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PRIMARY RESEARCH PAPER

Trophic overlap between native and invasive stream crayfish

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Abstract We examined trophic dynamics of a stream food web where invasive *Orconectes neglectus* appear to be displacing native *O. eupunctus* in the Spring River drainage of the Ozark Highlands, Missouri and Arkansas, USA. We collected crayfish species and possible food sources seasonally from a site of sympatry on the South Fork Spring River. We determined diet overlap and potential for competition between *O. eupunctus* and *O. neglectus*, and investigated seasonal variation using carbon and nitrogen stable isotope analyses and gut content analyses. Gut content analysis showed both species of crayfish consumed mainly detritus during summer and spring, with other prey categories varying by species and season. Stable isotope analysis showed that *O. eupunctus* and *O. neglectus* relied on invertebrates as a major energy and nutrient source throughout summer, autumn, and spring, and the two species showed differences in their stable isotope signatures during spring and summer, but not autumn. Given the trophic overlap between *O. eupunctus* and *O. neglectus*, there is a potential for the two species to compete for food and to be ecologically redundant. Ecological redundancy can lead to reduced effects on ecosystem function post-invasion, and therefore examining ecological redundancy of potential invaders should be a conservation priority.

Keywords *Orconectes eupunctus* · *Orconectes neglectus* · Food webs · Diet · Energy and nutrient sources · Invasive species · Temporal variation

Introduction

Crayfish introductions have elicited drastic changes in aquatic systems, both to native crayfish faunas (Capelli, 1982; Berrill, 1985; Momot, 1996) and to other members of the aquatic communities (Olsen et al., 1991; Gamradt et al., 1997; Nilsson et al., 2012; Ercoli et al. 2015). Invasive crayfish can negatively impact native crayfishes via reproductive interference (Butler & Stein, 1985; Perry et al., 2001), transmission of the crayfish plague (Alderman et al., 1990; Evans & Edgerton, 2002; Westman et al., 2002), interspecific competition (Hill & Lodge, 1994; Usio et al., 2001; Gherardi & Cioni, 2004), and habitat displacement with subsequent selective predation by fish (DiDonato & Lodge, 1993; Garvey et al., 1994).

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In the Ozark highlands of Arkansas and Missouri, the crayfish *Orconectes neglectus* Faxon, 1885 has recently invaded portions of the Spring River drainage, apparently displacing two native crayfish species, *Orconectes eupunctus* Williams, 1952 and *Cambarus hubbsi* Creaser, 1931 (Flinders & Magoulick, 2005; Magoulick & DiStefano, 2007). *Orconectes neglectus* is native to the White River drainage in southern Missouri and northern Arkansas (Pflieger, 1996) and the likely vector of introduction was via bait bucket. Research suggests that; (1) *O. neglectus* was introduced into the West Fork of the Spring River between 1984 and 1998 (Flinders & Magoulick, 2005; Magoulick & DiStefano, 2007), (2) *O. neglectus* may be negatively impacting the native crayfish community, especially *O. eupunctus* (Rabalais & Magoulick, 2006a, b; Larson & Magoulick, 2009; Larson et al., 2009), and (3) *O. neglectus* has the potential to expand its distribution in the Spring River drainage and may negatively affect other species including the imperiled *Orconectes marchandi* Hobbs, 1948 (Flinders & Magoulick, 2005; Taylor et al., 2007). Mechanisms driving this apparent displacement have not been determined, although seasonal drought and stream drying likely act as at least a partial mechanism (Larson et al., 2009).

Orconectes eupunctus and *O. neglectus* show similar habitat use, mainly selecting riffles, suggesting interspecific competition as a potential mechanism involved in the displacement (Magoulick & DiStefano, 2007). In previous studies, habitat use and selection by *O. eupunctus* and *O. neglectus* juveniles and adults did not shift in sympatry versus allopatry suggesting the two species did not compete for habitat (Rabalais & Magoulick, 2006a). Additionally, densities of adult and juvenile male *O. eupunctus* and *O. neglectus* were manipulated in field experimental enclosures, but no evidence of interspecific competition was found (Rabalais & Magoulick, 2006b; Larson & Magoulick, 2009). However, laboratory experiments showed that *O. neglectus* aggressively dominated *O. eupunctus* when food resources were limited (Larson & Magoulick, 2009). Therefore, it is necessary to examine prey resource use between species in situ to determine the potential for interspecific competition.

Most studies that use gut content analysis have described crayfish as omnivores with detritus, periphyton, sediment, and macrophytes making up the majority of the diet (Whitledge & Rabeni, 1997; Whitmore & Huryn, 1999; Helms & Creed, 2005). This diet composition is further substantiated by studies on ecosystem level effects of crayfish, specifically their impact on periphyton, macrophytes, and terrestrial leaf decomposition (Lodge & Lorman, 1987; Olsen et al., 1991; Hart, 1992; Creed, 1994; Charlebois & Lamberti, 1996; Nyström et al., 1999; Ludlam & Magoulick, 2010; Lodge et al., 2012). However, in laboratory experiments crayfish have been shown to have very little or no growth when fed only detritus, periphyton, and macrophytes (Hill et al., 1993). Gut content analysis only provides insight into a very short time frame and may not be indicative of what is being assimilated into crayfish tissue growth. Recent studies have expanded on the use of gut content analysis by using stable isotopes as a method of determining energy and nutrient source (Parkyn et al., 2001). The use of δ^{13}C and δ^{15}N allows for the determination of the assimilated fraction of the diet over an extended period of time as well as identifying carbon and nitrogen sources not obvious in gut content analysis (DeNiro & Epstein, 1978; Deniro & Epstein, 1981; Fry & Sherr, 1984; Peterson & Fry, 1987). The application of stable isotopes in determining crayfish food web structure has suggested that crayfish may be assimilating more protein and energy rich food than has been previously shown with gut content analysis (Whitledge & Rabeni, 1997; Nyström et al., 1999; Parkyn et al., 2001; Rudnick & Resh, 2005; Roth et al., 2006). Therefore, crayfish in many systems may need animal food sources. If these are in limited supply, or if less dominant species are unable to secure these food sources, then it could have a negative effect on crayfish fitness (Hill & Lodge, 1999).

In most streams, hydrologic regimes vary dramatically temporally which might affect food web structure (Closs & Lake, 1994). However, most studies examining food web structure and feeding relationships have ignored temporal variation. In particular, Ozark streams undergo dramatic seasonal shifts from high flows in autumn through spring and low flows in summer and early autumn. This seasonal variation in flows is likely important in the apparent displacement of *O. eupunctus* by *O. neglectus* (Larson et al., 2009) and may also effect feeding relationships and food web structure.

Given that *O. eupunctus* and *O. neglectus* use similar structural habitats but do not appear to compete for space, while they may potentially compete for food, we examined prey use by *O. eupunctus* and *O. neglectus* to determine the potential for interspecific competition. Additionally, we were interested in whether the native and invasive crayfish species may be ecologically redundant in these systems (i.e., species or functional groups that have similar effects on ecosystem structure and function; Walker, 1992). We also sought to determine how food web structure and feeding relationships among *O. eupunctus* and *O. neglectus* varied seasonally. Our objectives were to determine whether (1) *O. eupunctus* and *O. neglectus* used similar prey, and (2) *O. eupunctus* and *O. neglectus* feeding relationships varied temporally. We used gut content and stable isotope analyses to address these questions.

Materials and methods

This study was conducted on the South Fork Spring River in north central Arkansas (36°27′53″N, 91°51′48″W) where the invasive *O. neglectus* co-occurs with the native *O. eupunctus*. Because *O. eupunctus* and *O. neglectus* select primarily riffle and run habitats (Rabalais & Magoulick, 2006b; Magoulick & DiStefano, 2007) the study site consisted primarily of riffle and run habitats and associated stream margin.

Crayfish were collected during summer (August 2002), autumn (November 2002) and spring (April 2003). Crayfish were collected during daylight hours using a kick net and Smith-Root Model 12 backpack electrofisher. Collected crayfish were identified to species, sexed, and carapace length recorded to the nearest mm before being placed in a sample container. Potential foods were also collected during each sampling event. Fish were collected with a kicknet and electrofisher, and invertebrates were collected with a Hess sampler. Repeat collections were made within the site to ensure enough material was collected for stable isotope analysis. Periphyton were scraped from rocks using scalpels and placed in sample containers. Leaf detritus (hereafter detritus), filamentous green algae, wood, and aquatic vegetation were collected by hand and using forceps. All samples collected were placed in coolers on ice and transported to the laboratory within 5 h.

Crayfish were classified as juveniles (≤12 mm CL) and adults (>12 mm CL) for analysis. Adult crayfish typically ranged 15–27 mm CL. This was based on length-frequency histograms of *O. eupunctus* and *O. neglectus* collected in a concurrent study (Rabalais & Magoulick, 2006b). Both species showed similar growth rates and had similar juvenile and adult sizes in this system (Larson & Magoulick, 2008).

At the laboratory, all samples were immediately lyophilized (LabConco Corp.) and frozen. Invertebrates were analyzed whole and all other samples were homogenized using a pestle and mortar. Ground material was passed through a 4 mm mesh screen to reduce sample heterogeneity. Samples were stored in a vacuum desiccator until analyzed at the University of Arkansas Stable Isotope Laboratory. Individual crayfish abdomen muscle tissue was ground and 0.2–0.3 mg/sample used in analysis. Invertebrates were weighed and analyzed as whole organisms with the exception of Chironomidae which were sometimes paired to obtain 0.2–0.3 mg/sample. Filamentous green algae, periphyton, and detritus samples were subsampled to obtain 1.5–2.5 mg/sample of material for analysis. All samples were weighed into tin capsules on a microbalance (Sartorius) prior to analysis.

Elemental and isotopic analyses were performed using an elemental analyzer (Carlos Erba NA 2500) coupled with an isotope ratio mass spectrometer (Thermo Finnigan Delta Plus). Stable isotope ratios are reported in the δ notation where δ^{13}C or δ^{15}N $= ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$ where R_{sample} is ^{13}C/^{12}C or ^{15}N/^{14}N of the sample and R_{standard} is ^{13}C/^{12}C of Pee Dee belemnite carbonate or ^{15}N/^{14}N of atmospheric N_2. Internal standards of known relation to above-listed international standards were used every six samples. Reproducibility of internal standards at 2 standard deviations was 0.2‰ for δ^{13}C and 0.4‰ for δ^{15}N.

To determine prey ingested, crayfish from stable isotope analyses were dissected and foreguts were removed. Foregut contents were placed in a Petri dish and distributed evenly across the plate following Whitledge & Rabeni (1997). Gut contents were viewed under a dissecting microscope at ×20 magnification. Percent of the total area of the dish of detritus, invertebrates, algae, and inorganic material (i.e., sand and silt) was estimated. Autumn crayfish stomach contents were not determined due to a freezer malfunction.

We used mixing models in IsoSource (Phillips & Gregg, 2003) to determine the percent contribution of various energy and nutrient sources to crayfish. The potential sources were allochthonous detritus (leaves), invertebrates, filamentous green algae, and periphyton. We focused on Trichoptera, Ephemeroptera, and Chironomidae for this analysis because they were the most abundant invertebrate taxa. Sources were determined to be isotopically distinct by examining means and standard errors. We input δ^{13}C and δ^{15}N signatures of each source (prey) and mixture (crayfish) and set the increment size to 1% and the tolerance to 0.1‰. Before running IsoSource, values were adjusted for trophic fractionation from diet items to crayfish (2.3‰ for δ^{15}N and 0.5‰ for δ^{13}C) based on fractionation values determined from literature (France & Peters, 1997; Vanderklift & Ponsard, 2003). We report the ranges of feasible solutions for all possible combinations of source proportions for the population rather than means and standard deviations because they are more informative for mixing model stable isotope analysis (Phillips & Gregg, 2003).

We used ANOVA to determine differences in prey categories ingested by crayfish species. We used MANOVA to determine differences in δ^{13}C and δ^{15}N signatures of crayfish species by season. Significant differences in MANOVA were followed by ANOVA to determine differences in each response variable. We did not correct for differences in basal resource signatures among seasons as only filamentous green algae showed substantial variation in signatures among seasons and primary consumers varied little indicating this variation did not carry up the food web.

Results

Feeding relationships

Gut content analysis showed all species-age classes of crayfish consumed mainly detritus, with other prey categories varying by species and season (Fig. 1). Percent of each prey category consumed did not differ significantly among species in either season (ANOVA $P > 0.250$).

Invertebrates appeared to be the main energy and nutrient source for both species of crayfish (Fig. 2).

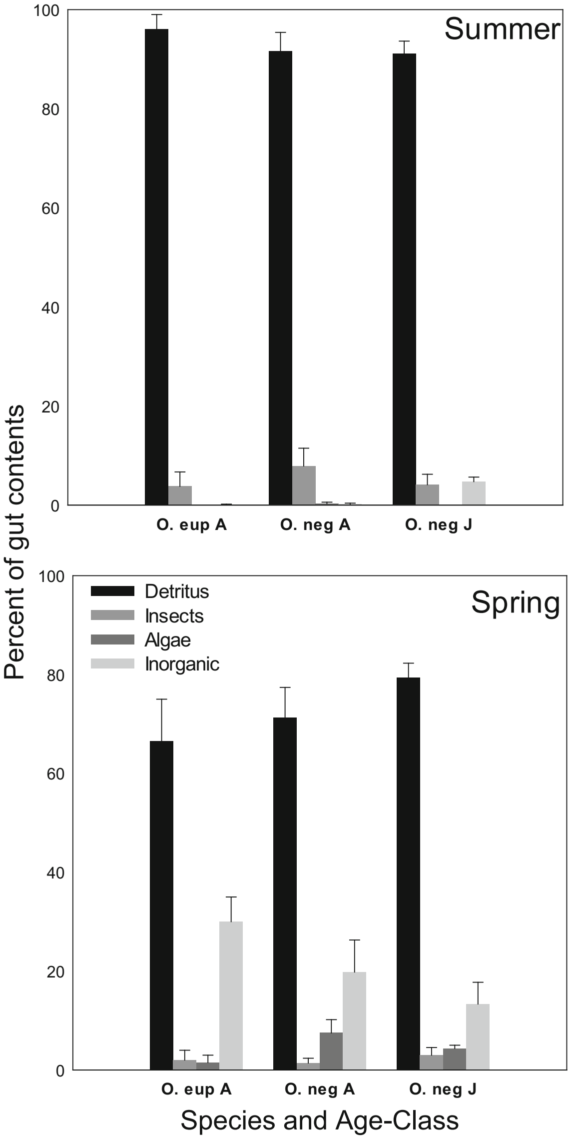

Fig. 1 Mean (±SE) percent gut contents of *O. eupunctus* adults (A) and *O. neglectus* juveniles (J) and adults (A) in South Fork Spring River during summer 2002 and spring 2003. Sample sizes were 10, 10, 8 in summer and 3, 10, 3 in spring, respectively

Mixing models showed that invertebrates were the largest contributing source to all crayfish stable isotope signatures, although there was an overlap among invertebrates, algae, and periphyton for *O. eupunctus* in summer (Table 1). Periphyton was the second largest crayfish energy and nutrient source in spring. In autumn, invertebrates made up a greater proportion of prey of *O. eupunctus* than of *O. neglectus* (Table 1).

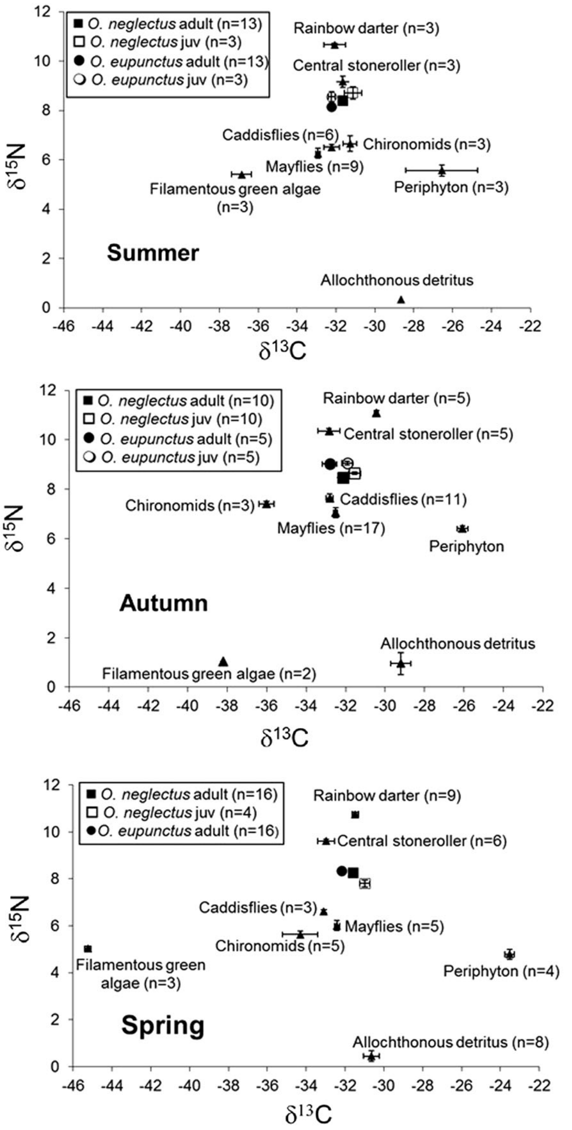

Fig. 2 Mean (±SE) δ^{13}C and δ^{15}N signatures (‰) of *O. eupunctus* and *O. neglectus* juveniles and adults and those of other consumers (central stonerollers and rainbow darters) and potential food sources in South Fork Spring River during summer 2002, autumn 2002 and spring 2003

Temporal variation

Percent detritus consumed decreased and percent inorganic material consumed increased from summer to spring (Fig. 1). Adult crayfish showed a significant species by season interaction in δ^{15}N and δ^{13}C stable isotope signatures (MANOVA Pillai Trace $P = 0.029$) driven by differences in δ^{15}N of *O. eupunctus* among seasons (Fig. 3). *Orconectes eupunctus* δ^{15}N signatures were significantly greater in autumn than in summer or spring (Tukey's test $P < 0.001$), whereas *O. eupunctus* δ^{13}C signatures did not differ among seasons (ANOVA $P = 0.123$). *Orconectes neglectus* δ^{15}N and δ^{13}C signatures did not differ significantly among seasons (MANOVA Pillai's Trace $P = 0.288$).

When examined on a seasonal basis, adult *O. eupunctus* and *O. neglectus* δ^{15}N and δ^{13}C combined signatures differed significantly in summer (Pillai Trace $P = 0.013$) and spring (Pillai Trace $P = 0.011$), but not in autumn (Pillai Trace $P = 0.063$). In summer, *O. neglectus* adults had significantly greater δ^{15}N (ANOVA $P = 0.048$) and δ^{13}C (ANOVA $P = 0.037$) than *O. eupunctus* adults (Fig. 3), whereas in spring only δ^{13}C (ANOVA $P = 0.004$) was significantly greater (Fig. 3). Although the combined δ^{15}N and δ^{13}C signatures did not differ in autumn, *O. eupunctus* adults had significantly greater δ^{15}N (ANOVA $P = 0.016$) than *O. neglectus* adults in autumn (Fig. 3). The δ^{15}N difference between *O. eupunctus* and *O. neglectus* in autumn was mainly due to increased consumption of invertebrates by *O. eupunctus* from summer to autumn (Table 1). Stable isotope signatures of *O. eupunctus* and *O. neglectus* were significantly different in autumn (Pillai Trace $P = 0.002$), but not in summer (Pillai Trace $P = 0.063$; Fig. 3). In autumn, *O. eupunctus* juveniles had significantly greater δ^{15}N (ANOVA $P = 0.001$) than *O. neglectus* juveniles (Fig. 3). We collected no *O. eupunctus* juveniles in spring.

Discussion

Gut content analysis showed that native *O. eupunctus* and invasive *O. neglectus* consumed mainly detritus, whereas stable isotope mixing models showed that both species gained most of their nutrients from invertebrates. Statistical analysis showed that *O. eupunctus* and *O. neglectus* adults differed in their stable isotope signatures in some seasons. Therefore, the former two analyses indicate that *O. eupunctus* and *O. neglectus* prey resources overlap and show the potential for competition, whereas the latter analysis suggests that prey resources of *O. eupunctus* and *O. neglectus* did not overlap during some seasons and may not show potential for competition. The

Table 1 Ranges of percent prey consumed by crayfish species in South Fork Spring River during summer, autumn 2002 and spring 2003 based on IsoSource mixing models

Season	Species	Prey categories			
		Invertebrates	Algae	Periphyton	Detritus
Summer	*O. eupunctus*	27–77	16–46	0–28	0–9
	O. neglectus	53–93	2–26	0–22	0–6
Autumn	*O. eupunctus*	79–91	0–10	0–12	0–11
	O. neglectus	59–79	0–16	2–25	0–20
Spring	*O. eupunctus*	89–90	0	10–11	0
	O. neglectus	83–84	0	16–17	0

Sample sizes are as in Fig. 2

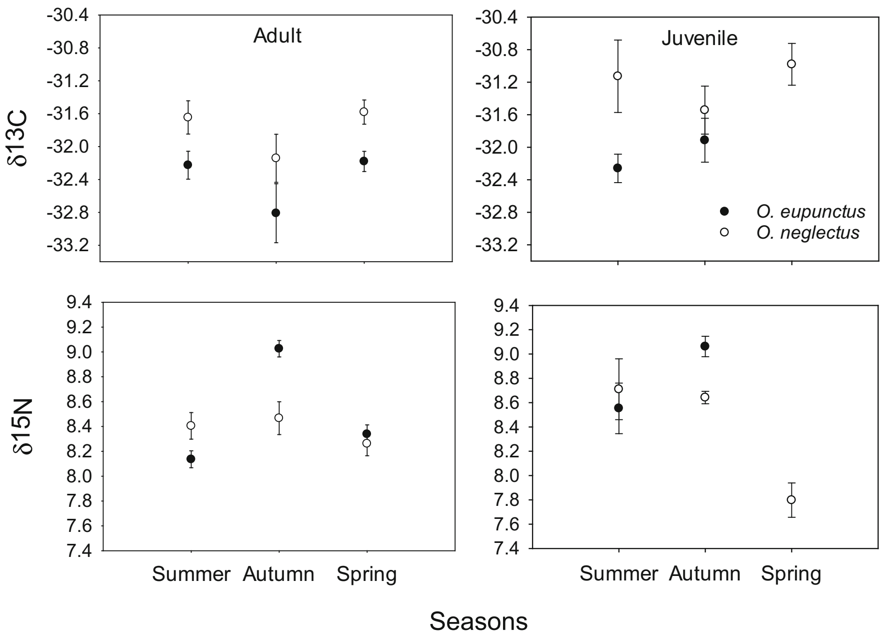

Fig. 3 Mean (±SE) δ^{13}C and δ^{15}N signatures (‰) of *O. eupunctus* and *O. neglectus* adults and juveniles during summer, autumn and spring at middle site in South Fork Spring River. Sample sizes are as in Fig. 2

discrepancy between the analyses may be due to subtle seasonal changes in diet between the two species that are not picked up by gut content analysis. It is also possible that the differences in stable isotope concentrations between the species in some seasons may not indicate differences in prey categories, but rather may be due to subtle differences in proportion of prey types. The δ^{15}N difference between *O. eupunctus* and *O. neglectus* adults in autumn appears to be an exception with increased consumption of invertebrates by *O. eupunctus* leading to increased δ^{15}N values from summer to autumn. On the other hand, gut contents analysis and stable isotope mixing models provided strong evidence that native *O. eupunctus* and invasive *O. neglectus* were consuming similar diets and gaining the majority of their energy and nutrients from similar prey types.

Others have found strong overlap between native and invasive crayfish diets. In Scandinavia, stable isotope analysis showed that native noble crayfish and introduced signal crayfish did not differ in their niche widths in boreal streams (Olsson et al., 2009) and lakes (Ercoli et al., 2014) and isotopic niches of the two species strongly overlapped in lakes (Ercoli et al., 2014). Using stable isotope analysis in an Australian river, Beatty (2006) found that the native marron and introduced yabbie occupied similar predatory trophic positions in summer, but the two species differed in their trophic positions in winter.

We also found temporal variation in crayfish gut contents and δ^{15}N and δ^{13}C stable isotope signatures. Few studies have examined temporal variation in freshwater food webs based on gut contents and stable isotope analysis, especially related to crayfish trophic dynamics. Stenroth et al. (2006) found that δ^{15}N and δ^{13}C signatures of *Pacifastacus leniusculus* Dana, 1852 did not differ between August and September or between 2001 and 2003 in lentic systems. Beatty (2006) found that native marron and introduced yabbie showed strong trophic overlap in summer, with most of their energy coming from fish, whereas in winter the yabbie trophic position shifted to herbivory.

Although *O. eupunctus* and *O. neglectus* were often using similar prey resources in the South Fork Spring River, competition will not occur unless food is limiting in this system and that has not been established. Field experiments have shown that adult and juvenile male *O. eupunctus* and *O. neglectus* did not compete for space and food when enclosed at typical densities in the South Fork Spring River (Rabalais & Magoulick, 2006b; Larson & Magoulick, 2009). Fortino & Creed (2007) also found no evidence for competition between two native crayfish species in Appalachian streams and suggested that predation was more important in structuring these communities. Competition for shelter has also been suggested as an important mechanism in structuring some crayfish communities (Bovbjerg, 1970; Rabeni, 1985; Garvey et al., 1994; Gherardi et al., 2004; Gherardi & Cioni, 2004), but little evidence exists for food competition among crayfish. Food and space may not be limiting crayfish populations in the Spring River.

Our finding that crayfish consume mostly detritus, but gain most of their energy and nutrients from animals or algae has been found in other systems (Whitledge & Rabeni, 1997; Parkyn et al., 2001; Hollows et al., 2002). Momot (1995) suggested that animal nitrogen is important in the diet of all crayfish, but that juvenile crayfish should require more animal protein than adult crayfish. We found that diets and isotopic signatures of juvenile and adult crayfish were similar and that both age classes gained most of their energy and nutrients from consumption of invertebrates. Some studies have found that juvenile crayfish consume more invertebrates and adult crayfish consume more detritus (Whitledge & Rabeni, 1997; Parkyn et al., 2001; Hollows et al., 2002). However, Bondar et al. (2005) found that both juvenile and adult *P. leniusculus* consumed mainly detritus when presented a choice of detritus and insects even though they grew faster on insects. Stenroth et al. (2006) found that juvenile and adult *P. leniusculus* were both dependent on animal matter in their diet based on stable isotope analysis. Although crayfish function as omnivores, their high use of animal matter as an energy and nutrient source has led some to suggest that crayfish occupy the trophic role of predators (Parkyn et al., 2001; Roth et al., 2006). Conversely, Stenroth et al. (2006) suggested that carbon and nitrogen may follow different pathways in omnivorous crayfish with plant material contributing to the carbon budget and invertebrates contributing to the nitrogen budget. Therefore, crayfish could be viewed as detritivores with respect to carbon and predators with respect to nitrogen. Our results support the idea that crayfish function as omnivores consuming mainly detritus, but act as trophic predators being relatively enriched in δ^{15}N, placing them as predators in the food web along with omnivorous central stonerollers (a grazing minnow) and below insectivorous rainbow darters.

Additionally, overlap in the food resources of native *O. eupunctus* and invasive *O. neglectus* suggests potential for ecological redundancy. This has important implications because if native and invasive species are ecologically redundant then species replacement should have little, if any, effects on ecosystem structure and function. In a stream mesocosm experiment, Magoulick (2014) found that native *O. eupunctus* and invasive *O. neglectus* were largely ecologically redundant, although subtle differences in crayfish effects on periphyton and sediment could potentially cascade through the food web. Usio et al. (2006) also found that the functional roles of a native and exotic crayfish were similar in Japan streams. In boreal lakes, Ercoli et al. (2015) found that introduced signal crayfish and native noble crayfish were ecologically equivalent in their effects on littoral macroinvertebrate assemblages. In a study on these two species in Swedish streams, Olsson et al. (2009) suggested the two species are likely to have similar impacts at the stream scale, but the invader is likely to have greater impacts at the regional scale due to their ability to occupy a greater range of stream conditions. Others have found that crayfish that replace native species can have large direct and indirect effects on ecosystem structure and function (Wilson et al., 2004; Lodge et al., 2012). Magoulick (2014) suggested that most studies that have found large effects of invasive species relative to native species have examined extraregional (invaded another continent or crossed major drainage boundaries within a continent) versus extralimital (invaded a drainage or state adjacent to their native range) invasions (Larson & Olden, 2010). Therefore, it is possible that extraregional invasions fundamentally differ from extralimital invasions in terms of ecological redundancy. Further research is needed to address this question.

Identifying crayfish gut contents has associated error and it is possible that this led to part of the discrepancy between gut contents and stable isotope analysis. However, given the large differences in the importance of detritus versus invertebrates it is unlikely that this source of error was responsible for the substantial differences we found using these two approaches. Whitledge & Rabeni (1997) found that *Orconectes* spp. had high assimilation efficiencies on insects (92%) and low assimilation efficiencies on detritus (14%) and this likely explains the discrepancy between gut content and stable isotope mixing models for crayfish. However, even using higher assimilation efficiencies for animal matter (70%) than leaf detritus (15%), detritus contributed most to production of *Orconectes* spp. (45%) followed by animal matter (30%) in a Kansas stream (Evans-White et al., 2003).

We found that native *O. eupunctus* and invasive *O. neglectus* consumed mainly detritus, but both species gained most of their energy and nutrients from invertebrates and this was the case during three seasons. Our results support the idea that crayfish function as omnivores consuming mainly detritus, but act as trophic predators in the food web. In our study stream and elsewhere, the trophic role of crayfish is not easily generalized, as omnivorous crayfish may function as detritivores or predators depending on techniques used to analyze feeding relationships. Given this trophic overlap, there is a potential for the two species to compete for food in this system as well as display ecological redundancy.

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