Influence of amino acid concentrations on foraging and feeding in the rusty crayfish *Faxonius rusticus* (Girard, 1852) (Decapoda: Astacidea: Cambaridae), assayed in flow-through mesocosms

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ABSTRACT

Organisms use chemical cues in their environment to extract relevant information to perform a variety of tasks, including foraging, finding shelter, and locating mates, and must locate and assess the quality of food sources based on these chemical cues. Crayfishes use chemical cues in the form of amino acids to locate food and to regulate consumption when determining the quality of food sources. It is currently unknown, however, whether crayfish foraging and feeding behavior in experimental flow-through systems are altered by differing amino acid concentrations. We collected individuals of the rusty crayfish, *Faxonius rusticus* (Girard, 1852), from two different watershed locations in Michigan, USA and exposed them to fish gelatin containing increasing concentrations of the amino acids β-alanine (excitatory amino acid) and L-tyrosine (inhibitory amino acid). The gelatin was weighed before and after each 24-hour trial to determine consumption. The addition of an excitatory amino acid (β-alanine) caused a significant drop in consumption but only for crayfish collected from one of the locations (\(P = 0.04\)). The addition of an inhibitory amino acid (L-tyrosine) had no effect on consumption from either location. This study demonstrates that feeding behaviors of *F. rusticus* are influenced by the presence of amino acids (β-alanine) in food sources.

KEY WORDS: amino acids, Crustacea, feeding behavior, taste perception

INTRODUCTION

Animals use their senses to extract relevant information about their environment to perform a number of behavioral tasks, including foraging for food, locating shelter, and finding mates (Pohnert et al., 2007; Hay, 2009). The chemical senses are a primary source of information for behavioral decisions in aquatic environments (Blaxter & Hallers-Tjabbes, 1992). Many aquatic organisms also defend themselves against predators by using chemical defenses in their tissues or by releasing chemicals into the environment (Williams & Gong, 2007; Thoms & Schupp, 2008; Walling, 2009). Some can also use information found in chemical compounds from other individuals to find potential mates (Kamio & Derby, 2017), and use sensory information to perform ecologically relevant behaviors and to assess features in the environment (Von Der Emde & Bleckmann, 1998). Changes in the composition and distribution of the chemical landscape of any aquatic realm has the ability to alter behavioral choices and the ecological impacts that result from those choices. These changes can have unforeseen consequences when keystone species like crayfishes are considered.

The ability of keystone species to extract information from the environment ensues the continuance of the ecosystem as a whole (Power et al., 1996). One key piece of information is the spatial and temporal location of objects that forms the basis of their ecological interactions (Moore & Crimaldi, 2004). Such information allows animals to locate stimuli that indicate objects that confer benefits (food, shelter, and mates) relative to threats (predators). When exposed to the cues given off by a predator, prey will reduce their vulnerability to those predators by changing their behavior, morphology, or their life history strategy (Brönnmark & Hansson, 2000). The behavioral use of ecological

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information can also be altered by the presence of environmental stressors.

Behaviors like foraging for food, finding mates, or evading predators can be altered by chemical stressors like acidity (Atema, 1988; Veselovsky, 2005; Bierbower et al., 2013). When exposed to acidity, metals, or interacting with complex water chemicals, aquatic invertebrates and vertebrates exhibited behavioral changes (Gerhardt, 2001). Farah et al. (2004) exposed freshwater fishes, Heteropneustes fossilis (Bloch, 1794), Clarias batrachus (Linnaeus, 1758), and Channa punctatus (Bloch, 1793) to PCP, butachlor, and 2,4-D and found that the fish displayed behavioral changes in the form of loss of balance, anorexia, body jerks, restlessness, and abnormal swimming (Farah et al., 2004).

In another example, abnormal foraging behavior was observed in the glass shrimp Parathya australiensis (Kemp, 1917) when exposed to zinc in untreated stormwater after exposure to both untreated and treated storm water (Oulton et al., 2014). These examples demonstrate how alterations in the chemical composition in the environment leads to changes in behavior. The impact of a changed chemical composition is acutely evident with foraging behavior.

To forage effectively, animals need to perform two different behavioral tasks, finding food sources and assessing the quality of those food sources. Animals use their senses to extract meaningful information about their environment to orient themselves towards attractive stimuli (Louis et al., 2008). This information often contains temporal and/or spatial information that controls or influences movement patterns within environments (Wolf et al., 2004). Most crayfish species are both opportunistic and exhibit polytropic behavior as crayfish consume a wide variety of food, including preferences towards insect larvae, algae, and macrophytes (Whitledge & Rabeni, 1997; Geiger et al., 2004). To access and orient themselves towards food sources, crayfishes use the information found in the spatial and temporal distribution of chemical signals to make foraging decisions (Moore & Grills, 1999). Crayfishes, who are ecosystem engineers and key-stone species, can facilitate or regulate macrophyte populations in aquatic habitats by their foraging choices (van der Wal et al., 2013). The chemical composition of those macrophytes influence foraging choices in crayfishes.

When determining the quality of food items prior to consumption, crustaceans primarily use amino acids as chemical cues for the quality of the available food sources (Adron & Mackie, 1978). To perceive these chemicals, crayfishes may use the amino acid-sensitive receptors found on crayfish antennules (Hodgson, 1958; Tierney & Atema, 1988). Several species of macrophytes, like species of the aquatic fern Azolla, have been found to have increased amino acid concentrations in the water (Fiogbe et al., 2004; Cruz et al., 2011). Various amino acids, like alanine, glycine, and tyrosine, alter behavior and increase the time crayfishes spent feeding (McLeese, 1970; Kay, 1971; Hamner & Hammer, 1977; Hartman & Hartman, 1977; Tierney & Atema, 1988). Tierney & Atema (1988) determined that two crayfishes, Faxonius virilis (Hagen, 1870) and F. rusticus (Girard, 1852), responded to different chemical feeding stimulants in the form of amino acids. Tierney & Atema (1988) defined “feeding movement” as the time a crayfish spends touching their first and second pair of legs to the ground. The addition of β-alanine elicited feeding movements in F. virilis, but not with tyrosine. Instead, grooming behavior increased when L-tyrosine was introduced (Tierney & Atema, 1988). Differential responses to amino acids in crayfishes is explained by one of the dactyl chemoreceptors is sensitive to alanine, histidine, and serine, but not to glutamate, lysine, and tyrosine (Hatt, 1984). We examined the behavioral changes in F. virilis due to the alteration in the amino acids β-alanine and L-tyrosine mixed into gelatin.

Bauer et al. (1981) and Hatt (1984) showed by studying leg chemoreceptors that β-alanine acts as an excitatory amino acid, whereas L-tyrosine is an inhibitory amino acid in crayfishes. We studied the particular behavioral changes taken place in F. rusticus when exposed to amino acids added to gelatin caps. We predicted that feeding activity would result in an increased feeding activity and consumption of the gelatin, but not when L-tyrosine is added to the gelatin.

METHODS

Collection and housing of crayfish

Ninety-seven form II (non-reproductive) male rusty crayfish (F. rusticus) were captured using hand nets from Maple Bay, Burt Lake in Cheboygan County, Michigan, USA (45.4873°N, 84.7065°W). One hundred and ten form II male rusty crayfish were also collected from Carp Lake River in Emmet County, Michigan, USA (45.7497°N, 84.8292°W) using modified minnow traps baited with sardines. Crayfish were collected from these two locations because while the locations were from the same watershed, both exhibit different selective pressures. All crayfish were stored in a flow-through steel cattle tank (200 × 60 × 60 cm) provided with unfiltered water from the East Branch of Maple River (45.5280°N, 84.7738°W). Water entered the tank through a PVC delivery pipe and exited via an overflow standpipe, which kept the water depth at approximately 60 cm. Crayfish fed on natural detritus which was contained within the unfiltered river water.

Shelters made from PVC pipes were provided in the housing tank to reduce resource-based aggression. Crayfish were housed separately, dependent on the site of collection. The post-rostrum carapace length, maximum carapace width, and left chelae length of each crayfish were measured to the nearest 0.5 mm before use in a trial. Body size measurements of Burt Lake crayfish included 40.00 ± 0.65 mm (mean ± SEM, carapace length) and Carp River crayfish were 31.6 ± 0.41 mm (mean ± SEM, carapace length). Burt Lake crayfish were 34.7 ± 0.97 mm (mean ± SEM, chelae length) and Carp River crayfish were 22.9 ± 0.56 mm (mean ± SEM, chelae length). Housing conditions included a natural light/dark cycle (12:12) at 23 °C ambient water temperature. Each crayfish was used only once in trials, then frozen per collecting-permit requirements.

Experimental design

All trials were made at the University of Michigan Biological Station (UMBS) Stream Research Facility, Pellston, MI, USA (45.5641°N, 84.7508°W). We used a two 2 × 4 factorial assay (Lahman & Moore, 2015) to examine the impacts of diet-supplemented amino acids on crayfish foraging and consumption behavior. The first factor was amino acid type (β-alanine and L-tyrosine) as these amino acids can increase or decrease
neuronal firing of dactyl chemoreceptors in crayfishes (Bauer et al., 1981; Hatt, 1984). The second factor was concentration, with four different concentrations added to the gelatin food source. Gelatin with no added amino acids were the control groups.

Treatment concentrations were modeled after environmentally relevant levels of amino acids reported by Carr et al. (1984). We used concentrations of 0.214 mM, 2.14 mM, 21.4 mM, or 214 mM for β-alanine treatments and 0.0101 mM, 0.101 mM, 1.01 mM, and 10.1 mM of L-tyrosine (Table 1). Approximately the same number of crayfish individuals (± 5 individuals) from Burt and Carp Lake sampling sites were assigned to each treatment. We used a total of 243 individuals for a total of 207 observations. Thirty-six individuals were removed from the data analysis due to escaping from the stream, molting, or death.

Preparation of diet regime
Fish gelatin, which has been used to measure consumption in other studies (Edwards et al., 2018; Jackson & Moore, 2019), was utilized as the food source. Plastic scintillation vial caps (20 ml) containing gelatin were placed at the upstream end of the arena, close to the head tank, for a consumption assay. Gelatin was made by homogenizing 7 g sardines with 175 ml of river water in a blender. The solution was then poured into a 1,000 ml beaker together with 7 g of Knox® unflavored gelatin. After 1 min, and placed on a hot plate to boil. The solution was mixed periodically during the boiling process to prevent burning and removed from the hot plate for 5 min to cool. A powdered form of β-alanine or L-tyrosine (Sigma-Aldrich, St. Louis, MO, USA) was added to the gelatin approximately 5 min after the gelatin was made before the gelatin solidified. The solution was cooled 5 min prior to adding amino acids to prevent the amino acids from denaturing. The solution was then poured into scintillation vial caps (20 ml) and placed in a refrigerator to for 24 h to set.

All gelatin vial caps had a strip of Velcro® (1 cm × 1 cm) attached to the bottom. A piece of plexiglass (11 cm × 16 cm) with the same number of crayfish individuals (± 5 individuals) from Burt and Carp Lake sampling sites were assigned to each treatment. We used a total of 243 individuals for a total of 207 observations. Thirty-six individuals were removed from the data analysis due to escaping from the stream, molting, or death.

Experimental stream mesocosms
All trials were performed in a flow-through experimental streams constructed from cinderblocks and plastic sheeting. Such streams have been used to imitate the natural aquatic habitat of crayfishes (Wood et al., 2018; Jackson & Moore, 2019). Concrete cinderblocks were stacked to make the stream mesocosm frame and lined with 6-mil polyethylene sheeting to hold water (1.5 × 0.5 × 0.28 m) (Moore & Grills, 1999; Wolf et al., 2004). The bottom of each stream was lined with a layer of pea stone (0.97 ± 0.04 cm × 0.75 ± 0.035 cm × 0.75 ± 0.035 cm; N = 50) approximately 2 cm thick. Past research has used a 2 cm thick layer of pea stone to mimic the natural habitat of crayfish (Alacantara et al., 1994). We placed egg crating over each stream to prevent crayfish from escaping.

A 208 l plastic drum in each stream served as a constant head tank that fed the stream with water from Maple River. The plastic drum fed into the stream via two 1.0 cm diameter garden hoses. Water flowed through the streams at a flow rate of 0.1 ± 0.05 l sec⁻¹. We used nylon stockings placed over the 7.6 cm PVC pipe that delivered the water to filter out macro invertebrates and fine organic matter. The water then exited the artificial stream through a cinderblock fitted with mesh to prevent escape (0.1 cm mesh size). The mesh-ﬁtted cinderblock was placed on the opposite side of the stream from the plastic drum. The water re-entered the river approximately 200 m downstream of the research-facility intake.

Table 1. Treatment and sample sizes of Faxonius rusticus from two Michigan locations

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Burt Lake samples</th>
<th>Carp River samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>N = 10</td>
<td>N = 15</td>
</tr>
<tr>
<td>β-alanine 0.214 mM</td>
<td>N = 10</td>
<td>N = 10</td>
</tr>
<tr>
<td>β-alanine 2.14 mM</td>
<td>N = 13</td>
<td>N = 12</td>
</tr>
<tr>
<td>β-alanine 21.4 mM</td>
<td>N = 10</td>
<td>N = 15</td>
</tr>
<tr>
<td>β-alanine 214 mM</td>
<td>N = 10</td>
<td>N = 11</td>
</tr>
<tr>
<td>L-tyrosine 0.0101 mM</td>
<td>N = 10</td>
<td>N = 10</td>
</tr>
<tr>
<td>L-tyrosine 0.101 mM</td>
<td>N = 11</td>
<td>N = 11</td>
</tr>
<tr>
<td>L-tyrosine 1.01 mM</td>
<td>N = 13</td>
<td>N = 14</td>
</tr>
<tr>
<td>L-tyrosine 10.1 mM</td>
<td>N = 10</td>
<td>N = 12</td>
</tr>
</tbody>
</table>

Experimental protocol
A gelatin cap and a single crayfish were used per trial. The crayfish was placed in the middle of the stream at the downstream end and the gelatin was placed 0.5 m upstream from the crayfish to allow individuals to receive odors from the food source. The gelatin was weighed before and after each trial.

Each trial was started around 0900 and ran overnight for 24 h. A crayfish was taken from the housing tank and placed in the middle of the stream at the downstream end. Crayfish were marked on the carapace before each trial using a 1 cm² white patch using a non-toxic correction pen (BIC® Wite-Out® 2 in 1 Correction Fluid, Shelton, CN, USA). Crayfish behavior was not altered by the Wite-Out application (Martin & Moore, 2007; Fero & Moore, 2008; Jurcak & Moore, 2018). Each gelatin cap was weighed on an Ohaus® scout scale (model H-5851; OHAUS, Parsippany, NJ, USA) and then was placed exactly 0.5 m upstream from the crayfish. The crayfish was placed downstream, furthest away from the head tank, while the gelatin was the closest to the head tank. Gelatin was removed from each mesocosm the following morning and was surface-dried in a salad spinner (Farberware 176 Basics, Farberware, Fairfield, CA, USA) for 30 rotations to remove excess water before being weighed. The crayfish was removed from the stream and the water in the mesocosms was rinsed for 120 seconds to allow enough water to flow through and replace itself 24 times during the flush period.

Gelatin consumption
Consumption of the gelatin was calculated as percentage consumed. The absolute value of the final weight of the gelatin minus the initial weight which was then divided by the initial weight
was used as a measure of consumption. Fish gelatin showed no mass loss or water weight gain over 48 h (Wolf et al., 2004; personal observation).

\[
\text{Gelatin consumption} = \left( \frac{G_f}{G_i} \right) \times 100,
\]

Where \(G_f\) = gelatin final weight; \(G_i\) = gelatin initial weight

The dependent variable consisted of percent consumption of the gelatin. Data treatment followed Zuur et al. (2009). The first step was to construct dotcharts to examine potential outliers. A Shapiro-Wilk test of normality was performed, and the data were not normally distributed. BestNormalized was performed to determine which data transformation was likely to produce the best normalized data (Peterson, 2021). Subsequent transformation of percent consumption using an ordered normality transformation resulted in a normally distributed dataset. Consumption of each gelatin cap was assessed using a linear mixed effects model by running the lmer function from the lme4T est package in R (Kuznetsova et al., 2017; R Core Team, 2019). Each gelatin consumption model was constructed with using a single continuous factor (weight of amino acid addition), and a two-crossed random effects terms (mesocosm and location of collection). Following model construction, the outputs were extracted using the ANOVA function from the car package in R (Fox & Weisburg, 2018). Because of the differences in concentrations of the two amino acids, separate models were performed for each. The statistical significance of each model was determined by extracting Cohen’s D (Cohen, 2013) using the effectsize package in R (Ben-Shachar et al., 2020). If significant differences were found with the linear mixed models, post-hoc comparison across concentrations of amino acids was performed with the emmeans package in R (Length, 2021).

RESULTS

Crayfish collected from Carp Creek had lower consumption of food, and this consumption decreased significantly with increasing concentrations of β-alanine (Fig. 1; \(P = 0.04\)). While crayfish collected from Burt Lake had lower consumption with increasing β-alanine when compared to the lowered consumption with crayfish collected from Carp Creek, the decrease in consumption was not as drastic (Fig. 1, Table 2). Post hoc analyses showed that the highest addition of β-alanine (19.1 g) was significantly different than all other concentrations \((P = 0.013 \text{ for } 1.91 \text{ g}), \ P < 0.001 \text{ for } 0.191 \text{ g}, \text{ and } P = 0.0486 \text{ for } 0.0191 \text{ g})\) and that the second highest addition (1.91 g) was significantly different than the highest and lowest two concentrations \((P = 0.037 \text{ for } 0.191 \text{ g}, \text{ and } P = 0.005 \text{ for } 0.0191 \text{ g})\).

The addition of L-tyrosine to a food source had no effect on crayfish (Fig. 2), and the location of capture did not alter rates of consumption of fish gelatin with tyrosine.

DISCUSSION

The addition of an excitatory amino acid (β-alanine) significantly decreased food consumption in crayfish in artificial streams (Fig. 1). Specifically, the addition of β-alanine decreased consumption across all concentrations, but the magnitude of the decrease was greater for crayfish from the Carp Creek river system (Table 2, \(P = 0.01\)) than the Burt Lake system (Table 2, \(P = 0.23\). We hypothesize that consumption decreased when β-alanine concentrations increased because the consumption was determined by how the crayfish perceived the chemical landscape. Due to the flowing nature of this experiment, crayfish had to locate and consume the gelatin. Because of these two variables, crayfish might have interpreted the chemosensory information differently than what has been found in past experiments that occurred under laboratory conditions using stagnant water. Conversely, altering the concentration of an inhibitory amino acid (L-tyrosine) did not alter consumption regardless of

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**Table 2.** Statistical output of main and interaction effects on the experimental consumption of β-alanine and L-tyrosine in individuals of *Faxonius rusticus.* Significant \(P\) values are in bold

<table>
<thead>
<tr>
<th>β-alanine</th>
<th>Model</th>
<th>(F)</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>12.3</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td>Concentration</td>
<td>27.0</td>
<td>&lt; 0.001</td>
<td></td>
</tr>
<tr>
<td>Location:Concentration Interaction</td>
<td>6.8</td>
<td>0.04</td>
<td></td>
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<table>
<thead>
<tr>
<th>L-tyrosine</th>
<th>Model</th>
<th>(F)</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>0.06</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>Concentration</td>
<td>0.07</td>
<td>0.8</td>
<td></td>
</tr>
<tr>
<td>Location:Concentration Interaction</td>
<td>1.2</td>
<td>0.27</td>
<td></td>
</tr>
</tbody>
</table>

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**Figure 1.** Scatter plot of mass and percentage of consumption of β-alanine by *F. rusticus.* The red circles represent responses of crayfish and red shading a 95% confidence interval around the predicted response of crayfish from Carp Creek, Michigan. The grey squares represent responses of crayfish and grey shading a 95% confidence interval around the predicted response of crayfish from Burt Lake, Michigan. Consumption and location were significantly affected \((P < 0.001)\) by the concentration of β-alanine.
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more significantly by the Pacific white shrimp Litopenaeus vannamei (Boone, 1931). Juvenile carp (Cyprinus carpio (Linnaeus, 1758)) showed significant effects on habitat exploration and attraction due to the presence of non-polar amino acids after being exposed to synthetic amino acids (Saglio et al., 1990). Basic amino acids and polar, uncharged amino acids, however, did not attract individuals of C. carpio, while exploration behavior significantly increased (Saglio et al., 1990). Previous investigations indirectly support the hypothesis that amino acids do influence foraging and feeding behavior, either positively or negatively, in aquatic animals. Foraging and feeding appear to be influenced differentially by the addition of amino acids.

Foraging involves the identification and location of a potential food source (Galef & Giraldeau, 2001). Olfactory chemoreceptors such as those involved in olfaction, can detect distant chemical stimuli (Giordano et al., 2017). Feeding, typically involving taste chemoreceptors has evolved for a more localized odor source (Giordano et al., 2017). These two systems overlap across different animal species (Devine & Atema, 1982; Ache, 1987). Amino acids can serve as chemoattractants (during foraging), feeding stimulants (during feeding), or as both as a feeding stimulant in aquatic animals. Foraging behavior involving amino acids such as betaine and taurine is species specific among decapod crustaceans. Glycine, taurine, and betaine have been found to act as both feeding stimulants and chemoattractants in a wide variety of decapods (Deshimaru & Yone, 1978; Tolomei et al., 2003; Truong, 2008). Glycine was found to increase searching behavior in the banana prawn Fenneropenaeus merguiensis (De Man, 1888) (Hindley, 1975, as Peneaus merguiensis), but not in the kuruma shrimp Peneaus japonicus (Bate, 1888), even though individuals experienced an increase in feed consumption (Deshimaru & Yone, 1978).

Foraging and feeding play a significant role in aquaculture industry. The use of artificially enhanced diets with amino acids can increase both the attractiveness and feeding rates of aquaculture diets. In general, decapods are slow feeders and because of delays in food detection, nutrients will be lost from the food (Mendoza et al., 1997; Smith et al., 2005). To prevent this loss, crystalline amino acids have been used in the past to act as both feeding stimulants and chemoattractants in decapods (Nakamura, 1987; Coman et al., 1996; Felix & Sudharsan, 2004). Most free amino acids, including glutamic acid (Hindley, 1975), alanine (Archdale & Nakamura, 1992), arginine (Harpaz et al., 1987), serine (Archdale & Nakamura, 1992), and cysteine (Lynn et al., 1994), act as chemoattractants in decapods.

We found that β-alanine was neither a feeding stimulant or a chemoattractant under the realistic feeding conditions of the use of natural flow and light settings and that foraging and feeding significantly decreased (Fig. 1). Crayfish exhibited no significant change in the presence of L-tyrosine (Fig. 2). Our results differ from those of past studies due to our use of flow-through. In these trials, crayfish needed to find and consume the food, two separate behaviors that possibly integrate chemosensory information differently. Overall, the presence of amino acids in aquatic systems can influence foraging and feeding behaviors of aquatic animals, but such effects are different in realistic flow-through mesocosms compared to static tanks.

Figure 2. Scatter plot of mass and percentage of consumption of L-tyrosine by F. rusticus. The red circles represent responses of crayfish and red shading a 95% confidence interval around the predicted response of crayfish from Carp Creek, Michigan. The grey squares represent responses of crayfish and grey shading a 95% confidence interval around the predicted response of crayfish from Burt Lake, Michigan. Consumption and location were not significantly affected (P = 0.8) by the concentration of L-tyrosine.
Amino acids are widely distributed and can be found freely in freshwater (Thurman, 2012), macrophyte tissues (Boyd, 1971), and in the tissues of many prey animals (Carr et al., 1996). Amino acids are released into water by a wide variety of organisms including vertebrates (Olsén, 1986), phytoplankton (Daumas, 1976), and zooplankton (Nicol, 1967). The concentrations of total dissolved amino acids in oligotrophic lakes are on the average of 100 μg l⁻¹, 600 μg l⁻¹ in eutrophic lakes (Burnison & Morita, 1974; Tuschall & Brezonik, 1980). Thomas & Eaton (1996) similarly found that the concentrations of individual free amino acids was much higher in eutrophic than in oligotrophic lakes. The total amount of amino acids account for 14–35% of the dissolved organic nitrogen (Tuschall & Brezonik, 1980). Given the ubiquitous and fluctuating presence of amino acids in the aquatic environment, omnivorous foragers, like crayfishes, may be faced with changing perceptions of foraging landscapes. The responsiveness to potential food items, like macrophytes or carrion, could be influenced by the differences in the natural background concentrations of amino acids (Johnson & Atema, 1986) and/or changes in the relative concentrations of amino acids in prey tissues (Derby & Zimmer, 2012). If foragers are altering prey selection based on changes in background amino acid levels, changes in food-web dynamics can have ripple effects throughout the ecosystem (Stewart et al., 2004).

The abundance and distribution of freshwater macrophytes are influenced by nutrient availability and the release of amino acids (Chambers & Kalff, 1985), which results in freshwater grazers undergoing selective pressure over food sources (Dale, 1986). The selective foraging of freshwater macrophytes by grazers influences the diversity, distribution, and abundance of these macrophytes (Jupp & Spence, 1977). Because β-alanine decreases food consumption, grazers may not select such macrophytes if the macrophytes have an abundance of the amino acid. Aquatic animals will likely remove submerged macrophytes containing amino acids like isoleucine and glycine (Tierney & Atema, 1988) that stimulate feeding in ponds and lakes (Saki & Tash, 1979; Feminella & Resh, 1986). When in abundance, amino acids can therefore play an important role in the selection of food sources.

Some behaviors or foraging choices have larger or more profound effects for ecosystem dynamics (Naiman, 1988; Guariento et al., 2014). Crayfish function as keystone species and ecosystem engineers both lentic and lotic habitats (Statzner et al., 2000; Reynolds et al., 2013; Albertson & Daniels, 2018). As such, the foraging choices of a crayfish impact macrophyte community dynamics such as abundance, diversity, and species-richness (Chambers et al., 1990). Increased foraging led to the decimation of water vegetation in lakes in northern Wisconsin (Lorman, 1980), and crayfish diets may shift from leaf detritus to macrophytes with elevated CO₂ levels due to human activities (Adams et al., 2003). We saw a decrease in consumption effort with increasing β-alanine concentrations, which clearly indicates that consumption is highly dependent on the chemical landscape perceived by crayfishes and possibly many other herbivores. Altering consumptive choices in keystone species like crayfishes has community-wide effects that need to be understood as ecosystems and their abiotic compositions are further altered by human activities (Giling et al., 2009).

ACKNOWLEDGEMENTS

The authors would like to thank the University of Michigan Biological Station for the use of facilities and the funding provided through the Marian P. and David M. Gates Graduate Student Endowment Fund. We acknowledge that the University of Michigan was formed and grown through connections with the land stewarded by Niswi Ishkodewan Anishinaabeg: The Three Fires People. We also thank the members of the Laboratory for Sensory Ecology for their help with comments on the manuscript, collection of crayfish, and experimental setup. Finally, we would also like to thank the anonymous reviewers for their comments to the manuscript. We have no conflicts of interest to declare.

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