

## Population dynamics of the invasive crayfish (*Procambarus clarkii* Girard, 1852) at two marshes with differing hydroperiods

Pedro Manuel Anastácio<sup>1\*</sup>, Ana Sofia Leitão<sup>2</sup>, Maria José Boavida<sup>3</sup>  
and Alexandra Marçal Correia<sup>2,4</sup>

<sup>1</sup> IMAR – Institute of Marine Research a/c. Departamento de Paisagem, Ambiente e Ordenamento, Universidade de Évora, Rua Romão Ramalho 59, 7000-671 Évora, Portugal

<sup>2</sup> Museu Nacional de História Natural, Universidade de Lisboa, R. Escola Politécnica 56/58, 1250-102 Lisboa, Portugal

<sup>3</sup> Centro de Biologia Ambiental, Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisboa, Portugal

<sup>4</sup> Instituto de Medicina Molecular, Faculdade de Medicina, Universidade de Lisboa, Av. Prof. Egas Moniz, Ed. Egas Moniz Piso 1B, 1649-028 Lisboa, Portugal

Received 5 August 2009; Accepted 22 September 2009

**Abstract** – The population dynamics of the red swamp crayfish (*Procambarus clarkii* Girard, 1852) was studied from May 2005 to May 2006 in a pond (PCD) subjected to drought between June and December and in a continuously flooded rice field drainage channel (PMG) located in the Tejo river basin, Portugal. The proportion of females in the population was not independent from the season and was negatively correlated with both female and male maturation status. Male and female maturation was synchronous but males remained in a reproductive form after recruitment while females reverted quickly to lower maturation indexes. At PCD and PMG, respectively 2 and 5 cohorts were detected by modal analysis. Large crayfish were abundant in spring, summer and early autumn and juveniles were abundant in autumn, especially at PCD. Crayfish density at PCD was lower than at PMG and mortality rate ( $Z$ ) was 3.99 at PCD and 2.43 at PMG. The average lifespan of the crayfish populations was 91 days at PCD and 150 days at PMG. Our study indicated faster growth and larger maximum sizes at the site with the more stressed environment and lowest relative crayfish densities (PCD), suggesting that any exploitation or control strategies for these two populations should consider management of the hydroperiod and of maximum crayfish densities.

**Key words:** Red swamp crayfish / growth / rice fields / sex ratio / recruitment

### Introduction

Nowadays, the introduction and invasion of new species is one of the most important issues in conservation biology and recent analyses suggest that biodiversity in freshwater ecosystems tends to decline faster than in most terrestrial ecosystems (Ricciardi and Rasmussen, 1999). If this process of homogenization continues, in less than 100 years most of these freshwater habitats will be dominated by an array of cosmopolitan species that will replace most of the native ones (Gherardi, 2006). In this context, the invasion by crayfish species has been held responsible for the biological homogenization of many freshwater systems since they cause significant alterations on community

structure especially on aquatic food webs (Lodge *et al.*, 1998).

The red swamp crayfish, *Procambarus clarkii* Girard, 1852, has been introduced in many countries of Europe, Asia and Africa for aquaculture purposes (Huner and Avault, Jr., 1979). This exotic species causes damage to local benthic fauna and flora (Gutierrez-Yurrita *et al.*, 1999) all over the world, being a potential threat to biodiversity (Correia and Anastácio, 2008). In fact, for the majority of *P. clarkii* introductions negative consequences were reported (Lodge *et al.*, 2000), although positive effects on predators are also noticeable (Adrian and Delibes, 1987; Correia, 2001). *P. clarkii* life cycle is characterized by a considerable plasticity, invading diversified environments where it adapts to extreme conditions such as temporary streams and polluted habitats

\*Corresponding author: [anast@uevora.pt](mailto:anast@uevora.pt)

(Gutierrez-Yurrita and Montes, 1999; Gherardi *et al.*, 2000). In Portugal this species was introduced from Spain in the 1970's (Ramos and Pereira, 1981) and spread rapidly. It is considered an agricultural pest because of its burrowing activity which causes serious damage in dams and levees and because it consumes young rice plants (Grigarick, 1984; Anastácio *et al.*, 2005a, 2005b).

Similar to other organisms, the population dynamics of the red swamp crayfish is highly dependent on the interaction between environmental and biological factors. If environmental conditions are favourable, the population acts as a r-strategist, because of its fast growth rate and high fertility (Gherardi, 2006). The objective of this study was to examine several aspects of the population dynamics of *P. clarkii* in areas with different conditions so that, in the future, more efficient predictions of the invasion success in new areas can be obtained and more effective management or exploitation is possible. The issue is particularly relevant in the studied area, since new legislation regarding invasive species is being prepared and predicts the implementation of state managed control programs for invasive species.

## Methods

### Study area

This study took place in two freshwater marshes, Paul da Casa de Cadaval (39°N, 8°30'W) and Paul de Magos (38°58'W, 8°45'W), located at the Salvaterra de Magos County in the Tejo river basin. Paul da Casa de Cadaval (PCD) is a freshwater marsh of about 14 km<sup>2</sup>, with agricultural fields, ponds and reservoirs (Correia, 2001). This freshwater marsh is surrounded by riparian vegetation and is linked to the Lamarosa stream. The peripheral land is occupied by oaks, reeds and eucalyptus. Paul de Magos (PMG) is a rice (*Oryza sativa*) field area of 7 km<sup>2</sup>, characterized by a continuously flooded spring-summer culture which development and growth is strongly influenced by the water level (Correia, 1995). Fields are prepared for cultivation in March–April, sown in April–May, harvested in September–October and water level is controlled during most of the rice growth period. The purpose of this is to control aquatic weeds and animal pests. In the adjacent areas of this marsh there are oaks and pinewoods (Correia, 1995, 2003).

### Crayfish sampling and laboratory procedures

From May 2005 to May 2006, crayfish were sampled monthly in a pond at PCD and in irrigation channels at PMG. Crayfish were caught with a dip net (65 cm × 40 cm frame; 3 mm mesh size) and traps and sampling was replicated three times during the same day at both sites. Several environmental variables were recorded during sampling: depth, dissolved oxygen, conductivity, ammonium ion (NH<sub>4</sub><sup>+</sup>) and pH. A temperature logger was set to a 30 min interval and placed in the water at both locations.

In each replicate, three traps with bait (canned sardine) were set out at sunset with a distance of 5 m among them. After 12 h, crayfish were collected from the traps and in the same area of 15 m<sup>2</sup> crayfish were sampled with a dip net, using an effort of 15 min. Samples obtained by both methods were separately kept in bags, previously identified, and preserved in 70% alcohol for further analysis. The pond at PCD dried from July to October 2005, therefore during these months the sampling and the measurement of environmental variables did not take place. In the laboratory, each specimen was weighted to the nearest 0.001 g, and the CL (carapace length from the tip of rostrum to the carapace end) was measured to the nearest 0.01 mm. For each individual with a carapace length longer than 13 mm, sex was verified by the presence of developed gonopodia (Suko, 1953).

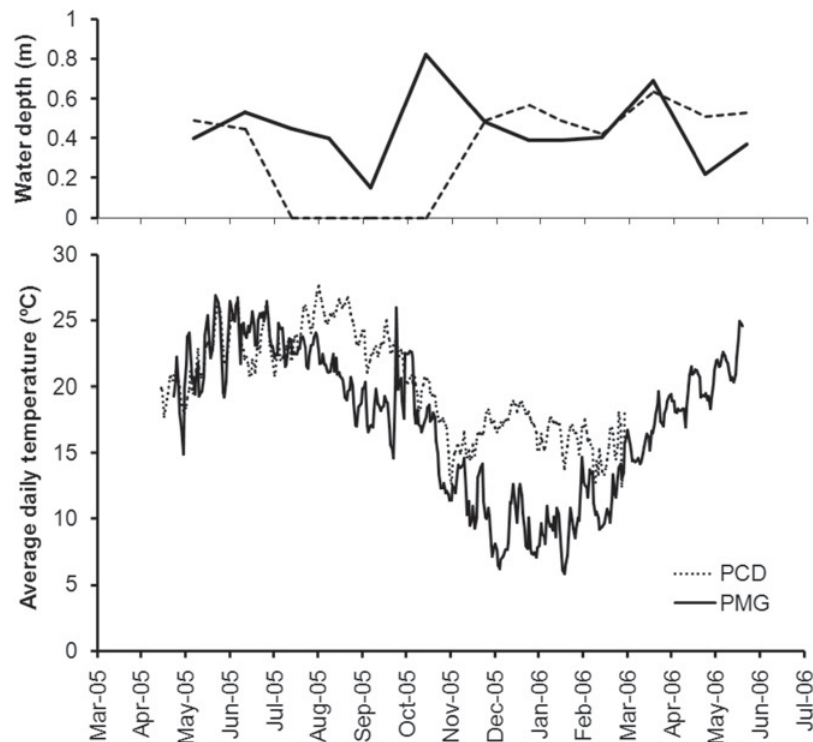
### Analysis of the population structure

Size-frequency distributions (mm) of the two studied populations were constructed using 5 mm class intervals. We used the FISAT II computer program (version 1.2.2, FAO-ICLARM) and applied modal progression analysis to size-frequency distribution data from each marsh. Normsep's method with the Simplex algorithm was used, after an initial analysis with the Bhattacharya method (Sparre *et al.*, 1992). For each cohort identified by Normsep's method the mean carapace length (CL) and the standard deviation (SD) were calculated.

The maturation index (MI) was estimated monthly for females at each study area by the equation (Guerra and Niño, 1996):  $MI = \frac{\sum (\text{status } K * n^{\circ} \text{ of } K \text{ individuals})}{N}$ . The possible *K* status for females are: 1 – white gonad; 2 – yellow gonad; 3 – orange gonad; 4 – brown gonad. *N* is the total number of females analysed. Sex ratio (SR) was calculated as the ratio between the females and the total number of individuals with a CL over 13 mm (F/total) for each month, at each marsh. Likewise, the proportion of Form I males on the adult male population was also calculated.

### Analysis of growth and mortality

Growth parameters were estimated using FISAT (FAO–ICLARM Stock Assessment Tools) computer program. Asymptotic length ( $L_{\infty}$ ) and corresponding 95% confidence limits were estimated by the maximum length estimation method, using as input the maximum length ( $L_{\text{max}}$ ) recorded at each area. For each site, a non-oscillating von Bertalanffy growth equation (von Bertalanffy, 1957) was fitted using Appeldorn's method. The equation is  $L_{(t)} = L_{\infty} [1 - \exp(-K(t - t_0))]$ , where  $L_{(t)}$  is the crayfish carapace length (CL) at time *t*;  $L_{\infty}$  is the theoretical maximum CL of the crayfish; *K* is the curvature parameter which records the rate at which the  $L_{\infty}$  is obtained; and  $t_0$  is a theoretical value for time when the CL is equal to 0. The starting value of  $L_{\infty}$  was the estimate obtained by the maximum length estimation



**Fig. 1.** Average daily water temperature at the two marshes obtained from logger measurements. PCD – Paul da Casa de Cadaval; PMG – Paul de Magos.

method, allowing for a variation within the 95% confidence limits. The used software did not calculate  $t_0$  but it can be estimated assuming a CL of 5 mm at recruitment.

The mortality index ( $Z$ ) was calculated using the length converted catch curve analysis by the FISAT software using the estimated values of  $L_\infty$  and  $K$ . Based on  $Z$ , the mean lifespan of each population ( $t_i$ ) was given by the ratio  $1/Z$ , assuming that  $Z$  is constant and that both populations did not undergo migration (Allen, 1971).

### Statistical analysis

Statistical analysis was performed using SPSS version 17. The values of the environmental variables collected at each sampling were compared by means of a Wilcoxon signed ranks test in which the pairs consisted of the values of the variable at both sites at each date. Temperature data from the loggers were used to calculate average temperature for each 24 hours period and these values were compared at both sites by a paired samples t-test after checking for normality and homogeneity of variances. Chi-square tests on contingency tables were used to verify differences in proportions among sexes or among male reproductive status throughout the year, at each site. We explored the possibility of significant correlations among the variables “sex ratio” (females/total adults), “proportion of Form I males” (Form I/total males) and “female maturation index” at each sampling site. A Wilcoxon signed ranks test was used to test for differences in the number of crayfish captured at both sites, pairing data for each sampling occasion.

## Results

### Environmental variables

Average daily water temperatures were generally higher throughout the year at PCD (Fig. 1). At this location the logger stopped working the 13 March 2005, *i.e.* approximately 2 and a half months before the last sample was taken. Average temperature at PCD and at PMG was respectively 20.2 °C and 16.9 °C during the period when both loggers were operating. A paired samples t-test was applied to temperature data from these loggers indicating very highly significant differences ( $t = 16.866$ ,  $d.f. = 308$ ,  $P < 0.001$ ). The temperature on the two sites differed on average by 3.35 °C. An analysis of the data from the physico-chemical variables at both sites using a Wilcoxon signed ranks test on data obtained at each sampling occasion, indicated no significant differences for all the variables considered except conductivity (Table 1). Conductivity was considerably higher at PMG, with an average value of 848 *versus* 324 ( $\mu\text{s}\cdot\text{cm}^{-1}$ ) at PCD.

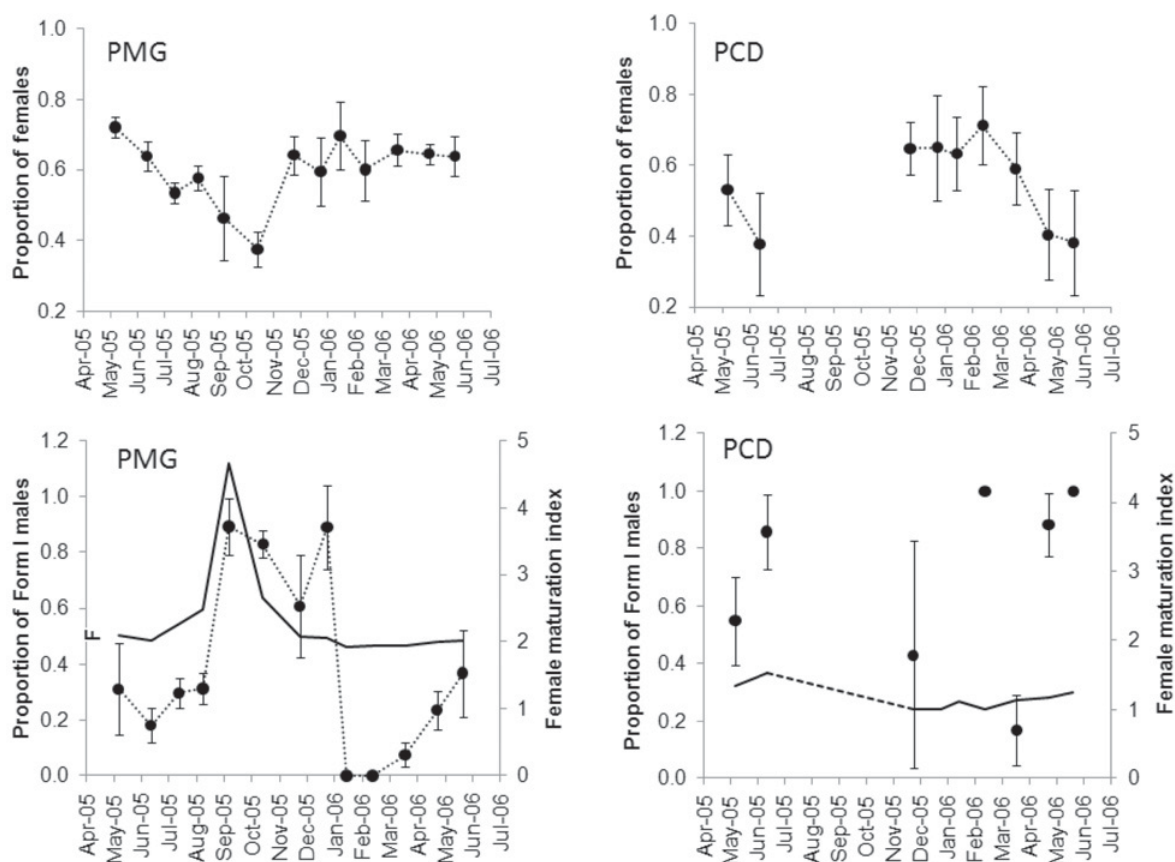
### Sex ratio and reproductive status

At PMG the proportion of females decreased from May to October–November (Fig. 2). The minimum proportion of females in the population was attained just after the end of the peak in the maturation index. Female maturation index (Fig. 2) was highest in October which is coincident with a sharp increase in the presence of reproductive (Form I) males. Form I males were abundant

**Table 1.** Wilcoxon signed ranks test comparing the values of each environmental variable at both of the studied marshes and descriptive statistics for each variable. Paul de Magos (PMG) and Paul de Cadaval (PCD).

	O <sub>2</sub> (mg.L <sup>-1</sup> )	pH	Conductivity (μs.cm <sup>-1</sup> )	Ammonium (mg.L <sup>-1</sup> )	Depth (m)
<b>Wilcoxon</b>					
Z	-0.415	-1.481	-2.666	-0.512	-0.314
Asymp. Sig. (2-tailed)	0.678	0.139	<b>0.008</b>	0.609	0.753
<b>Descriptive statistics</b>					
<i>N</i> (PMG)	13	13	13	13	13
Mean	6.80	6.26	848.41	0.65	0.44
Std. deviation	8.39	1.09	297.70	0.36	0.17
Minimum	0.41	3.49	432.33	0.00	0.20
Maximum	32.76	7.19	1268.67	1.20	0.80
<i>N</i> (PCD)	9	9	9	9	13
Mean	5.17	6.46	323.85	0.92	0.35
Std. deviation	2.87	0.26	63.26	0.50	0.25
Minimum	2.19	6.07	231.00	0.60	0.00
Maximum	10.22	6.76	432.00	2.10	0.64

Note: *N* for Wilcoxon is the minimum value of *N* for the two sampling stations.



**Fig. 2.** Proportion of females, proportion of reproductive (Form I) males and female maturation index of the crayfish populations from the two marshes. The proportions are within 95% confidence limits. Female maturation index is represented by a line without confidence limits. PCD – Paul da Casa de Cadaval; PMG – Paul de Magos.

until the beginning of January, and disappeared completely from the population until the end of March. At this date the proportion of Form I males started to increase once again. At PCD the absence of water prevented sampling

from the end of June to the beginning of December. The proportion of females was highest when the lowest values of their maturation index were obtained, and *vice versa* (Fig. 2). A generally low number of adult males was

obtained in comparison to that of PMG. The proportion of Form I males was quite irregular (Fig. 2), with large uncertainties and with missing values caused by the lack of adult males.

The Chi-square test applied on a contingency table demonstrated that the proportion of Form I males was not independent from the season, at both sites. At PMG  $X^2 = 383.64$ , d.f. = 12 and  $P < 0.001$  and at PCD  $X^2 = 66.82$ , d.f. = 4 and  $P < 0.001$ . A much lower number of samples was used in Cadaval because of insufficient numbers of males and a long dry period. The proportions of females were not independent from the season, at both sites. At PMG  $X^2 = 185.11$ , d.f. = 12 and  $P < 0.001$  and at PCD  $X^2 = 31.56$ , d.f. = 8 and  $P < 0.001$ . The lower value of degrees of freedom obtained at PCD was justified by a long dry period which prevented sampling.

At PMG all the three variables related to sex ratio and reproductive stage were significantly correlated. The female maturation index and the proportion of females in the population were negatively correlated ( $r = -0.627$ ,  $P = 0.022$ ,  $N = 13$ ) and so were the proportion of reproductive (FI) males and the proportion of females ( $r = -0.624$ ,  $P = 0.018$ ,  $N = 13$ ). The proportion of FI males and the female maturation index were positively correlated ( $r = 0.593$ ,  $P = 0.033$ ,  $N = 13$ ). Data from PCD were scarce because of the long dry period and insufficient number of males, therefore the analysis of correlations involving males was not performed. At PCD the female maturation index and the proportion of females in the population were negatively correlated as well ( $r = -0.79$ ,  $P = 0.011$ ,  $N = 9$ ).

### Population size structure and recruitment

In Figure 3 size frequency histograms can be seen for crayfish populations throughout the year at both sites. There were clear differences in population structure with *e.g.* distinct recruitment patterns at both sites. The population from PCD exhibited a single recruitment period, starting in December, immediately after the dry period. On the contrary, multiple recruitment periods were observed at PMG where water was found all over the year. Recently recruited animals were not abundant at PCD during the months of May and June, while this situation occurred from September to November at PMG. Adult individuals were found all year round at both sites but dominated the population in May–June at PCD, while at PMG this occurred during the months of September–October.

### Growth, density, mortality and mean lifetime

Two cohorts were identified at PCD and 5 cohorts at PMG (Fig. 4). In this population (PMG), cohorts 2 and 3 merged during September 2005 and were followed until the end of the sampling program, in June 2006. These two cohorts were statistically distinguishable at the

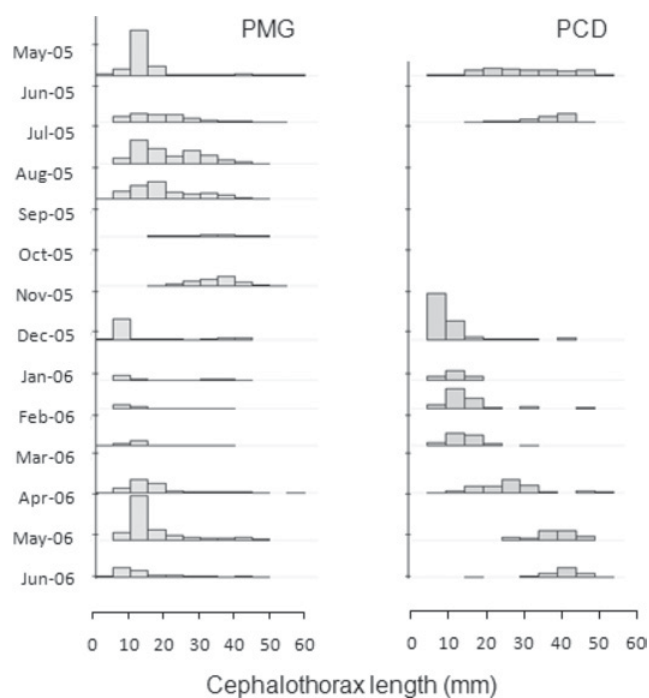


Fig. 3. Size-frequency histograms for the crayfish populations sampled at the two marshes, obtained from cephalothorax length measurements. PCD – Paul da Casa de Cadaval; PMG – Paul de Magos.

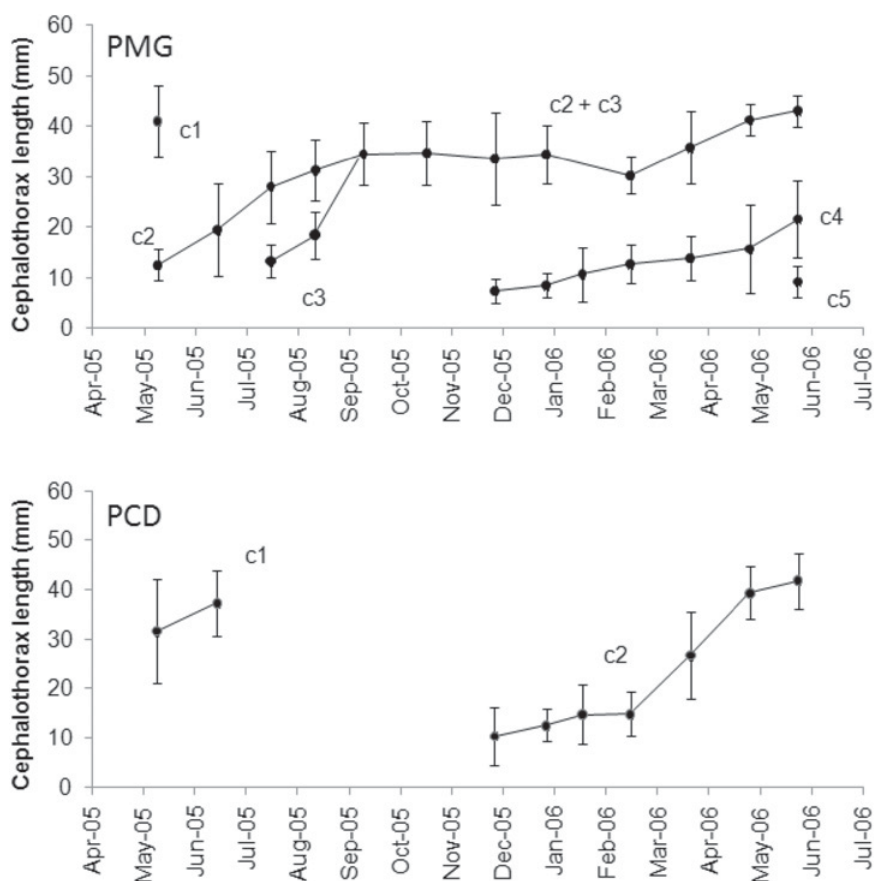
recruitment stage but the possibility of a single and long recruitment period should not be discarded. Cohort 5 was detected the first of June but it is possible that its recruitment was already initiated at the previous sampling date, as can be seen by the large error bars of cohort 4 at that date. Modal analysis identified 3 new cohorts per year in PMG and 1 new cohort each year in PCD. The only cohort recruited into the crayfish population from PCD was detected at the 6/12/2005. The adjustment of a von Bertalanffy growth curve to data from the two sites, using Appeldoorn's method, resulted in different growth parameter values (Table 2). Although a larger number of cohorts (and individuals) were released each year at PMG, crayfish grew faster, as shown by a larger  $k$  value, and individuals reached larger size ( $L_{\infty}$ ) at PCD.

The number of captures at each sampling date, based on an equal capture effort, was very different at both sites as demonstrated by the Wilcoxon test ( $Z = -2.666$ ,  $n = 9$ ,  $P < 0.001$ ). This indicates much higher densities at PMG and in fact the maximum number of individuals caught was obtained at this site during spring and early summer (Fig. 5). Mortality was higher at PCD and consequently mean lifetime was much lower (Table 2).

## Discussion

### Environmental variables

Habitat conditions are more adequate for the populations of *P. clarkii* at PMG because of the constant



**Fig. 4.** Results of the modal analysis applied to the crayfish populations from the two marshes, with average size and standard deviation. PCD – Paul da Casa de Cadaval; PMG – Paul de Magos; c1 to c5 – cohort 1 to cohort 5.

**Table 2.** Growth and mortality related parameters obtained for the crayfish populations from the two marshes. Paul de Magos (PMG) and Paul de Cadaval (PCD).

	PMG	PCD
<i>Maximum length estimation</i>		
Observed extreme length (mm)	57.5	52.5
Predicted extreme length (mm)	60.6	63.98
<i>Appeldoorn's method</i>		
$L_{\infty}$ (mm)	54.97	74.77
$K$	0.95	1.32
<i>Length-converted catch curve</i>		
$Z$	2.43	3.99
95% conf. lim.	1.79–3.06	1.92–6.06
Mean lifetime (days)	150	91

presence of water. PMG is a permanent rice field channel with an average depth of approximately 0.44 m and its higher conductivity values do not indicate a factor of stress because the species is tolerant to brackish water with salinities up to 10 ppt (Huner, 1988). In fact, Alcorlo *et al.* (2008) sampled crayfish from 11 stations in the Lower Guadalquivir basin (Spain) with conductivities ranging

from 1000 to 4000  $\mu\text{S}\cdot\text{cm}^{-1}$  in rice field and channel habitats.

In the pond at PCD hydrology and temperature seem to be the key variables structuring the population. There is a long phase without water, forcing crayfish to confinement inside burrows and therefore reducing the period of growth and reproduction. In spite of this constraint, which makes the habitat more stressed, temperature is higher at PCD and this can accelerate growth rates within certain limits. This seems to be the case at this site because average temperatures are within the tolerance values for the species (Anastácio *et al.*, 1999). Other possible explanations for the faster growth at PCD are a different reproductive cycle and a lower population density therefore causing less intraspecific competition.

**Sex ratio and reproductive status**

The decrease of the proportion of females at maximum maturation is in accordance with the hypothesis of mature females spending most of the time inside burrows. The sex ratio results obtained for both marshes were favourable to females, which is similar to what was found by other authors (Huner, 1978; Oluoch, 1990; Adão and Marques, 1993; Anastácio, 1993; Anastácio and Marques, 1995; Correia, 1995; Fidalgo *et al.*, 2001; Scalici and

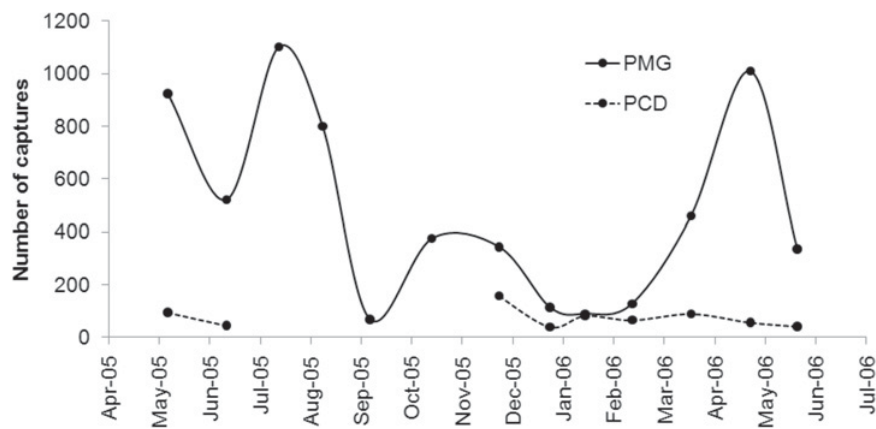


Fig. 5. Number of crayfish captured at both marshes throughout the year. PCD – Paul da Casa de Cadaval; PMG – Paul de Magos.

Gherardi, 2007; Ligas, 2008). Nevertheless, the proportion of females was largest in the population from PCD, probably in response to the presence of a long dry period. Anastácio and Marques (1995), while noticing geographical variations in the values of the sex ratio, hypothesized that an increase in the number of females in the population can be an adaptation strategy to unfavourable conditions. Other species of crustaceans may exhibit larger proportions of males at high population densities or can even change sex throughout their life (Heinle, 1970; Fleminger, 1985).

At PCD the proportion of females was highest during the post-flooding period but the maturation state of both sexes did not show a consistent pattern throughout the year. The proportions of Form I males were very irregular because of the low number of captures and the female maturation index was always lower than at PMG. Maximum values of the female maturation index were obtained in June of both years, but were very low. In temporary freshwater marshes such as PCD, which dry in summer and are flooded in winter, the best strategy of females should be to associate the end of ovarian maturation with periods of flooding and adequate temperatures (Gutierrez-Yurrita and Montes, 1999).

The abundance of reproductive males is a good indicator of the reproduction state of a population (Huner and Romaine, 1979), and positive correlations among the abundance of Form I males and mature females were found by Alcorlo *et al.* (2008). In our study, the abundance of reproductive males was highly synchronous with the increase of female's maturation index. This positive correlation may be caused by one or more of the following factors: (1) a simultaneous response of the two sexes to favourable environmental conditions leading to the sexual maturation; (2) sexual maturation emerging simply as a stage in growth, therefore occurring simultaneously in both sexes; (3) a mechanism of mutual induction of maturation in males and females. In spite of these three hypotheses it seems clear (and in accordance with the available literature) that males maintain their reproductive stage (Form I) for a certain period after

female maturation. This is because they need a moult to change reproductive status (Taketomi *et al.*, 1990).

The negative correlation found between the proportion of reproductive (FI) males and the proportion of females may in fact be an indirect consequence of the synchronous maturation of males and females. Mature females may be less prone to be captured, as shown by the negative correlation of the proportion of females to female reproductive status. This is probably linked to the fact that females raise their broods during burrowing (Correia and Ferreira, 1995; Hasiotis, 1995) and in fact techniques for producing *P. clarkii* young (*e.g.* Gooch method) involve simulating burrow conditions (Huner and Barr, 1991).

#### Population size structure and recruitment

The crayfish population from PCD was composed of large animals in spring and summer and juveniles at the end of autumn and winter, while at PMG large individuals were more abundant in late spring, summer and early autumn. The presence of juveniles, especially in winter, and the abundance of adults in spring, summer and autumn can be related to the temperature. In fact, the low water temperatures during winter ( $< 10^{\circ}\text{C}$ ) inhibit adult activities (Huner and Barr, 1991) whereas the activities of the juveniles are stimulated in this same period (Sommer, 1984). The section dedicated to environmental variables highlighted several differences between the two sites and these are known to cause strong variations in population structure and recruitment. Hydrology is fundamental for the timing of release of the young and recruitment frequently occurs after water input into the system *i.e.* after dry periods (Romaine and Lutz, 1989; Gutierrez-Yurrita and Montes, 1999; Alcorlo *et al.*, 2008). Because water is limiting the system, crayfish can only reproduce and grow during a certain period and therefore the population adapts to these conditions.

At PCD, recruitment occurred mainly after flooding, in November, which is similar to Central and Northern

**Table 3.** Comparative values of the parameters for von Bertalanffy growth curves obtained by other authors for *Procambarus clarkii*. TL – total length; CL – carapace length; POCL – post orbital carapace length; TLES – length measured from tip of rostrum to end of abdominal somites.

	$L_{\infty}$ (mm)	$K$	Comments
(Chien and Avault, Jr., 1979, 1980)	123.2 (TL)	0.153	Rice ponds (USA)
	106.9 (TL)	0.184	Natural ponds (USA)
(Chien and Avault, Jr., 1983)	92.2 (CL)	0.055	Early flooded (USA)
	82.7 (CL)	0.090	Late flooded (USA)
(Anastácio and Marques, 1995)	56 (POCL)	0.682	Oscillating curve (Portugal)
(Correia, 1995)	173 (TL)	0.440	Paul de Magos (Portugal)
	192 (TL)	0.656	Paul da Casa Cadaval (Portugal)
(Emam and Khalil, 1995)	77.0 (CL)	2.21	River Nile (Egypt)
	76.8 (CL)	2.23	
(Xiaoming)	134 (TLES)	0.4620	Unpublished abstract
	144 (TLES)	0.3567	
(Fidalgo <i>et al.</i> , 2001)	62.01 (CL)	0.23	Portugal
(Chiesa <i>et al.</i> , 2006)	62.1 (CL)	0.79	Italy
(Dorr <i>et al.</i> , 2006)	80.8 (CL)	0.85	Italy. Oscillating curve
(Scalici and Gherardi, 2007)	62.71–65.53 (CL)	0.61–0.69	Italy

Portugal, Northern Italy and the United States (Huner and Barr, 1991; Anastácio and Marques, 1998; Gherardi *et al.*, 2000; Fidalgo *et al.*, 2001; Mueller, 2007). At PMG, recruitment occurred throughout most of the year but with two main seasons: The first was from spring to early summer and the second during November–December. Data from Correia (1995) also suggest the existence of a continuous reproductive period at this marsh, although concentrated on two major periods. Other authors reported continuous recruitment in the Louisiana marshes (Penn, Jr., 1943) as well as in commercial ponds (Huner, 1978) and in Kenya (Oluoch, 1990). In Egypt two main periods of recruitment were reported, respectively in May and in December (Emam and Khalil, 1995), which is not very different from what was observed at PMG. Alcorlo *et al.* (2008) reported that, in permanent water bodies, most recruitment took place in late autumn and spring, whereas in water bodies that dry out in the summer, recruitment was mainly observed in autumn or early winter. In fact, PMG is a rice field drainage channel that exhibits water throughout the year and PCD dries during summer, which explains the similarities observed with the recruitment periods in the two former ecosystem types.

### Growth, density, mortality and mean lifetime

Modal analysis distinguished 2 cohorts for the crayfish population from PCD and 5 from that of PMG. Correia (1995) also obtained a larger number of cohorts at PMG than at PCD, with 4 and 6 cohorts respectively, and referred the difficulty in performing a modal analysis at PCD because of the low number of individuals caught. *P. clarkii* age classes or cohorts may vary considerably in number: Anastácio and Marques (1995) distinguished 7 cohorts, Guerra and Niño (1996) and Chiesa *et al.* (2006) distinguished 3 cohorts while Scalici and Gherardi (2007) found 5 cohorts. Other authors (*e.g.* Oluoch,

1990) refer continuous recruitment therefore rendering rather fuzzy the concept of cohorts for those populations.

The relative density of crayfish was much higher in PMG than in PCD. This agrees with Correia's work (1995) at the same locations and corroborates the comparative study of habitats performed by Alcorlo *et al.* (2008) which found the highest densities in rice fields and adjacent channels. *Procambarus clarkii* is a density-regulated species (McClain, 1995a, 1995b; Ramalho *et al.*, 2008) and crayfish populations in general can deal with environmental modifications by changing their life-span, age at maturity, age-specific fecundity or mortality rates and growth rate (Momot, 1984). We would however add to these mechanisms a possibility of changes in sex ratio (Anastácio and Marques, 1995). Caution should be taken because these changes are masked by differential activity patterns of females throughout their reproductive cycle.

Our study indicated faster growth and larger maximum sizes at the site with the more stressed environment and lowest relative density (PCD). In fact, there is a large variation in the literature values for the von Bertalanffy growth parameters depending on the method used for the calculations, the units of time, the body measurement and the local conditions (Table 3).

Results regarding mortality were not very different from those obtained by Scalici and Gherardi (2007) which report a range of  $Z$  from 2.99 to 5.16. In our case mortality was higher at PCD than at PMG *i.e.* it was highest at the location with the lowest relative density. This is an indication that the larger mortality is one of the main causes for the lower density observed at PCD. Both in this work and in the work by Scalici and Gherardi (2007) the mean lifetime did not overreach 12 months, which in fact is lower than the limit of 18 months proposed by Huner (1981). Once more this agrees with earlier generalist work by Momot (1984) and indicates a possible mechanism of population regulation.



Cruz and Rebelo (2007) suggested that temporary waters may be less at risk of being colonized and may be less able to sustain *P. clarkii* populations. Moreover, both our study and that of Alcorlo *et al.* (2008), in a geographically near region, indicated smaller crayfish size at higher population densities. Therefore, any exploitation strategy for these two populations should take into account a trade-off between maximum size and speed of growth in one hand and larger densities on the other hand. If the aim is the control of the crayfish populations, then hydroperiod should be reduced in the rice field channel. In this last situation some negative effects on the remaining aquatic fauna would be expected. The preferential dry period for a more effective population control and for larger crayfish size would be during the warmer months of the year. This would in fact mimic the natural hydrological cycle of the area.

*Acknowledgements.* The authors are very grateful to D. Carvalho for her field assistance. Ricardo Ramalho and Sergio Barradas shared with us their water temperature data from the two sampling locations. This work was funded by the Fundação para a Ciência e a Tecnologia project POCTI/BSE/46862/2002, by FEDER (“Fundo Europeu de Desenvolvimento Regional” – European Fund for Regional Development) and by the Museu Nacional de História Natural and Centro de Biologia Ambiental, Universidade de Lisboa.

## References

- Adão M.H.S.M. and Marques J.C., 1993. Population biology of the red swamp crayfish *Procambarus clarkii* (Girard, 1852) in southern Portugal. *Crustaceana*, 65, 336–345.
- Adrian M.I. and Delibes M., 1987. Food habits of the otter (*Lutra lutra*) in two habitats of the Doñana national park, SW Spain. *J. Zool., Lond.*, 212, 399–406.
- Alcorlo P., Geiger W. and Otero M., 2008. Reproductive biology and life cycle of the invasive crayfish *Procambarus clarkii* (Crustacea: Decapoda) in diverse aquatic habitats of South-Western Spain: Implications for population control. *Arch. Hydrobiol.*, 173, 197–212.
- Allen K.R., 1971. Relation between production and biomass. *Journal of the Fisheries Research Board of Canada*, 28, 1573–1581.
- Anastácio P.M., 1993. Ciclo biológico e produção do lagostim vermelho da Louisiana (*Procambarus clarkii*, Girard) na região do baixo Mondego. M.Sc. Thesis, University of Coimbra, Coimbra, 120 p.
- Anastácio P.M. and Marques J.C., 1995. Population biology and production of the red swamp crayfish *Procambarus clarkii* (Girard) in the lower Mondego river valley, Portugal. *J. Crust. Biol.*, 15, 156–168.
- Anastácio P.M. and Marques J.C., 1998. Crayfish (*Procambarus clarkii*) condition throughout the year in the lower Mondego River valley, Portugal. *Crustaceana*, 71, 593–602.
- Anastácio P.M., Nielsen S.N. and Marques J.C., 1999. CRISP – crayfish rice integrated system of production. 2. Modelling crayfish (*Procambarus clarkii*) population dynamics. *Ecol. Model.*, 123, 5–16.
- Anastácio P.M., Correia A.M. and Menino J.P., 2005a. Processes and patterns of plant destruction by crayfish: effects of crayfish size and developmental stages of rice. *Arch. Hydrobiol.*, 162, 37–51.
- Anastácio P.M., Parente V. and Correia A.M., 2005b. Crayfish effects on seeds and seedlings: identification and quantification of damage. *Freshwat. Biol.*, 50, 697–704.
- Chien Y.H. and Avault J.W., Jr., 1979. Double cropping rice, *Oryza sativa* and red swamp crawfish, *Procambarus clarkii*. *Freshw. Crayfish*, 4, 263–272.
- Chien Y.H. and Avault J.W., Jr., 1980. Production of crayfish in rice fields. *Progr. Fish-Cult.*, 42, 67–71.
- Chien Y.H. and Avault J.W., Jr., 1983. Effects of flooding dates and disposal of rice straw on crayfish, *Procambarus clarkii* (Girard), culture in rice fields. *Aquaculture*, 31, 339–359.
- Chiesa S., Scalici M. and Gilbertini G., 2006. Occurrence of allochthonous freshwater crayfishes in Latium (Central Italy). *Bull. Fr. Pêche Piscic.*, 380-381, 883–902.
- Correia A.M., 2001. Seasonal and interspecific evaluation of predation by mammals and birds on the introduced red swamp crayfish *Procambarus clarkii* (Crustacea, Cambaridae) in a freshwater marsh (Portugal). *J. Zool., Lond.*, 255, 533–541.
- Correia A.M., 2003. Food choice by the introduced crayfish *Procambarus clarkii*. *Ann. Zool. Fennici*, 40, 517–528.
- Correia A.M. and Anastácio P.M., 2008. Shifts in aquatic macroinvertebrate biodiversity associated with the presence and size of an alien crayfish. *Ecol. Res.*, 23, 729–734.
- Correia M.A. and Ferreira O., 1995. Burrowing behavior of the introduced red swamp crayfish *Procambarus clarkii* (Decapoda: Cambaridae) in Portugal. *J. Crust. Biol.*, 15, 248–257.
- Correia P.A.C.M., 1995. Biologia populacional e interações tróficas de *Procambarus clarkii* (Crustacea, Decapoda, Cambaridae) no sistema hidrográfico do rio Tejo (Ribatejo, Portugal). Doctoral Dissertation, Faculdade de Ciências, Universidade de Lisboa, Lisboa, 255 p.
- Cruz M.J. and Rebelo R., 2007. Colonization of freshwater habitats by an introduced crayfish, *Procambarus clarkii*, in Southwest Iberian Peninsula. *Hydrobiologia*, 575, 191–201.
- Dorr A.J.M., La Porta G., Pedicillo G. and Lorenzoni M., 2006. Biology of *Procambarus clarkii* (Girard, 1852) in lake Trasimeno. *Bull. Fr. Pêche Piscic.*, 380-381, 1155–1170.
- Emam W.M. and Khalil M.T., 1995. Population dynamics and stock assessment of the newly introduced crayfish *Procambarus clarkii* in the river Nile, Egypt. *Proc. Zool. Soc. A. R. Egypt*, 26, 131–143.
- Fidalgo M.L., Carvalho A.P. and Santos P., 2001. Population dynamics of the red swamp crayfish (*Procambarus clarkii*) (Girard, 1852) from the Aveiro region, Portugal (Decapoda, Cambaridae). *Crustaceana*, 74, 369–375.
- Fleminger A., 1985. Dimorphism and possible sex change in copepods of the family Calanidae. *Mar. Biol.*, 88, 273–294.
- Gherardi F., 2006. Crayfish invading Europe: the case study of *Procambarus clarkii*. *Mar. Freshw. Behav. Phy.*, 39, 175–191.
- Gherardi F., Raddi A., Barbaresi S. and Salvi G., 2000. Life history patterns of the red swamp crayfish (*Procambarus clarkii*) in an irrigation ditch in Tuscany, Italy. In: Von Vaupel Klein J.C. and Schram F.R. (eds.), The biodiversity crisis and crustacea, Balkema, 99–108.
- Grigarick A.A., 1984. General problems with rice invertebrate pests and their control in the United States. *Prot. Ecol.*, 7, 105–114.

- Guerra J.L. and Niño A.E., 1996. Ecology of red swamp crayfish (*Procambarus clarkii*, Girard) in the central meseta of Spain. *Freshw. Crayfish*, 8, 179–200.
- Gutierrez-Yurrita P.J. and Montes C., 1999. Bioenergetics and phenology of reproduction of the introduced red swamp crayfish, *Procambarus clarkii*, in Donana National Park, Spain, and implications for species management. *Freshwater Biol.*, 42, 561–574.
- Gutierrez-Yurrita P.J., Martínez J.M., Bravo-Utrera M.A., Montes C., Ilhéu M.A. and Bernardo J.M., 1999. The status of crayfish populations in Spain and Portugal. In: Gherardi F. and Holdich D.M. (eds.), *Crayfish in Europe as alien species – How to make the best of a bad situation?*, Balkema, 161–192.
- Hasiotis S.T., 1995. Notes on the burrow morphologies and nesting behaviours of adults and juveniles of *Procambarus clarkii* and *Procambarus acutus acutus* (Decapoda: Cambaridae). *Freshw. Crayfish*, 8, 623–634.
- Heinle D.R., 1970. Population dynamics of exploited cultures of calanoid copepods. *Helgoland Mar. Res.*, 20, 360–372.
- Huner J.V., 1978. Crawfish population dynamics as they affect production in several small, open commercial crawfish ponds in Louisiana. *Proc. Ann. Meet. World Maricult. Soc.*, 9, 619–640.
- Huner J.V., 1981. Information about the biology and culture of the red swamp crawfish, *Procambarus clarkii* (Girard, 1852) (Decapoda, Cambaridae) for fisheries managers in Latin America. *An. Inst. Cien. del Mar Y Limnol. Univ. Nal. Autón. México*, 8, 43–50.
- Huner J.V., 1988. *Procambarus* in North America and elsewhere. In: Holdich D.M. and Lowery R.S. (eds.), *Freshwater crayfish – Biology, management and exploitation*, London, Croom Helm, 239–261.
- Huner J.V. and Avault J.W., Jr., 1979. Introductions of *Procambarus* spp. – a report to the introductions committee of the International Association of Astacology, Fourth biannual meeting Thonon-les-Bains, France, 28–31 August 1978. *Freshw. Crayfish*, 4, 191–194.
- Huner J.V. and Barr J.E., 1991. Red swamp crawfish: Biology and Exploitation, Louisiana Sea Grant College Program, Baton Rouge, Louisiana, 128 p.
- Huner J.V. and Romaine R.P., 1979. Size at maturity as means of comparing populations of *Procambarus clarkii* (Girard) (crustacea, decapoda) from different habitats. *Freshw. Crayfish*, 4, 53–64.
- Ligas A., 2008. Population dynamics of *Procambarus clarkii* (Girard, 1852) (Decapoda, Astacidea, Cambaridae) from Southern Tuscany (Italy). *Crustaceana*, 81, 601–609.
- Lodge D.M., Stein R.A., Brown K.N., Covich A.P., Broenmark C., Garvey J.E. and Klosiewski S.P., 1998. Predicting impact of freshwater species on native biodiversity: Challenges in spatial scaling. *Aust. J. Ecol.*, 23, 53–67.
- Lodge D.M., Holdich D.M. and Skurdal J., 2000. Reducing impacts of exotic crayfish introductions: New policies needed. *Fisheries*, 25, 21–23.
- McClain W.R., 1995a. Growth of crayfish *Procambarus clarkii* as a function of density and food resources. *J. World Aquacult. Soc.*, 26, 24–28.
- McClain W.R., 1995b. Investigations of crayfish density and supplemental feeding as factors influencing growth and production of *Procambarus clarkii*. *Freshw. Crayfish*, 10, 512–520.
- Momot W.T., 1984. Crayfish production: a reflection of community energetics. *J. Crust. Biol.*, 4, 35–54.
- Mueller K.W., 2007. Reproductive habits of non-native red swamp crayfish (*Procambarus clarkii*) at Pine lake, Sammamish, Washington. *Northwest Sci.*, 81, 246–250.
- Oluoch A.O., 1990. Breeding biology of the Louisiana red swamp crayfish *Procambarus clarkii* Girard in lake Naivasha, Kenya. *Hydrobiologia*, 208, 85–92.
- Penn G.H., Jr., 1943. A study of the life history of the Louisiana red-crawfish, *Cambarus clarkii* Girard. *Ecology*, 24, 1–19.
- Ramalho R.O., Correia A.M. and Anastácio P.M., 2008. Effects of density on growth and survival of juvenile Red Swamp Crayfish, *Procambarus clarkii* (Girard), reared under laboratory conditions. *Aquac. Res.*, 39, 577–586.
- Ramos M.A. and Pereira T.M., 1981. Um novo astacidae para a fauna portuguesa: *Procambarus clarkii* (Girard, 1952). *Bol. Inst. Nac. Invest. Pescas*, 6, 37–47.
- Ricciardi A. and Rasmussen J.B., 1999. Extinction rates of North American freshwater fauna. *Conserv. Biol.*, 13, 1220–1222.
- Romaine R.P. and Lutz C.G., 1989. Population dynamics of *Procambarus clarkii* (Girard) and *Procambarus acutus acutus* (Girard) (Decapoda: Cambaridae) in commercial ponds. *Aquaculture*, 81, 253–274.
- Scalici M. and Gherardi F., 2007. Structure and dynamics of an invasive population of the red swamp crayfish (*Procambarus clarkii*) in a Mediterranean wetland. *Hydrobiologia*, 583, 309–319.
- Sommer T.R., 1984. The biological response of the crayfish *Procambarus clarkii* to transplantation into California rice-fields. *Aquaculture*, 41, 373–384.
- Sparre P., Ursin E. and Venema S.C., 1992. Introduction to tropical fish stock assessment, Part 1 – Manual, FAO, Report 306, 337 p.
- Suko T., 1953. Studies on the development of the crayfish. I. The development of secondary sex characters in appendages. *Sci. Rept. Saitama Univ.*, 1B, 77–96.
- Taketomi Y., Murata M. and Miyawaki M., 1990. Androgenic gland and secondary sexual characters in the crayfish *Procambarus clarkii*. *J. Crust. Biol.*, 10, 492–497.
- von Bertalanffy L.V., 1957. Quantitative laws in metabolism and growth. *Q. Rev. Biol.*, 32, 217–231.