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Food choice by the introduced crayfish *Procambarus clarkii*

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Predicting the effects of invasive species demands detailed studies on intra and interspecific trophic interactions. To better understand the trophic role of *Procambarus clarkii* in rice fields, I quantified stomach contents and assessed temporal, ontogenetic and sexual trophic selection of macroinvertebrates. Detritus and plants occurred frequently in the stomach of *P. clarkii*, but animals formed the highest fraction of the diet. A seasonal pattern in the proportion of animals in the diet was observed for the total population, different sizes and both sexes. Pre-adults and adults tended to be more herbivorous, whereas juveniles tended to be predatory. Trophic selection of macroinvertebrates appeared related to their availability. Food choice by different life stages indicates that alterations in the demography or abundance of *P. clarkii* may change its structural and functional trophic role in rice field aquatic ecosystems.

Introduction

The introduction of exotic species can threaten native species through predation, competition, and through the introduction of new diseases (Holdich 1999, van der Velde *et al*. 2000). Explosive growth in the population size of a newly introduced species may have dramatic effects on resident communities. Interactions between native and introduced species will most probably influence vertical and horizontal food-chain processes leading to structural and functional changes in the ecosystem (van der Velde *et al*. 2000). Among crustaceans, freshwater crayfishes are often important and successful invaders, and *Procambarus clarkii* (Girard 1855) provides a good example of such species. Native to the northeast of Mexico and central south of USA, *P. clarkii* has been introduced worldwide, with the exception of Australia and Antarctica (Hobbs *et al*. 1989).

Procambarus clarkii was introduced to Portugal in the late 1970's (Ramos & Pereira 1981) and it has since expanded its range throughout the country due to its fast population growth and the abundance of favourable habitats (Correia 1995). This species is considered a pest in rice fields because it causes physical damage to the irrigation systems and levees, and interferes with the establishment of rice seedlings (Correia 1993, Correia & Ferreira 1995, Anastácio & Marques 1996, Anastácio *et al*. 1999, Gutiérrez-Yurrita *et al*. 1999). A number of studies have documented the role of *P. clarkii* as a vector of the crayfish fungus plague *Aphanomyces astaci* (Bernardo *et al*. 1997, Gutiérrez-Yurrita *et al*.

1999), as a prey of diverse avian, mammalian and fish predators (Godinho & Ferreira 1994, Correia 2001), and details of its trophic ecology (Ilhéu & Bernardo 1993a, 1993b, 1995, Gutiérrez-Yurrita *et al.* 1999, Correia 2002). However, the information about the effects of *P. clarkii* on native species and habitat changes induced by its introduction is still limited, and there is an urgent need to assess the impact of *P. clarkii* on aquatic communities.

Procambarus clarkii is an important polytrophic consumer that may act as a keystone species (Huner & Barr 1991, Ilhéu & Bernardo 1993a, 1993b, 1995, Gutiérrez-Yurrita *et al.* 1998, Gutierrez-Yurrita *et al.* 1999). Omnivores can play complex roles in aquatic communities, and their ecological impact can hence be large (Lodge *et al.* 1994, Nyström 1999, Nyström *et al.* 2001, Parkyn *et al.* 2001, Buck *et al.* 2003). The identification of resources consumed by *P. clarkii* will provide information critical to the assessment of its trophic role, and what impact it may exert on aquatic ecosystems. Food choice depends on several factors, namely resource availability, preference, and size (Parkyn *et al.* 2001, Buck *et al.* 2003). Resource partitioning among conspecifics may lead to trophic selection (Parkyn *et al.* 2001). Previous studies on the trophic ecology of *P. clarkii* have suggested that, in spite of its opportunistic habits, this species may feed selectively on macrophytes and macroinvertebrates (Feminella & Resh 1989, Ilhéu & Bernardo 1993a, 1993b, 1995, Gutiérrez-Yurrita *et al.* 1998). By feeding selectively, *P. clarkii* can have a strong negative impact on the selected resources. The purpose of this study was to investigate the attributes of temporal, ontogenetic and sexual food choice by *P. clarkii* by quantifying stomach contents from a rice field population.

Materials and methods

Study site

Samples of *P. clarkii* and other aquatic macroinvertebrates were obtained from a rice field located in the lower river Tagus (Tejo) drainage system (38°–39°N, 8°–9°W), Portugal. The rice field has an area of 7 km^2 where rice (*Oriza sativa*) is cultivated from April to September. Water level is controlled through a drainage and irrigation system of boxes and channels. The wetland area is filled with rain water from October to March when soil preparation takes place.

Sampling and laboratory treatment

Crayfish were captured at dawn, every month from February 1991 to October 1993, with a dip net (65 cm × 40 cm frame; 3 mm mesh size) in irrigation channels. Animals were injected with 4% formalin in the cephalothorax immediately after capture (modified from Hessen & Skurdal 1986, Saffran & Barton 1993) to preserve stomach contents. In the laboratory crayfish were washed with running water for 24 hours to remove formalin, and then measured from the tip of the rostrum to the tip of the telson (total length) and sexed. Their stomachs were removed and placed into a gridded Petri dish. Each stomach content was identified and quantified under a stereomicroscope. The identification of macroinvertebrates was based upon the presence of diagnostic rigid structures and on characters of complete or almost complete specimens.

A macroinvertebrate reference collection was made using specimens captured at the same area as crayfish, from February 1991 to October 1993. Animals were collected with a dip net (1 mm mesh size) using a catch per unit effort (CPUE) of 5 minutes (Afonso 1989). This period was subdivided in two shorter time intervals of 3 and 2 minutes each, to target benthic and pelagic specimens respectively (Fontoura 1985). Efforts were made to document and sample various macrohabitats within the irrigation channels (edge, open area, macrophytes). Macroinvertebrates were live sorted into Gastropoda, Isopoda and Coleoptera and preserved in 70% alcohol. Other taxa were preserved in 4% formalin (Fontoura 1985, Collado & Martinez-Ansemil 1991). Prior to their identification, macroinvertebrates preserved with formalin were maintained for 24 hours under flowing water. Snails were identified to species, and the other taxa to genera or family. Relative abundance of each taxon was also determined.

Diet composition of *P. clarkii*

The diet of *P. clarkii* was quantified through stomach content analysis by estimating the percentage of occurrence (%O) as the number of occurrences of each item (i) divided by the total of analyzed stomachs, and mean volumetric percentages (V) as the sum of the volumetric percentage of the ith category over the total analyzed stomachs (Hellawell & Abel 1971, Capitoli 1992). Food composition was determined seasonally for the total population, each sex and different size classes. Three size classes (SC) were considered: SCI < 50 mm, SCII 50–82 mm, SCIII > 82 mm. These size classes corresponded to the minimal (50 mm total length) and mean size (82 mm total length) at sexual maturity of *P. clarkii* for this site (Correia unpubl. data).

A MANOVA was applied to test the temporal, size and sex differences in the consumption of different food types. The analyzed factors were season (4 levels — spring, summer, autumn, winter), size (3 levels — SCI, SCII, SCIII), sex (2 levels — males, females) and food type (3 levels — detritus, plant material and animal matter). The tested variable was (V), after an arc sin transformation. Bartlett's test was used to determine the homogeneity of variances and normality was tested according to Sokal and Rholf (1982). The Tukey's post-hoc test for unequal n, was used when the significant effect among means was detected (Zar 1984).

Due to the small size of some samples, months were grouped into seasons: spring (March, April, May), summer (June, July, August), autumn (September, October, November), winter (December, January, February).

Trophic selection of aquatic macroinvertebrates by *P. clarkii*

The trophic selection measure of Kohler and Ney (1982) was adopted to determine whether *P. clarkii* feeds selectively on aquatic macroinvertebrates. This method consists of the application of the nonparametric "two-sided, Wilcoxon signed ranks test", used for pairwise comparisons, through the equation:

$$Z = r_i - p_i \qquad (1)$$

where r_i and p_i are respectively the relative frequencies (expressed in proportion) of the ith item in the stomach and in the habitat.

The statistic Z was determined with the expression:

$$Z = \frac{T^+ - \frac{N(N+1)}{4}}{\sqrt{\frac{N(N+1)(2N+1)}{24}}} \qquad (2)$$

T^+ is the sum of positive ranks and N the number of pairs (minus any pairs whose difference is zero; Siegel & Castellan 1988). The null hypothesis that $\Sigma r_i - p_i = 0$ was tested (random exploitation of the ith item). When the null hypothesis was rejected ($P < 0.05$), trophic selectivity was considered to be positive if $Z > 0$ (exploitation of the ith category was significantly greater than its availability) or negative if $Z < 0$ (ingestion of the ith category was significantly lower than its abundance, it does not mean avoidance). Given the high number of comparisons, the P values were adjusted using the sequential Bonferroni technique, which detects if more than one H_0 is false (Rice 1989). Resource abundance was estimated directly through the assessment of the relative abundance of aquatic macroinvertebrates.

Results

Diet composition of *P. clarkii*

The diet composition of *P. clarkii* expressed as percentage of occurrence is shown in Fig. 1. Detritus, plants (green plants, seeds, remains of seeds and other) and animals occurred frequently in the stomachs of *P. clarkii*. Animals consisted of various taxa (Fig. 1). Cannibalism was due to the predation of juvenile crayfish by both sexes. Only pre-adults and adults presented cannibalism.

Significant seasonal differences were found in the use (V) of detritus, plants and animals (Manova, Table 1; Tukey's post-hoc, unequal n, Table 2). The consumption of detritus was high, varying significantly throughout time (Table 2), and a seasonal pattern in their use

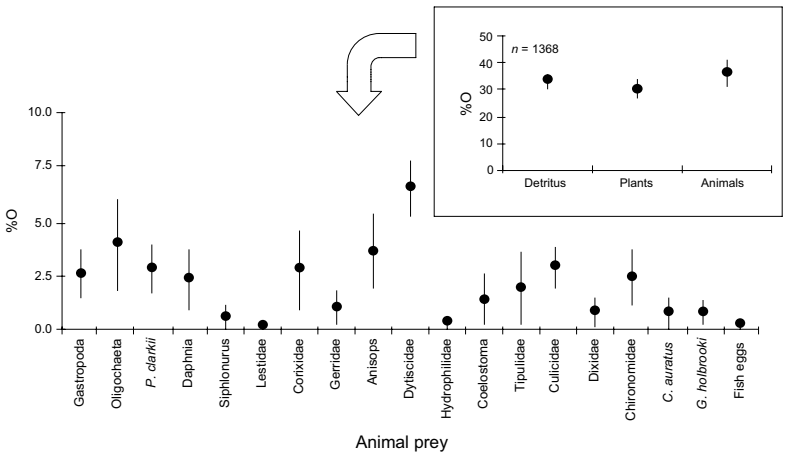

Fig. 1. Diet composition of *P. clarkii* expressed as percentage of occurrence (%O) ± SE. *n* = total number of analyzed stomachs.

Table 1. Statistical test (MANOVA) of the temporal, ontogenic and sex differences in the consumption of different food types.

MANOVA	*P*	Significance
Season	0.613	n.s.
Size	0.807	n.s.
Sex	0.728	n.s.
Food Type	0.001	*
Season × Size	0.538	n.s.
Season × Sex	0.482	n.s.
Size × Sex	0.948	n.s.
Season × Food type	0.001	*
Size × Food type	0.001	*
Sex × Food type	0.026	*
Season × Size × Sex	0.843	n.s.
Season × Size × Food type	0.002	*
Season × Sex × Food type	0.065	n.s.
Size × Sex × Food type	0.585	n.s.
Season × Size × Sex × Food type	0.488	n.s.

was not evident (Figs. 2, 3, 4). The consumption of plants by the total population (Fig. 2) and both sexes (Fig. 4) revealed a seasonal pattern. Plants were most consumed in summer, and a decrease in their use was registered from autumn to winter with an increase in spring (Table 2). Concerning size, plants were most consumed in summer, but there was not a clear pattern in their seasonal use (Fig. 3). A seasonal pattern relative to the consumption of animals was also observed for the total population (Fig. 2), different sizes (Fig. 3) and both sexes (Fig. 4). Animals were most consumed in winter, and a decrease in their use was registered from spring to summer with an increase in autumn (Table 2).

Significant ontogenic and sex differences were found in the use of detritus, plants and ani-

Table 2. Tukey's post-hoc (unequal *n*) comparisons between season and food type. Numbers listed are *P* values; n.s. = differences non significant.

Season × Food type	2	3	4	5	6	7	8	9	10	11	Winter × Animals
1 Spring × Detritus	0.001	0.002	n.s.	n.s.	0.011	0.007	0.002	n.s.	n.s.	0.005	n.s.
2 Spring × Plants	–	n.s.	0.039	0.002	n.s.	n.s.	n.s.	0.021	n.s.	n.s.	0.001
3 Spring × Animals	–	–	n.s.	0.002	0.011	n.s.	n.s.	n.s.	n.s.	n.s.	0.001
4 Summer × Detritus	–	–	–	0.001	0.018	n.s.	n.s.	n.s.	n.s.	n.s.	0.038
5 Summer × Plants	–	–	–	–	0.001	0.001	0.001	n.s.	0.016	0.001	0.001
6 Summer × Animals	–	–	–	–	–	0.019	n.s.	0.001	n.s.	n.s.	0.001
7 Autumn × Detritus	–	–	–	–	–	–	n.s.	n.s.	n.s.	n.s.	0.006
8 Autumn × Plants	–	–	–	–	–	–	–	0.027	n.s.	n.s.	0.002
9 Autumn × Animals	–	–	–	–	–	–	–	–	n.s.	n.s.	n.s.
10 Winter × Detritus	–	–	–	–	–	–	–	–	–	n.s.	0.005
11 Winter × Plants	–	–	–	–	–	–	–	–	–	–	0.001

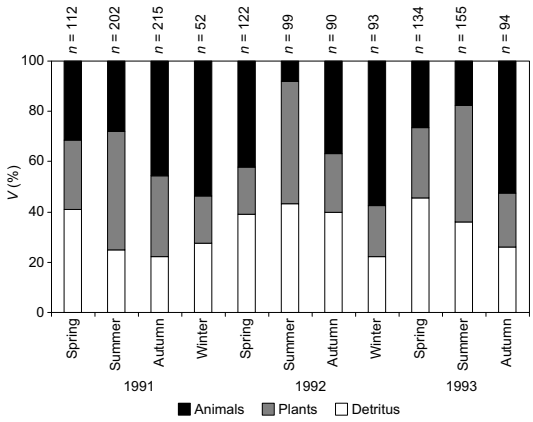

Fig. 2. Seasonal consumption of three main trophic categories by *P. clarkii* expressed as mean volumetric percentage (*V*). *n* = number of analyzed stomachs.

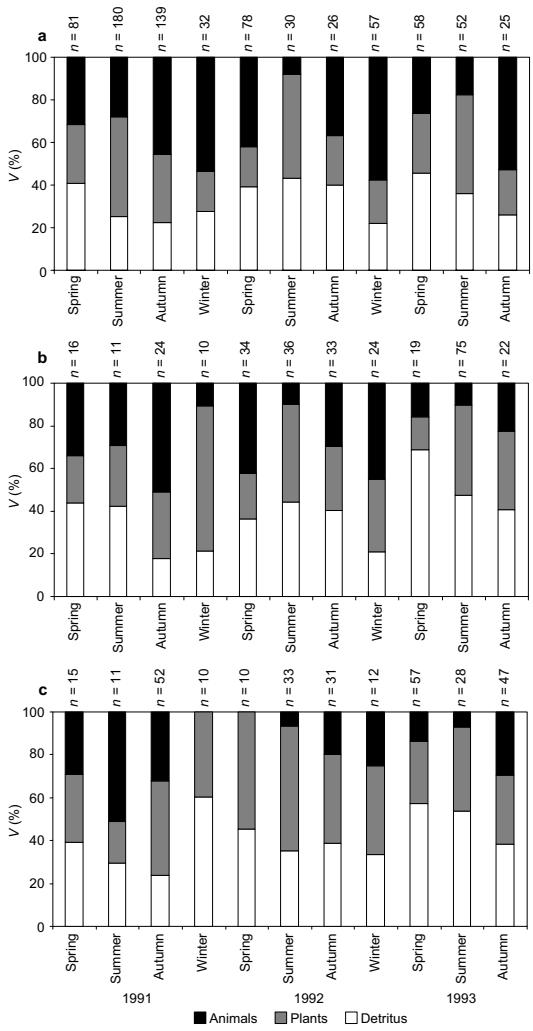

Fig. 3. Consumption of three main trophic categories by different ontogenic phases expressed as mean volumetric percentage (*V*): — **a**: size class I (SCI < 50 mm total length); — **b**: size class II (SCII 50–82 mm total length); — **c**: size class III (SCIII > 82 mm total length). *n* = number of analyzed stomachs.

mals (Manova, Table 1). The intake of animal prey was significantly different among size classes (Tukey's post-hoc, unequal *n*, Table 3). Juveniles (SCI) (Table 3), presented the highest consumption of animal matter (V = 44%) followed by detritus (V = 29%) and plants (V = 27%). Pre-adults (SCII) and adults (SCIII) (Table 3) consumed significantly more detritus (V = 39% and 41%, respectively) and plants (V = 34% and 39%, respectively) than animals (V = 27% and 20%, respectively). These results indicate that there was a decrease in the use of animal prey and an increase in the consumption of detritus and plants with size of *P. clarkii* individuals (Table 3). Both sexes (Tukey's post-hoc, unequal *n*, $P < 0.05$) consumed significantly more animal prey (males: V = 37%; females: V = 38%) and detritus (males: V = 35%; females: V = 34%) than plants (males and females: V = 28%).

Trophic selection of aquatic macroinvertebrates by *P. clarkii*

Mostly, *P. clarkii* presented a random selection ($Z \approx 0.000$, $P > 0.05$) of prey over time, but a negative selection ($Z < 0.000$, $P < 0.05$) also occurred (Fig. 5). These results suggest that macroinvertebrate exploitation was proportional to or lower than their availability. This pattern was consistent among size classes and between sexes (Fig. 6a and b) with a few exceptions in this case. Males selected ($Z > 0.000$, $P < 0.05$) Dytiscidae in summer 1991; Culicidae in winter 1991; *Daphnia*, Hydrophilidae, Culicidae and Chironomidae in spring 1992; Hydrophilidae in spring 1993 (Fig. 6a). Females selected ($Z > 0.000$, $P < 0.05$) *Daphnia* and Culicidae in autumn 1991; Corixidae in winter 1991; *Anisops* in summer 1992; Hydrophilidae in winter 1992 (Fig. 6b).

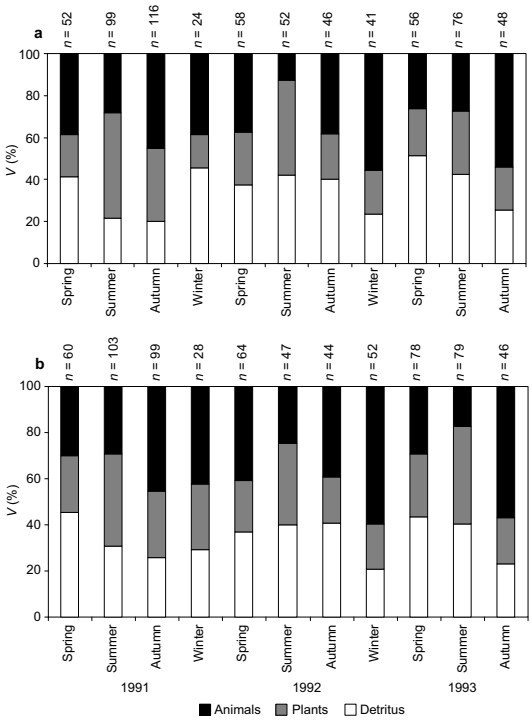

Fig. 4. Consumption of three main trophic categories by (**a**) males and (**b**) females expressed as mean volumetric percentage (*V*). *n* = number of analyzed stomachs.

Discussion

Methodological constraints

One of the major constraints to the study of the trophic ecology of omnivores is the absence of a practical and accurate method to determine their diet composition. Stomach contents of *P. clarkii* are often a mixture of small particles of invertebrates, detritus and plant material that are difficult to separate manually and to use conventional methods of counting and weighing (Ahlgren & Bowen 1992). The percentage of occurrence is not a quantitative method but is a good indicator of prey absence/presence. It may be argued that stomach contents do not accurately reflect resource exploitation by the consumer. According to Hellawell and Abel (1971) the volumetric technique used in this study is a valid measure for quantifying stomach contents, including detritus and plant material otherwise difficult to assess.

Trophic selection is influenced by various unknown variables that together with inherently biased field data will complicate the interpretation of results. The Wilcoxon's signed-rank test avoids the assumptions related to population distribution and variance, and because it evaluates date-specific pair differences it provides the best measure for the trends of trophic selection (Kohler & Ney 1982). In this sense it reflects a broad and accurate estimate of food selection, since it weighs individual diets. To determine trophic selection it is necessary to assess resource availability, which is the "Achilles heal" of *in situ* feeding studies. Information on resource availability can be estimated by the determination of the relative abundance of prey items in the environment. Some criticism has arisen to the application of this technique, because habitat samples may not accurately reflect resource availability to the consumer (Kohler & Ney 1982). Nevertheless, it is more desirable to use this method than determining selection based only on proportional consumption. It is important to keep in mind that trophic selection measurements are site and time specific

Table 3. Tukey's post-hoc (unequal *n*) comparisons between size and food type. Numbers listed are *P* values; n.s. = differences non significant.

Size × Food type	2	3	4	5	6	7	8	SCIII × Animals
1 SCI × Detritus	0.006	0.032	n.s.	n.s.	0.015	n.s.	n.s.	0.009
2 SCI × Plants	–	0.024	n.s.	n.s.	0.016	n.s.	n.s.	0.031
3 SCI × Animals	–	–	0.041	0.009	0.001	0.037	0.021	0.012
4 SCII × Detritus	–	–	–	n.s.	0.001	n.s.	n.s.	0.038
5 SCII × Plants	–	–	–	–	0.009	n.s.	n.s.	0.043
6 SCII × Animals	–	–	–	–	–	0.025	0.018	n.s.
7 SCIII × Detritus	–	–	–	–	–	–	n.s.	0.039
8 SCIII × Plants	–	–	–	–	–	–	–	0.029

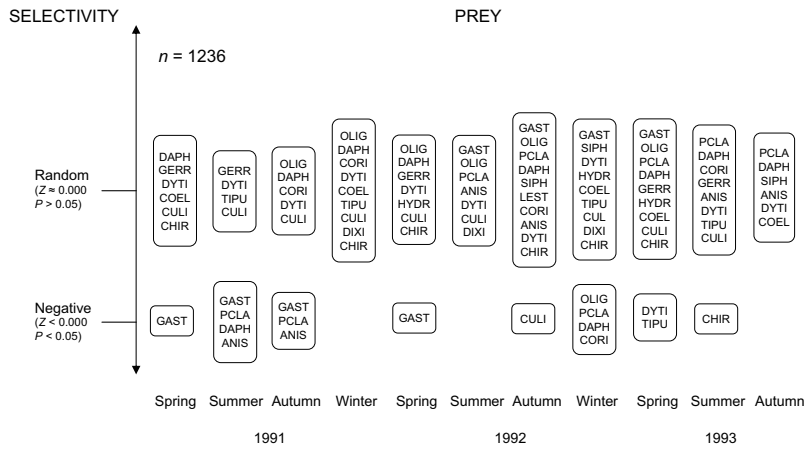

Fig. 5. Temporal trophic selection of aquatic macroinvertebrates by *P. clarkii*. *Z* = index of trophic selectivity (random = exploitation of the *i*th category was proportional ($P > 0.05$) to its availability; negative = ingestion of the *i*th category was significantly lower ($P < 0.05$) than its abundance, it does not mean avoidance). *P* values adjusted with the sequential Bonferroni test. GAST = Gastropoda; OLIG = Oligochaeta; PCLA = *P. clarkii*; DAPH = *Daphnia* spp.; SIPH = *Siphlonurus*; LEST = Lestidae; CORI = Corixidae; GERR = Gerridae; ANIS = *Anisops*; DYTI = Dytiscidae; HYDR = Hydrophilidae; COEL = *Coelostoma*; TIPU = Tipulidae; CULI = Culicidae; DIXI = Dixidae; CHIR = Chironomidae. *n* = total number of analyzed stomachs.

and should be interpreted in a perspective of tendency and not absolute evaluation of a species food preference.

Diet composition and trophic selection by *P. clarkii*

Information on food choice by a species contributes to understanding the trophic niche it occupies, i.e., its structural and functional role in the community. *Procambarus clarkii* behaved as an omnivore consuming resources from several trophic levels (i.e. acting as detritivore, herbivore and predator). According to Buck *et al.* (2003) omnivory may be advantageous since a varied diet includes complimentary nutrients that will enhance individual growth. Results from this study indicate that the consumption of detritus by *P. clarkii* was high throughout the year regardless of size or sex, which is in accordance with Avault and Brunson (1990), and Ilhéu and Bernardo (1993a). Detritus probably represent the main trophic component of aquatic ecosystems forming an energetic flow through biota being the microdistribution of detritivore taxa frequently influenced by the ecosystem detritic composition (Culp *et al.* 1983). According to Wiernicki (1984) and McClain *et al.* (1992a) most of the nutritional value of detritus is associated with its rich microbial layer that makes up half of the carbon source ingested by juveniles. These seem to be able to grow on a diet based only of decomposing material depending on the nutritional value of the microbial fraction of detritus (McClain *et al.* 1992a). Nevertheless, McClain *et al.* (1992a, 1992b) concluded that detritus have a reduced contribution to weight gain of juveniles of *P. clarkii*. Likewise, Parkyn *et al.* (2001) found that detritus did not contribute significantly for the growth of *Paranephrops planiformis,* although this material probably provided energy for respiration and maintenance. Ingestion of detritus will speed up the rate of decomposition by modifying its chemical composition, increasing the leaching area and microbial colonization (Oberndorfer *et al.* 1984) and releasing nitrogen and phosphorus. These will enter their respective nutrient cycles serving as support for primary production (Kristiansen & Hessen 1992, Golterman & Groot 1994). However, Lodge (1991), Hessen *et al.* (1993), and Parkyn *et al.* (2001) argue that the contribution of crayfish to primary production is very limited, and their major functional role as detritivores is to breakdown dead organic material into FPOM.

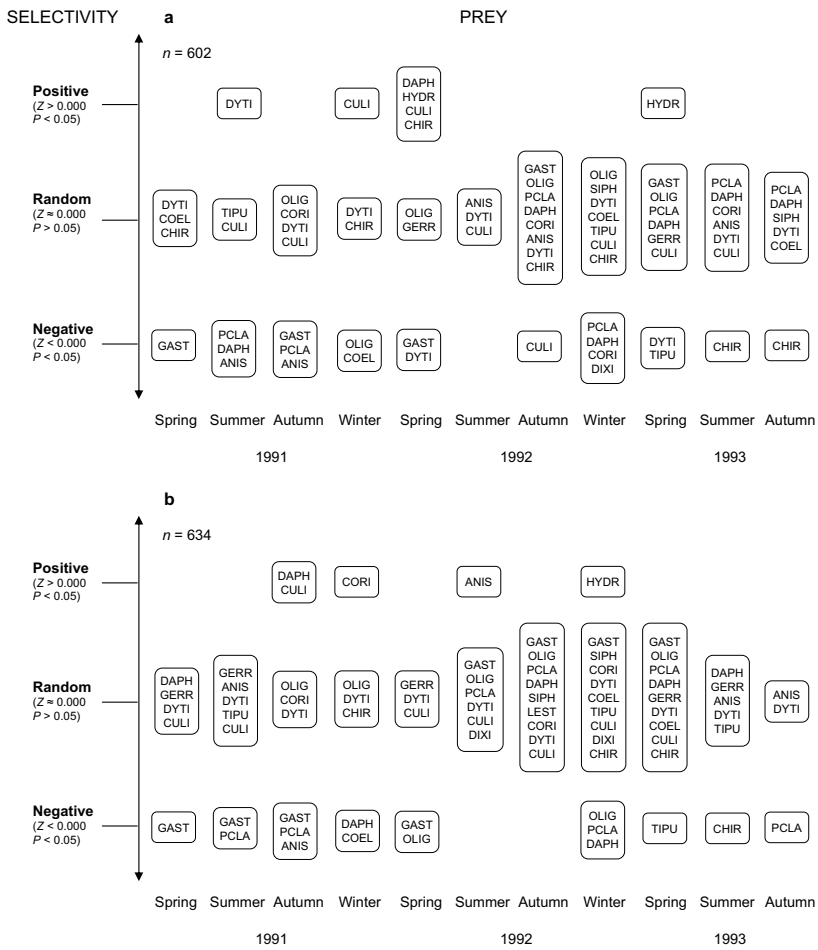

Fig. 6. Trophic selectivity of aquatic macroinvertebrates by (**a**) males and (**b**) females. *Z* = index of trophic selectivity (positive = exploitation of the *i*th category was significantly greater ($P < 0.05$) than its availability; random = exploitation of the *i*th category was proportional ($P > 0.05$) to its availability; negative = ingestion of the *i*th category was significantly lower ($P < 0.05$) than its abundance, it does not mean avoidance). *P* values adjusted with the sequential Bonferroni test. GAST = Gastropoda; OLIG = Oligochaeta; PCLA = *P. clarkii*; DAPH = *Daphnia* spp.; SIPH = *Siphlonurus*; LEST = Lestidae; CORI = Corixidae; GERR = Gerridae; ANIS = *Anisops*; DYTI = Dytiscidae; HYDR = Hydrophilidae; COEL = *Coelostoma*; TIPU = Tipulidae; CULI = Culicidae; DIXI = Dixidae; CHIR = Chironomidae. *n* = total number of analyzed stomachs.

Plant consumption was always lower than that of detritus which is in accordance with the suggestion that *P. clarkii* has a more important role as a detritivore than as an herbivore (Ilhéu & Bernardo 1993a). Oliveira and Fabião (1998) demonstrated a low consumption of fresh plants by *P. clarkii*, and the authors suggest that this is because of its poor nutritional value. In fact, McClain *et al*. (1992a) argued that although green plants can be a source of carotenoids and phytosterols, they are not suitable for the maximal potential growth of *P. clarkii*. Nevertheless, the use of vegetable matter by *P. clarkii* in this study was substantial, with higher consumption in spring and summer than in autumn and winter. Gutiérrez-Yurrita *et al*. (1998) found that *P. clarkii* consumed mostly plant material in the marshes of the Doñana National Park, Spain, and attributed this feeding behaviour to resource availability. However, other studies (e.g., Feminella & Resh 1989, for *P. clarkii*, Carpenter & Lodge 1986, Lodge & Lorman 1987, Chambers *et al*. 1990, Olsen *et al*. 1991, Matthews *et al*. 1993, Lodge *et al*. 1994, Nyström & Strand

1996, Nyström *et al*. 1999 for other species) have shown that crayfish could feed selectively on plants, especially aquatic macrophytes, leading to significant reduction of their biomass. Because crayfishes are known to be the most important consumers of aquatic macrophytes (Carpenter & Lodge 1986, Lodge & Lorman 1987, Chambers *et al*. 1990, Olsen *et al*. 1991, Lodge *et al*. 1994, Nyström 1999) further estimates of grazing rates by *P. clarkii* on submersed and emergent vegetation are needed, particularly *in situ* measurements.

Animal prey are considered to be of high quality and essential resources especially during the growth phase of *P. clarkii* (McClain *et al*. 1992a, 1992b, Ilhéu & Bernardo 1993a, Oliveira & Fabião 1998). In this study, the seasonal pattern relative to the consumption of animal prey was such that their exploitation was highest in winter decreasing during spring and summer. Furthermore, *P. clarkii* presented an ontogenic shift of the diet with juvenile feeding more intensively on aquatic invertebrates, and pre-adults and adults consuming more detritus and plants. These results are in agreement with Ilhéu and Bernardo (1993a) who observed a diet shift from zoophagy to herbivory with growth increment. As discussed by McClain *et al*. (1992a) juveniles can not be classified as true detritivores or herbivores since they rely on animal prey for their rapid growth. Although Ilhéu and Bernardo (1993b) found that also adults feed preferentially on macroinvertebrates at least in laboratory experiments, in this study the role of herbivory seems to apply more to pre-adults and adults than to juveniles, whereas all age classes function as detritivores. These findings indicate, as suggested by Buck *et al*. (2003) that, in spite of consuming primarily one food type, animals will eat other food types to obtain nutrients lacking in their primary diet. Studies from Hanson *et al*. (1990), Olsen *et al*. (1991), Matthews *et al*. (1993), Lodge *et al*. (1994), Nyström *et al*. (1996, 1999), Lodge *et al*. (1998), Nyström and Pérez (1998), Turner *et al*. (2000), Nyström *et al*. (2001) have shown that crayfish strongly affect aquatic macroinvertebrate communities, although the observed impact was species dependent and may be indirect. In this study, trophic selection towards aquatic macroinvertebrates was mostly random or negative indicating exploitation proportional to or lower than their availability. In fact, Correia (2002) found that, in rice fields, *P. clarkii* adjusted its trophic behaviour to the availability of aquatic macroinvertebrates. There was a positive trophic selection of *Daphnia*, Dytiscidae, Hydrophilidae, Culicidae, Chironomidae by males, and *Daphnia*, Corixidae, *Anisops,* Hydrophilidae and Culicidae by females. The selection of Chironomidae larvae by males may be beneficial since larvae of *Chironomus* are important rice pests that destroy the rice plant and its roots. However, the selection of different animal resources by both sexes is somewhat puzzling and may be related to methodological constraints. Nevertheless, these results raise some questions that remain to be answered: is there any connection between trophic selection and sexual dimorphism? Is trophic selection related with reproductive needs of mature males and females? What mechanisms could be implied in trophic selection by *P. clarkii*?

Overall, the impact of *P. clarkii* on the rice fields seems to be exerted on various trophic levels, and food choice seems to be dependent on resource availability. These findings suggest that this species is able to switch between resources so fluctuations in their abundance would tend to cancel out, stabilizing the total resource availability. By consuming a great amount of detritus, *P. clarkii* may have a positive influence in the sense that it promotes nutrient recycling. Predation on aquatic macroinvertebrates may induce changes in their abundance and diversity, but because their consumption by *P. clarkii* was generally lower or identical to resource availability no dramatic effects on rice field aquatic macroinvertebrates are expected to occur. The trophic behaviour presented by different functional groups indicate that alterations in the population structure and abundance of *P. clarkii* may change its structural and functional trophic role that will have further implications on rice field aquatic food webs. The omnivory presented by *P. clarkii*, along with the seasonal changes of its trophic connections, and its ontogenic diet shifts, makes it difficult to position in food webs. Therefore, predicting the consequences of the invasion of this species underlies some complexity that demands thorough approaches

of food web linkages involving intra and interspecific interactions. Despite this complexity, I hope this research contributes to fill in the puzzle providing information for understanding basic questions on the effects of *P. clarkii* on aquatic communities.

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