Feeding Preference of the Red Swamp Crayfish *Procambarus clarkii* (Girard) on Living Macrophytes in a Spanish Wetland

Santos Cirujano
Real Jardín Botánico (C.S.I.C.)
Plaza de Murillo 2, 28014 Madrid, Spain
Julio A. Camargo[a]
Departmento Interuniversitario de Ecología
Universidad de Alcalá
28871 Alcalá de Henares (Madrid), Spain
and
Carmen Gómez-Cordovés
Instituto de Fermentaciones Industriales (C.S.I.C)
Juan de la Cierva 3, 28006 Madrid, Spain

ABSTRACT

We carried out field studies and laboratory experiments to investigate (1) the possible feeding preference of the red swamp crayfish *Procambarus clarkii* on living macrophytes, and (2) the influence that such a feeding preference can cause on the distribution and bundance of *P. clarkii* in wetland systems. Field studies, at two sampling areas of the Spanish wetland Tablas de Daimiel National Park (TDNP), showed that *P. clarkii* had significantly higher mean values of density and biomass at S-2 (with *Chara hispida* as the dominant macrophyte) than at S-1 (with *Ceratophyllum submersum* as the dominant macrophyte). Laboratory experiments showed that *P. clarkii* had a significant feeding preference for *C. hispida* versus *C. submersum*. Analyses of the biochemical composition of each macrophyte species showed that the unpreferred macrophyte (*C. submersum*) had higher amounts (per unit of biomass) of total protein, nitrogen, phosphorus, sodium, potassium, magnesium and phenolic compounds than the preferred macrophyte (*C. hispida*). By contrast, *C. hispida* had more calcium per unit of biomass than *C. submersum*. Overall, we conclude that the presence of higher amounts of phenolic compounds in *C. submersum* might be the foremost factor responsible for the observed feeding preference of *P. clarkii* on living macrophytes in TDNP.

INTRODUCTION

Aquatic ecologists have been debating for a long time the extent to which animals feed on living macrophytes. Several authors (Hutchinson 1975, Gregory 1983, Margalef 1983, Polunin 1984), following Shelford's (1918) traditional viewpoint, assumed that living macrophytes are not a major component of the diet of herbivores in lentic and lotic ecosystems. They argued that macrophytes enter aquatic food webs primarily as organic detritus. In contrast, other authors (Welch 1935, Frohne 1956, Gaevskaya 1969, Kiorboe 1980, Lodge 1991, Newman 1991, Cyr and Pace 1993), on the basis of empirical evidence, agreed that living macrophytes may be an important element in the food chains of freshwater ecosystems because they are grazed by a great variety of animals (e.g., macroinvertebrates, fishes, birds, mammals). Among those animals, crayfishes appear to be opportunistic and catholic herbivores that can feed readily on living macrophytes, being able to produce marked changes in the abundance and diversity of submersed macrophyte communities (Lodge and Lorman 1987, Feminella and Resh 1989, Chambers et al. 1990, Hobbs 1991, Lodge 1991, Ilhéu and Bernardo 1993a, Matthews et al. 1993, Creed 1994).

[a]Corresponding author

At present, the red swamp crayfish *Procambarus clarkii* (Girard), a freshwater crayfish from wetlands of eastern North America, has successfully invaded many other wetland areas around the world (Hobbs et al. 1989). *P. clarkii*, like other crayfish species, usually develops a polytrophic strategy by switching from detritivore/scavenger to herbivore/carnivore in response to food availability (Hobbs 1991). Although significant amounts of organic detritus, macroinvertebrates (including crayfishes), and fishes are often present in stomach contents of *P. clarkii* (Lowery and Mendes 1977, Wiernicki 1984, Ilhéu and Bernardo 1993a), field studies suggest that living macrophytes may be a major component of its diet when macrophytes are abundant in the aquatic environment (Ilhéu and Bernardo 1993a). Moreover, laboratory experiments have shown that *P. clarkii* can exhibit feeding preference for vegetal food versus animal food if the energetic cost involved in active predation is high (Ilhéu and Bernardo 1993b).

Several field and laboratory investigations with other crayfish species, such as *Austropotamobius pallipes*, *Orconectes immunis*, *O. Rusticus*, and *O. virilis* have shown that these crayfishes may exhibit feeding preferences for some macrophytes versus other macrophytes as a likely consequence of the differential concentration of chemical constituents in the tissues of macrophyte species (Seroll and Coler 1975, Chambers et al. 1991, Lodge 1991, Matthews et al. 1993). Nevertheless, with regard to the red swamp crayfish *P. clarkii*, little is known about its possible feeding preference on living macrophytes. Furthermore, little is known about the influence that such a feeding preference on macrophytes can cause on the distribution and abundance of *P. clarkii* in wetland systems.

In a previous study on aquatic vegetation (Cirujano et al. 1996), we observed that *P. clarkii* was able to reduce dramatically the macrophyte biomass at areas dominated by *Chara hispida*, whereas at other areas dominated by *Ceratophyllum submersum* the macrophyte biomass experienced a much lower reduction. Subsequently, we carried out field studies and laboratory experiments with *P. clarkii* and report those results here.

METHODS AND MATERIALS

Field studies were conducted in Tablas de Daimiel National Park (TDNP) during the summer (July) of 1997. TDNP is situated within the province of Ciudad Real (Central Spain) and constitutes a SW-oriented continental wetland with a maximum inundated area of about 1640 ha. Red swamp crayfish were weekly collected using traps (like baskets; see Bateman 1977) with chicken and carp meat at two different sampling sites. At the first site (S-1), the macrophyte community was dominated by *Ceratophyllum submersum*, with a mean biomass (fresh weight) of 18.2±4.7 kg/m^2 and an approximate covering of 80%. At the second site (S-2), the macrophyte community was dominated by *Chara hispida*, with a mean biomass (fresh weight) of 13.8±2.5 kg/m^2 and an approximate covering of 85%. Sampling sites had an area of 0.5-0.6 ha and an average depth of 0.95 m. Every week, five traps were randomly placed at each sampling site and left for 24 hours. Subsequently, traps were removed and crayfish counted and weighed (fresh weight). Average concentrations of major ions in the area of sampling sites were 410 mg SO_4^{2-}/L, 328 mg Ca^{2+}/L, 189 mg Cl^-/L, 184 mg HCO_3^-/L and 117 mg Mg^{2+}/L (Alvarez and Cirujano 1996). In addition, we weekly analyzed water physicochemical characteristics (temperature, conductivity, dissolved oxygen, chemical oxygen demand and pH) according to standard methods described in APHA (1992).

Laboratory experiments were performed using crayfish of three different body sizes (large, medium and small). To avoid the potential effect of previous feeding experiences, crayfish were collected from a small area in TDNP where the submersed

macrophyte community was more diverse and mainly composed by *Chara vulgaris*, *Potamogeton pectinatus*, *Ranunculus peltatus* and *Tolypella glomerata*. In the laboratory, crayfish were selected and distributed into three glass aquaria (40 x 40 x 40 cm): one aquarium with four large crayfish and a total crayfish biomass of 163 g (mean crayfish fresh weight of 40.8±5.72 g); a second aquarium with six medium crayfish and a total crayfish biomass of 155 g (mean crayfish fresh weight of 25.9±2.80 g); and a third aquarium with 11 small crayfish and a total crayfish biomass of 168 g (mean crayfish fresh weight of 15.3±1.25 g). Each aquarium had a sandy bottom and a water column of about 10 cm. Slight water oxygenation was produced with air pumps and airstones. Prior to the beginning of experiments, crayfish were acclimatized to laboratory conditions for six days, being indiscriminately fed with macrophytes.

Experiments on the feeding preference of *P. clarkii* on either *C. hispida* or *C. submersum* were conducted for eight days. During the first three days, crayfish were fed only with *C. submersum*. Through the following three days, only *C. hispida* was used as food. Finally, during the last two days, crayfish were fed simultaneously with both *C. hispida* and *C. submersum*. A total macrophyte biomass of 100 g (fresh weight) was daily used at each aquarium. The relationship between fresh weight and its respective dry weight in each macrophyte species was estimated at 90 °C for 24 hours. The amount of macrophyte biomass (fresh and dry weights) daily consumed by crayfish was calculated as the difference between the initial macrophyte biomass and the final macrophyte biomass. The water of aquaria was changed daily. Average water quality conditions were 22.7 °C for temperature, 3.1 mS/cm for conductivity, 7.6 mg O_2/l for dissolved oxygen, and 7.7 for pH.

After finishing laboratory experiments, the concentration of total soluble protein in shoot biomass of *C. hispida* and *C. submersum* was determined according to the rapid and sensitive method developed by Bradford (1976). Concentrations of inorganic constituents (N, P, Na, K, Mg, Ca) also were determined in accordance with standard methods described in MAPA (1994). In addition, phenolic family compounds (total polymeric polyphenols, high polymeric polyphenols, low polymeric polyphenols, o-diphenols, catechins, and procyanidins) were analysed for each macrophyte species following traditional methods described in Paronetto (1977).

Physicochemical and biological differences between sampling sites (field studies) and between treatments (laboratory experiments) were examined by the analysis of Student's t-test to compare means (Elston and Johnson 1987). Because the analysis of Student's t-test is fairly robust against non-normality of data and non-homogeneity of variances when sample sizes are equal (Elston and Johnson 1987), data were not transformed. Normality of data and homogeneity of variances were however assumed.

RESULTS AND DISCUSSION

Mean values of water temperature, pH, dissolved oxygen, conductivity and chemical oxygen demand were similar between sampling sites (Table 1). Indeed, there were no significant ($P>0.05$) physicochemical differences between stations. However, mean crayfish density and biomass were significantly ($P<0.01$) different between sampling sites, with S-2 (where *C. hispida* was the dominant macrophyte) exhibiting higher values (Table 2). All in all, 536 crayfish were captured at S-2, whereas 149 crayfish were captured at S-1.

Crayfish of the three sizes consumed more *C. hispida* biomass than *C. submersum* biomass throughout the laboratory experiments. In fact, during the last two days (where crayfish were fed simultaneously with both *C. hispida* and *C. submersum*), small, medium and large crayfish showed clear preference for consuming *C. hispida*. Mean

Table 1. Mean (n=4) values of physicochemical parameters analyzed at sampling stations (S-1 and S-2) in Tablas de Daimiel National Park.

	S-1	S-2
Water temperature (°C)	24.3±0.8	24.8±0.7
Dissolved oxygen (mg O_2/l)	8.2±1.3	7.5±1.1
Conductivity (mS/cm)	2.7±0.1	2.6±0.1
Chemical oxygen demand (mg O_2/l)	15.2±2.8	16.4±3.4
pH	7.9±0.2	7.6±0.2

values of macrophyte biomass (fresh and dry weights) daily consumed by small, medium and large crayfish were significantly ($P<0.01$) higher for *C. hispida* than for *C. submersum* (Table 3). Furthermore, the per capita crayfish consumption of macrophyte biomass was clearly dependent on crayfish size, with large crayfish exhibiting significantly ($P<0.01$) a greater consumption than medium and small crayfish (Table 3). However, there were no significant ($P>0.05$) differences between crayfish sizes for the ratio total macrophyte biomass daily consumed/total crayfish biomass at each aquarium (Table 3).

Analyses of total soluble protein, nitrogen, phosphorus, sodium, potassium, magnesium, and calcium in shoot biomass of macrophytes (Table 4) showed that *C. submersum* had significantly ($P<0.01$) greater amounts of total soluble protein, N, P, Na, K, and Mg than *C. hispida*. By contrast, *C. hispida* had a significantly ($P<0.01$) greater amount of Ca than *C. submersum* (Table 4). Regarding phenolic compounds, though it was not possible to determine significant differences between macrophyte species because analyses were performed only once, it is worth noting that concentrations of total polymeric polyphenols, high polymeric polyphenols, low polymeric polyphenols, o-diphenols, catechins, and procyanidins were clearly higher in *C. submersum* than in *C. hispida* (Table 5).

It should be evident from the obtained results that the red swamp crayfish, *Procambarus clarkii*, may exhibit feeding preferences not only for vegetal food versus animal food (Ilhéu and Bernardo 1993b) but also for some macrophyte species (e.g., *Chara hispida*) versus other macrophyte species (e.g., *Ceratophyllum submersum*). Additionally, this feeding preference on living macrophytes might influence the distribution and abundance of *P. clarkii* in wetland systems. For example, in Tablas de Daimiel National Park, greater abundances of *P. clarkii* were found in wetland areas where the preferred macrophyte species (*C. hispida*) was the dominant macrophyte, whereas much lower densities of *P. clarkii* were found in wetland areas where the unpreferred macrophyte species (*C. submersum*) was the dominant macrophyte.

Table 2. Mean (n=5) values of crayfish density (number per trap) and crayfish biomass (grams per trap) at sampling stations (S-1 and S-2) in Tablas de Daimiel National Park during each week of sampling.

	S-1		S-2	
	Density	Biomass	Density	Biomass
1st week	7.8±2.6	207±49	29.6±7.2	482±113
2nd week	6.6±3.1	169±52	27.8±5.5	475±94
3rd week	7.4±2.7	192±48	25.4±5.9	421±95
4th week	8.0±3.2	210±59	24.6±5.2	397±91

Table 3. Mean (n = 5) values for daily consumption of *C. hispida* and *C. submersum* by crayfish of different sizes when the two macrophytes were offered simultaneously in aquarium experiments. The ratio of total daily macrophyte consumption to total crayfish biomass in test aquaria is also given.

	Small crayfish	Medium crayfish	Large crayfish
Wet weight (g) consumed			
C. hispida	31.7±7.1	23.1±7.0	33.2±5.28
C. submersum	10.8±7.2	7.7±7.3	7.8±5.0
Dry weight (g) consumed			
C. hispida	3.0±0.7	2.1±0.6	3.1±0.5
C. submersum	0.7±0.4	0.5±0.5	0.5±0.3
Wet weight (g) consumed per crayfish			
C.hispida	2.9±0.6	3.9±1.2	8.3±1.3
C. submersum	1.0±0.7	1.3±1.2	2.0±1.3
Total daily consumption (wet, g) / Total crayfish biomass (wet, g)			
C. hispida	0.19±0.04	0.15±0.05	0.20±0.03
C. submersum	0.06±0.04	0.05±0.05	0.05±0.03

Selective grazing on living macrophytes has been previously observed in other aquatic animals such as fishes (Prejs 1984, Wiley et al. 1986), snails (Sheldon 1987, Brönmark 1989), insects (Cronin et al. 1999, Dorn et al. 2001) and other crayfish species (Seroll and Coler 1975, Chambers et al. 1991, Lodge 1991, Matthews et al. 1993). Nevertheless, in most cases, the biotic and abiotic factors responsible for the observed selective grazing were unclear. Lodge (1991), after reviewing and evaluating data from several of these works (Seroll and Coler 1975, Prejs 1984, Wiley et al. 1986, Sheldon 1987, Brönmark 1989), found that concentrations of protein, cellulose, and lignin in tissues of preferred and unpreferred macrophytes did not differ significantly among preference categories. Lodge (1991) also found that phenolic content, but not alkaloid content, in tissues of preferred and unpreferred macrophytes was negatively related to the grazing preference of *Orconectes rusticus* (crayfish), *Physa gyrina* (snail), and *Ctenopharyngodon idella* (fish), suggesting that phenolic compounds can negatively affect macrophyte choice by a diversity of aquatic grazers. Chambers et al. (1991), after studying the effect of macrophyte chemical constituents on feeding selectivity by the crayfish *Orconectes virilis*, reported that grazing preference was unrelated to plant fibre

Table 4. Mean (n = 10) concentrations (mg/g dry biomass) of total soluble protein, nitrogen, phosphorus, sodium, potassium, magnesium, and calcium in shoots of *C. hispida* and *C. submersum*.

	C. hispida	*C. submersum*
Total soluble protein	4.0±0.71	11.0±2.69
Nitrogen	0.8±0.13	1.8±0.27
Phosphorus	0.1±0.02	0.6±0.05
Sodium	0.3±0.02	0.5±0.03
Potassium	1.5±0.14	2.8±0.22
Magnesium	0.6±0.03	1.8±0.10
Calcium	23.7±1.05	10.3±1.82

(i.e., digestibility) and alkaloid content, but was negatively related to nutritional content, with macrophytes of low nutritional content, such as *Chara* species, being consistently preferred. Similarly, Matthews et al. (1993), after carrying out field experiments (enclosures) in the mesotrophic lake Lough Lene (Ireland), found that *Chara desmacantha* was markedly grazed by the crayfish *Austropotamobius pallipes*. Regarding aquatic insects, Dorn et al. (2001) reported that relative growth rates, chemical cues, and previous feeding experiences were important factors determining feeding preferences of semi-aquatic lepidopteran larvae of *Munroessa gyralis* on macrophytes, whereas protein content, polyphenolic content, and toughness were less important.

In our case, the preferred macrophyte (*C. hispida*) had lower content of protein, nitrogen, phosphorus, sodium, potassium, magnesium, and phenolic compounds than the unpreferred macrophyte (*C. submersum*), but higher calcium content. These findings agree in part with the fact that other crayfish species have shown grazing preference for *Chara* species (Chambers et al. 1991, Matthews et al. 1993) and with the suggestion that phenolic compounds can negatively affect selective grazing by aquatic animals (Lodge 1991). Polyphenols constitute the most widely distributed class of plant secondary metabolites and several thousand different compounds have been identified in tissues of terrestrial plants (Hättenschwiler and Vitousek 2000). An important role of phenolic compounds in terrestrial plants seems to be as defensive agents against hervibores and pathogens (Hättenschwiler and Vitousek 2000). Although the number of studies that have examined phenolic compounds in tissues of aquatic plants is minimal (see, for example, McClure 1970, Zapata and McMillan 1979, Planas et al. 1981, Lodge 1991, Aliotta et al. 1992), it may be that phenolic compounds also play a deterring role in the action of aquatic grazers (e.g., crayfishes).

Table 5. Concentrations (μg/g dry biomass) of phenolic compounds in shoots of *C. hispida* and *C. submersum*.

	C. hispida	*C. submersum*
Total polymeric polyphenols	162	1,077
High polymeric polyphenols	38	425
Low polymeric polyphenols	124	652
o-Diphenols	31	157
Catechins	225	1,050
Procyanidins	782	1,653

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