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Predatory efficiency of crayfish: comparison between indigenous and non-indigenous species

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Abstract

The invasive crayfish *Procambarus clarkii* is highly dispersed within lentic waters in northern and central Italy. It is a polytrophic predator, exerting a strong influence on animal communities, including amphibians, fish, gastropods, and insect larvae. The indigenous species *Austropotamobius italicus*, inhabiting lotic waters, behaves as a generalist – but not opportunistic – species. The object of this study was to compare the predatory pressure exercised by the two species on potential prey, i.e., anuran tadpoles, urodelan larvae, fish fry, larvae of insects, and gastropods. Three main conclusions were drawn: (1) both species are skilled predators, adopting a sit-and-wait strategy, (2) the two crayfish seemed to form a 'search image' of familiar prey, as the result of either visual or chemical perceptual changes, and (3) at least in the laboratory, *P. clarkii* readily switched to naive prey for it (tadpoles of *Rana italica* and larvae of Limnephilidae), unlike the less opportunistic *A. italicus*. These results furnish suggestions on the trophic preferences of the two crayfish species and provide a partial understanding of the effects that the invasive species have on the community dynamics.

Introduction

Crayfish are the largest vagile invertebrates acting as keystone species in many ecosystems (Nyström et al. 1996). Their predatory behaviour plays an important role in regulating the structure of trophic chains. These macro-invertebrates directly influence freshwater communities and control the energy flow (Holdich 1987; Momot 1995). Crayfish are omnivorous and consume macrophytes, invertebrates, algae, and detritus (reviewed in Nyström 2002). They are also prey for a number of larger predators (Foster and Slater 1995).

Although generalists in their feeding behaviour, crayfish are selective consumers. Their influence on communities is complex and difficult to predict, being exerted at several trophic levels in direct and indirect ways. Crayfish act upon invertebrates and periphyton biomass by reducing macrophytes, and periphyton can

be facilitated through reduction of snail grazers because of crayfish predation (reviewed in Nyström 2002).

Both laboratory experiments and field observations showed that non-indigenous species exercise a strong effect on the lower trophic levels (reviewed in Nyström 2002). The potential to be invasive by a crayfish, depends on its ability to withstand environmental extremes and to a number of features, such as polytrophism, early maturity, rapid growth rate, high fecundity, disease resistance (Lindqvist and Huner 1999), plasticity in the biological cycle (Gherardi et al. 1999), and responsiveness to a wide array of danger signals (Hazlett 2000; Gherardi et al. 2002). In addition, active dispersal capabilities can increase its extent of habitat occupation (Gherardi and Barbaresi 2000).

The introduction of the invasive *Procambarus clarkii* in Spain in 1974 caused, and is still causing in many European countries, changes in both the structures of

ecological communities and the function of ecosystems. Today, *P. clarkii* is certainly the most widespread crayfish in the world, and is represented on every continent, except Australia and obviously Antarctica (Hobbs et al. 1989). The success of this crayfish is mainly due to its ecological plasticity, which allowed its introduction and stabilisation in diversified environments (Hobbs et al. 1989; Huner and Barr 1991), including those previously occupied by indigenous species (Huner and Barr 1991).

This crayfish yielded minimal economic benefits (except, possibly, for Spain) (Ackefors 1999), and negative consequences to the invaded habitats (Hobbs et al. 1989), being responsible for the loss of biodiversity in aquatic communities (Lodge et al. 1985; Holdich 1987). Information on *P. clarkii*'s diet is from aquaculture studies (Huner and Meyers 1979; Avault et al. 1981) and laboratory experiments (Covich et al. 1980; Ilhéu and Bernardo 1993b). If we exclude stomach content analyses (Ilhéu and Bernardo 1993b), there are a few studies on field populations (Ilhéu and Bernardo 1993a).

Austropotamobius pallipes complex, indigenous to Western Europe (Lowery and Holdich 1988), is one of the most demanding crayfish in terms of habitat quality. Populations of this species are in decline because seriously threatened throughout its range by oomycete fungus *Aphanomyces astaci* Schikora (Unestam 1969); other threats include over-fishing, habitat destruction, water acidification, pollution, competition with foreign introduced crayfish species, and extreme weather conditions (drought, floods) (Westman 1985). The feeding habit of this species has been investigated through the analysis of their diet from stomach content and laboratory food-preference studies (Gherardi et al. 2004), and indirectly through their impact on seedlings and adult macrophytes (Nyström et al. 1996; Nyström 1999).

Our main objective here was to compare the predatory behaviour of *P. clarkii* and *Austropotamobius italicus* (belonging to the *A. pallipes* complex and native to Italy) towards natural prey. We analysed the preference of those predators for a number of amphibian larvae, fish fry, larvae of insects, and gastropods that we have selected for their common occurrence in Italian lotic and lentic habitats. Several authors (reviewed by Nyström 2002) reported that crayfish behave like predators on these species. One shortcoming of this work was that it was restricted to a confined and artificial setting. However, the results

can furnish suggestions on the predatory potentials of non-indigenous species.

Materials and methods

The study animals

Crayfish

The white-clawed crayfish, *A. italicus*, is restricted to headwater streams and distributed across all the Italian peninsula, with the exception of the north-west of Italy inhabited by *A. pallipes* (Grandjean et al. 2000; Largiadér et al. 2000). The Convention for the Conservation of European Wildlife and Natural Habitats ('Bern Convention' Appendix III) listed *A. pallipes* complex as protected species, but did not forbid the introduction of non-indigenous species.

Native to north-eastern Mexico and the south-central USA, after its introduction into Spain, *P. clarkii* successfully colonised several European countries, including northern and central Italy (Gherardi et al. 1999). Its distribution is enlarging in the Po River and Reno River basins, in Tuscany, Umbria, the Marches, Latium, and Abruzzo (Gherardi et al. 1999). There are reports that this species lives already in syntopy with the indigenous crayfish in a number of water bodies in Lombardy, Tuscany, and Latium (F. Gherardi, pers. comm.).

Anurans

The common toad, *Bufo bufo*, is widely distributed in temperate zones of the British Isles, western Europe, and as far as Japan. This species moves to water during the breeding season and lays up to 7000 eggs in gelatinous strings of 3–5 m (Lanza 1983; Ballasina 1984; Duellman and Trueb 1994). Eggs and feeding larvae are found both in lotic and lentic waters.

Rana kl. *esculenta*, the green frog, inhabits the same lentic waters occupied by *P. clarkii*. This hybrid is a cross between *Rana ridibunda* and *Rana lessonae*. Eggs are deposited in relatively large, amorphous clumps in shallow water (Lanza 1983; Ballasina 1984). *Rana italica* lives in lotic waters and deposits clutches of eggs anchored at submerged stones (Lanza 1983).

Urodelans

Triturus vulgaris is widely distributed and occurs in polluted waters more commonly inhabited by *P. clarkii*

than *A. italicus*. Newt larvae are easily found in ponds, streams, and ditches, whereas adults are difficult to detect because of their secretiveness outside the mating season and their avoidance of daylight (Ballasina 1984). Females lay fertilised eggs singly, or in very small clutches (Ballasina 1984).

Fish

The brown trout, *Salmo trutta fario*, is one of the most widespread European fish (Greenhalgh 1999). Adult trout pair and spawn in small, shallow streams between late September and December. Eggs are laid by the female in pea-sized gravel, fertilised by the male and then covered with gravel by the female. Fry develop a camouflaged colouration, including dusky markings along the sides, and are known as parr (Greenhalgh 1999). Wild trout occur in most unpolluted European lakes and rivers with suitable spawning areas. In many rivers and some lakes the effects of pollution and over-fishing have caused a collapse of brown trout stocks.

Tricoptera

Limnephilidae frequently deposit egg masses on branches overhanging water (Herbert 1948), that swell and liquefy, and hatch during rain. The gelatinous drops run down twigs and drop into the water, carrying the larvae along (Herbert 1948). The larvae feed on small aquatic animals or micro-organisms, which encrust decayed organic matter in the water (Herbert 1948). Tricoptera larvae live in the same high quality flowing water as *A. italicus*.

Gastropods

The pulmonate *Physa acuta* is resistant to thermal pollution (Girod et al. 1980) and lives in diversified freshwater systems (streams, rivers, ponds, rice-fields, swamps), particularly those still or slow flowing, on all kinds of substrata and on grasses. This gastropod is spread in western Europe and in the Mediterranean countries and is present in Italy, Sicily, and Sardinia (Girod et al. 1980).

Planorbis corneus is a polymorphic snail inhabiting hard water, canals, rivers and lakes. It has a Palearctic distribution and in Italy, is present in all regions (Girod et al. 1980). This mollusc is insensitive to organic pollution, low concentrations of dissolved oxygen, and elevated summer temperatures (Girod et al. 1980).

The experimental protocol

The work was carried out during spring and summer, 1999 and 2000. Individual *P. clarkii* were captured in cylindrical, baited traps (80 cm long, 28 cm in diameter, and 4 mm in mesh size) from a ditch system near Florence (Italy) and from the Padule di Fucecchio, a freshwater swamp 60 km far from Florence. *A. italicus* were collected by hand in Fosso di Farfereta, a third-order stream 40 km far from Florence at an altitude of 450 m above sea level.

For at least one week before testing, both crayfish species were kept in the laboratory under a natural L/D cycle regime and at ambient temperature. Specimens were kept in plastic tanks (30 × 16 cm) containing 3 l of well water and fed on earthworms 3 times a week. Water was changed every second day.

For 'satiated' individuals we mean crayfish that were fed several times per day until one day before the experiment, while other crayfish were starved for about nine days ('starved' crayfish).

Amphibian larvae were collected from freshwater systems surrounding Florence and raised in communal tanks isolated by species; water was changed twice a week. Anuran tadpoles were fed with boiled lettuce while urodelan larvae were fed with larvae of midges (Chironomidae) and *Daphnia*. Tadpoles that were used dead in the experiments were killed in a freezer at -30 °C where death occurred in a few seconds.

Salmo trutta fario fry were from the trout-farm 'Puccini' in Papiano (FI). Specimens were raised in mass in plastic tanks, where water was filtered, and fed on a granular food once per week.

Limnephilidae larvae and gastropods were collected near Florence and fed with detritus from the same place.

At the end of the experiments, surviving prey were released in the same location where they had been collected.

For every treatment, we used one adult *A. italicus* of 29.3–45.8 mm cephalothorax length or one adult *P. clarkii* of 32.6–73.15 mm cephalothorax length (20 replicates per species). Individuals were tested in circular aquaria (diameter 30 cm) containing 5 l of well water. Potential prey were placed in the aquarium immediately after the introduction of the experimental crayfish.

The experimental design for each treatment was:

1. Observation of the crayfish behaviour for 90 min towards the prey. Latency time was the time from the introduction of prey to the first contact by the

crayfish. Handling time was the time spent by the crayfish to eat the prey.

- If the prey were not eaten, aquaria were checked after 24 h. If crayfish did not catch the prey, we assigned an arbitrary latency time of two days.

At the end of each test, sex and cephalothorax length of every experimental crayfish were recorded. Nine experiments were carried out, with twenty replicates per crayfish species per test; each specimen was used only once.

The experiments were distinguished into:

Experiment 1. Either one or three live tadpoles of *B. bufo* was/were offered to starved crayfish of both species to investigate the ‘confusion effect’ (Bertram 1978) on crayfish. According to the ‘confusion effect’ theory, a group of prey may confuse the predator, therefore reducing its success and decreasing the risk of the members of the group to be eaten (Bertram 1978).

Experiment 2. One live tadpole of *B. bufo* was offered to starved crayfish comparing experimental aquaria having either light or dark bottoms to test crayfish capability to capture a mimetic prey.

Experiment 3. One live tadpole of *B. bufo* was offered to starved crayfish to analyse the potential unpalatability of Bufonid tadpoles.

Experiment 4. Fifty eggs of *B. bufo* were offered to starved crayfish to assess their predatory pressure on them.

Experiment 5. One live larva of either *B. bufo* or *R. kl. esculenta* or *R. italica* or *T. vulgaris* were offered to starved crayfish to identify their eventual preference.

Experiment 6. Either one dead or live fry of *Salmo trutta fario* was offered to starved crayfish to understand their ability to prey on mobile animals like fish.

Experiment 7. Two live larvae of Limnephilidae were offered to starved crayfish.

Experiment 8. Three live *P. acuta* were offered to starved crayfish.

Experiment 9. Three live *P. corneus* were offered to starved crayfish.

Experiments 7, 8 and 9 were designed to test the ability of predators to identify unknown species or to form a potential ‘search image’ of familiar prey. Following the definition of Tinbergen (1960), a search image is the mental image of a prey that is possessed by an animal searching for that prey and that requires a continual reinforcement to be sustained.

Statistical analyses

Parametrical statistical techniques were used following Zar (1984), when the scores appeared to be drawn from a normally distributed population. Comparisons between species and among treatments were done using the Student’s *t*-test or a two-way ANOVA. Figures give mean values + standard error. The level of significance under which the null hypothesis was rejected is $\alpha = 0.05$.

Results

Experiment 1 (Figure 1)

The two starved crayfish required significantly more time in preying on one live *B. bufo* tadpole than three ones ($F = 4.716$, $df = 1,77$, $P = 0.033$), without any difference between crayfish species ($F = 1.291$, $df = 1,77$, $P = 0.2594$) and in the interaction ($F = 0.222$, $df = 1,77$, $P = 0.6386$). Handling time was significantly shorter in *P. clarkii* (one tadpole: 0.54 ± 0.07 min, $n = 15$; 3 tadpoles: 0.45 ± 0.08 min, $n = 18$) than in *A. italicus* (1 tadpole: 53.79 ± 40.59 min, $n = 16$; 3 tadpoles: 52.66 ± 30.42 min, $n = 18$) ($F = 4.122$, $df = 1,64$, $P = 0.0451$). No difference was found between the number of tadpoles ($F = 0.001$, $df = 1,64$,

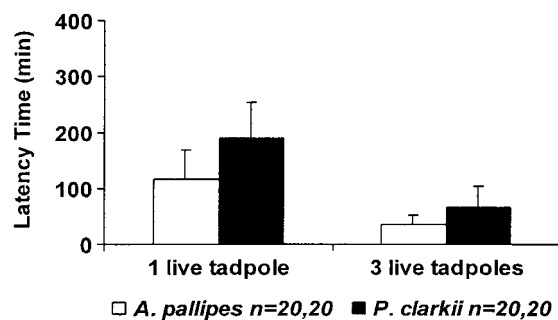


Figure 1. Time spent in capturing one or three live tadpoles of *B. bufo* by starved crayfish.

$P = 0.9810$) and in the interaction ($F = 0.001$, $df = 1, 64$, $P = 0.9843$).

Experiment 2 (Figure 2)

In the presence of one live *B. bufo* tadpole inside aquaria with light or dark bottoms, Latency time did not differ between crayfish species ($F = 0.005$, $df = 1,77$, $P = 0.9415$), between bottoms ($F = 0.437$, $df = 1,77$, $P = 0.5105$), and in the interaction ($F = 1.780$, $df = 1,77$, $P = 0.1861$). Similarly, handling time did not differ between predators ($F = 1.539$, $df = 1,60$, $P = 0.2197$), between bottoms ($F = 1.268$, $df = 1,60$, $P = 0.2646$), and in the interaction ($F = 1.505$, $df = 1,60$, $P = 0.2246$).

Experiment 3 (Figure 3)

All the individuals of both crayfish species consumed one live *B. bufo* tadpole.

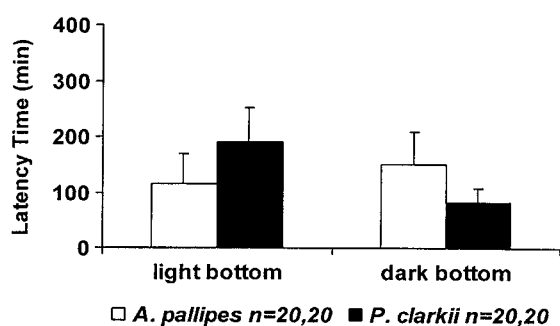


Figure 2. Time spent in capturing one live *B. bufo* tadpole by starved crayfish compared between experimental aquaria having either light or dark bottoms.

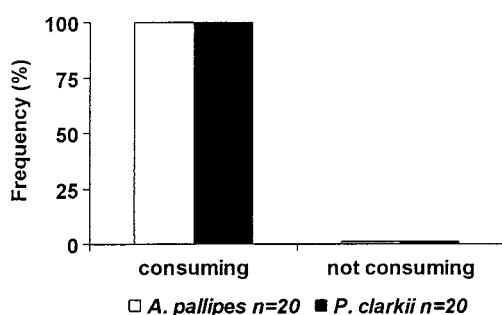


Figure 3. Consumption of one live tadpole of *B. bufo* by starved crayfish.

Experiment 4 (Figure 4)

Starved *P. clarkii* preyed on eggs faster than *A. italicus* (Student's t -test = 3.232, $df = 38$, $P = 0.0025$).

Experiment 5 (Figure 5)

Latency Time was longer for *A. italicus* than for *P. clarkii* to prey on *T. vulgaris* ($t = 4.107$, $df = 38$, $P < 0.0002$) and *R. kl. esculenta* ($t = 2.289$, $df = 38$, $P = 0.0277$), while it did not differ between crayfish species for *R. italica* ($t = 0.556$, $df = 38$, $P = 0.5817$) and *B. bufo* ($t = 0.896$, $df = 38$, $P = 0.3759$). Handling time was the same for the two predators in all the examined prey (*T. vulgaris*: $t = 0.918$, $df = 5$, $P = 0.4009$; *R. kl. esculenta*: $t = 0.577$, $df = 24$, $P = 0.5695$; *R. italica*: $t = 0.738$, $df = 11$, $P = 0.4760$; *B. bufo*: $t = 1.229$, $df = 29$, $P = 0.2291$).

Experiment 6 (Figure 6)

When presented with fry of *Salmo trutta fario*, no significant difference was found for latency time in *A. italicus* between one dead or live fry ($t = 0.072$, $df = 38$, $P = 0.9431$). On the other hand,

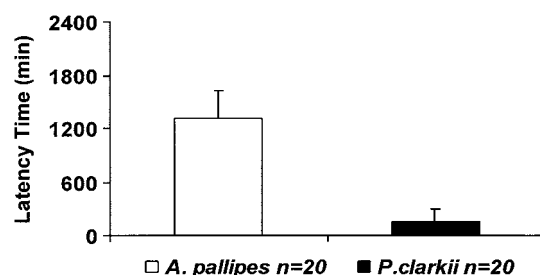


Figure 4. Time spent in capturing 50 eggs of *B. bufo* by starved crayfish.

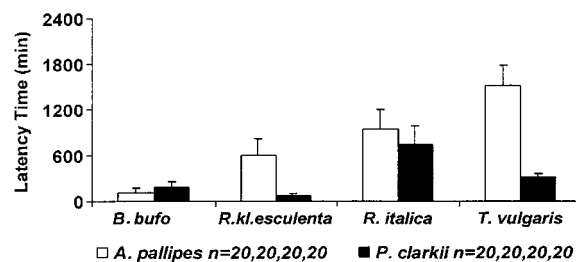


Figure 5. Time spent in capturing one live larva of either *B. bufo* or *R. kl. esculenta* or *R. italica* or *T. vulgaris* by starved crayfish.

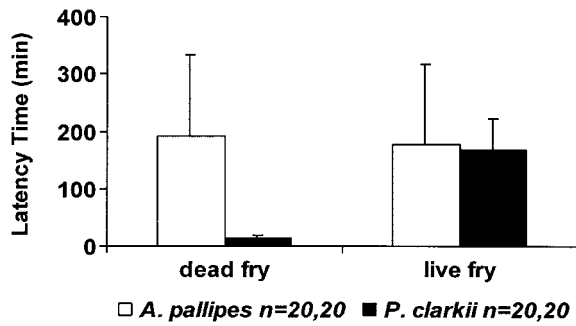


Figure 6. Time spent in capturing either one dead or live fry of *Salmo trutta fario* by starved crayfish.

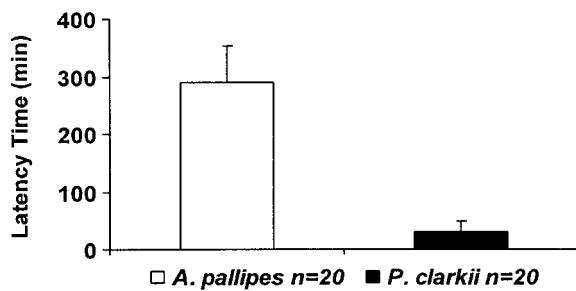


Figure 7. Time spent in capturing the first of two live larvae of Limnephilidae by starved crayfish.

P. clarkii preyed on dead fry faster than on live ones ($t = 2.625$, $df = 38$, $P = 0.0124$). However, on the overall, latency time did not differ between crayfish species ($F = 0.773$, $df = 1,77$, $P = 0.3820$). Handling time did not differ between conditions of fry ($F = 0.026$, $df = 1,64$, $P = 0.8724$), between predators ($F = 2.900$, $df = 1,64$, $P = 0.0934$), and in the interaction ($F = 0.015$, $df = 1,64$, $P = 0.9036$).

Experiment 7 (Figure 7)

Latency time was shorter in *P. clarkii* than in *A. italicus* when offered with larvae of Limnephilidae ($t = 3.799$, $df = 38$, $P < 0.0005$). Similarly, handling time was shorter in the non-indigenous species (5.07 ± 1.45 min, $n = 19$) than indigenous one (53.40 ± 25.40 min, $n = 10$) ($t = 2.516$, $df = 27$, $P = 0.0181$).

Experiment 8 (Figure 8)

Latency Time did not significantly differ between species when offered with *P. acuta* gastropods ($t = 1.140$, $df = 38$, $P = 0.2615$). Handling time was shorter in *P. clarkii* (5.97 ± 0.71 min, $n = 17$) than

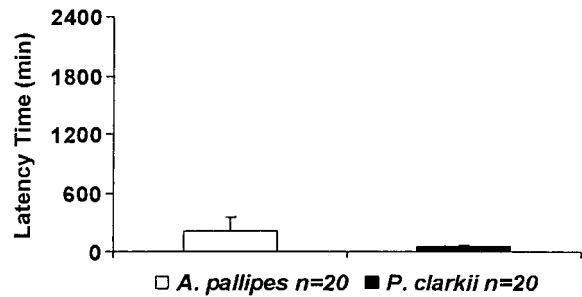


Figure 8. Time spent in capturing the first of three live gastropods of *P. acuta* by starved crayfish.

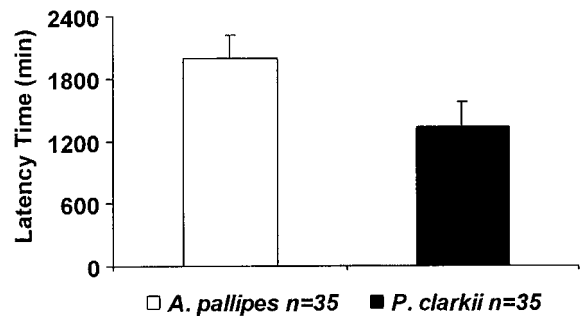


Figure 9. Time spent in capturing the first of three live gastropods of *P. corneus* by starved crayfish.

in *A. italicus* (88.51 ± 41.86 min, $n = 8$) ($t = 2.755$, $df = 23$, $P = 0.0113$).

Experiment 9 (Figure 9)

Twenty males and fifteen females per species were tested to evaluate whether sexes differed for latency time and handling time when offered with three *P. corneus* gastropods. No intersexual difference was found (*A. italicus* latency time: $t = 1.261$, $df = 33$, $P = 0.216$; handling time: $t = 0.015$, $df = 9$, $P = 0.988$; *P. clarkii* latency time: $t = 2.032$, $df = 33$, $P = 0.050$; handling time: $t = 0.053$, $df = 17$, $P = 0.958$). Moreover latency time ($t = 1.977$, $df = 68$, $P = 0.052$) and handling time ($t = 0.105$, $df = 28$, $P = 0.917$) did not differ between the two crayfish species.

Discussion

Predation on amphibian larvae

In Europe, the survival of amphibians is threatened by habitat loss and alteration and by the introduction of non-indigenous crayfish (Corbett 1989; Fog et al.

1997). The spread of *P. clarkii* in ephemeral habitats, where European indigenous crayfish are not able to survive, constitutes a risk for the amphibians breeding in these environments. In fact, the species with ineffective anti-predatory defence live in temporary ponds to avoid aquatic predators, such as fish (Skelly 1996). In the laboratory, Reynolds (1978) and Axelsson et al. (1997) observed that indigenous and non-indigenous European crayfish, like *A. pallipes* complex, *P. clarkii*, *Pacifastacus leniusculus*, and *Astacus astacus*, prey on amphibian larvae. Our experiments emphasised the ability of the first two predators to consume live tadpoles of *B. bufo* without any difference between species.

Amphibians have evolved anti-predator behaviours, like: reduction of mobility (Woodward 1983), cryptic colouration (Wassersug 1971), chemical repellents (Kruse and Francis 1977; Brodie et al. 1978), changes in activity pattern (Taylor 1983), and escape reactions to chemical cues produced by predators, and particularly by fish (Petranka et al. 1987). On the contrary, the mimetic colouration did not seem here to turn out an efficient system of defence, possibly because *A. italicus* and *P. clarkii* use a sit-and-wait predatory strategy or are able to recognise chemical cues emitted by tadpoles.

Bufonid tadpoles are usually avoided by predators with chewing mouthparts because of their unpalatability (Henrikson 1990), as observed by Axelsson et al. (1997) for *A. astacus* and *P. leniusculus*. On the contrary, *A. italicus* and *P. clarkii* were efficient predators, without need of producing sub-lethal damage (Figiel and Semlitsch 1991), such as cutting tails (Gamradt and Kats 1996). In addition, Gamradt and Kats (1996) showed that newt adults and eggs of *Taricha torosa* produced a tetrodotoxin poison and that this was a useful defence against indigenous predators. Tetrodotoxin was inefficacious against *P. clarkii* (Diamond 1996). Similar results were obtained in the present study that showed that eventual poisons produced by the amphibians we used had no effect on crayfish, since the tested individuals survived for at least a month.

Predator responses to a potential prey can vary in relation to its different developmental stage (Formanowicz and Brodie 1982; Denton and Beebee 1991). In Europe, *B. bufo* eggs, as well as tadpoles, are unpalatable for newts and invertebrates with chewing mouthparts (Kruse and Stone 1984; Henrikson 1990). Laboratory experiments by Axelsson et al. (1997) showed that *A. astacus* and *P. leniusculus* did not eat *B. bufo* eggs. On the contrary, *P. clarkii* and *A. italicus* are able to feed on *B. bufo* eggs and the

non-indigenous species is a more voracious predator on them. Both predators handled the prey and separated eggs from the protective gelatin that they avoided.

Aggregations of *B. bufo* tadpoles that might produce a 'confusion effect' were not efficacious against predators. On the contrary, the density of prey increased the speed of capture, possibly because crayfish use a sit-and-wait predatory strategy. Furthermore, the non-indigenous species was faster to handle prey than the indigenous one, without any difference between the number of tadpoles.

A comparison of the latency time to capture the four amphibian larvae tested here showed that *A. italicus* captured live larvae of *T. vulgaris*, living in lentic waters, slower than *P. clarkii*, while the non-indigenous species required more time to prey on tadpoles of *R. italica* living in lotic waters. Therefore, both predators seem to have a 'search image' of species they are familiar to and are able to capture these prey faster.

Predation on Salmo trutta fario fry

Rubin and Svensson (1993) and Guan and Wiles (1997) reported that some crayfish are able to produce damage to the fish directly with their predatory activity, even if capture is nearly exclusively limited to eggs (Savino and Miller 1991; Xinya 1995). Moreover these predators, like *Orconectes rusticus*, can alter habitat through cropping macrophytes, where macro-invertebrates live (Lodge and Lorman 1987), reducing the trophic resources for fish. However, crayfish cannot capture mobile animals (D'Abramo and Robinson 1989), often preferring detritus (Ilhéu and Bernardo 1993b).

Lowery and Mendes (1977) demonstrated that the opportunistic *P. clarkii* preferred animal food when it consisted of dead, dying, or immobilised fish. Within the frame of foraging theory, this behaviour can be interpreted in terms of cost-benefit ratios (Schoener 1971). Adult crayfish prefer animal food, but choose different foraging strategies according to the costs of their predatory activity (Ilhéu and Bernardo 1993b). In agreement with Lowery and Mendes (1977) and Ilhéu and Bernardo (1993b), *P. clarkii* required less time to capture dead fry than live ones. In contrast, in *A. italicus* latency time did not differ for the two conditions of fry.

Predation on macro-invertebrates

In 40 Swedish ponds, Nyström et al. (1996) observed that a high density of *P. leniusculus*

influenced the invertebrates associated with macrophytes, especially those equipped with weak escape reactions (gastropods, leeches, and mussel *Pisidium*) (Nyström et al. 1996; Nyström and Granély 1996). The composition of macro-invertebrates favoured sediment-dwelling taxa, like oligochaetes, chironomids, and Sialidae or alderflies (*Sialis* sp.), and skilful swimmers, like Ephemeroptera (mayflies), Coleoptera, Odonata, Heteroptera, and *Gammarus* sp. (Nyström et al. 1996, 1999). Abrahamsson (1966) and Nyström (1999), in agreement with Nyström et al. (1996), found a similar community in the presence of *A. astacus* and *P. leniusculus*.

Nyström et al. (1996) observed that *P. leniusculus* did not prey on microcaddisfly larvae because of the difficulty to manipulate their large sheaths constructed with sand grains, while the small *Triaenodes* sp. (using small pieces of fresh macrophytes to build mobile shelters) was easily consumed. Experiments conducted by Charlebois and Lamberti (1996) on the benthic community in Middle Branch in Wisconsin showed that some species were frequently avoided by *O. rusticus*, like the microcaddisfly *Leucotrichia*, which builds a silken case tightly appressed to the rock surface. The architecture of the sheath guarantees protection (Charlebois and Lamberti 1996).

In agreement with the majority of other field studies, we showed that *A. italicus* and *P. clarkii* are both able to prey on larvae of microcaddisflies. The non-indigenous crayfish was more able to capture and handle this prey than the indigenous species. This result underlines the plasticity of *P. clarkii*'s feeding behaviour, the non-indigenous species being able to consume an unknown prey like microcaddisflies living in lotic waters typical of *A. italicus*. On the contrary, the indigenous predator consumed these larvae, probably recognising them through chemical or visual cues (O'Keeffe 1986).

Predation on gastropods

Many studies hypothesise that molluscs are the favourite prey of *P. clarkii* (Covich et al. 1980; Ilhéu and Bernardo 1993b) and of its congeners. Ilhéu (1991) and Ilhéu and Bernardo (1993b) observed that Planorbidae in Alentejo (Portugal) are the highest percentage of invertebrates contained in the stomachs of *P. clarkii*. In the National Park of Doñana (Spain), Montes et al. (1993) demonstrated the influence of *P. clarkii* on aquatic ecosystems by preying on several gastropods species. On the contrary, in temporary

swamps of the same area, Gutiérrez-Yurrita et al. (1998) did not record any predation by crayfish on molluscs, but laboratory studies showed that *P. clarkii* preferred these prey with respect to other food items (Gutiérrez-Yurrita 1997). This preference has been interpreted like a mean to obtain calcium (Ilhéu and Bernardo 1993b). In the laboratory, the majority of *P. corneus* survived in the presence of both *A. italicus* and *P. clarkii*.

In agreement with Covich et al. (1980) and Warner (1995), crayfish used their second and third pairs of walking legs, maxillipeds, and mandibles to eat the prey, unlike to marine crabs that use chelae to break-off and to consume gastropods (e.g., Zipser and Vermeij 1978; Cunningham and Hughes 1984). The behaviour displayed by *A. italicus* and *P. clarkii* towards *P. corneus* is similar to that described for *P. leniusculus* towards thin *Lymnaea peregra* and *L. stagnalis* molluscs (Warner 1995), and for both *Cambarus bartonii* and *P. clarkii* towards *Corbicula* (Covich et al. 1980). Also in these cases, chelae did not have a primary role.

The results of our experiments with *P. corneus* showed that this prey was not favoured by both predators, although in nature plano-spiral molluscs, like this, are preferred by crayfish (Lodge et al. 1998). Probably, the thickness of the shell, more than the shape, influenced the choice of the prey by *A. italicus* and *P. clarkii*. Indeed, both crayfish species showed high predatory ability towards the thin and spiralled *P. acuta*, but the non-indigenous predator was faster to handle this gastropod.

Conclusions

These laboratory experiments allowed us to estimate the trophic preference of *A. italicus* and *P. clarkii* and provided a contribution to the knowledge of the feeding ecology of the non-indigenous species and of its potential effects on freshwater communities. Some of our results can be explained by the potential of the two crayfish to create a 'search image' of the familiar prey. Future researches will be directed to analyse the actual ability of crayfish to hunt by 'search images' and to switch their 'search image' formation from familiar to novel prey.

Both predators were able to prey on species with fast escape reactions like amphibian larvae and trout fry and their capture was not made easier by producing

sub-lethal damage (Figiel and Semlitsch 1991). Possibly, the ability of *A. italicus* and *P. clarkii* to capture mobile prey is related to the adopted sit-and-wait strategy, which seems to thwart the 'confusion effect' (Bertram 1978). On the contrary, the density of prey increased the speed of capture of both predators, at least when the potential prey are *B. bufo* tadpoles. Moreover, anti-predator defences, such as their unpalatability, were ineffective to both crayfish species that not only were able to consume *B. bufo* tadpoles, but also survived for at least a month after the capture. Also, dark bottoms did not seem to prevent crayfish to capture *B. bufo* tadpoles (that are apparently mimetic on that background), possibly because these crayfish are able to recognise prey from their odours. Additional experiments should confirm this hypothesis.

Further studies are certainly needed to assess the impact of *P. clarkii* on natural habitats. However, our work showed the wide potential of this species as a predator. The predatory ability of this and other non-indigenous crayfish has been considered by other authors as one of the factors responsible for the rapid decrease of biodiversity in aquatic communities (Lodge et al. 1985; Holdich 1987; Olsen et al. 1991).

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References

- Abrahamsson SAA (1966) Dynamics of an isolated population of the crayfish *Astacus astacus*. *Linnè-Oikos* 17: 96–107
- Ackefors H (1999) The positive effects of established crayfish introductions in Europe. *Crustacean Issues* 11: 281–292
- Avault JW Jr, Romaire RP and Miltner MR (1981) Feeds and forages for red swamp crayfish, *Procambarus clarkii*: 15 years research at Louisiana State University. Reviewed. *Freshwater Crayfish* 5: 362–369
- Axelsson EP, Nyström P, Didenmark J and Brönmark C (1997) Crayfish predation on amphibian eggs and larvae. *Amphibia-Reptilia* 18: 217–228
- Ballasina D (1984) *Amphibians of Europe: A Colour Field Guide*. David & Charles, London
- Bertram BCR (1978) Living in groups: predators and prey. In: Krebs JR and Davies NB (eds) *Behavioural Ecology. An Evolutionary Approach*, pp 64–96. Blackwell Scientific Publications, Oxford
- Brodie ED Jr, Formanowicz DR Jr and Brodie ED III (1978) The development of noxiousness of *Bufo americanus* tadpoles to aquatic insect predators. *Herpetologica* 34: 302–306
- Charlebois PM and Lamberti GA (1996) Invading crayfish grazing in Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. *Journal of the North American Benthological Society* 15: 551–563
- Corbett K (1989) *Conservation of European Reptiles and Amphibians*. London, Christopher Helm
- Covich AP, Dye LL and Mattice JS (1980) Crayfish predation on *Corbicula* under laboratory conditions. *American Midland Naturalist* 105: 181–188
- Cunningham PN and Hughes RN (1984) Learning of predatory skills by shorecrabs, *Carcinus maenas*, feeding on mussels and dogwhelks. *Marine Ecology Progress Series* 16: 21–26
- D'Abramo LR and Robinson EH (1989) Nutrition of crayfish. *Reviews in Aquatic Sciences* 1: 711–728
- Denton T and Beebe TJ (1991) Palatability of anuran eggs and embryos. *Amphibia-Reptilia* 12: 111–112
- Diamond JM (1996) A-bomb against amphibians. *Nature* 383: 386–387
- Duellman WE and Trueb L (1994) *Biology of Amphibians*. The Johns Hopkins University Press, Baltimore and London
- Figiel CR Jr and Semlitsch RD (1991) Effects of nonlethal injury and habitat complexity on predation in tadpole populations. *Canadian Journal of Zoology* 69: 830–834
- Fog K, Schmedes A and Rosenørn de Lasson D (1997) *Nordens padder og krjbdjr*. G.E.C. Gad København, 365 pp
- Formanowicz DR Jr and Brodie ED Jr (1982) Relative palatabilities of members of a larval amphibian community. *Copeia* 1982: 91–97
- Foster J and Slater FM (1995) A global review of crayfish predation with observations on the possible loss of *Austropotamobius pallipes* in the Welsh wye due to crayfish plague. *Freshwater Crayfish* 8: 589–613
- Gamradt SC and Kats LB (1996) Effect of introduced crayfish and mosquitofish on California newts. *Conservation Biology* 10: 1155–1162
- Gherardi F and Barbaresi S (2000) Invasive crayfish: activity patterns of *Procambarus clarkii* in the rice fields of the Lower Guadalquivir (Spain). *Archiv für Hydrobiologie* 150: 153–168
- Gherardi F, Acquistapace P and Santini G (2004) Food selection in omnivores: a case study of *Austropotamobius pallipes*. *Archiv für Hydrobiologie* (in press)
- Gherardi F, Baldaccini GN, Barbaresi S, Ercolini P, De Luise G, Mazzoni D and Mori M (1999) In: Gherardi F and Holdich DM (eds) *Crayfish in Europe as Alien Species: How to Make the Best of a Bad Situation?*, pp 107–128. A.A. Balkema, Rotterdam, the Netherlands
- Gherardi F, Acquistapace P, Hazlett BA and Whisson G (2002) Behavioural responses to alarm odours indigenous and non-indigenous crayfish species: a case study from Western Australia. *Marine & Freshwater Research* 53: 93–98
- Girod A, Bianchi I and Mariani M (1980) *Gastropoda, Pulmonata, Prosobranchia, Neritidae, Viviparidae, Bythyniidae, Valvatidae*. Guide per il riconoscimento delle specie animali delle acque interne, vol. 7, AQ/1/44. Consiglio Nazionale delle Ricerche, Rome
- Grandjean F, Harris DJ, Souty-Grosset C and Crandall KA (2000) *Systematic of the European endangered crayfish species*

- Austropotamobius pallipes* (Decapoda: Astacidae). Journal of Crustacean Biology 20(3): 522–529
- Greenhalgh M (1999) Freshwater Fish. Mitchell Beazley, London
- Guan R and Wiles PR (1997) Ecological impact of introduced crayfish on benthic fishes in a British lowland river. Conservation Biology 11(3): 641–647
- Gutiérrez-Yurrita PJ (1997) El papel ecológico del cangrejo rojo de la marisma *Procambarus clarkii* (Crustacea: Decapoda: Cambaridae), en el Parque Nacional de Doñana. Una perspectiva bioenergética con implicaciones en la gestión. PhD thesis, Facultad de Ciencias Universidad Autónoma de Madrid, Madrid, Spain
- Gutiérrez-Yurrita PJ, Sancho MA, Baltanàs A and Montes C (1998) Diet of the red swamp crayfish *Procambarus clarkii* in natural ecosystems of the Doñana National Park temporary freshwater marsh (Spain). Journal of Crustacean Biology 18: 120–127
- Hazlett BA (2000) Information use by an invading species: do invaders respond more to alarm odors than native species? Biological Invasions 2: 289–294
- Henrikson BI (1990) Predation on amphibian eggs and tadpoles by common predators in acidified lakes. Holarctic Ecology 13: 201–206
- Herbert H Ross (1948) A Textbook of Entomology. John Wiley, New York/Chapman & Hall, London
- Hobbs HH, Jass JP and Huner JV (1989) A review of global crayfish introductions with particular emphasis on two North American species (Decapoda Cambaridae). Crustaceana 56: 299–316
- Holdich DM (1987) The danger of introducing alien animals with particular reference to crayfish. Freshwater Crayfish 7: 15–30
- Huner JV and Barr JE (1991) Red Swamp Crayfish, Biology and Exploitation. 3rd revised edition. – Louisiana Sea Grant College Program, pp 1–36. Baton Rouge, Louisiana
- Huner JV and Meyers SP (1979) Dietary protein requirements of the red crayfish *Procambarus clarkii* (Girard) (Decapoda, Cambaridae), grown in a closed system. Proceedings of the World Mariculture Society 10: 751–760
- Ilhéu M (1991) Aspectos da ecologia trófica do lagostim vermelho da Louisiana (*Procambarus clarkii* Girard). Dissertation for Zootechnical Degree, University of Evora, Portugal, 129 pp
- Ilhéu M and Bernardo JM (1993a) Aspects of trophic ecology of red swamp crayfish (*Procambarus clarkii* Girard) in Alentejo, South Portugal. Actas VI Congreso Español de Limnología Granata, Mayo de 1993, pp 417–423
- Ilhéu M and Bernardo JM (1993b) Experimental evaluation of food preference of red swamp crayfish, *Procambarus clarkii*: vegetal versus animal. Freshwater Crayfish 9: 359–364
- Kruse KC and Francis MG (1977) A predation deterrent in larvae of the bullfrog, *Rana catesbeiana*. Transactions of the American Fisheries Society 106: 248–252
- Kruse KC and Stone BM (1984) Large mouth bass (*Micropterus salmoides*) learn to avoid feeding on toad (*Bufo*) tadpoles. Animal Behaviour 32: 1035–1039
- Lanza B (1983) Guide per il riconoscimento delle specie animali delle acque interne italiane. 27. Anfibi, Rettili. (Amphibia, Reptilia). Consiglio Nazionale delle Ricerche, Rome
- Largiadèr CR, Herger F, Lörtscher M and Choll A (2000) Assessment of natural and artificial propagation of the white-clawed crayfish (*Austropotamobius pallipes* species complex) in the Alpine region with nuclear and mitochondrial markers. Molecular Ecology 9: 25–37
- Lindqvist OV and Huner JV (1999) Life history characteristics of crayfish: What makes some of them good colonizers? In: Gherardi F and Holdich DM (eds) Crayfish in Europe as alien species. How to make the best of a bad situation? pp 23–30. A.A. Balkema, Rotterdam, the Netherlands
- Lodge DM and Lorman JG (1987) Reductions in submerged macrophyte biomass and species richness by the crayfish *Orconectes rusticus*. Canadian Journal of Fisheries and Aquatic Sciences 44: 591–597
- Lodge DM, Beckel AL and Magnuson JJ (1985) Lake-bottom tyrant. Natural History 94: 32–37
- Lodge DM, Stein RA, Brown KB, Covich AP, Bronmark C, Garvey JE and Klosiewski SP (1998) Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. Australian Journal of Ecology 23: 53–67
- Lowery RS and Holdich DM (1988) *Pacifastacus leniusculus* in North America and Europe, with details of the distribution of introduced and native crayfish species in Europe. In: Holdich DM and Lowery RS (eds) Freshwater Crayfish: Biology, Management and Exploitation, pp 283–308. Croom Helm, London
- Lowery RS and Mendes AJ (1977) *Procambarus clarkii* in Lake Naivasha, Kenya, and its effects on established and potential fisheries. Aquaculture 11: 111–121
- Momot WT (1995) Redefining the role of crayfish in aquatic ecosystems. Reviews in Fisheries Science 3(1): 33–63
- Montes C, Bravo-Utrera MÁ, Baltanàs C, Duarte Á and Gutiérrez-Yurrita PJ (1993) Bases ecológicas para la gestión del cangrejo rojo de las marismas en el Parque Nacional de Doñana. Instituto Nacional para la Conservación de la Naturaleza (ICONA), Spain, 270 pp
- Nyström P (1999) Ecological impact of introduced and native crayfish on freshwater communities: European perspectives. In: Gherardi F and Holdich DM (eds) Crayfish in Europe as Alien Species: How to Make the Best of a Bad Situation? pp 63–85. A.A. Balkema, Rotterdam, the Netherlands
- Nyström P (2002) Ecology. In: Holdich DM (ed) Biology of Freshwater Crayfish. School of Life and Environmental Sciences, pp 192–235. University of Nottingham, Nottingham, UK
- Nyström P and Granéli W (1996) The effect of food availability on survival, growth activity and the number of mature females in crayfish populations. Freshwater Crayfish 11: 170–181
- Nyström P, Brönmark C and Granéli W (1996) Patterns in benthic food webs: a role for omnivorous crayfish? Freshwater Biology 36: 631–646
- Nyström P, Brönmark C and Granéli W (1999) Influence of an exotic and a native crayfish species on a littoral benthic community. Oikos 85: 545–553
- O’Keeffe C (1986) The ecology of two populations of the freshwater crayfish *Austropotamobius pallipes* (Lereboullet) in Ireland. PhD thesis, Department of Zoology, University of Dublin, Ireland, 254 pp
- Olsen TM, Lodge DM, Capelli GM and Houlihan R (1991) Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners snails and macrophytes. Canadian Journal of Fisheries and Aquatic Sciences 48: 1853–1861

- Petranka JW, Kats LB and Sih A (1987) Predator–prey interactions among fish and larval amphibians: use of chemical cues to detect predatory fish. *Animal Behaviour* 35: 420–425
- Reynolds JD (1978) Crayfish ecology in Ireland. *Freshwater Crayfish* 4: 215–220
- Rubin JF and Svensson M (1993) Predation by the noble crayfish, *Astacus astacus* (L.), on emerging fry of sea trout, *Salmo trutta* (L.). *Nordic Journal of Freshwater Research* 68: 100–104
- Savino JF and Miller JE (1991) Crayfish (*Orconectes virilis*) feeding on young lake trout (*Salvelinus namaycush*): effect of rock size. *Journal of Freshwater Ecology* 6: 161–170
- Schoener TW (1971) Theory of feeding strategies. *Annual Review of Ecology and Systematics* 2: 369–403
- Skelly DK (1996) Pond drying, predators, and the distribution of *Pseudacris* tadpoles. *Copeia* 1996: 599–605
- Taylor JT (1983) Orientation and flight behaviour of a neotenic salamander (*Ambystoma gracile*) in Oregon. *American Midland Naturalist* 109: 40–49
- Tinbergen L (1960) The natural control of insects in pine woods. I. Factors influencing the intensity of predation in song birds. *Archives Neerlandaises de Zoologie* 13: 265–343
- Unestam T (1969) Resistance to the crayfish plague in some American, Japanese and European crayfishes. Institute of Freshwater Research, Drottningholm, Report 49: 202–209
- Warner GF (1995) Choice and consumption of aquatic weeds by signal crayfish (*Pacifastacus leniusculus*). *Freshwater Crayfish* 8: 360–363
- Wassersug RJ (1971) On the comparative palatability of some dry-season tadpoles from Costa Rica. *American Midland Naturalist* 86: 101–109
- Westman K (1985) Effects of habitat modification on freshwater crayfish. In: Alabaster JS (ed) *Habitat Modification and Freshwater Fisheries* (EIFAC Symp.) Butterworth, London
- Woodward BD (1983) Predatory–prey interactions and breeding-pond use of temporary-pond species in a desert anuran community. *Ecology* 64: 1549–1555
- Xinya S (1995) Effect of the crayfish *Procambarus clarkii* on the survival of the fry and fingerlings of fishes cultivated in China. *Freshwater Crayfish* 8: 528–532
- Zar JH (1984) *Biostatistical Analysis*, Prentice Hall, Englewood Cliffs, New Jersey
- Zipser E and Vermeij GJ (1978) Crushing behaviour of tropical and temperate crabs. *Journal of Experimental Marine Biology and Ecology* 31: 155–172