallace (1980), Ahlgren (1990), and Whitledge and Rabeni (1997). Net production efficiency (production/assimilation = NPE) was not directly estimated for either *C. anomalum* or *Orconectes* spp. during our study, but for macroinvertebrates it is often ~50% (Benke and Wallace 1980, Benke 1996), and this value is also similar to averages reported for ectothermic vertebrates (Burton and Likens 1975, Pough 1980). Therefore, a value of 50% was used for the NPE of each food type for both crayfish and stonerollers. All AE and NPE percentages were converted to proportions to estimate the relative amount each food source contributed to production.

Orconectes spp. and *C. anomalum* consumption and the trophic basis of production for each were estimated using the procedure of Benke and Wallace (1980). Consumption of each food source was estimated using the following equation:

TABLE 2. Mean abundance, biomass, instantaneous growth rate (IGR), and daily and interval production for each size class of *Orconectes nais* and *O. neglectus* during each sampling interval. Mean stream temperature was used to estimate IGR for individuals ≤25 mm carapace length (CL) and an average growth rate was used for individuals >25 mm CL. Annual production is the sum of interval production. Interval production is the product of daily production and the number of days in each interval, which were 25, 38, and 56 in the June to July, July to August, and August to October sampling intervals, respectively. AFDM = ash-free dry mass.

Sampling interval	Mean stream temp. (°C)	CL class (mm)	Mean abundance (ind./m^2)	Mean biomass (mg AFDM/m^2)	IGR (/d)	Production	
						Daily (mg AFDM m^{-2} d^1)	Interval (mg AFDM/m^2)
O. nais							
26 Mar–8 Jun 99	12.9	≤25	0.05	27	0	0	0
		>25	0.03	58	0	0	0
9 Jun–14 Jul 99	17.1	≤25	0.84	116	0.017	1.97	69
		>25	0.06	119	0.003	0.36	13
15 Jul–20 Aug 99	18.8	≤25	1.71	283	0.022	6.23	237
		>25	0.03	79	0.003	0.24	9
21 Aug–15 Oct 99	16.8	≤25	2.04	418	0.016	6.69	375
		>25	0.09	94	0.003	0.28	16
Annual production							719
O. neglectus							
26 Mar–8 Jun 99	12.9	≤25	0.23	119	0	0	0
		>25	0.01	9	0	0	0
9 Jun–14 Jul 99	17.1	≤25	0.25	71	0.017	1.21	42
		>25	0.04	59	0.003	0.18	6
15 Jul–20 Aug 99	18.8	≤25	0.66	123	0.022	2.71	103
		>25	0.07	96	0.003	0.29	11
21 Aug–15 Oct 99	16.8	≤25	2.68	369	0.016	5.9	330
		>25	0.09	98	0.003	0.29	16
Annual production							508

$$\text{consumption} = \frac{\text{production}}{(\text{AE})(\text{NPE})} \tag{3}$$

where production is the secondary production attributed to each food source.

Results

Density and biomass patterns

Monthly mean densities of *O. nais* ranged from 0.05 to 2.04 individuals/m^2 for young-of-the-year (YOY) individuals (≤25 mm CL) and 0.03 to 0.09 ind./m^2 for adult individuals (Table 2). Mean monthly densities for *O. neglectus* ranged from 0.23 to 2.68 ind./m^2 for YOY individuals and 0.01 to 0.09 ind./m^{-2} for adult individuals. Mean densities (ind./m^2) for *C. anomalum* ranged from 0.02 to 0.19 for age-0, 0.21 to 0.29 for age-1, and 0.03 to 0.08 for age-2 individuals (Table 3). Mean coefficients of variation (±1 SE) of density for all population estimates were 44.9 ± 12.5%, 64.7 ± 14.0%, and 44.6 ± 9.6% for *O. nais*, *O. neglectus*, and *C. anomalum*, respectively.

Orconectes spp. biomass was lower than *C. anomalum* biomass only in March, when all *Orconectes* spp. individuals collected were <25 mm CL. However, *Orconectes* spp. biomass from March may have been low because crayfish were sampled during daylight hours. Subsequent nocturnal collections yielded more individuals and a more balanced size structure. April 2000 nocturnal biomass estimates of *Orconectes* spp. were higher than the 1999 March (211 vs 31 mg AFDM/m^2, respectively). Mean annual biomasses (mg AFDM/m^2 ± 1 SE) of *O. nais* (296 ± 81.2), *O. neglectus* (244 ± 64.9), and *C. anomalum* (202 ± 61.8) were not significantly different ($p > 0.05$). However, the mean annual biomass of both *Orconectes* spp. combined (541

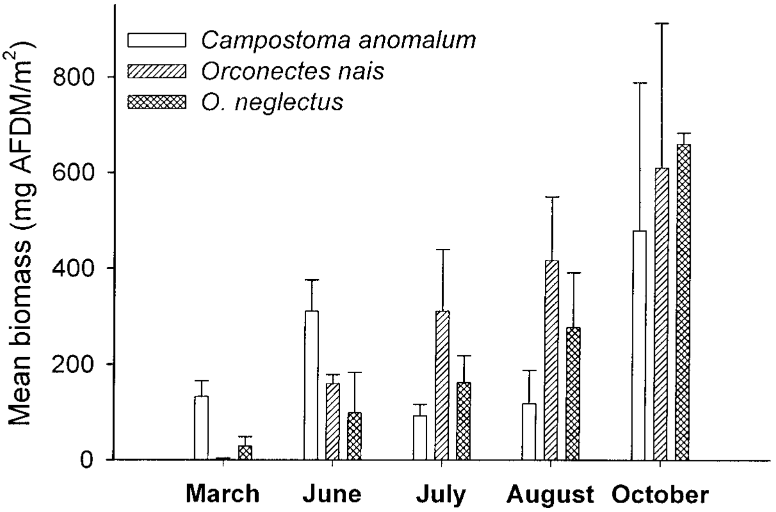

FIG. 2. Mean monthly ash-free dry mass (AFDM) biomass of *Campostoma anomalum*, *Orconectes nais*, and *O. neglectus* in Kings Creek in 1999. Error bars are +1 SE.

± 132.4) was significantly greater than the mean annual biomass of *C. anomalum* (F = 5.0, p = 0.03).

Seasonal patterns of abundance were different between *O. nais* and *O. neglectus*. The abundance of *O. nais* ≤25 mm CL began to increase in the June to July sampling period, whereas the abundance of *O. neglectus* ≤25 mm CL did not increase until the July to August sampling period (Table 2). These increases in abundance in both species corresponded with the appearance of newly hatched individuals (5–10 mm CL), which suggests that the peak hatching time for *O. neglectus* occurs later in the growing season than *O. nais*. Different seasonal patterns in biomass were also observed between *Orconectes* spp. and *C. anomalum*. *Orconectes nais* and *O. neglectus* biomass increased each successive month during the study, whereas *C. anomalum* biomass decreased from June to July and increased again from August to October (Fig. 2).

IGRs

Orconectes nais IGRs were both size and temperature dependent. No significant linear relationship between CL and IGR was found for individuals >25 mm CL ($p > 0.05$). A significant

TABLE 3. Mean abundance, biomass, instantaneous growth rate (IGR), and daily and interval production for each age class of *Campostoma anomalum* from March to October 1999. Annual production is the sum of interval production. the number of days within the March to July and the July to October sampling increments were 110 and 94, respectively. AFDM = ash-free dry mass.

Sampling interval	Age	Mean abundance (ind./m^2)	Mean biomass (mg AFDM/m^2)	IGR (/d)	Production Daily (mg AFDM m^{-2} d^{-1})	Production Interval (mg AFDM/m^2)
26 Mar–13 Jul 99	0	0.02	2	0.041	0.08	7
	1	0.21	57	0.008	0.46	51
	2	0.08	53	0.009	0.48	53
14 Jul–15 Oct 99	0	0.19	38	0.013	0.49	54
	1	0.29	187	0.004	0.75	82
	2	0.03	59	0002	0.12	13
Annual production						260

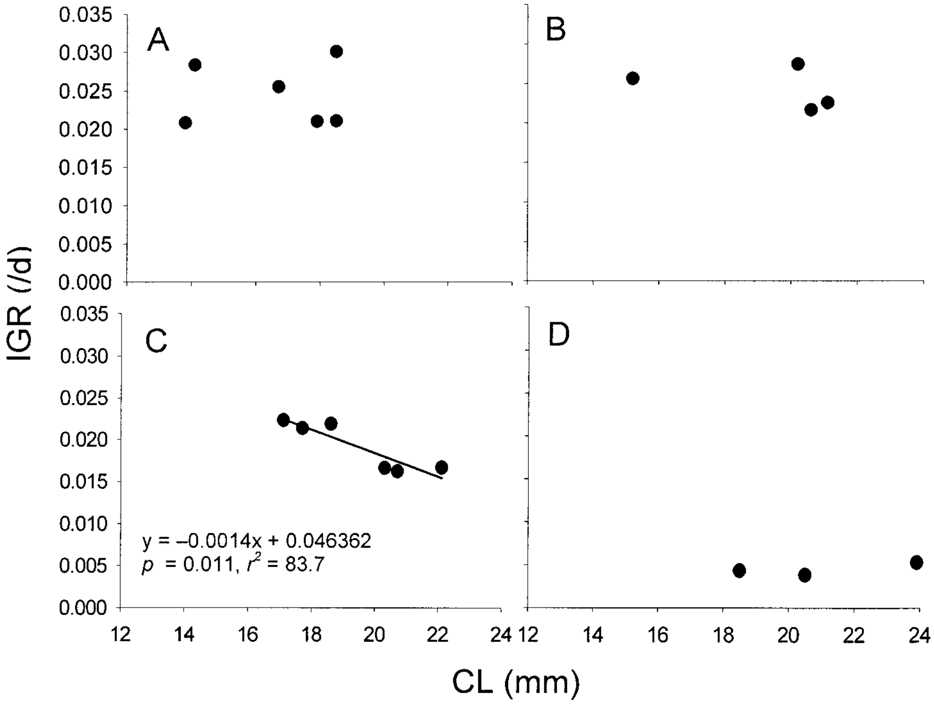

FIG. 3. Relationship between carapace length (CL) and instantaneous growth rate (IGR) for *Orconcetes nais* ≤25 mm CL for 24°C (A), 19.5°C (B), 18.5°C (C), and 14.0°C (D). The equation in panel C corresponds to the line shown.

relationship was found between IGR and CL for individuals ≤25 mm CL at 18.5°C, but not at other temperatures (Fig. 3). Individuals ≤25 mm CL had a 6-fold higher mean IGR than those >25 mm CL when data from all temperature regimes were combined ($F = 28$, $p = 0.0001$).

No significant linear or nonlinear relationship was observed between the mean stream temperature and the IGR of *O. nais* >25 mm CL (Fig. 4A, mean IGR = 0.003/d). However, the trend of IGR with stream temperature appeared to be hump-shaped. A quadratic equation described the relationship between mean stream temperature and the IGR of *O. nais* ≤25 mm CL (Fig. 4B). The squared parameter in this equation was significant ($p = 0.0005$) and, thus, was more efficient at modeling IGR than a simple linear regression. Based on this relationship, peak growth occurred at 22°C and no growth occurred below 13.6°C.

Growth rates of *C. anomalum* ranged from 0.013 to 0.041/d for age-0, 0.004 to 0.008/d for age-1, and 0.002 to 0.009/d for age-2. Growth rates were slightly lower from July through October than from March through July (Table 3). Average length of age-1 and age-2 individuals from 1999 March (Fig. 5A) coincided with the average length of age-0 and age-1 individuals from 1999 October (Fig. 5C), suggesting little growth occurs during winter. Age-0 individuals first appeared in the 1999 July sample (Fig. 5B).

Production

Orconectes nais and *O. neglectus* ≤25 mm CL made up most of the daily and interval production in all months (Table 2), and most annual production of *Orconectes* spp. took place from July to October. Total annual production of *O. nais* and *O. neglectus* was 719 and 508 mg AFDM/m^2, respectively. Annual production to biomass ratios (P/B) for *O. nais* and *O. neglectus* were 2.4 and 2.1, respectively.

Age-1 and -2 *C. anomalum* made the largest contribution to production in the March to July sampling interval (Table 3). Age-0 and -1 made the most significant contribution to production

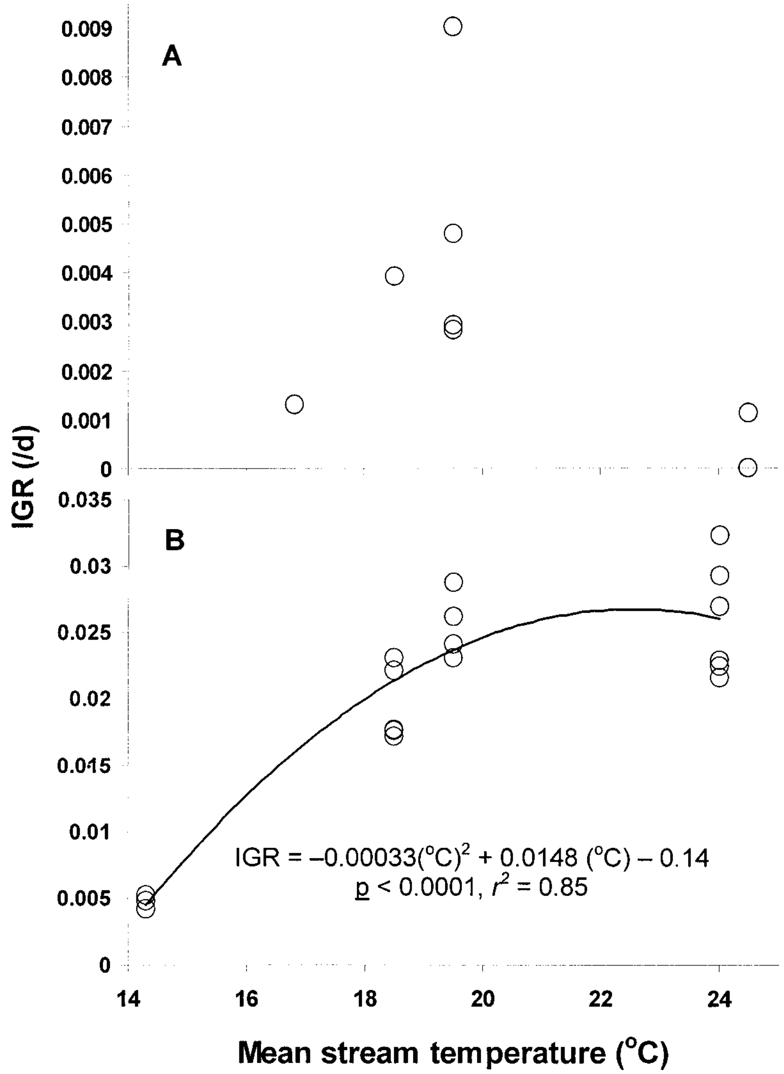

FIG. 4. Relationship between mean stream temperature and instantaneous growth rate (IGR) for *Orconectes nais* >25 mm carapace length (CL) (A) and le;25 mm CL (B). The equation in panel B corresponds to the line shown.

in the July through October sampling interval. Total annual production of *C. anomalum* was 260 mg AFDM/m^2, with an annual P/B of 1.3.

Gut contents

There were no significant differences in the % of each type of gut contents of *O. nais* and *O. neglectus* in spring, summer, or autumn samples ($F < 3.31$, $p > 0.05$). Therefore, gut content data for both species were combined for subsequent statistical analyses. Significant seasonal differences were found in the relative % of terrestrial vascular plant detritus ($F = 13.1$, $p = 0.001$), filamentous green algae ($F = 12.75$, $p = 0.0001$), and animal matter ($F = 3.6$, $p = 0.002$) in *Orconectes* spp. gut contents (Fig. 6). The % of terrestrial vascular plant detritus in *Orconectes* spp. guts was significantly higher in the summer than in the spring or the autumn ($p < 0.05$). However, the mean (±1 SE) % presence of leaves available at gut content analysis sites was

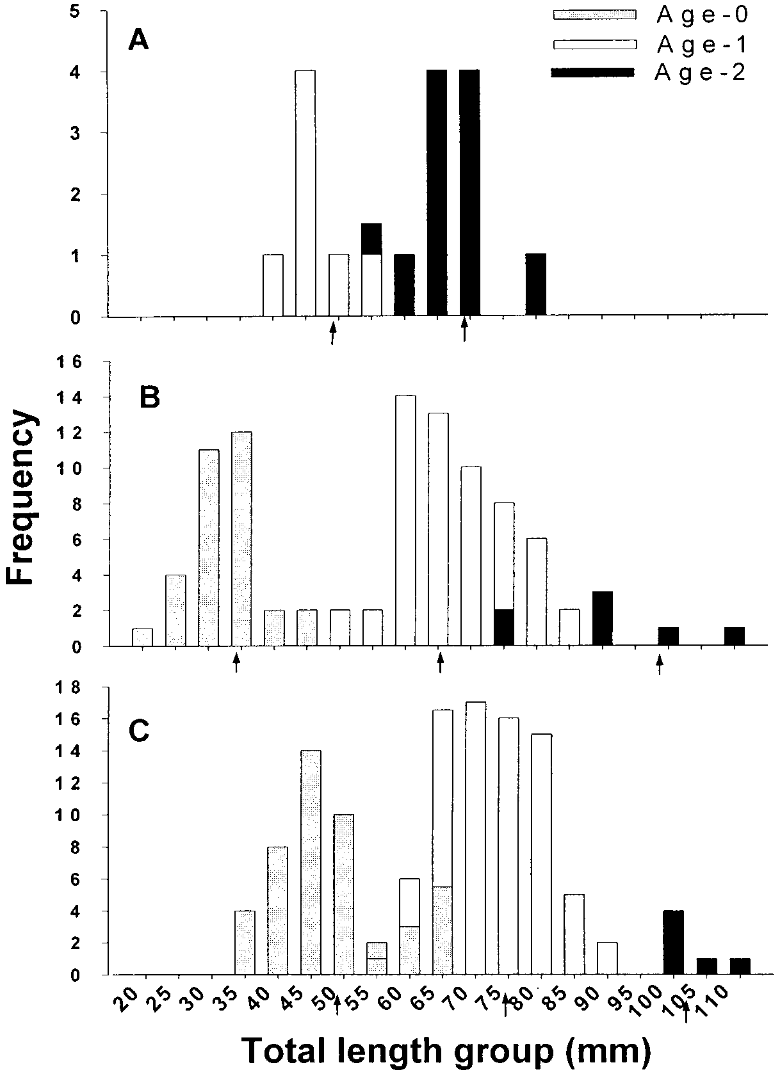

FIG. 5. *Campostoma anomalum* length–frequency and age structure in March (A), July (B), and October (C) 1999. Arrows represent mean total length for each age class used to calculate instantaneous growth rates for each sampling period.

significantly lower in the summer (5 ± 3.2) than in the spring (20 ± 7) and autumn (33 ± 15) ($p < 0.05$). The % of animal matter (primarily other crayfish, Odonata, and Ephemeroptera) in *Orconectes* spp. guts was significantly higher in the autumn than in the summer ($p < 0.05$). *Orconectes* spp. guts contained significantly more filamentous green algae in the spring than in the summer and autumn samples ($p < 0.05$), which were not significantly different ($p > 0.05$, Fig. 6). The mean (±1 SE) % presence of filamentous green algae available at gut content sites was also significantly higher in spring (38 ± 10) than in the summer (0) and autumn (2 ± 2) ($p < 0.05$).

The only significant seasonal difference in *C. anomalum* gut contents was the % of animal matter ($F = 9.16$, $p = 0.0004$), which was higher in the spring than in the summer or autumn ($p < 0.05$, Fig. 6). Chironomidae larvae were the most common invertebrates ingested by *C. anomalum*, followed by small heptageniid mayfly larvae.

Diatoms consistently made up a higher % of gut contents for *C. anomalum* than for *Orconectes*

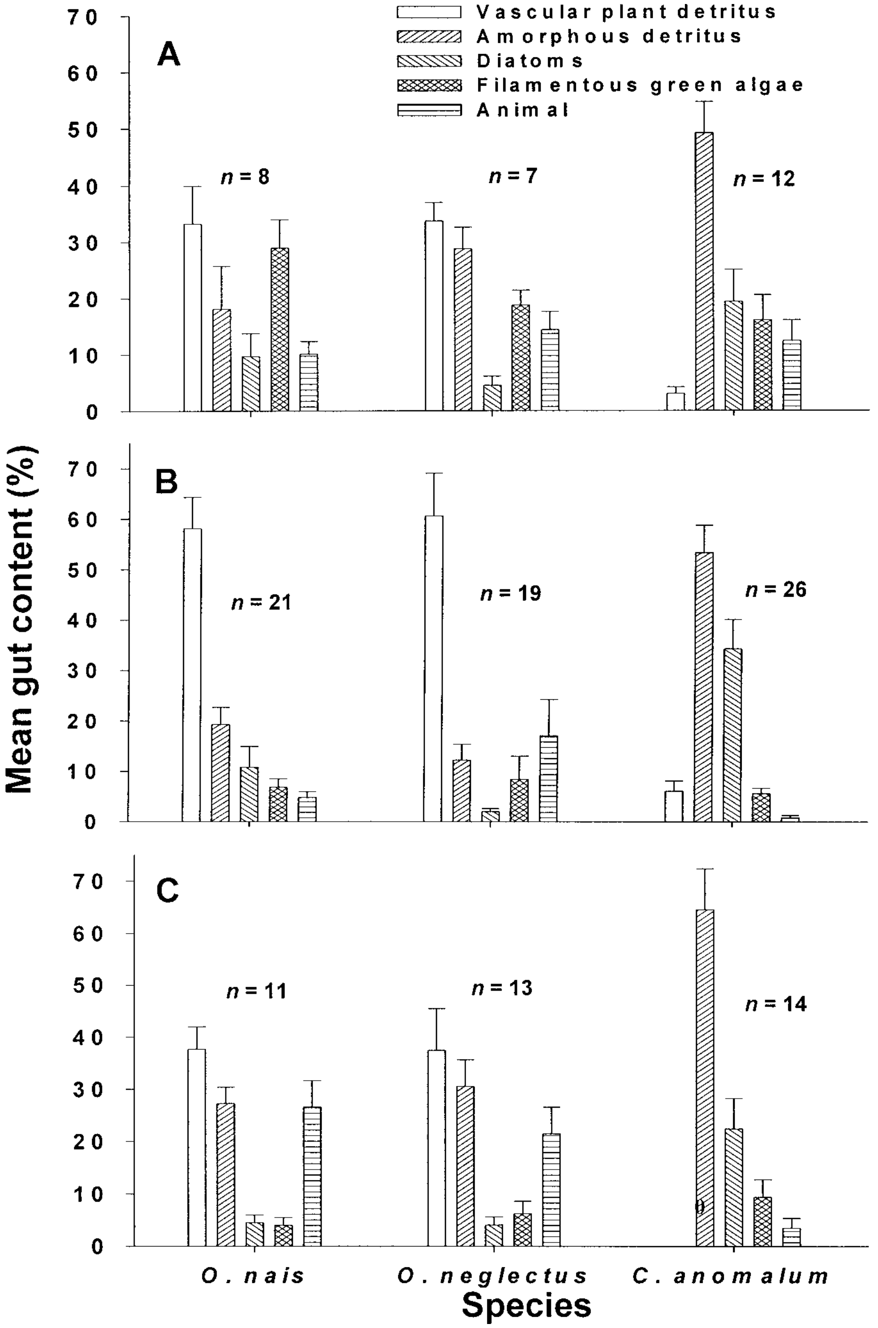

FIG. 6. Mean % (+1 SE) of food items found in the guts of *Orconectes nais*, *O. neglectus*, and *Campostoma anomalum* in spring (A), summer (B), and autumn (C) 1999.

spp. (Fig. 6). Guts of *Orconectes* spp. contained a higher % of filamentous green algae in the spring compared to guts of *C. anomalum* ($F = 4.67$, $p = 0.038$). *Campostoma anomalum* guts consistently contained a higher % of total algae (diatoms + filamentous green algae) than did *Orconectes* spp. guts, even though the % of total algae in the guts was similar for both species in

TABLE 4. The contribution of each food source to *Orconectes* spp. and *Campostoma anomalum* production. The *% production attributed to each food type* column is calculated by dividing each individual value in the *Relative amount to production* column by the total of all values in the *Relative amount to production* column. The *Production attributed to each food type* column is calculated by multiplying each individual value in the *% production attributed to each food type* column by the total of all values in the *Production attributed to each food type* column and dividing by 100.

	Amount in foregut (%)		AE		NPE		Relative amount to production	% production attributed to each food type	Production attributed to each food type (mg AFDM m^{-2} y^{-1})
***Orconectes* spp.**									
Leaves	42.2	×	0.42	×	0.5	=	8.86	46	564
Animal	16.1	×	0.70	×	0.5	=	5.64	29	356
Filamentous green algae	12.7	×	0.53	×	0.5	=	3.37	17	209
Amorphous detritus	22.6	×	0.10	×	0.5	=	1.13	6	73
Diatoms	6.4	×	0.15	×	0.5	=	0.48	2	25
Total							19.48	100	1227
C. anomalum									
Amorphous detritus	55.7	×	0.10	×	0.5	=	2.79	30	78
Diatoms	25.3	×	0.18	×	0.5	=	2.28	24	64
Filamentous green algae	10.4	×	0.41	×	0.5	=	2.13	23	59
Animal	5.6	×	0.70	×	0.5	=	1.96	21	55
Leaves	3.0	×	0.10	×	0.5	=	0.15	2	4
Total							9.30	100	260

the spring samples (*C. anomalum* = 35.5%, *Orconectes* spp. = 31.5%). *Orconectes* spp. and *C. anomalum* gut contents often were composed of similar amounts of detritus, but guts of *Orconectes* spp. contained mainly terrestrial vascular plant detritus, whereas guts of *C. anomalum* guts contained mainly fine, amorphous detritus. *Orconectes* spp. and *C. anomalum* guts contained similar percentages of animal matter in the spring months (12.4% and 12.1%, respectively), but in the summer and autumn samples the % of animal matter in *Orconectes* spp. guts was consistently higher than in *C. anomalum* guts (Fig. 6).

Consumption and trophic basis of production

Terrestrial vascular plant tissue contributed most to *Orconectes* spp. production, followed by animal matter, filamentous green algae, amorphous detritus, and diatoms (Table 4). Amorphous detritus, diatoms, filamentous green algae, and animal matter all made important contributions to *C. anomalum* production. Total algae accounted for 47% of *C. anomalum* production and 19% of *Orconectes* spp. production. Leaves and amorphous detritus and animal matter contributed more to *Orconectes* spp. production (52% and 29%, respectively) than to *C. anomalum* production (32% and 21%, respectively).

Both *C. anomalum* and *Orconectes* spp. were important consumers of total algae and total detritus (leaves and amorphorus detritus) in Kings Creek (Fig. 7). *Orconectes* spp. consumed more terrestrial vascular plant detritus (CPOM), filamentous green algae, and animal matter than did *C. anomalum*, whereas *C. anomalum* consumed more diatoms than *Orconectes* spp.

Discussion

Density and biomass patterns

Densities of age-0 *Orconectes* spp. in Kings Creek were often higher than densities of age-0

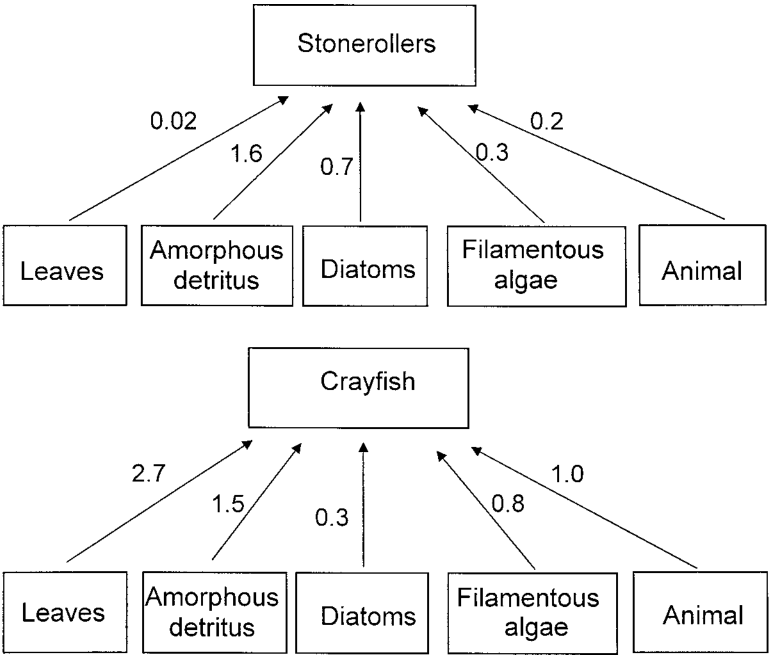

FIG. 7. Estimated annual consumption (g ash-free dry mass [AFDM] m^{-2} y^{-1}) of various food sources by stonerollers (top) and crayfish (bottom) in Kings Creek.

C. anomalum, whereas densities of adult *C. anomalum* were often higher than adult *Orconectes* spp. It is possible that we were more efficient at sampling age-0 *Orconectes* spp. than age-0 *C. anomalum*. However, all species were measured using sampling techniques that were likely biased against small individuals. Efficiency of capture by electrofishing increases with fish size (Reynolds 1989). The average size of post-yolk sac *C. anomalum* is between 9 and 13 mm TL. We caught none <20 mm TL. Age-0 *O. nais* and *O. neglectus* are ~4 mm CL (~8 mm TL) when they first leave their mothers protection (MAE-W, personal observation). We collected no individuals <7 mm CL (~14 mm TL). Therefore, densities of age-0 *C. anomalum* and age-0 *Orconectes* spp. were probably both underestimated.

Our depletion-removal sampling may also have resulted in conservative estimates of population size. We did not use block-nets for population estimates when well-defined shallow riffles (<2.5 cm deep) bounded our sampling reach. Therefore, some movement could have taken place into and out of the sampling reach, violating the closed-population assumption of a Leslie depletion estimate. However, we believe that these shallow riffles did impede movement into and out of the sampling reach during our sampling events for several reasons. First, block-nets were placed in these shallow riffles twice during sampling and no target organisms were captured. Second, large numbers of *C. anomalum* were often caught at the base of upstream riffles, whereas few to none were caught within these upstream riffles. We sampled from downstream to upstream, so that *C. anomalum* were corralled at the base of the riffle and were unable or unwilling to escape in appreciable numbers. Third, the mean r^2 of relationships between catch per unit effort and accumulated catch were high for all species ($r^2 > 80$), indicating successful depletion, obviating significant movement into the study reach. Overall, the biomass of *Orconectes* spp. was higher than that of *C. anomalum* throughout the growing season. Given that sampling of all species was biased in a similar manner, it is likely that the relative difference in the biomass of *Orconectes* spp. and *C. anomalum* is real and conservative.

IGRs and production

IGR of *O. nais* decreased with increasing size and decreasing temperature. However, temperature effects on IGR dominated over size effects. Our experiment included no individuals <13.8 mm CL because these individuals could escape from the cage through the mesh windows. It is possible that more significant relationships would have been found between CL and stream temperature if these smaller individuals had been included. It is also likely growth rates of individuals <10 mm CL exceed those of the larger individuals (13–23 mm CL) included in our experiment, which would lead to an underestimate of growth and production for small *Orconectes* spp. in our study. In addition, individuals ≤25 mm CL were stocked in growth chambers at a higher density than was generally found in the stream, so it is possible that some competition occurred that might decrease growth rates. However, food was provided in excess to minimize competition for food resources, so any competition would have been intraspecific interference competition.

A quadratic relationship like the one between *O. nais* growth rate and average stream temperature (Fig. 4B) may be useful for examining and modeling relationships between growth and stream temperature for other species of crayfish and other macroinvertebrates. Mundahl and Benton (1990) also found significant quadratic relationships between temperature and % CL increase and % mass increase of *O. rusticus*. A similar quadratic relationship has also been demonstrated for Chironomini, Tanytarsini, and total Chironomidae growth rates and stream temperature (Benke 1998). Once known, these relationships represent valuable tools for estimating invertebrate growth and production.

Although the relationship between stream temperature and IGR was strong for small individuals, it is possible that other factors besides stream temperature and CL affected *Orconectes* spp. IGR. IGR sites had variable canopy cover and groundwater input that resulted in the different temperature regimes observed. These differences could result in differences in food resources available at each site. However, we tried to provide crayfish with similar algal food sources at all sites. Stream water velocity was also slightly different among sites, but all cages were located in pools and water velocity did not appear to differ significantly among sites. Stream temperature explained >80% of the variation in *O. nais* growth rates, and it appears to be the primary factor explaining the growth rate of *O. nais* in Kings Creek.

IGRs of *C. anomalum* were higher in the spring (March–July) than in the autumn months (July–October). The significance of this decrease in growth rates during autumn could not be statistically tested because there were no replicates of growth rate for *C. anomalum*. However, Lotrich (1973) observed a similar phenomenon whereby daily growth increments for age-1 cyprinids, including *C. anomalum*, sampled from 1st- to 3rd-order streams in eastern Kentucky, were twice as high from May to August compared to August to September. We observed this pattern for all age classes of *C. anomalum* in Kings Creek, and it could be related to size-dependent growth-rate changes, reduced feeding, and increased metabolism. Water levels fell and some reaches dried completely in the late summer and autumn of 1999, as is typical for most years in Kings Creek. Drying of intermittent reaches on KPBS results in a series of pools connected only by hyporheic flow in which temperatures rise and dissolved oxygen (DO) decreases (Gerlanc 1999). This drying confines large populations of fish into pools that get progressively smaller. Competition for food could become an important factor limiting growth, as could physicochemical stress and increased metabolic demands associated with a rise in water temperature and a decrease in dissolved oxygen.

Orconectes spp. and *C. anomalum* may use different strategies for existing in intermittent streams. *Orconectes* spp. total biomass increased with each sample over the growing season, whereas *C. anomalum* populations decreased in the late summer months when intermittent reaches dried, indicating mortality, emigration, or both. This result suggests *C. anomalum* was more negatively influenced by stream drying than were crayfishes. Crayfishes are likely better at surviving in drying stream reaches because they can burrow to reach moisture and tolerate low oxygen conditions (Hobbs 1981, Berrill and Chenowith 1982). Crayfish can successfully emigrate from drying pools to deeper pools or perennial reaches because they can move over land, at least for short distances (Hobbs 1991), a behavior not shared by *C. anomalum*. Thus, crayfish appear better adapted for surviving in a given stream reach throughout the year, whereas *C. anomalum* are stronger swimmers and can more easily recolonize from wetter reaches downstream.

Gut contents

Orconectes spp. guts had a higher % of total detritus than total algae or invertebrates during all seasons, which is consistent with gut content information for other species of *Orconectes* (Charlebois and Lamberti 1996, Whitledge and Rabeni 1997). However, we found significant seasonal differences in the % of terrestrial vascular plant detritus, algae, and invertebrates in *Orconectes* spp. guts. Our data indicated the peak hatch time for *O. nais* is earlier in the year than that of *O. neglectus*, but no trophic resource partitioning between the 2 species. However, future studies using larger sample sizes may be needed to distinguish small differences in resource use.

The % of certain food items in *Orconectes* spp. guts was related to their abundance in the environment. Filamentous green algae were the most abundant food resource in the stream in March when they made up the greatest % of items in *Orconectes* spp. guts. In addition, the % of invertebrates in *Orconectes* spp. guts increased in the autumn, when *Orconectes* spp. densities were highest. The pattern was different for terrestrial vascular plant detritus. The % of terrestrial vascular plant detritus in *Orconectes* spp. guts was higher in the summer than in the autumn, despite the high abundance of leaf litter in the stream during autumn, which suggests that *Orconectes* spp. chose animal matter over leaf litter when both were abundant, but that leaf litter was consumed when other resources were not as abundant.

The % of invertebrates in *C. anomalum* guts also varied with season. The highest % of macroinvertebrates occurred in spring, which coincided with *C. anomalum* spawning. Invertebrate presence in guts also coincided with higher growth rates and is likely an important, high-quality food source for *C. anomalum* growth as well as reproduction. *Campostoma anomalum* guts often contain only small amounts of invertebrates (Kraatz 1923, Schmulbach 1953, Burkhead 1980), but invertebrate tissue still makes a significant contribution to *C. anomalum* production in Kings Creek and possibly other streams because invertebrates are more easily digested and are more nutritious than algal and detrital food sources (Ahlgren 1990, Evans-White 2000). The significant seasonal differences found in both *Orconectes* spp. and *C. anomalum* gut contents underscore the importance of analyzing samples throughout the growing season to obtain an accurate assessment of resource use and trophic dynamics.

Orconectes spp. and *C. anomalum* are both omnivorous, but they did not eat identical items in Kings Creek. *Campostoma anomalum* guts always contained a higher % of diatoms than did *Orconectes* spp. guts. However, *Orconectes* spp. guts contained a higher % of filamentous green algae than did *C. anomalum* guts when it became abundant in the stream. The types of animal matter found in *Orconectes* spp. and *C. anomalum* were also different. *Orconectes* spp. guts contained mainly other *Orconectes* spp., odonates, and mayfly larvae, whereas *C. anomalum* guts contained mainly chironomids. Thus, although both omnivores ingested detritus, algae, and invertebrates, the relative proportions ingested and the specific food type differed.

Orconectes spp. ingested a higher % vascular plant detritus and a lower % of fine amorphous detritus than did *C. anomalum* during all seasons. *Orconectes* spp. and *C. anomalum* may eat different types of detritus because of morphological differences that constrain acquisition, handling, and ingestion of food items. Crayfishes hold food items in place with their walking legs and tear off pieces with the mandible, the maxillae, and the maxillipeds, whereas *C. anomalum* rely only on their mouth to initially reduce particles to a size they are able to ingest. Thus, leaves and other forms of coarse particulate organic matter would be more difficult for *C. anomalum* than *Orconectes* spp. to consume.

Consumption and trophic basis of production

Campostoma anomalum are generally considered herbivores, but both amorphous detritus and invertebrates contributed significantly to their production in Kings Creek. Therefore, *C. anomalum* should be considered omnivorous. Invertebrates often made up <20% of their diet, but contributed significantly to *C. anomalum* production, which was consistent with prior stable isotope analyses in this stream (Evans-White et al. 2001). Evans-White et al. (2001) also provided evidence from stable isotopes that *C. anomalum* may be more predaceous than *Orconec-*

tes spp. in Kings Creek. Our study provided evidence that both fish and crayfish ingest animal matter but did not indicate that *C. anomalum* ingests more animal matter than *Orconectes* spp.

Our results demonstrated that crayfish and *C. anomalum* both ingested filamentous green algae and diatoms, but suggested that each might affect different components of stream algal communities. *Orconectes* spp. consumed more filamentous green algae than did *C. anomalum*, which were more important consumers of diatoms than were crayfish. Crayfish also are important consumers of filamentous green algae in other systems (Hart 1992, Creed 1994). Both omnivores are potentially important consumers of benthic algae in prairie streams in central North America. Therefore, future experiments that examine and compare the responses of algal communities to crayfish and *C. anomalum* grazing, and interactions between these 2 consumers, will provide further insight on their relative importance in stream ecosystems.

Other studies have shown that crayfish and *C. anomalum* play a significant role in structuring benthic stream communities (Power et al. 1985, 1988, Creed 1994, Charlebois and Lamberti 1996, Gelwick and Matthews 1997, Evans-White et al. 2001). Our study represents the first comparison of the relative roles of these 2 abundant and often co-occurring omnivores in organic matter processing and energy flow in streams. These animals used different components of the same resource base for their production and, thus, played unique roles in Kings Creek. These differences in resource use should be considered when designing both community- and ecosystem-level studies that involve both *Orconectes* spp. and *C. anomalum*.

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