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Seasonal Diet Shifts in the Rusty Crayfish, *Faxonius rusticus* (Girard)

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Abstract: The rusty crayfish, *Faxonius rusticus* (Girard), is a species of great management concern due to its rapid range expansion across the northeastern United States and southern Canada. The rusty crayfish is an opportunistic omnivore that has been shown to disrupt invaded ecosystems by outcompeting native crayfish species for food and shelter. While numerous studies have demonstrated the community and ecosystem effects of rusty crayfish invasions, relatively little attention has been given to understanding the species' ecological needs, especially in their native range. In particular, relatively little is known about their foraging habits within their native range. This study aims to elucidate the feeding habits of rusty crayfish within their native range of the Ohio River Valley to determine (1) the most commonly consumed food items, and (2) how the diet of the species changes across seasons. Results show seasonal shifts in the diets of the rusty crayfish that likely coincide with seasonal abundance of food resources. Detritus was the dominant food item across months of study. The percent contribution of animal tissue and plants to the diets varied seasonally. The results elucidate the plasticity of rusty crayfish diets, which may be an important contributor to their success as an invasive species.

Keywords: diet, foraging, invasive species, crayfish

Introduction

The rusty crayfish (*Faxonius rusticus*) has undergone rapid range expansion in recent decades (Olden et al. 2006). While the species is native to the Ohio River Valley, its range has expanded to include much of the northeastern United States and Canada, including the Great Lakes region (Olden et al. 2006). The surprising rate of the species' range expansion, paired with the major ecological effects of its introduction (Gherardi 2007; Lodge et al. 1987, 1994; Olden et al. 2006; Morse et al. 2013) has made rusty crayfish a species of great management concern. Rusty crayfish are commonly used by anglers as live bait, and their range expansion is linked to the release of unused baits in waterbodies outside of the natural range of the species (Lodge et al. 2000, Ludwig and Leitch 1996). Therefore, management efforts to date have focused on lowering the rate of introductions and using intensive trapping mechanisms to lower population sizes in invaded areas. These efforts have remained largely ineffective at lowering non-native rusty crayfish populations (Lodge et al. 2000).

The ecological effects of rusty crayfish on invaded habitats have been well documented. Rusty crayfish invasions decrease population sizes of native crayfish species (Lodge et al. 2000), disrupt food webs (Lodge et al. 1994), and lead to a general loss of biodiversity (Lodge and Lorman 1987). While numerous studies elucidate the ecological effects of this species, less attention has been given to understanding the characteristics that make this species such a successful invader (Gherardi 2007). Behavioral studies have focused on understanding the competitive dynamics between rusty crayfish and native crayfish species (e.g., Pintor et al. 2008), and genetic studies have focused on understanding hybridization dynamics that may accelerate the decline of native crayfish populations (e.g., Perry et al. 2001). However, the plasticity of their diet has received comparatively little attention as a plausible mechanism permitting rusty crayfish range expansion.

The northern range expansion of rusty crayfish has introduced the species to more extreme seasonal weather patterns than it experiences in its native range (e.g., northern Wisconsin versus southern Ohio). Consequently, this exposes rusty crayfish to new metabolic and foraging challenges that must be overcome to survive and reproduce. In order to survive in areas with seasonal shifts in temperature and resource abundance, organisms must exhibit considerable plasticity in their diets and be able to utilize a variety of nutritional resources to meet their physiological demands (Ebling and Barrett 2008, Heng et al. 2018). In particular, organisms in these seasonally variable environments must shift their diet to match the availability of seasonally abundant food resources (Correia 2002). Rusty crayfish are opportunistic omnivores that can feed on a variety of food items across trophic levels (Roth et al. 2006). Thus, it is reasonable to predict that rusty crayfish can undergo seasonal diet shifts to match their resource use to the available resources in their environment. This study aims to elucidate the use of food resources by rusty crayfish across seasons. We tested the hypothesis that rusty crayfish exhibit seasonal variation in their diet by analyzing the gut contents of specimens collected monthly. The study was conducted in the native range of the species in the Ohio River Valley to better understand their natural foraging habits as they relate to the invasion success of the species and their overall ecological impacts on invaded regions (Gherardi 2007). Additionally, understanding the feeding habits of rusty crayfish in their native range will allow managers to better identify habitats susceptible to invasions and develop more effective trapping strategies (Olden et al. 2006).

Methods

Specimen Collection. Male and female rusty crayfish were collected by hand netting from Sharon Creek (Sharonville, Ohio, USA) monthly from April–November 2016. Due to the inactivity of the animals at low environmental temperatures and frozen water surfaces, collections were unsuccessful at capturing a sufficient number of samples in colder winter months (December–March).

Upon collection, specimens were placed in an ice bath to lower their metabolic rates and slow the progress of food through the alimentary canal. After collection, specimens were immediately transported to the lab and euthanized in a laboratory freezer (approximately -20°C), where they remained frozen until analysis. Only non-molting individuals were analyzed for stomach contents. Sample sizes for analyses were N = 16 (April), N = 15 (May, June, and July), N = 14 (August), N = 12 (September), N = 11 (October), and N = 8 (November).

Gut Content Analysis. Immediately prior to dissection, specimens were removed from the freezer and thawed to room temperature. Morphometric measurements including wet mass, carapace length, and cephalothorax length were measured for each animal. Animals were sexed by visual examination of the reproductive organs. The stomachs were removed by dissection and placed in a 2 mL snap-cap tube containing 0.5 mL of distilled water. The stomachs were ruptured manually using a dissection probe so that the contents could be removed and homogenized by mixing by hand with the dissection probe; 0.25 mL of homogenized stomach contents was placed on a microscope slide and viewed at 100X total magnification. All identifiable material in the stomach contents was classified into one of the following categories: detritus, animal tissue, plant tissue, algae, diatoms, cyanobacteria, and protozoa. Once all identifiable material within the visual field was categorized, the stage of the microscope was moved to create a new visual field, and the material within that field was identified. This procedure was repeated until ten total visual fields were inspected for each specimen. The frequency of each food item was tallied across the ten visual fields. 400X total magnification was used to help identify contents when needed. To determine the percent contribution of each food item to the diet of the crayfish each month, the total tally of each food category was divided by the total number of identifiable food items found in that month and multiplied by 100.

Statistical Analysis. Kruskal-Wallis tests were used to test for differences in morphometric characteristics of the specimens across months. Chi-squared analysis was used to determine whether the proportions of food materials in the stomachs varied across months. A Pearson's correlation was used to test the *a posteriori* hypothesis of correlation between the contributions of animal tissue and diatoms across months.

Results

No significant differences were found among monthly collections for body mass ($H = 7.691$, $df = 7$, $P > 0.05$), carapace length ($H = 13.65$, $df = 7$, $P > 0.05$), or cephalothorax length ($H = 9.768$, $df = 7$, $P > 0.05$; Figure 1). The percent contributions of diet items in the guts of rusty crayfish varied significantly by collection month (X^2 (35) = 97.05, $P < 0.0001$; Figure 2). Detritus was the most abundant food item in the guts across months, ranging from 44–65% of the overall diet. Cyanobacteria and protozoa were not commonly found in the gut contents. Plant material and algae were found in all collection months, but contributed a relatively small proportion to the overall diet of the crayfish. The abundance of both plant material and algae in the guts increased during summer months and decreased during fall and early spring months. Interestingly, the abundance of diatoms and animal tissue were negatively correlated across months ($R^2 = 0.8722$, $P < 0.001$; Figure 3). When diatom contributions to the diet were highest in spring months, animal contributions to the diets were their lowest. When the frequency of animal content peaked during summer and early fall months, diatom contributions to the diets decreased.

Discussion

Because of the opportunistic, omnivorous nature of their feeding, we expected rusty crayfish to exhibit varied diets that

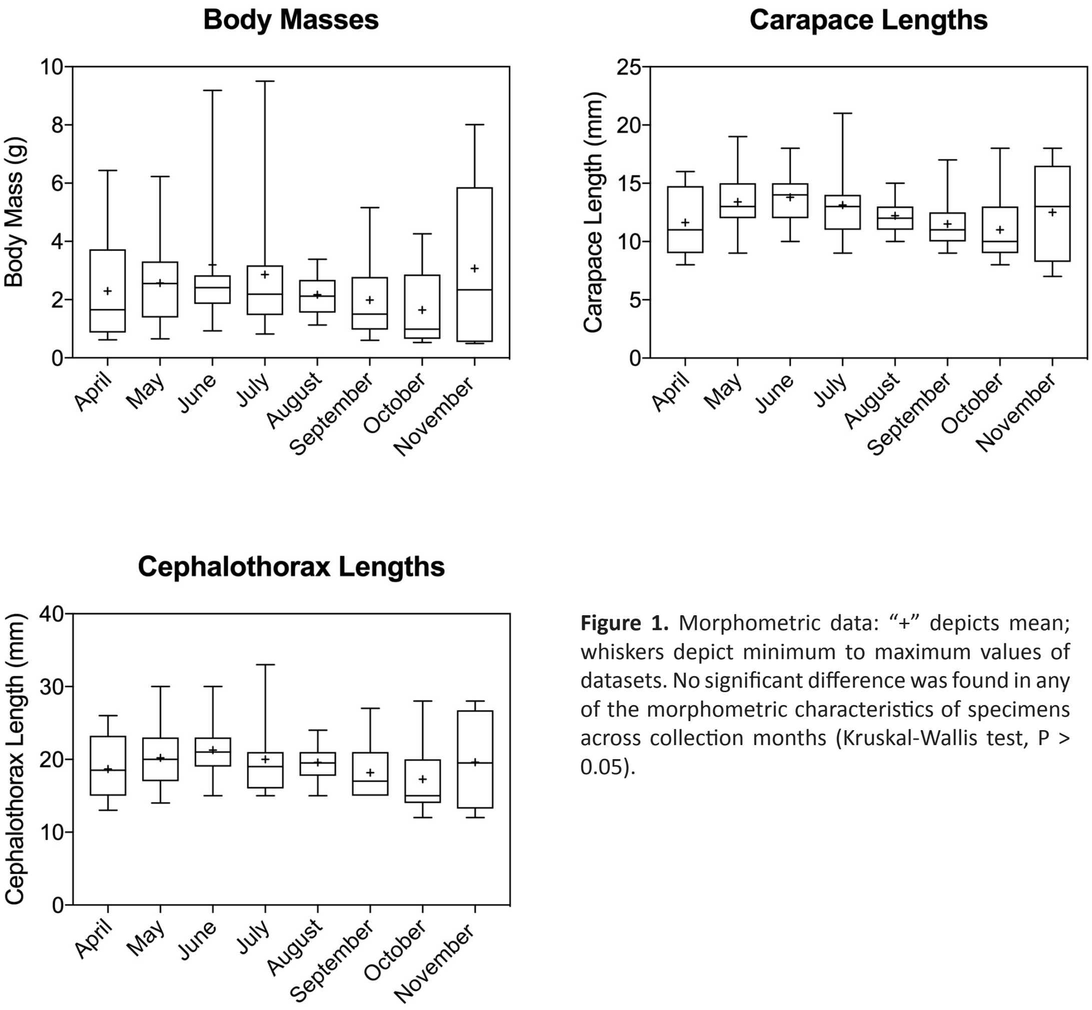

Figure 1. Morphometric data: “+” depicts mean; whiskers depict minimum to maximum values of datasets. No significant difference was found in any of the morphometric characteristics of specimens across collection months (Kruskal-Wallis test, $P > 0.05$).

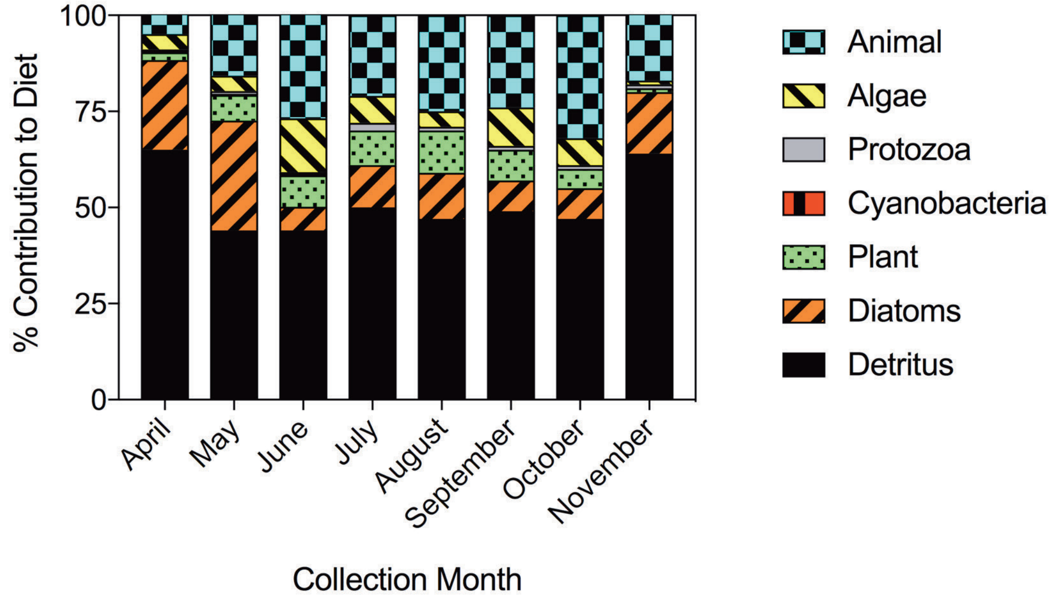

Figure 2. Percent contributions of different food items to the diets of rusty crayfish. X^2 (35) = 97.05, $P < 0.0001$.

incorporate a number of food resources across trophic levels. The ability to utilize a variety of food items has been suggested as an important determinant of range expansion and invasion success (Vázquez 2006). Species that are able to consume a variety of food resources are more likely than specialists to encounter suitable food resources in non-native habitats (Vázquez 2006). Expansion into non-native habitats increases the likelihood of an organism encountering novel food resources, and omnivorous crustaceans have been shown to readily track and consume novel foods (Tran 2015). The ability to shift diets seasonally within their natural range of the Ohio River Valley suggests a high level of plasticity in the diet that likely benefits rusty crayfish during their invasion of new habitats.

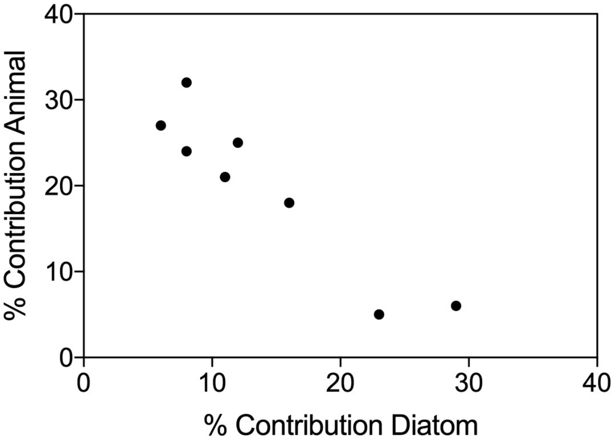

Figure 3. Correlation between diatom and animal tissue abundances. Pearson $R^2 = 0.08722$, $P < 0.001$.

The food resources consumed by rusty crayfish in our study were consistent with those consumed by other crayfish species (Parkyn et al. 2001, Whiteledge and Rabeni 1997). Our data suggest that rusty crayfish vary their diets to match seasonally abundant food resources. For example, aquatic insect larvae emerge during late spring and early summer in the Ohio River Valley (DeWalt et al. 2016), and this corresponds with the increase in animal tissue abundance in the stomachs of rusty crayfish during summer. In our study, April had the lowest percent contribution of animal tissue to the diets of rusty crayfish. It is possible that this was caused by the lack of animal tissue resources for consumption prior to events such as the emergence of aquatic insect larvae.

The negative correlation between the percent contributions of diatoms and animal tissue to the diets of rusty crayfish was an unexpected result, but shows the ability of rusty crayfish to feed at different trophic levels. Our data suggests that rusty crayfish may increase their diatom consumption in response to low environmental abundance of animal tissue for consumption. Morphological studies have confirmed that crayfish have the oral appendage structure necessary for filter-feeding (Budd et al. 1977). It is unknown whether rusty crayfish are ingesting these diatoms by filter-feeding or through the consumption of other food items on which the diatoms are found. However, evidence suggests that other crustaceans (e.g., copepods) show strong growth efficiency when fed a diet including diatoms (Jones and Flynn 2005). Thus, it is plausible that rusty crayfish are supplementing their diets with diatoms ingested through filter-feeding during certain times of the year. This ability to supplement their diet with less nutritionally desirable foods may allow for better invasion potential in rusty crayfish as they encounter novel food resources in spatially and temporally variable habitats.

Previous research on rusty crayfish has focused extensively on the ecological impacts of their invasion. However, more attention should be given to studying this species in their native range to better understand the evolutionary and ecological pressures that have shaped their resource needs and behaviors. In particular, more studies comparing the behaviors and ecological roles of rusty crayfish in native versus invaded ranges are needed (Gherardi 2007). By doing so, researchers will better understand how the plasticity of traits influences the invasion potential of species and how successful invaders cope with the ecological pressures of newly invaded habitats.

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