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Invasive crayfish in Europe: the impact of *Procambarus clarkii* on the littoral community of a Mediterranean lake

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SUMMARY

1. Despite the growing number of non-indigenous crayfish species introduced worldwide, little scientific attention has been given to their effects on the recipient communities. Here, we quantified the impact of adult red swamp crayfish (*Procambarus clarkii*) on key components of the littoral community of a mesotrophic lake in central Italy. We used two densities of crayfish plus a no-crayfish control, and two complementary methods –*in situ* enclosures and a laboratory study.

2. Both experiments showed that *P. clarkii* strongly affects the community even at a low density (4 m^{-2}), although a high crayfish density (8 m^{-2}) showed a more pronounced impact in a shorter time.

3. In enclosures, *P. clarkii* quickly consumed the pond snail *Haitia acuta*, notwithstanding its anti-predator behaviour, but not the mosquitofish *Gambusia affinis*. The biomass of the hydrophytes *Nymphoides peltata* and *Potamogeton* spp. was strongly reduced by crayfish grazing, coupled with their non-consumptive plant clipping and uprooting, which were particularly intense in the case of *Potamogeton crispus*. In contrast, *Utricularia australis* was avoided by *P. clarkii*, even when other resources were exhausted.

4. The introduction of *P. clarkii* could reduce biodiversity and increase biotic homogenisation in a short time.

Keywords: biological invasions, field enclosures, Mediterranean lakes, non-indigenous crayfish, *Procambarus clarkii*

Introduction

The anthropogenic introduction of species outside their native ranges is now recognised as one of the five most important determinants of global environmental change (Sala *et al.*, 2000). This is particularly true in inland waters that have been subject to extensive unintentional (e.g. via ship ballast) and intentional (e.g. stocking of invertebrates and fish) releases of organisms (Ricciardi, 2001).

It is broadly accepted that non-indigenous species often affect other species, communities and ecosystems, and can exacerbate the negative effects of both global climatic warming and other anthropogenic

sources of disturbance (Lodge, 1993, 2001). However, little scientific attention has yet been placed on developing either theoretical or operational generalisations about their impact. In a challenging article, Parker *et al.* (1999) lamented the lack, particularly in fresh water, of a framework within which to discuss and predict the impact of different non-indigenous species and in different systems. This is unfortunate, because our main concern for the introduction of species is ultimately a function of the impact on other species in their new range, the ways in which they affect ecosystem processes and how these effects may persist or increase over time (McMahon, Cadotte & Fukami, 2006).

Crayfish are the largest and amongst the longest lived invertebrates in temperate freshwater environments, and often occur at high density. Most species are keystone consumers (Nyström, Brönmark &

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Granéli, 1996), feeding on benthic invertebrates, detritus, hydrophytes and algae in lotic and lentic waters (e.g. Whitley & Rabeni, 1997). They also constitute the main prey of several species, including otters (Slater & Rayner, 1993), fish (e.g. Blake, 1995) and birds (Rodríguez *et al.*, 2005). Because of their capability to integrate into the food web at many levels and to persist on the substantial energy reserves of the detrital pool, crayfish are likely invaders of aquatic systems (Moyle & Light, 1996).

Where potentially invasive crayfish colonise, the combination of their rapid population increase and omnivorous feeding habits may have consequences for the structure of freshwater food webs (Lodge *et al.*, 1998). In the short term, non-indigenous crayfish have the potential to reduce the biomass and species richness of macroinvertebrates, hydrophytes, periphyton and pelagic/surface microalgae (e.g. Lodge & Lorman, 1987; Charlebois & Lamberti, 1996; Nyström & Strand, 1996; Gutiérrez-Yurrita *et al.*, 1998; Nyström & Pérez, 1998; Nyström *et al.*, 2001; Correia, 2002; Cronin *et al.*, 2002; Gherardi & Lazzara, 2006). They may also cause direct economic damage due, for instance, to the reduced recruitment of commercially valuable fish stocks, such as trout (Nyström, 1999), or to the destruction of rice plants (Anastácio, Correia & Menino, 2005a; Anastácio, Parente & Correia, 2005b). In the long term, non-indigenous crayfish may induce drastic habitat changes with the consequent decline of several invertebrate taxa, amphibians and fish (e.g. Guan & Wiles, 1997).

There are many examples of non-indigenous crayfish being stocked throughout the world (Hobbs, Jass & Huner, 1989). Because of their high commercial value, the introduction and cultivation in Europe of several species have increased during the last few decades (e.g. Pérez *et al.*, 1997), so that today most European countries have at least one introduced species (Gherardi & Holdich, 1999). Indeed, more than 90% of the total crayfish production in Europe derives from the red swamp crayfish *Procambarus clarkii* (Girard) (Ackefors, 1999). This species, native to north-eastern Mexico and south-central U.S.A., has, since the 1950s, been introduced to 25 other countries for aquaculture (Gherardi *et al.*, 1999). Where it has been introduced, whether by escape or purposefully released, *P. clarkii* has colonised natural water bodies giving rise to breeding populations. The further spread of this species has contributed to the biodiver-

sity loss and habitat degradation recorded in many freshwater systems of south-central Europe (Gherardi, 2006).

Unfortunately, apart from a few studies on some invasive populations in the Iberian peninsula (e.g. Angeler *et al.*, 2001; Rodríguez, Bécares & Fernández-Aláez, 2003; Cirujano, Camargo & Gómez-Cordovés, 2004; Correia, Bandeira & Anastácio, 2005; Rodríguez *et al.*, 2005), much of the discussion about the ecological effects of *P. clarkii* has been anecdotal; as a consequence, the case against introducing this and other non-indigenous crayfish is often weakly supported (Gherardi, 2006). On the contrary, forecasting the ecological consequences of invasions is critical for setting priorities for intervention (Vander Zanden *et al.*, 2004) and for guiding restoration efforts (Zavaleta, Hobbs & Mooney, 2001).

In this study, we attempted to quantify the impact of adult *P. clarkii* crayfish at two densities on some key components of the littoral community of a lake in central Italy. We used two complementary methods – field enclosures and a laboratory study. While enclosure experiments provide more realistic data, it is sometimes difficult to identify the mechanisms underlying the impact. By comparison, laboratory experiments can lack realism, but may be more effective in understanding such mechanisms (Diamond, 1986).

Methods

Rationale

The study lake, Lago della Doccia, Province of Pistoia (43° 46' 42"N, 10° 48' 12"E; about 15 m above sea level) is a small (6 ha) and shallow (maximum water depth: 4 m) mesotrophic lake in central Italy. It was selected for study because it has been subject to a recent invasion of *P. clarkii*. This crayfish was first recorded in the lake in 2001 and, by the time of the study (summer 2003), had reached only a relatively low mean density of 0.2 m⁻².

In both the enclosure and laboratory experiments, we manipulated crayfish density at three levels: (i) a no-crayfish control, (ii) low crayfish density (4 m⁻²) and (iii) high crayfish density (8 m⁻²). Densities were in the range of natural field densities recorded in the adjacent wetland, Padule di Fucecchio (F. Gherardi, unpublished data), where *P. clarkii* was first recorded in the area. All the experimental crayfish (intact, adult

and reproductive (Form I) males, with an average cephalothorax length of 47 mm for field enclosures and 45 mm for the laboratory experiment) were collected from the study lake at least 4 days before the start of the experiment. In this pre-experimental phase, they were kept isolated in 5-L aerated plastic tanks containing clay pipes (5 cm in diameter) as shelters and maintained in natural light:dark cycle at room temperature (22 °C), and fed *ad libitum* with live *Calliphora* sp. larvae. Water was changed daily. Each animal was used only once.

The species on which the impact of *P. clarkii* was tested were selected because they are representative of the dominant taxa in the littoral zone of many lakes in the area. Therefore, in the enclosure experiment we used adult individuals of both the pond snail *Haitia acuta* (Draparnaud) (average length: 5.5 mm) and the western mosquitofish *Gambusia affinis* (Baird & Girard) (average total length: 26 mm), and established plants of the hydrophytes *Nymphoides peltata* (S.G. Gmel.) Kuntze, *Potamogeton filiformis* Pers. and *Utricularia australis* R. Br. *Haitia acuta* and *G. affinis* are both native to North America but their introduction into Italy dates back to the 1850s (Cianfanelli, Lori & Bodon, 2007) and 1922 (Sommani, 1967) respectively. They are now widely distributed and abundant, being well-integrated components of Italian lentic waters.

In the laboratory, our analysis was focused on the three hydrophytes above plus *Potamogeton crispus* L. The hydrophytes used in this study shared a morphology that makes them easy for crayfish to handle and to consume. They include floating-leaved species anchored to the bottom by rhizomes (*N. peltata*), species with branched stems and submerged leaves (*Potamogeton* spp.) and floating plants with submerged branched stems (*U. australis*).

Enclosure experiment

The experiment took place in August 2003, when water temperature in the lake ranged between 19 and 24 °C and pH between 6 and 7. On 25–31 July 2003, 12 enclosures were installed at a water depth of 0.95–1.30 m along 30 m of shoreline exposed to full sunlight from dawn to noon. Enclosure bottom area was 0.5 m² and height was 80 cm. We used a randomised block design, consisting of four experimental blocks each with the three densities as above (no crayfish, low crayfish density and high crayfish

density) placed randomly within each block. Low and high crayfish densities were obtained by introducing two and four individuals, respectively, per enclosure. Each block was 2 m from other blocks and, within each block, enclosures were placed about 1 m apart.

Enclosures had a steel frame, covered on all four sides by aluminium window screening (mesh size: 1 mm²), and were provided with a solid steel base, a removable 1-mm aluminium mesh lid to prevent the crayfish from escaping, and 0, 2 or 4 clay pipes (according to the assigned density) as shelters (see above). The bottom was covered with a 10 cm-thick layer of sediment (sand and gravel) collected from the lake from which any potential prey has been removed. One week before the experiment began we provided each enclosure with a similar wet mass of the test species. We used a mean of 2.7 g of *H. acuta*, 13.3 g of *G. affinis* and 69.8 g, 66.1 g and 161 g of *N. peltata*, *U. australis* and *P. filiformis* respectively.

The experiment started on 7 August with the introduction of 0, 2 or 4 crayfish into each enclosure, and lasted 3 weeks. During the experiment the sides and tops of the enclosures were brushed twice per week to prevent the build up of debris. Crayfish mortality was low, with only two individuals in the high-density enclosures being lost. These were replaced by other crayfish of a similar size. At the end of the experiment, enclosures were sampled destructively, and the surviving snails, fish and hydrophytes were collected and weighed to 0.1 mg after drying (24 h) at 65 °C. The final dry weight per m² was used to infer the impact of crayfish on each test species.

We also assessed the time course of any impact on each of the three hydrophytes by measuring shoot development of *N. peltata* (number of leaves m⁻²) and density of *P. filiformis* plants (number of plants m⁻²) once every 3 days, and coverage of *U. australis* (percentage of the total area occupied) once every 5 days.

Laboratory experiment

The experiment was conducted during September 2003 in nine round plastic pools (1.75 m² × 35 cm height) filled with dechlorinated tap water (water depth: 25 cm) at a temperature of 25 °C. Each pool was provided with 0, 7 or 14 clay pipes as above, according to crayfish density, and was aerated. The bottom was covered with a 15 cm-high layer of sand

and gravel. As in the field enclosure experiment, each pool was randomly assigned to one of the three densities (no crayfish, low crayfish density and high crayfish density). Low and high crayfish densities were obtained by placing 7 and 14 individuals into the pools respectively.

One week before the experiment began, we added to each pool approximately the same wet mass per species of four hydrophytes collected from Lago della Doccia: *N. peltata*, *P. crispus*, *P. filiformis* and *U. australis* (mean wet mass per pool: 50.9 g, 20 g, 54.2 g and 63.8 g respectively). The experiment started on 2 September with the introduction of the crayfish and lasted for 10 days. No crayfish died.

To assess the damage to hydrophytes from crayfish other than by direct consumption, once every second day we collected plant fragments found floating on the water surface or lying on the bottom, and weighed them to 0.1 mg after drying (24 h) at 65 °C. At the end of the experiment, plants were harvested by species and weighed after drying as above to obtain the dry mass.

The impact of crayfish on the hydrophytes was assessed by calculating for each species the dry mass loss per pool, i.e. the difference between the initial and the final dry mass which had been lost by either direct consumption or other damage. Dry mass was used instead of wet mass (WM) because the latter was found to decrease with time in the absence of crayfish due to natural leaching. The initial dry mass (DM) of each hydrophyte species was inferred by regressing the linear equations of the type $DM = a + b \text{ WM}$, obtained from a preliminary test in which dry mass was measured for 30 samples of the same hydrophyte of known wet mass (a and b : *N. peltata*, 0.042 and 0.108; *P. crispus*, 0.007 and 0.059; *P. filiformis*, -0.009 and 0.095; and *U. australis*, -0.004 and 0.050).

Statistical analyses

To reduce the risk of type I error, we first applied a randomised block design two-way MANOVA to the data from the enclosure experiment to assess whether the initial wet mass of the test species was different between the enclosures assigned to the three levels of crayfish density and whether the three levels and blocks had a diverse impact on the dry mass of the test species. Similarly, for the laboratory experiment, a one-way MANOVA was used to assess the overall

effect of the three density levels on the dry mass of the test species that was lost. To clarify the interpretation of the MANOVA, single randomised block design two-way ANOVAs for the enclosure experiment, and single one-way ANOVAs for the laboratory experiment, tested the effects of enclosures/density/blocks and pools/density on each single test species respectively. Prior to MANOVA and ANOVA, the data were $\log(x + 1)$ transformed to normalise distributions and stabilise variances.

Two-way, repeated-measures ANOVAs (density level \times day) were used in the enclosure experiment to assess the time-related impact of crayfish density on shoot development in *N. peltata* and on plant density of *P. filiformis* (after $\log(x + 1)$ transformation), and on the coverage of *U. australis* (after arcsine square-root transformation). Differences among hydrophyte species in the percentage of non-consumptive loss of dry mass were tested by a two-way, repeated-measures ANOVA on arcsine square-root transformed data. Where significant F -ratios were obtained, Tukey's *post hoc* tests were computed to identify which density level differed from each other.

Results

Enclosure experiment

The initial wet mass of the test species was found to be significantly different among enclosures (after a two-way MANOVA, $F = 4.593$, d.f. = 2, 6, $P = 0.038$). However, individual ANOVAs indicated that this difference was exclusively due to *N. peltata* having a significantly lower wet mass in the control enclosures than in the others ($F = 6.174$, d.f. = 2, 6, $P = 0.035$).

The overall effect of crayfish density on the biomass of the test species was weak after a two-way MANOVA ($F = 3.393$, d.f. = 2, 6, $P = 0.074$), but individual ANOVAs showed that the final dry masses of *H. acuta*, *N. peltata* and *P. filiformis* were all significantly lower in the enclosures containing crayfish than in the control (Table 1; Fig. 1). In contrast, the final dry masses of *G. affinis* and *U. australis* did not change with the density level.

The analysis of the impact of crayfish over time on the hydrophytes showed that the effect on shoot development in *N. peltata* and on plant density in *P. filiformis* was greater in the first week of the experiment in the enclosures with a high density of

Table 1 *In situ* enclosure experiment. Two-way ANOVAs for the effects of crayfish density (0, 4 or 8 m⁻²) on the final wet biomass of the pond snail *Haitia acuta*, the mosquitofish *Gambusia affinis* and the hydrophytes *Nymphoides peltata*, *Potamogeton filiformis* and *Utricularia australis* after 3 weeks.

Source	d.f.	MS	F	P
<i>Haitia acuta</i>				
Block	3	0.067	1.799	0.247
Density level	2	0.875	23.451	0.001
Error	6	0.037		
<i>Gambusia affinis</i>				
Block	3	0.020	4.490	0.874
Density level	2	0.135	3.512	0.299
Error	6	0.090		
<i>Nymphoides peltata</i>				
Block	3	0.272	1.024	0.446
Density level	2	11.355	21.398	0.002
Error	6	1.592	0.265	
<i>Potamogeton filiformis</i>				
Block	3	0.040	1.047	0.437
Density level	2	8.824	228.589	<0.001
Error	6	0.039	0.265	
<i>Utricularia australis</i>				
Block	3	0.103	3.457	0.092
Density level	2	0.038	1.272	0.346
Error	6	0.030		

Significant values in bold.

crayfish. This was shown by analysing the interaction between crayfish density and time (*N. peltata*: $F = 13.19$, d.f. = 12, 36, $P < 0.001$; *P. filiformis*: $F = 14.36$, d.f. = 12, 36, $P < 0.001$). In contrast, no effect of either crayfish density ($F = 0.05$, d.f. = 2, 6, $P = 0.952$) or time ($F = 4.56$, d.f. = 6, 12, $P = 0.062$) was found for the coverage of *U. australis* (Fig. 2).

Laboratory experiment

The presence of crayfish at either low or high densities was accompanied by the almost complete loss of three of the test hydrophytes (*N. peltata*: 98.05%, SE = 1.68; *P. filiformis* and *P. crispus*: 100%), but not the fourth, *U. australis* (41.5%, SE = 8.88). Although the overall effect of crayfish density on the dry mass loss of the test hydrophytes only approached significance (after a one-way MANOVA, $F = 3.767$, d.f. = 8, 8, $P = 0.062$), individual ANOVAs indicated, as in the enclosure experiment, that the presence of crayfish at either low or high densities (Tukey test: $P > 0.05$) led to the reduction of most of the dry mass of *N. peltata*, *P. crispus* and *P. filiformis*, but not of *U. australis* (Table 2; Fig. 3).

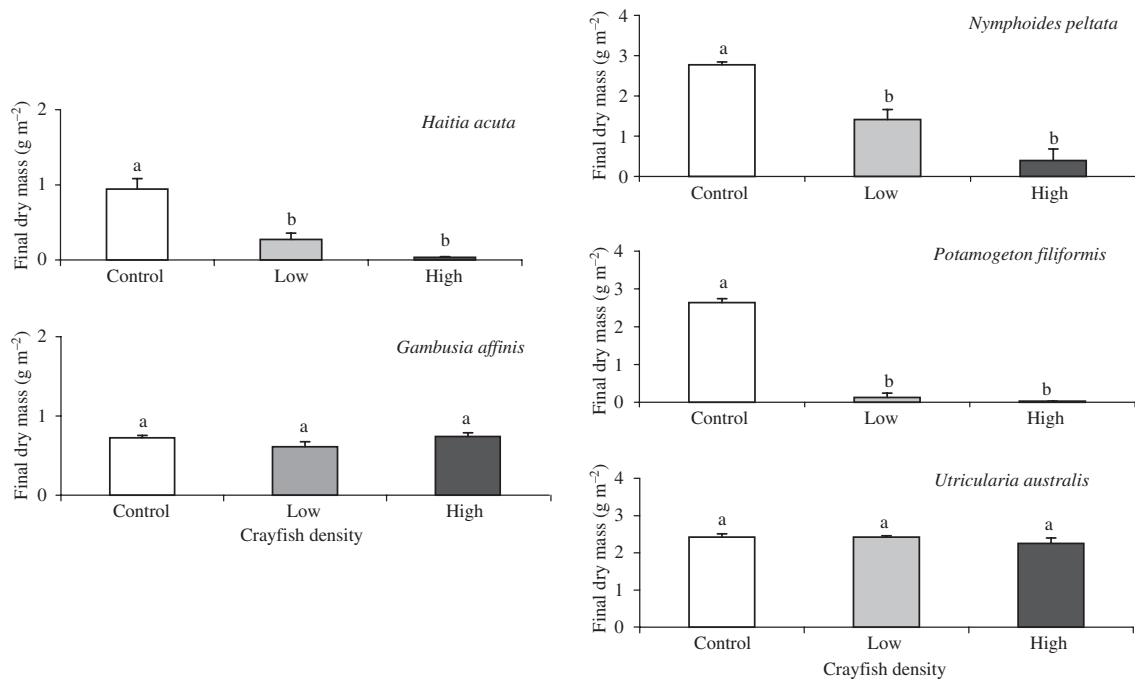


Fig. 1 Enclosure experiment. Mean (+SE) final dry mass (g m⁻²) of the pond snail *Haitia acuta*, of the western mosquitofish *Gambusia affinis* and of the hydrophytes *Nymphoides peltata*, *Potamogeton filiformis* and *Utricularia australis* 3 weeks after the introduction of different densities (0, 4 or 8 m⁻²) of the crayfish *Procambarus clarkii* in field enclosures. Letters over bars denote differences after Tukey's *post hoc* tests.

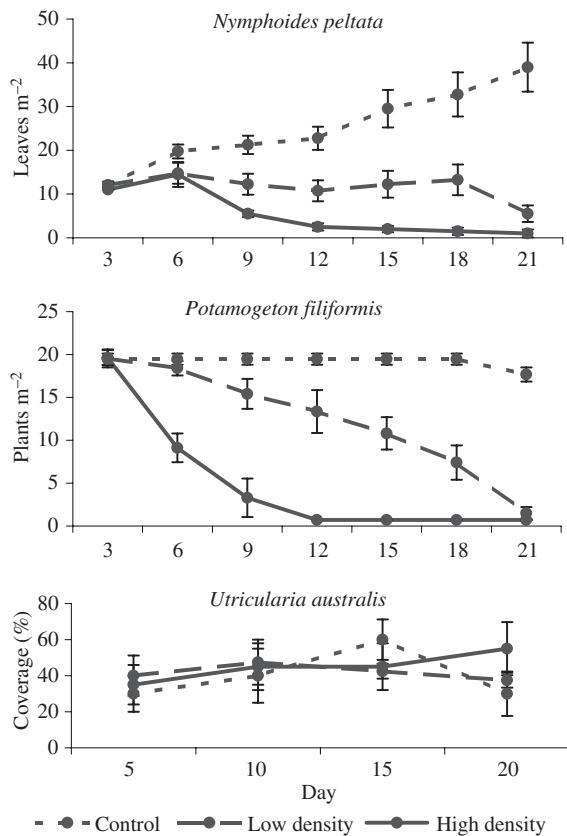


Fig. 2 Enclosure experiment. Changes with time in the mean (\pm SE) number of leaves per m^2 , number of plants per m^2 , and % of coverage of the hydrophytes *Nymphoides peltata*, *Potamogeton filiformis* and *Utricularia australis* respectively, over 3 weeks of the experiment with differing crayfish densities.

Table 2 Laboratory experiment. One-way ANOVAs for the effects of different levels of crayfish density (0, 4 or 8 m^{-2}) on the loss of dry mass of *Nymphoides peltata*, *Potamogeton crispus*, *P. filiformis* and *Utricularia australis* consumed during 10-day experiment in pools.

Source	d.f.	MS	F	P
<i>Nymphoides peltata</i>				
Density level	2	22.137	6.177	0.035
Error	6			
<i>Potamogeton crispus</i>				
Density level	2	1.153	11.073	0.01
Error	6			
<i>Potamogeton filiformis</i>				
Density level	2	38.637	19.661	0.002
Error	6			
<i>Utricularia australis</i>				
Density level	2	0.064	0.025	0.976
Error	6			

Significant values in bold.

Crayfish, independently of their density (low versus high density, $F = 0.556$, d.f. = 1, 22, $P = 0.465$), broke off leaves and stems but did not consume more than 60% of the initial dry mass of *P. crispus*. This was a significantly larger fraction than that of *N. peltata*, *P. filiformis* or *U. australis* ($F = 4.502$, d.f. = 1, 22, $P = 0.047$ and after Tukey's test on data from the two densities pooled; Fig. 4).

Discussion

Both field and laboratory experiments showed that *P. clarkii* can exert strong effects on other littoral species in a Mediterranean lake, even at a relatively low density. Not surprisingly, high crayfish densities exerted an effect on hydrophytes more quickly. Our results also showed that the crayfish is selective in its direct consumption and destruction of the hydrophytes tested. It is of course possible that our experiments may have exaggerated the predatory effect of crayfish (McCarthy & Dickey, 2002). Nevertheless, our experimental setting mimics conditions in many Mediterranean lakes, which often dry out during late summer and early autumn giving rise to isolated small ponds (Correia, 2003).

Previous experiments, most often conducted in the littoral zone of lentic systems (an exception is Stenroth & Nyström, 2003), have described some direct and indirect trophic effects that several other non-indigenous crayfish exert on food web structure (reviewed in Nyström, 1999, 2002). Their impacts were often shown to be density-dependent (e.g. Charlebois & Lamberti, 1996). On the other hand, as found for *Orconectes rusticus* (Girard) (e.g. Lodge *et al.*, 1994) and *O. virilis* (Hagen) (Chambers *et al.*, 1990), even relatively low densities of *P. clarkii* drastically reduced the biomass and species-richness of hydrophytes, and the abundance of snails.

In enclosures, *P. clarkii* quickly consumed the pond snail *H. acuta*. This is despite the anti-predator behaviour shown by the snail (Correia, Bandeira & Anastácio, 2005), which crawls to the water surface and may thereby reduce encounters with the crayfish (Alexander & Covich, 1991). The ability of *P. clarkii* to capture and consume snails, and in particular *H. acuta*, is well documented in the laboratory (Renai & Gherardi, 2004). Gastropods, particularly thin-shelled and small-bodied snails (Nyström & Pérez, 1998), are among macroinvertebrates most affected by

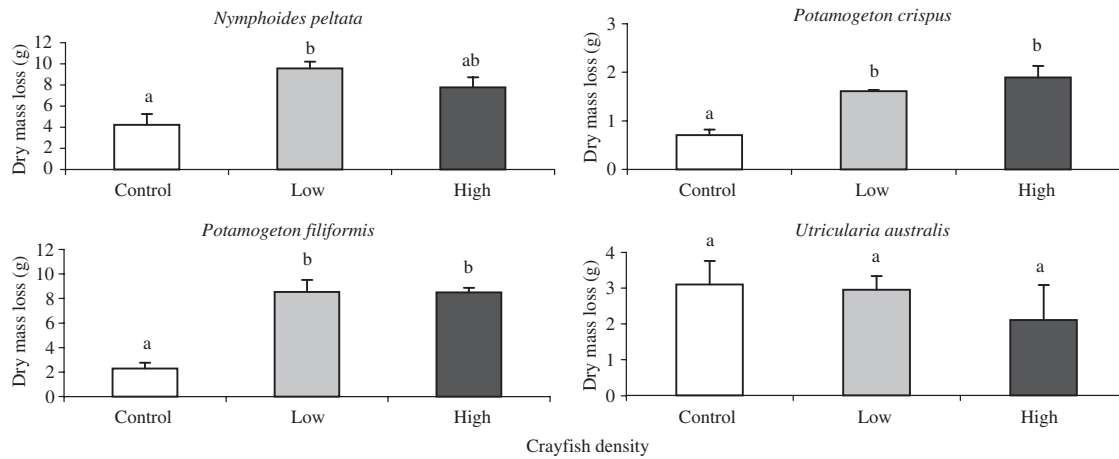


Fig. 3 Laboratory experiment. Mean (\pm SE) dry mass loss (g m^{-2}) of the hydrophytes *Nymphaoides peltata*, *Potamogeton crispus*, *P. filiformis* and *Utricularia australis* 10 days after the introduction of different densities (0, 4 or 8 m^{-2}) of the crayfish *Procambarus clarkii* in laboratory pools. Letters over bars denote differences after Tukey's *post hoc* tests.

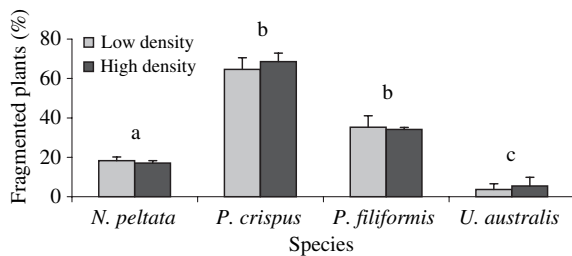


Fig. 4 Laboratory experiment. Mean (\pm SE) percentage of the initial dry mass of the four test hydrophytes that was fragmented but not consumed 10 days after the introduction of crayfish at low (4 m^{-2} , $n = 3$) or high (8 m^{-2} , $n = 3$) densities. Letters over bars denote differences between plant species after Tukey's *post hoc* tests on data from the two densities pooled.

non-indigenous crayfish. This may be by direct consumption or indirectly by destroying the hydrophytes on which the snails live (Nyström *et al.*, 1996). Snails can be drastically reduced (from $>10\,000$ to <5 individuals m^{-2} after 19 years of colonisation by *O. rusticus* in Trout Lake, Wisconsin, U.S.A.; Wilson *et al.*, 2004) and can even be eliminated (Charlebois & Lamberti, 1996). Due to their relatively large body-size, long generation time and relatively low productivity, snails show less resilience in the long term than the other invertebrates and are slow to respond numerically following any reduction in crayfish density (McCarthy *et al.*, 2006). The impact of crayfish on snails may have indirect consequences for littoral communities. Because snails are particularly important grazers (Lodge *et al.*, 1994; Nyström *et al.*, 2001),

crayfish may indirectly increase the abundance of microalgae by releasing them from herbivory, thus inducing a trophic cascade in the littoral food web.

In contrast to snails, *G. affinis* was not affected by *P. clarkii*. This contrasts with the results of Correia (2002, 2003) and Leite *et al.* (2005), who showed in Portugal that this crayfish preyed on the related *Gambusia holbrooki* (Girard) and that mosquitofish lack anti-predator responses when exposed to the crayfish. Our results are not wholly surprising, however. In fact, apart from ideal conditions in very small temporary pools (Ilhéu, Bernardo & Fernandes, 2007), the opportunistic *P. clarkii* usually feeds only on dead, dying or immobilised fish (Lowery & Mendes, 1977; Renai & Gherardi, 2004) and on eggs (Xinya, 1995). Non-indigenous crayfish such as *Pacifastacus leniusculus* (Dana), however, may be able to inflict direct damage through their predatory activity to benthic fish or may outcompete them for the access of shelters (Guan & Wiles, 1997).

Our data confirm the ability of non-indigenous crayfish to reduce the biomass of hydrophytes. Indeed, intense grazing by crayfish (Lodge *et al.*, 1994; Nyström *et al.*, 1996), coupled with the damage they do by clipping and uprooting plants (Lodge *et al.*, 1994; Nyström & Strand, 1996; Smart *et al.*, 2002), can cause a decline in hydrophyte abundance. This has been shown previously by Lodge & Lorman (1987) in *O. rusticus*, where a crayfish density of 19 gm^{-2} reduced total hydrophyte biomass by 64%, while a density $>140 \text{ gm}^{-2}$ eliminated all hydrophytes

in 12 weeks. Similarly, more than 80% of hydrophyte biomass was lost about 20 years after the introduction of *P. clarkii* to the Doñana National Park (Spain) (Gutiérrez-Yurrita *et al.*, 1998).

A further result is that much of the destruction (>60% in the case of *P. crispus*) made by *P. clarkii* was by non-consumptive means. Such behaviour is common among consumers of freshwater plants (Lodge, 1991; Olsen *et al.*, 1991; Lodge *et al.*, 1994) and of marine macroalgae (e.g. Elner & Vadas, 1990). Certainly, the negative impact of crayfish on the abundance of most plant species is assumed to be the same, whether plant tissue is eaten or fragmented. However, the destruction of much more plant tissue than the crayfish can eat might even have a positive effect on the system (Lodge, 1991). For instance, species that readily root adventitiously (such as *Elodea* spp.) or species without roots (such as *Ceratophyllum* spp.) may benefit from crayfish fragmentation (Lodge *et al.*, 1994). Fragments of most species would join the detritus pool and produce nutritious coarse particulate organic matter (CPOM) (e.g. Allan & Johnson, 1997). However, hydrophyte destruction in nutrient-rich conditions, particularly in mesotrophic-eutrophic shallow lakes, is generally followed by a switch from a clear to a turbid state dominated by surface microalgae, e.g. *Microcystis* spp., growth (Scheffer *et al.*, 1997; Rodríguez *et al.*, 2003). In its turn, this may lead to decreased primary production by benthic hydrophytes and periphyton, due to the reduced light penetration. Changes in hydrophyte biomass may also have several non-trophic effects on the community, because of their role as protective cover, substratum or breeding sites for many organisms (Olsen *et al.*, 1991; Nyström *et al.*, 1996; Dorn & Wojdak, 2004).

Finally, we found that *P. clarkii* is selective in its action on hydrophytes, *N. peltata* and *P. filiformis* being more affected than *U. australis*. Also, *P. crispus* was more easily fragmented than the other test species. Probable consequences of this selectivity, which may also influence *P. clarkii*'s distribution (Cirujano, Camargo & Gómez-Cordovés, 2004), are a decreased diversity of the hydrophytes and an increased homogenisation of the recipient communities (Lodge & Lorman, 1987; Nyström *et al.*, 1996).

Crayfish feeding preferences are based on plant traits such as morphology, structure, chemical defences and nutritional value (Chambers *et al.*, 1990). Often, they feed upon plants whose finely branched or

filamentous morphologies seem to make them easier to handle and to consume (the four test species here), while avoiding plants that contain defensive chemical (Bolser *et al.*, 1998). However, as shown by Cronin *et al.* (2002), no single plant trait appears to be a good predictor of palatability to *P. clarkii*. Factors other than quality and morphology, such as cover or protection from predators afforded by the plant (e.g. Damman, 1987), hunger (e.g. Cronin & Hay, 1996) and prior feeding experience (e.g. Dorn, Cronin & Lodge, 2001), may also determine crayfish food choice. Differences in the impact of crayfish on hydrophytes were also found to be related to crayfish sex and activity, to the abundance of alternative foods (Chambers *et al.*, 1990) and to crayfish density. Since food may be limiting at high crayfish density, less preferred items may be included in the diet (Bolnick, 2001; Bondar *et al.*, 2005). Surprisingly, we did not find such a density-dependent effect of food consumption in the case of *U. australis*, which was avoided even when the other hydrophytes were almost exhausted. This suggests that the unpalatability of this plant for *P. clarkii* derives from some structural or, more probably, chemical factors. In support of this hypothesis, Prusak, O'Neal & Kubanek (2005) found that extracts of *Utricularia* sp. deterred feeding in the closely related *Procamburus acutus acutus* (Girard).

In conclusion, our results underline the ecological threat posed by *P. clarkii*. Indeed, an understanding of the impact of non-indigenous species is an important first step towards the ultimate goal of developing effective approaches towards conserving biodiversity and restoring pristine ecological conditions (Vitousek *et al.*, 1996). To reach this goal, further work is needed in quantifying this species' long-term effects, which might highlight how efforts to reduce crayfish populations influence the recovery of the community invaded. However, our study shows that *P. clarkii* affects several components of littoral communities in Mediterranean lakes. Such a strong impact should be of concern for any conservation effort, in light of the growing number of non-indigenous crayfish introduced worldwide (Gherardi & Holdich, 1999; Lodge *et al.*, 2000).

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