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Invasive dynamics of the crayfish Procambarus clarkii *(Girard, 1852) in the international section of the River Minho (NW of the Iberian Peninsula)*

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ABSTRACT

1. *Procambarus clarkii* (Girard, 1852) is a well-established invasive species in many worldwide aquatic ecosystems and is responsible for several ecological and economic impacts. This study examines the major factors responsible for its invasive dynamics in the international section of the River Minho (north-west Iberian Peninsula).

2. Data collected from June 2007 to May 2011 showed that abundance and biomass increased in the first 3 years of sampling, but suffered a decrease in the fourth year. Higher abundance and biomass were always found from May to October. These higher values have a clear relationship with water temperature and probably reflect higher activity and mobility.

3. The sex-ratio was 1.08:1 in favour of females; eggs start to appear in May/June and the majority of juveniles in August/September.

4. Information collected in this study is extremely important for future management actions that could be applied to this invasive species. Accordingly, we propose that control actions to minimize *P. clarkii* impacts in this system, such as intensive trapping, should be applied during late spring/early summer, when the catches are higher, the females are dominant, and before juvenile recruitment.

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KEY WORDS: abiotic factors; impacts; non-indigenous invasive species; *Procambarus clarkii*; spatial and temporal distribution

INTRODUCTION

The introduction of species outside their native range is now recognized as a leading threat to biodiversity and ecosystem functioning (Byrnes *et al*., 2007; Sousa *et al*., 2011). Inland waters are particularly vulnerable to intentional or accidental introduction of organisms, where human activities are clearly related to the recent increasing rates of non-indigenous invasive species (NIS) introductions (Cohen and Carlton, 1998; Vilà *et al*., 2010).

Procambarus clarkii (Girard, 1852) is a native crayfish from North America that has recently been introduced worldwide (Harper *et al*., 2002;

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Magalhães *et al*., 2005; Xu *et al*., 2006; Gherardi and Acquistapace, 2007). The history of its invasion is well documented in Europe: after introduction in Spain in the 1970s as a result of a successful import from Louisiana, *P. clarkii* became widespread in the continent (Barbaresi and Gherardi, 2000). This species has important characteristics that can increase its invasive behaviour – sufficient plasticity to adapt its ecology and life cycle to changing environmental conditions, high somatic growth and reproductive output, short development time, ability to tolerate high temperatures, dry periods and low dissolved oxygen conditions, and a flexible feeding strategy (Alcorlo *et al*., 2004; Gherardi, 2006; Jones *et al*., 2009). In addition to its natural dispersal capabilities, human activities have contributed significantly to its rapid expansion. In fact, the relative economic importance of *P. clarkii* has resulted in repeated translocations for commercial or recreational purposes (Geiger *et al*., 2005; Gherardi, 2006).

Given the great abundance and biomass attained in several aquatic ecosystems and since *P. clarkii* occupies an important position in the food web, interacting with different trophic levels, its introduction may bring about important ecological changes (Matthews and Reynolds, 1992; Anastácio *et al*., 2000; Angeler *et al*., 2001; Dorn and Wojdak, 2004; Cruz *et al*., 2006; Gherardi and Acquistapace, 2007). For example, the efficiency of *P. clarkii* in grazing macrophytes and its extensive burrowing activity can change a macrophyte-dominated area with clear water to a turbid area dominated by phytoplankton (Rodriguez *et al*., 2003; Geiger *et al*., 2005; Matsuzaki *et al*., 2009). On the other hand, this species provides an important food source for higher trophic levels, as it is consumed by mammals, birds and fishes (Matthews and Reynolds, 1992; Beja, 1996; Correia, 2001; Smart *et al*., 2002; Tablado *et al*., 2010). Its presence also affects the diversity of other invertebrates and vertebrates by competition and predation (Alcorlo *et al*., 2004; Gherardi and Acquistapace, 2007; Hernández *et al*., 2008), and acts as a vector of diseases of native crayfish (e.g. the introduction of crayfish plague *Aphanomyces astaci*) or functioning as an intermediate host for numerous helminth parasites of vertebrates (Kozubíková *et al*., 2009). In addition, by accumulating metals and other pollutants, this species is responsible for their transmission up the food chain (Gherardi *et al*., 2002; Alcorlo *et al*., 2006).

This study assesses the invasive dynamics of *P. clarkii* in the international section of the River Minho and aims to relate these dynamics with environmental factors. The international section of the River Minho is 70 km long and is classified as a Natura 2000 site. The conservation importance of this area emphasizes the need to use data collected during this study to develop management measures for application to this ecosystem and other invaded waters.

MATERIAL AND METHODS

Study area

The River Minho is about 300 km long from its origin in Serra de Meira (Spain) to its mouth at the Atlantic Ocean, with a mean annual freshwater discharge of 300 m^3s^{-1} and comprising a total basin area of 17 080 km^2. Its international section functions as a natural border between Portugal and Spain and includes the River Minho estuary, which is nearly 40 km long and has an area of 23 km^2 (Sousa *et al*., 2005).

Over the last decade several studies have been carried out on the fauna present in the international section of the River Minho, particularly its estuary. These studies were focused on macroinvertebrates (Sousa *et al*., 2007, 2008a), epibenthos (Costa-Dias *et al*., 2010) and fish (Antunes and Rodrigues, 2004), and some included invasive species (Sousa *et al*., 2008b, c, d). However, a basic understanding of *P. clarkii* ecology is still incomplete, despite its wide distribution and high abundance and biomass. For example, the date of introduction of *P. clarkii* in the River Minho has not been recorded, although local fishermen gave the end of the 1980s/beginning of the 1990s as the most plausible period.

Sampling strategy

The following abiotic variables were measured on each sampling occasion: temperature, conductivity, salinity, total dissolved solids, redox potential, dissolved oxygen and pH using a multi-parametric sea gauge YSI 6820 (YSI Incorporated). In addition, transparency was measured using a Secchi disk.

The biological study comprised a spatial and a temporal characterization of the *P. clarkii* population colonizing the international section of the River Minho. For the first part, smaller traps 1 m long, of 10 mm mesh and with two apertures were constructed to capture crayfish. These traps were first tested to check their efficiency and the results suggested that they were suitable for the aims of this study. Three traps were left for 48 h at each of the 21 sites along the 70 km study area (Figure 1) in April and August 2009. If no crayfish were captured, sites were re-sampled twice.

For the second part of the study large fyke-nets were used to capture crayfish from June 2007 to May 2011 at site S6 (Figure 1). These nets can be effectively deployed in all river conditions. Crayfish were collected using three to five fyke–nets (10 mm mesh, 0.7 m diameter mouth, 7 m long, 3.5 m central wing); in more than 90% of the surveys five fyke-nets were used. Fyke-nets were set facing downstream and were placed to cover the maximum habitat heterogeneity (i.e. submerged vegetation, without submerged vegetation, and with mud or sand bottoms). The number of days fished varied during the study period. For each sampling event all the specimens were counted and the wet biomass was recorded. From January to December 2010 total length (from the rostrum tip to telson rear edge), sex-ratio, presence of eggs or hatched young and absence of claws were determined for all *P. clarkii* captured.

Data analysis

Catches were standardized by dividing the total abundance and biomass by the number of fyke-nets and number of days fishing. The abundance and wet biomass were interpreted as dependent on abiotic conditions (mainly water temperature and river flow) and possible correlations were established. Temporal differences in abundance and biomass among the years (we define a year from June to May; e.g. Year 1 ran from June 2007 to May 2008) and months were analysed by the non-parametric Kruskall–Wallis ANOVA, since assumptions for parametric tests were not met. Changes in the mean length of *P. clarkii* in different months in 2010 were also assessed using one-way ANOVA and changes in the mean length of males and females were analysed using a Student's *t*-test. Changes in sex-ratio were checked by chi-square tests. All the statistical analyses were done using MINITAB 14 software.

RESULTS

Spatial distribution

The spatial distribution of *P. clarkii* along the River Minho is shown in Figure 1. Sites had different environmental characteristics: sparse submerged vegetation, shallow depth and sediments mainly consisting of sand (sites S1–S4, S9, S12, S14–S17, S20, and S21); abundant submerged vegetation, shallow depth and sediments mainly of mud (sites S5–S8 and S10); and sparse submerged vegetation, shallow depth and sediments mainly comprising gravel (sites S11, S13, S18, and S19). In addition, sites S1 to S4 can be subject to high salinities,

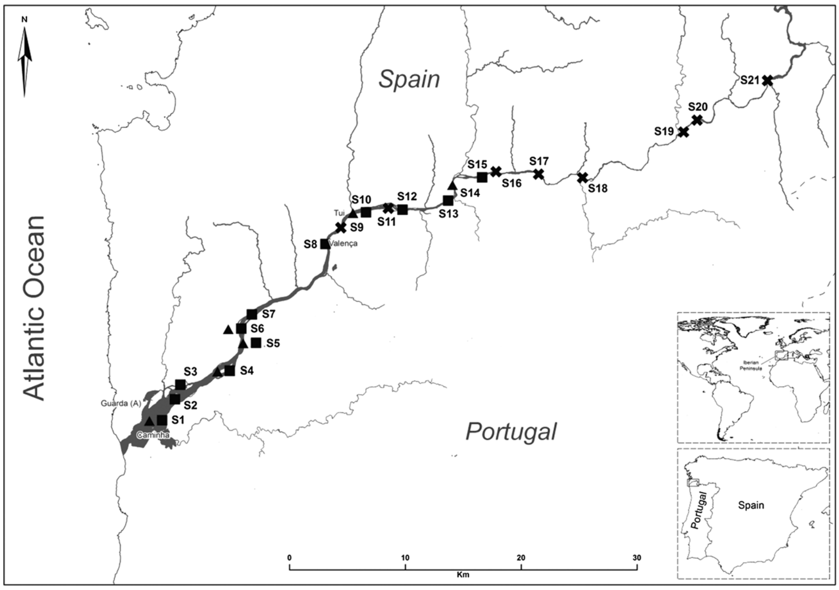

Figure 1. Presence and absence map for *P. clarkii* in the River Minho international section (▲ - present, April 2009; ■ - present, August 2009 and ✖ - absent).

especially during summer high tides, with salinities up to 25. Sites S5 and S6 may also experience brackish conditions, but only during high tides at the end of the summer, with values up to 5 in S5. Sites S7 to S21 are always exclusively freshwater.

In April 2009, *P. clarkii* was present in six of the 21 sampling sites, but in August the number had increased to 14 (Figure 1). Site S17 was the upstream limit of distribution. *Procambarus clarkii* was also captured in the brackish area (from S1 to S6) on both sampling occasions.

Temporal variation

A detailed description of the abiotic factors measured during the study period at site S6 is shown in Table 1. In the 4 years of sampling, 34 923 crayfish were captured, corresponding to a total wet biomass of 735.2 kg. Maximum values of abundance and biomass (standardized per day and per fyke-net) were recorded on 14 July 2010 with an abundance of 22.7 ind. CPUE (catch per unit effort) and a wet biomass of 568.5 g CPUE. Minimum values were obtained on 4 January 2011 with 0.3 ind. CPUE and 3.4 g CPUE, respectively (Figure 2a, b). Mean values of abundance and biomass throughout the 4 years were 5.2 ind. CPUE and 105.4 g CPUE, respectively.

There were significant differences in abundance (H = 22.3; $P < 0.01$) and biomass (H = 26.6; $P < 0.01$) of *P. clarkii* among the 4 years. Abundance and biomass values increased in the first 3 years of sampling, but decreased in the fourth year. Significant differences were also found between months, both for abundance (H = 116.7; $P < 0.01$) and biomass (H = 140.7; $P < 0.01$). Abundance and biomass began to increase after April/May, reaching a peak in July, and then declining. Abundance ($P < 0.01$) and biomass ($P < 0.01$) have clear positive relationships with water temperature (Figure 3a, b), but no relationship was found with river flow (data not shown).

During 2010, in total, 10 944 *P. clarkii* were measured; the smallest individual caught was 2.3 cm long (June) and the largest 13.5 cm (March). The mean length was significantly different among months (F = 153.8; $P < 0.01$), with the lowest mean values gathered during February (6.8 cm) and the higher ones during July (9.3 cm). Overall, data from 2010 also showed differences between the mean length of males and females (t-test = 5.95; $P < 0.01$), (males 8.8 cm, females 9.0 cm) (Figure 4).

Table 1. Abiotic characterization (mean, maximum, and minimum values) of the water column at site S6 during the 4 years of sampling

	January			February			March			April			May			June		
	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.
Temperature (°C)	9.8	10.8	9.1	9.3	9.9	8.8	11.2	13.0	9.9	14.3	17.4	11.1	17.9	22.8	14.5	20.0	23.3	17.6
Conductivity (mS cm^{-1})	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.6	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Salinity	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.1	0.1	0.1
Dissolved oxygen (mg L^{-1})	10.1	11.2	9.2	10.4	11.7	9.5	9.7	10.4	9.2	9.9	11.8	9.0	10.7	11.8	9.3	9.1	10.5	7.5
pH	7.6	8.0	7.0	7.7	8.0	7.0	7.6	7.7	7.4	7.6	8.0	7.4	7.4	7.9	7.1	7.4	7.8	7.1
Redox potential (mV)	124.7	154.3	107.8	132.4	173.2	91.4	130.4	189.3	103.7	123.4	148.1	65.5	112.2	121.1	100.6	113.6	149.7	88.7
Transparency (m)	1.7	2.2	1.0	2.1	2.3	1.7	1.5	2.5	0.5	1.9	2.5	1.5	1.7	2.0	1.5	1.5	2.3	1.0

(Continues)

Table 1. (Continued)

	July			August			September			October			November			December		
	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.
Temperature (°C)	22.7	25.0	21.3	23.6	24.7	22.8	20.8	23.6	18.7	16.6	17.3	15.4	14.2	15.6	12.2	8.5	11.0	8.5
Conductivity (mS cm^{-1})	0.1	0.1	0.1	0.2	0.4	0.1	0.2	0.5	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Salinity	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.2	0.0	0.0	0.1	0.0	0.1	0.1	0.1	0.0	0.1	0.0
Dissolved oxygen (mg L^{-1})	9.8	10.3	9.4	9.2	10.7	8.5	9.2	10.2	8.7	9.3	10.8	8.2	9.2	9.7	8.8	9.8	10.2	9.8
pH	7.8	8.0	7.8	7.9	8.0	7.8	7.8	8.0	7.8	7.9	8.0	7.9	7.9	7.9	7.8	7.8	8.0	7.8
Redox potential (mV)	92.1	140.7	71.9	99.0	115.7	85.2	121.7	128.0	115.5	92.2	94.9	90.2	139.4	151.8	127.6	112.9	160.1	112.9
Transparency (m)	1.8	2.0	1.2	1.6	1.8	1.3	1.5	2.0	1.0	1.5	1.7	1.3	2.4	2.5	2.2	2.3	3.0	2.3

The sex ratio was 1.08:1 in favour of females, which was significantly different from the expected 1:1 ($\chi^2 = 14.1$; $P < 0.01$) (Figure 5). The smallest female that carried eggs or hatched young had a total length of 6.7 cm. Females with eggs started to appear in May and continued to be found until November. Juveniles were captured from June to December with a higher preponderance during August/September. As well as determining the sex ratio, the percentage claw loss for males and females of *P. clarkii* was also checked during 2010. Males had a much higher percentage of claw loss than females (Figure 6); an increase in the percentage claw loss from June to August was also observed.

DISCUSSION

Spatial distribution

In the international section of the River Minho *P. clarkii* appears to be restricted to the first 45 km (from S1 to S17) with no traces of individuals in the upper sections. This may be explained by the increasing altitude and current velocity, which may act as a barrier to the species' upstream dispersal. Earlier studies showed that altitude, current velocity and oligotrophic conditions can constrain the distribution of *P. clarkii* (Gil-Sánchez and Alba-Tercedor, 2002; Cruz and Rebelo, 2007).

Although it is likely that altitude and current velocity were the main factors restricting upstream dispersal, others such as substrate type, availability of burrows, water depth and other physical factors, cannot be dismissed (Gherardi, 2006). For example, the compacted sediment can exclude crayfish by restraining burrow shelter construction (Barbaresi *et al.*, 2004; Cruz and Rebelo, 2007), and possibly explains the crayfish absence at site S11, which had mainly boulder sediment. The upstream section of the River Minho is dominated by the presence of boulders, gravel or bedrock, but some areas have suitable conditions for *P. clarkii*, and include the presence of natural refuges with shallow water (e.g. small arms of the river disconnected from the main river in the summer owing to lower river flow), presence of submerged vegetation, and some areas with mud and sandier sediments. Thus, although no specimens were caught during this study in the upstream area, it is possible that some individuals could colonize these regions, but with a much lower abundance and biomass than in downstream sites.

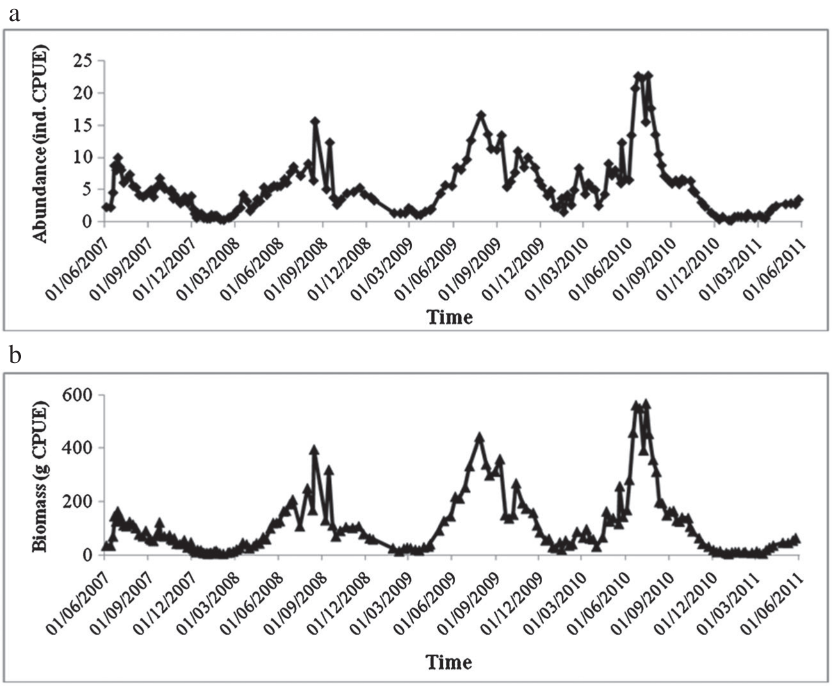

Figure 2. Abundance (a) and biomass (b) of *P. clarkii* present at site S6 during the 4 years of sampling. CPUE - catch per unit effort.

The spatial distribution of *P. clarkii* in the River Minho includes sites subject to high salinities (sites S1 to S4), mainly at high tides during the summer and early autumn (Sousa *et al.*, 2008a). Although survival in brackish waters has been reported for *P. clarkii*, the crayfish captured in the River Minho estuary are rare examples in European invasive populations (e.g. Palude di Torre Flavia and some estuarine and lagoonal brackish environments of the Adriatic coast (Italy), and Ria de Aveiro (Portugal); Fidalgo *et al.* (2001), Scalici *et al.* (2010), Casellato and Masiero (2011)). These findings contradict those of Geiger *et al.* (2005), who stated that salinity limits the distribution of *P. clarkii*. This present record in the lower estuarine areas shows the high ecological plasticity of *P. clarkii* and presents an additional concern as the crayfish may become more tolerant to adverse abiotic conditions (salinity) and cause further impacts on lower estuarine areas (e.g. salt marshes) where the effects are not well known or yet studied (Scalici *et al.*, 2010).

Temporal dynamics

Since crayfish are poikilothermic, temperature has a major influence on metabolic pathways, behaviour, distribution, growth, reproduction and life history (Olsson *et al.*, 2010). The present study data clearly show that higher abundance and biomass were recorded when temperatures increased above 18°C in late spring, summer, and early autumn. Also, behaviour depends on temperature; there are examples of *P. clarkii* ceasing movement when temperatures are below 10°C and above 35°C, and optimum values for oviposition range from 20 to 25°C and for copulation of about 22°C (Anastácio *et al.*, 1999). In the River Minho the highest temperature registered was 25°C and therefore the higher limiting temperature was never reached. Temperatures below 10°C were reported only in winter, with the lowest being 8.5°C, and this situation possibly explained the capture of specimens on all sampling occasions. The clear relationship of abundance (and biomass) and temperature has been observed previously in several invasive crayfish species and this may be explained by the enhancement of activity and mobility (Bubb *et al.*, 2002; Gherardi, 2006; Olsson *et al.*, 2010). However, mobility must also be dependent on other abiotic and biotic factors (e.g. current velocity, presence of predators and competitors, availability of food resources) since other studies have shown temporal differences in areas with higher temperatures all year round or areas without significant differences between seasons. For example, Gutiérrez-Yurrita and Montes (1998) showed that seasonal temperatures and hydrological changes (frequency of floods) had no effects, and crayfish activity was explained by oxygen availability and photoperiod.

Comparison of the present results with published data indicates that *P. clarkii* in the River Minho

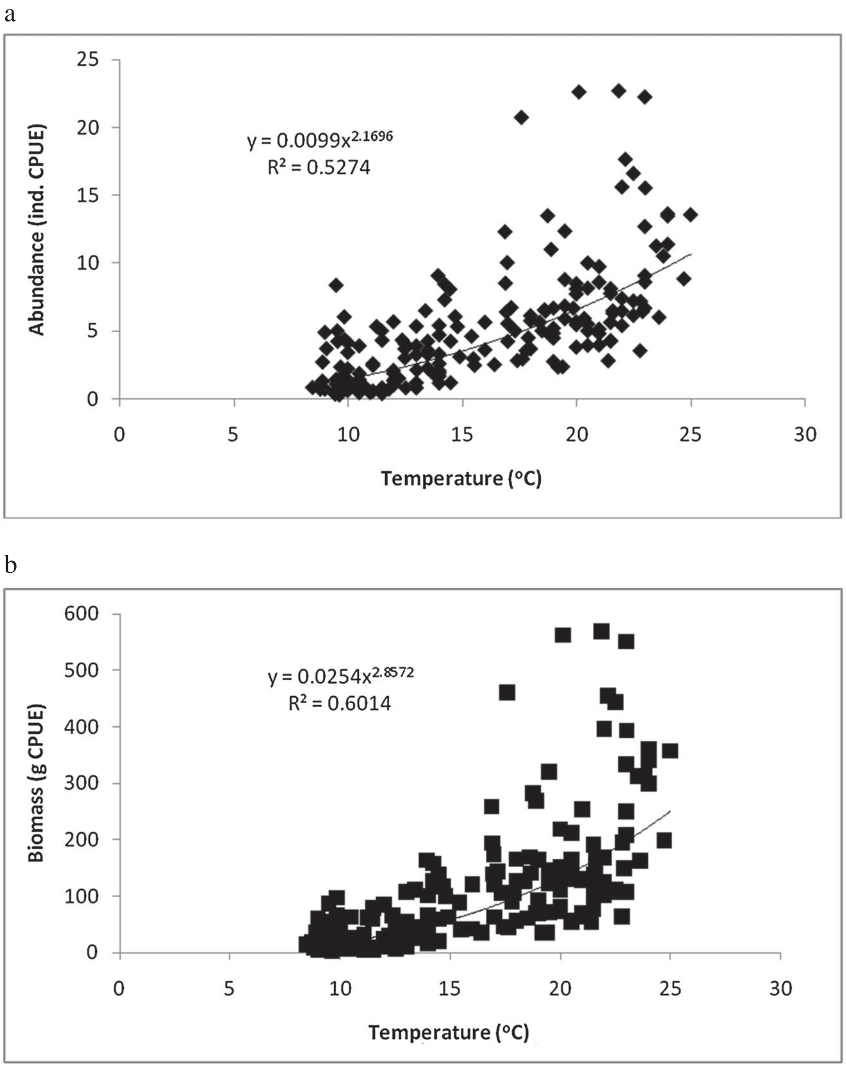

Figure 3. Relationship between temperature and abundance (a) and temperature and biomass (b) of *P. clarkii*. CPUE - catch per unit effort.

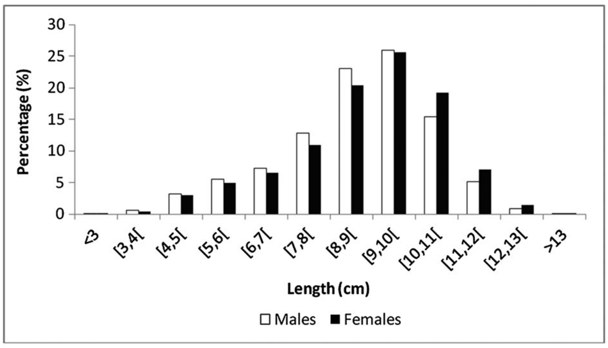

Figure 4. Length profiles of *P. clarkii* males and females during 2010 (data pooled).

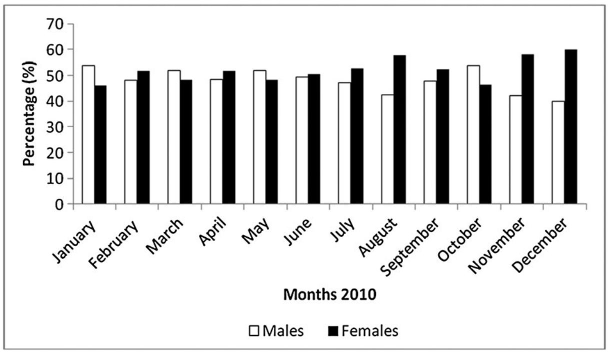

Figure 5. Monthly variation in the sex-ratio of *P. clarkii* during 2010.

grow longer than in warmer locations. No individuals from warmer wild populations studied exceed 12 cm either in the native range (11.6 cm in Louisiana (USA); Penn (1943)) or in the introduced range (10.5 cm in Doñana National Park (Spain) and 9.9 cm in São Miguel (Azores, Portugal); (Bravo *et al*., 1994; Costa *et al*., 1996). On the other hand, the results are similar to Lake Trasimeno, Italy (total length = 14 cm) (Dörr *et al*., 2006). Therefore, it appears that

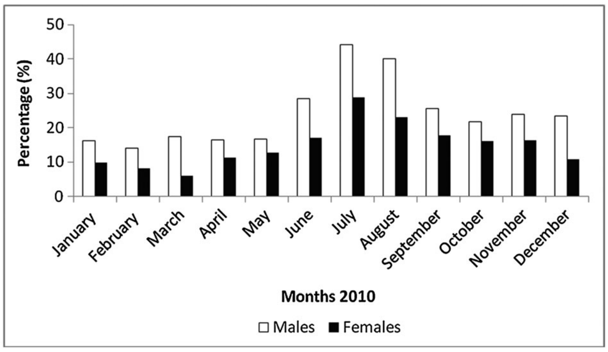

Figure 6. Monthly variation of the percentage claw loss during 2010.

P. clarkii lives considerably longer in northern regions than in its native or southern introduced habitats, where most males die at the end of their first year, and females rarely live longer than 2 years (Penn, 1943; Bravo *et al*., 1994). Assuming similar growth rates in the River Minho and some northern Italian populations it is possible that the larger animals in the River Minho may live for up to 4 years (Dörr *et al*., 2006; Scalici and Gherardi, 2007).

The sex-ratio for 2010 was near 1:1 with a small dominance of females. This female dominance has previously been described by several authors (Dörr *et al*., 2006; Scalici and Gherardi, 2007; Scalici *et al*., 2010). In addition, the period for the appearance of eggs and juveniles also matches results obtained in several other studies, suggesting that reproduction and spawning takes place mainly in summer and autumn (Dörr *et al*., 2006 and references therein).

This study measured the percentage claw loss with time and interpreted the results as a proxy of possible changes in *P. clarkii* aggressiveness. Higher values were recorded for males than for females and the results show a clear increase in aggressiveness from June to August, which corresponds to months of higher activity and therefore a greater probability of encounters and possible fights (Gherardi, 2006). In addition, this is the period of reproduction which may also increase aggressiveness in both males and females (Figler *et al*., 1995, 2001, 2005).

Ecological relevance and possible management actions

Based on the results obtained during the 4 years of sampling in the River Minho, *P. clarkii* has a widespread distribution and some sites may attain high abundance and biomass; this non-indigenous invasive species can be considered a relevant key species and may have possible effects on ecosystem processes and functions. Unfortunately, no study has been performed addressing the possible ecological and economic impacts resulting from this particular introduction in the River Minho. Therefore, we can only speculate about its effects, the most important of which are probably related to trophic interactions and physical disturbance (Geiger *et al*., 2005). One major concern could be the overall reduction in the abundance of macrophytes by grazing, and for invertebrates, amphibians and fishes by direct predation on eggs, larvae, juveniles, or adults. This can result in the loss of biodiversity, which has been described widely for other invaded areas (Renai and Gherardi, 2004; Cruz *et al*., 2006). However, several species may benefit from the presence of *P. clarkii*, mainly because this crayfish functions as an important food resource for higher trophic levels (Matthews and Reynolds, 1992; Correia, 2001; Tablado *et al*., 2010) for example, otter *Lutra lutra* (Delibes and Adrián, 1987; Beja, 1996) and the invasive American mink *Neovison vison* (Sousa, pers. obser.). Crayfish also affect aquatic invertebrates by changing sediment characteristics, acting as an ecosystem engineer by reducing fine particulate matter (Alcorlo *et al*., 2004; Creed and Reed, 2004; Usio and Townsend, 2004). This species can also promote bioturbation and resuspend nutrients bonded with sediments, thereby mediating matter flux and nutrient cycling in freshwater ecosystems (Angeler *et al*., 2001).

Given the potentially important ecological and economic impacts generated by the introduction of this non-indigenous invasive species, the information obtained in this study may be important for future management limiting further dispersal of *P. clarkii* to adjacent areas. Complete eradication in the international section of the River Minho will be almost impossible because *P. clarkii* is already widespread. However, some control measures can be applied following known methods already described, such as mechanical removal, physical methods, biological control, biocides, and autocidal methods (revised in Freeman *et al*. (2010) and Gherardi *et al*. (2011)). The use of biocides and microbial pathogens could be a strategy for *P. clarkii* control; however, these methods are almost impossible to implement, owing to its widespread distribution in the River Minho and the possible collateral impacts generated by these techniques, including high economic and social costs, as well as ecological concerns. Physical methods such as habitat destruction and drying out of some parts of the river are also impossible to implement in this area. However, because this species is adversely affected by current velocity, control of discharge by upstream dams can limit the crayfish population from reaching its maximum range by restricting it to downstream areas (Kerby *et al.*, 2005). In addition, as there are suitable habitats further upstream, human activities that might transport *P. clarkii* in an upstream direction need to be controlled because if crayfish became established in upstream areas downstream dispersal will probably occur (Barbaresi and Gherardi, 2000; Geiger *et al.*, 2005).

Other strategies may include the sterilization of *P. clarkii* males, which has had considerable success in the decrease of reproduction rates (Aquiloni *et al.*, 2009) or the use of biological control (for example, by eels *Anguilla anguilla*; Aquiloni *et al.* (2010)). In the River Minho, *A. anguilla* is still present, but the overall abundance and biomass has suffered a considerable reduction in recent decades (Sousa *et al.*, 2008b). However, given the environmental conditions in this river, intensive trapping may be the best option for reducing the abundance and distribution of *P. clarkii* (Hein *et al.*, 2007), complementing this measure with the use of pheromones to increase the success of trapping (Freeman *et al.*, 2010; Gherardi *et al.*, 2011). Given the good water quality in the River Minho with low concentrations of pollutants (Sousa *et al.*, 2008a), harvesting *P. clarkii* for human consumption and national commercialization might be another way to reduce its abundance and biomass (Smart *et al.*, 2002; Jones and Coulson, 2006; Hein *et al.*, 2007; Jones *et al.*, 2009; but see Nuñez *et al.* (2012) who advise caution before starting these harvesting programmes). In fact, control measures using fishing, supported by environmental education to avoid introducing crayfish beyond its present range, could help to limit the spread of the *P. clarkii* population (Jones *et al.*, 2009). If intensive trapping could be undertaken, we propose that this should take place during late spring or early summer, when catches are higher, the females are dominant, and because this period is earlier than juvenile recruitment.

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