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# Impact of an introduced Crustacean on the trophic webs of Mediterranean wetlands

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## Abstract

Based on a review and our own data, we present an overview of the ecological impacts on the trophic web of Mediterranean wetlands by an introduced Decapod Crustacean, the red swamp crayfish (*Procambarus clarkii*). *P. clarkii* lacks efficient dispersal mechanisms but is very well adapted to the ecological conditions of Mediterranean wetlands (fluctuating hydroperiods with regular intervals of drought). As an opportunistic, omnivorous species, which adapts its ecology and life history characteristics, such as timing and size at reproduction to changing environmental conditions, it became readily established in most of the Mediterranean wetland environments. High reproductive output, short development time and a flexible feeding strategy are responsible for its success as an invader. Like most crayfish, it occupies a keystone position in the trophic web of the invaded system and interacts strongly with various trophic levels. It efficiently grazes on macrophytes and is one of the main factors, besides the impact of flamingos, cattle and introduced fish, of the change of many water bodies from a macrophyte dominated, clear water equilibrium to a phytoplankton driven turbid water balance. Juveniles feed on protein rich animal food with the corresponding impact on the macroinvertebrate community in competition with other crayfish or fish species. At the same time, it serves as a prey for mammals, birds and fish. Due to its predatory and grazing activity, it efficiently canalises energy pathways reducing food web complexity and structure. Feeding also on detritus it opens, especially in marshlands, the detritic food chain to higher trophic levels which results in an increase of crayfish predators. As a vector of diseases, it has a severe impact on the preservation and reintroduction of native crayfish. *P. clarkii* accumulates heavy metals and other pollutants in its organs and body tissues and transmits them to higher trophic levels. Due to the long history of its presence, the complex interactions it established within the invaded ecosystems and the socio-economic benefits it provides to humans, prevention and control seem the most promising management measures to reduce the negative impact of this crayfish species.

## Introduction

Biological invasions and their negative impact on resident communities and ecosystem functioning are considered one of the major threats to biodiversity. Mediterranean ecosystems in particular have a long history of biological invasions be they anthropogenic or non-anthropogenic in origin (Di Castri 1990). Especially threatened are Mediterranean wetlands, which have to suffer the consequences of invasions and of anthropogenic alterations and transformations leading to habitat destruction and very often to their complete disappearance. Despite that these wetlands are second only to rainforests as reservoirs of biodiversity and productivity and are ranked second to estuaries in terms of ecosystem services provided to human welfare (Costanza et al. 1997) they have become only recently the object of increased protection.

Wetland ecosystems are characterised by high biodiversity and complex trophic interactions. Such systems are thought to be less vulnerable to invasions (Sakai et al. 2001), but recent studies have shown that the length of disturbance-free periods is equally important (Shea and Chesson 2002). Disturbance tends to disrupt existing interaction among species and opens new niches for potential invaders. Levels of both anthropogenic and non-anthropogenic disturbances in wetlands are high. A further characteristic of Mediterranean wetlands is the existence of frequent, regular periods of drought, which protects them against most of the invaders.

The impact of an invader also depends on its position in the trophic web of the invaded ecosystem. Species with strong interactions or which are keystone species in the sense of Power and Tilman (1996) will have a larger impact than species with weak or few interactions. Equally, species interacting with several trophic levels affect ecosystem structure and function more intensively than those which interact with a single trophic level. The removal of a species which has already established tight trophic links with native species might produce unpredictable secondary effects on the invaded community. Therefore, an understanding of the invader's role within the trophic web is crucial not only for predictive purposes but also for estimating the consequences of management measures.

Crayfish have been introduced in many water bodies for a long time. Omnivorous and highly active, they are known to occupy keystone positions in both their natural and host ecosystems (Holdich 2002). Therefore, the impact and changes they cause on natural ecosystems once introduced are expected to be high. Nevertheless, they lack efficient systems of dispersal such as easily transported resting eggs or highly mobile larval stages, and their natural potential of dispersal is low in comparison to plants or invertebrate species such as insects or molluscs. However, man has played a crucial role in helping crayfish to overcome this disadvantage by continuous translocations across natural boundaries. Once translated, crayfish establish stable populations followed by rapid range expansion within the invaded watershed.

In what follows, we will try to give an overview based on a literature review and our own studies on the manyfold impacts of an introduced crayfish species – the red swamp crayfish *Procambarus clarkii* – on the natural ecosystems of Mediterranean wetlands.

## The biological basis of invasiveness – the example of the red swamp crayfish *Procambarus clarkii*

Successful invaders are characterised by a number of biological and ecological features determining both the process of dispersion and the establishment in the new habitat (Table 1). Although most likely none of the species possesses all of these traits, it is evident that the more they have these traits, the higher their invasive potential is. In the case of *P. clarkii*, not all of these characteristics are equally well expressed. Natural dispersal ability across drainage basins is low, despite the mobility of adults, but this handicap is largely offset by human transport. Although it does not reproduce asexually nor parthenogenetically – but see the recent description of a close parthenogenetic relative in Germany (Scholtz et al. 2002) –

*Table 1.* Biological and ecological characteristics of successful invaders (Baker 1974) shared by *P. clarkii* (– absent; + low; ++ medium; +++ high).

| Biological characteristics of invaders | *Procambarus clarkii* |
|---|---|
| High dispersal capability through seeds, eggs or highly mobile larval stages | + |
| Ability to reproduce both sexually and asexually | – |
| High fecundity | ++ |
| Short generation and juvenile development times | ++ |
| Fast adaptation to environmental stress | +++ |
| High tolerance to environmental heterogeneity | +++ |
| Desirability to and association with humans (edibility, game species) | +++ |
| *Additional features* | |
| Omnivory | +++ |
| Brood care | +++ |

high reproductive investment of both males (spermatophore production) and females (high egg numbers) increases reproductive success (Gherardi 2002). The species is amongst the most prolific crayfish with more than 600 eggs/females. It reproduces more than once per year if conditions are favourable and adapts its size at maturity to environmental conditions (hydroperiod, food conditions). Newly hatched juveniles are carried by their mothers during the period where they are most vulnerable to predation and reach maturity within several months.

Environmental conditions in the home area of *P. clarkii* are similar to those encountered in Mediterranean wetlands both characterised by regular periods of drought, and this species is very well adapted to withstand these periods in burrows, where they also bear their offspring.

*P. clarkii* is an opportunistic, omnivorous feeder which readily accepts new food items another advantage when arriving in a new habitat. For these characteristics, which result in easy culturing and high yields, it is prized by humans as a food source, used for baiting and as a laboratory animal and pet. Therefore, it is not astonishing that such a productive species is also a successful invader.

## The history of introduction and expansion of *P. clarkii* in Europe and Spain

Crayfishing in Europe for human consumption has been a deep-rooted habit in most parts of the continent. For this reason, traditional management of native crayfish populations through additions and translocations of native species was common. Because overexploitation of this resource extinguished some of the populations, the introduction of exotic species during the XIX century was considered as a possible solution to restore crayfish populations (Lodge et al. 2000a). At least seven species of non-native crayfish have been introduced in Europe since then: five of them were introduced from North America (*Pascifastacus leniusculus, Orconectes limosus, O. immunis, Procambarus clarkii, P. zonangulus*), one from Australia (*Cherax destructor*) and, finally, one from eastern Europe (*Astacus leptodactylus*) (Hobbs 1988; Diéguez-Uribeondo 1998).

But overexploitation by fishing for recreational or commercial purposes is not the only cause of the dramatic decrease of native European crayfish populations, which led in some cases to their extinction. Anthropogenic alteration of river ecosystem quality due to contamination, the alteration of riverine vegetation or riverbed dredging (Alderman and Polglase 1988; Taugbol et al. 1993) the introduction of exotic species, carriers of diseases (Smith and Söderhäll 1986; Taugbol and Skurdal 1993; Diéguez-Uribeondo et al. 1997; Holdich 1997, 1999a) and competitors of native crayfish for shelter and food (Hill and Lodge 1999) contributed substantially to the decline of native crayfish.

One of the most widespread diseases carried by introduced crayfish from North America is a fungal plague called *aphanomicosis*, produced by the oomycete fungus *Aphanomyces astaci*, which is endemic to many North American crayfish but lethal to European crayfish (Unestam 1972; Diéguez-Uribeondo et al. 1995; Alderman 1996). Ironically, the extirpation of native European crayfish by the plague has increased the number of subsequent introductions of North American crayfish (*Orconectes limosus, O. immunis, Pacifastacus leniusculus* and *Procambarus clarkii*) into more than 20 European countries to replace the native stocks (Lodge et al. 2000a).

The introduction of red swamp crayfish (*Procambarus clarkii*), the subject of this review, in Europe is a very well documented example of the quick expansion of an alien species. It was first introduced in 1973 in Spain in two aquaculture installations located in Sevilla (Lower Guadalquivir River Basin, southwestern Spain) and Badajoz (southwestern Spain) (Habsburgo-Lorena 1983). The aim of the introduction was twofold: On the one hand, there were economic arguments; it was an attempt to improve the economy of an impoverished area by developing crayfish commercialisation plans. On the other hand, it was erroneously thought that the introduction of a non-native species into an area without native crayfish would cause no ecological problems, because the red swamp crayfish would occupy a new empty niche. The fact is, that, in only three decades, red swamp crayfish became widespread throughout the Mediterranean region and Europe. Several factors, all of them linked to human activity such as the increasing economic importance of *P. clarkii*, its *in vivo* commercialisation and repeated translocations for economical or recreational purposes, are responsible for its rapid spread. From southwestern Spain, *P. clarkii* populations expanded to the rest of the country including the Balearic (Majorca: (Hobbs et al. 1989)) and Canary Islands (Gutiérrez-Yurrita and Martínez 2002) and to Europe: Portugal (Ramos and Pereira 1981; Correia 1992; Adao and Marques 1993), Azores Islands (Correia and Costa 1994), Cyprus (Hobbs et al. 1989), United Kingdom (Holdich 1999b), France (Arrignon et al. 1999), Italy (Gherardi et al. 1999), Netherlands (Hobbs et al. 1989) and Switzerland (Stucki 1997; Stucki and Staub 1999).

## Effects of alien crayfish in food webs – general aspects

In many ecosystems, crayfish occupy a central position in the trophic web acting as both predator and prey. As opportunistic, omnivorous feeders, they include in their diet submerged macrophytes, algae, invertebrates and detritus (Lodge and Hill 1994; Momot 1995; Gutiérrez-Yurrita et al. 1998). In the words of Huner (1981), 'They eat any insect, crustacean, molluscs (especially snails), or annelid worm they can catch.'

Invasive crayfish species clear macrophyte beds thereby altering the ecosystem characteristics such as habitat heterogeneity (Lodge and Lorman 1987; Lodge et al. 2000b) or the composition of invertebrates associated with macrophytes. In addition, they feed directly on many invertebrate species, reducing their abundances (Nyström et al. 1996; Perry et al. 1997).

Crayfish diet is reported to change with body size. Small crayfish are mainly carnivorous, and larger individuals are primarily herbivorous (Abrahamsson 1966; Lorman and Magnuson 1978). This ontogenetic shift has also been observed in red swamp crayfish. Animal food is much more important for young, rapidly growing juveniles than for adults (Marçal-Correia 2003). Since crayfish cannot swim, foraging they concentrate on the bottom or benthic zone. However, some individuals, especially young ones, can catch planktonic organisms with their mouth parts acting as a filter. Living green plant material, an important source of dietary carotenoids (Huner 1981), also forms part of the red crayfish's diet. Other studies postulate that the principal food of the red crayfish is plant detritus (Lorman and Magnuson 1978). Once dead, submerged plants quickly become covered with a layer of living bacteria and fungi which use the dead plant material as an energy source. The dead plant material itself is of little energetic value to the red crayfish, but not so the rich protein layer of bacteria and fungi (Cronin 1998).

Besides these effects on lower trophic levels (top-down effect), they also serve as a prey to higher trophic levels (bottom up effect), and they are also known to compete with fish and other crayfish species for food (Momot 1995).

In the following chapters, we would like to examine in detail the impact of the introduced red swamp crayfish on the different trophic levels of the invaded ecosystems

## Impacts of *P. clarkii* on macrophytes

### *Crayfish feeding and macrophytes*

Several studies have demonstrated that crayfish consume freshwater macrophytes, with plants often accounting for over 75% of the diet (King 1883; Chidester 1908; Tack 1941; Momot 1967; Prins 1968). They are common and important omnivores which consume a lot of living plant tissue and detritus when favoured animal prey is not available (Momot 1995). Crayfish can reduce (Abrahamsson 1966; Rickett 1974; Saiki and Tash 1979; Carpenter and Lodge 1986; Feminella and Resh 1986), or eliminate submerged vegetation from the littoral zone of many lakes and ponds whether they are native (Dean 1969) or have been introduced (Lorman and Magnuson 1978, Chambers et al. 1990). Some species of crayfish are also considered to be large-bodied grazers with both low numerical and biomass density and large effects on filamentous alga (*Cladophora*). Grazer exclusion experiments with large *Orconectes propinquus* resulted in an algae biomass increase of an order of magnitude (Creed 1994). Little quantitative information exists about the relationship between introduced crayfish species density and macrophyte biomass or species composition (Appendix 1). However, some conclusions can be derived from biomanipulation experiments conducted in mesocosms – for example, that crayfish consumption of submerged macrophytes is species-selective and also density-dependent (Lodge and Lorman 1987; Chambers and Hanson 1990). Several authors report that the impact on macrophytes depend on crayfish density (Flint and Goldman 1975; Lodge and Lorman 1987). Chambers et al. (1990) manipulated sex ratios and densities of *Orconectes virilis* to show that macrophyte species are differentially affected by crayfish attack. Furthermore, their observations indicated that macrophyte attack is indiscriminate but that crayfish feeding is selective (Chambers et al. 1990).

In general, the impact of crayfish feeding on macrophytes depends on a combination of three factors: the type of macrophyte (e.g. differences between species, initial biomass, growth form, palatability), the crayfish (e.g. differences between species, sexes, individual crayfish size and activity), and the abundance of alternative prey.

### *The role of* P. clarkii

The dominant herbivorous feeding character of *Procambarus clarkii* has been documented in life history studies from their natural habitats in Louisiana (USA) (Penn 1943; Avault et al. 1983). But so far, little is known about the quantitative effects of this species on macrophytes once introduced elsewhere. Exceptions are the results of crayfish exclusion experiments and submerged macrophytes, performed *in situ*, in the freshwater marshes of Coyote Hills (California, USA), by Feminella and Resh (1986). They found that the exclusion of crayfish resulted in a sixfold increase in macrophytes and that crayfish abundance is strongly related to *Potamogeton pectinatus* clearance (Feminella and Resh 1989).

In multispecies laboratory experiments, Cronin (1998) found that red swamp crayfish avoided macrophyte species with structural or chemical deterrents and preferred undefended plants high in nitrogen. Plant structure (morphology, toughness, and/or surface features) and plant chemistry were important determinants of crayfish feeding choices (Cronin 1998; Cronin et al. 2002).

In Mediterranean environments, *P. clarkii* has been cited to be responsible for the disappearance of some macrophyte species in wetlands and fresh and brackish water marshes of southern Europe (Montes et al. 1993). In Spain, there are other examples where the composition of submerged macrophytes changed following the arrival of *P. clarkii* (e.g. Laguna de El Portil in Huelva, SW Spain (Enríquez et al. 1987); Lake Carucedo (Dpt. Ecología, UAM, unpubl.), Lake Chozas, León, northwestern Spain (Palacios and Rodríguez 2002)). However, at least in freshwater marshes, other factors such as the anthropogenic alteration of water quality and flooding regime or livestock trampling and flamingo treading (Duarte et al. 1990; Montes and Bernués 1991; Grillas et al. 1993) seem to have contributed to the decrease of macrophyte populations in this area. Livestock and flamingos directly damage the macrophyte seed bank (Montes and Bernués 1991), whereas crayfish has a lower impact on this important reservoir of macrophyte diversity.

Shredding of plants and bioturbation by *P. clarkii* are thought to be responsible for the change from a natural, macrophyte dominated, transparent water state equilibrium to a turbid, eutrophic balance, dominated by phytoplankton (Duarte et al. 1990; Nyström and Strand 1996). Angeler et al. (2001) showed in the Tablas de Daimiel wetland of La Mancha, Central Spain, that the benthic feeding of crayfish disturbs and resuspends the sediment, which leads to increased nutrient release. This results in a deterioration of water quality, increased turbidity and nutrient content and reduced light availability for submerged macrophytes. However, importance for nutrient recycling at the ecosystem level was found to be low (Angeler et al. 2001).

Rodríguez et al. (2002) described the disappearance of seven species of submerged macrophytes of a small lake in northwestern Spain (Lake Cabañas, León) after the introduction of *P. clarkii* in 1997. The recovery level of macrophytes in an exclusion experiment was 70%.

Additional quantitative studies directed towards the question on how crayfish density and population structure affect macrophytes and towards the role of other factors (nutrient enrichment, hydroregime changes) should clarify the role of this crayfish species in the disappearance and alteration of macrophyte communities.

## The impact of alien crayfish on the native invertebrate communities

### P. clarkii *as an invertebrate predator*

For a long time, crayfish were described to be mainly herbivores and detritivores as gut content analyses always contained large amounts of plant material and detritus (Webster and Patten 1979; Huryn and Wallace 1987). However, when correcting gut contents for assimilation efficiencies, the importance of animals as an energy source increases (Whiteledge and Rabeni 1997). Animals form, at least in the juvenile stage, when growth rates are the highest, an important part of a crayfish's diet (Hobbs 1993; Gutiérrez-Yurrita et al. 1998). A direct impact on its prey organisms is therefore to be expected. Crayfish feed mainly on aquatic invertebrates, with a clear preference for arthropods and gastropods (see for a review Momot 1995). The reduction of invertebrate populations by crayfish feeding has often cascading effects on lower trophic levels. In preference experiments, *P. clarkii* prefers animal food over macrophytes (Ilhéu and Bernardo 1993), whereas in the field, it mainly feeds on plant material and detritus (Feminella and Resh 1986, 1989; Gutiérrez-Yurrita et al. 1998).

Gutiérrez-Yurrita et al. (1998) showed that despite high occurrences of plant material and detritus, small arthropods (copepods, ostracods), insect larve and fish (*Gambusia holbrooki*) are consistently found in the guts. Fish is eaten only by large, adult individuals, whereas copepods are an important food source for small crayfish. Furthermore, these authors observed cannibalism in 20% of the larger sized (>30 mm carapax length) individuals. No differences were found in the feeding preferences of males and females.

Comparing rice fields and natural marshland ecosystems, we were able to demonstrate that crayfish feeding is highly flexible and is a function of prey availability in the field. Crayfish from natural marshlands fed on 17 different prey items, whereas the guts of individuals from rice fields only contained 12 taxa (Figure 1). In both systems, they mainly feed on macrophytes (>97% of occurrence), but the percentage of stomachs with animal food can be as high as 50% in natural marshlands, especially in spring, when prey diversity is the highest. Rice fields are characterised by an impoverished invertebrate fauna, and crayfish fulfill their need for animal protein by cannibalism and predation on fish (Table 2) (Alcorlo et al. in press). Predation on mosquito fish (*Gambusia holbrooki*), which occurs in high

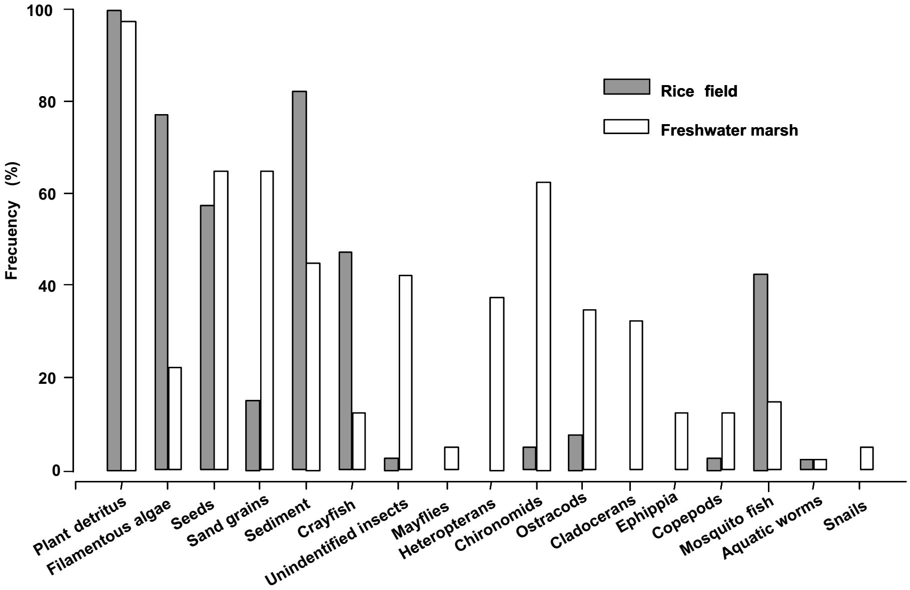

*Figure 1.* Frequency of occurrence of food items found in guts of *P. clarkii* from rice fields and marshlands of the Lower Guadalquivir basin (Spain).

*Table 2.* Frequency of occurrence of food items in gut contents of *P. clarkii.*

| Food items | Frequency of appearance | |
|---|---|---|
| | Rice field | Freshwater marsh |
| Plant debris | 100 | 97.5 |
| Filamentous algae | 77.5 | 22.5 |
| Seeds | 57.5 | 65 |
| Sand grains | 15 | 65 |
| Clay particles | 82.5 | 45 |
| Crayfish | 47.5 | 12.5 |
| Nonidentified Insects | 2.5 | 42.5 |
| Ephemeroptera | 0 | 5 |
| Heteroptera | 0 | 37.5 |
| Chironomidae | 5 | 62.5 |
| Ostracoda | 7.5 | 35 |
| Cladocera | 0 | 32.5 |
| Ephippia | 0 | 12.5 |
| Copepoda | 2.5 | 12.5 |
| Gambusia holbrooki | 42.5 | 15 |
| Oligochaeta | 2.5 | 2.5 |
| Gastropoda | 0 | 5 |

densities in the rice fields, is noteworthy as fish is not commonly found among crayfish prey.

### P. clarkii *and the extinction of macroinvertebrates including native crayfish*

As stated above, *P. clarkii* is thought to be responsible for the disappearance of some species of macroinvertebrates in aquatic ecosystems where it was introduced. An example is the coincidence between the extinction of two species of gastropods – *Lymnaea peregra* and *L. stagnalis* – in freshwater marshes of the Doñana National Park (southwestern Spain) and the introduction of the red swamp crayfish (Montes et al. 1993). Gastropods are known to be one of the favourite food items in the diet of crayfish (Covich 1977; Goddard 1988; Hanson et al. 1990; Olsen et al. 1991; Ilhéu and Bernardo 1993). *P. clarkii* has been introduced in Kenya to reduce snail populations and thereby snail-born diseases (Rosenthal et al. 2001). It has also been proposed as a control agent of the giant rams-horn snail, *Marisa cornuarietis* (Gastropoda: Pilidae) in the USA (T.L. Arsuffi, pers. comm.). Therefore, it is highly probable that the direct and indirect feeding effects of *P. clarkii* contributed to the disappearance of these two species, but the deterioration of the water quality and the damages to macrophyte stands by large herbivore grazing and trampling might have been equally important.

We face a similar problem when analysing the role of *P. clarkii* in the decline of autochtonous crayfish populations. As mentioned above, *P. clarkii* also successfully spreads to areas formerly populated by the native crayfish *Austropotamobius pallipes*. However, it remains unclear whether *P. clarkii* displaced the native species by direct competition or whether it invaded these systems after the populations of *A. potamobius* were already decimated by other mechanisms. In Portugal, *P. clarkii* is mainly restricted to the south-central part, where the native species has never been observed and overlap only occurs in the central part of the country (Anastácio and Marques 1995). Furthermore, the requirements with regard to temperature, water quality and substrate of the two species are quite different. *P clarkii* prefers high temperatures, clayey–silty substrates to construct its burrows and is more tolerant to low water quality, whereas *A. potamobius* lives in temperate to cold waters with coarse substrates and is sensitive to low oxygen and high nutrient concentrations (Gil-Sánchez and Alba-Tercedor 2002). At the moment, data on the autecology of *P. clarkii* from habitats formerly inhabited by the native species are lacking. In zones of abiotic niche overlap, biotic interactions should be intensive and competitive exclusion of the native species might occur. Whether there be direct interaction or not: with the red swamp crayfish present, any recovery of *A. pallipes* populations is unlikely, because *P. clarkii* is also a vector of the aphanomicosis, which is detrimental to the native species.

## *P. clarkii* – a new food item for higher trophic levels

Since its introduction in 1974, *P. clarkii* has been readily accepted as a prey item by fish, birds and mammals thus offering a new resource for higher trophic levels. In some areas such as the Lower Guadalquivir Basin, *P. clarkii* has opened new trophic pathways by transferring energy from the formerly underexploited detritus pool to primary and secondary predators.

Three fish species, six bird species and four mammal species commonly include *P. clarkii* in their diet (Table 3). However, the consumption of crayfish differs considerably according to species, season and study.

For the otter, where information from four quantitative studies over more than one season is available (Adrián and Delibes 1987; Beja 1996; Correia 2001; Ruíz-Olmo et al. 2002), the percentage of crayfish in the total amount of food varies between 1.6 and 76.3% with lowest values in winter and highest in summer (Table 3). All three studies coincide in that otter prey upon crayfish according to crayfish density and prefer small and medium sized individuals. Highest densities of *P. clarkii* in the water bodies coincide with the presence of young otters and feeding on them enhances juvenile survival (Ruíz-Olmo et al. 2002). However, the important bottleneck is in winter, when crayfish are not available, and otters have to rely on scarce native prey species (Beja 1996).

The same is true although to a lesser degree for other mammals such as the red fox (*Vulpes vulpes* L.), the common genet (*Genetta genetta* L.) or the Egyptian mongoose (*Herpestes ichneumon* L.) which also prey upon *P. clarkii* (Correia 2001) (Table 3). As in otters, the highest consumption of crayfish is in summer.

All mammal predators feed in an opportunistic manner on crayfish, and none of them selects this prey item. Diversity of prey in mammals decreases when they start feeding on *P. clarkii*, and crayfish are taken as a function of crayfish density (Correia 2001).

*P. clarkii* is also an important part of the diet of at least six bird species, in particular for most ciconiiform species. In the case of the white stork, night heron or little egret, crayfish can make up to 80% of the diet during summer, when densities of crayfish are high (Table 3). In addition, other bird species such as the black stork (Parkes et al. 2001) or the lesser black-backed gull (Amat and Aguilera 1988) are reported to feed on *P. clarkii*.

Birds, similar to mammals, consume crayfish above the minimum size for maturity but below the mean size for mature adults (Correia 2001). Predation in this size fragment reduces intraspecific competition among crayfish and produces large-sized adults which in turn produce a higher number of offspring (Correia 2001).

Thus, predation by birds and mammals should help in stock renewal and not negatively affect crayfish populations. Therefore, it remains unclear

*Table 3*. Frequency of occurrence and percentage of diet of *P. clarkii* in the stomachs of vertebrate predators.

| Species | % of occurrence | % of diet |  |  | Source |
|---|---|---|---|---|---|
|  |  | Mean | Maximum | Biomass |  |
| Fish |  |  |  |  |  |
| *Esox lucius* | 72.5 | 82.9 |  | 72.4 | Elvira et al. (1996) |
| *Micropterus salmoides* | 5.8 | 0.9 |  | 9.9 | García-Berthou (2002) |
| *M. salmoides* (> 250 mm; summer) |  |  |  | 50–100 | García-Berthou (2002) |
| *M. salmoides* | 72.2 |  |  |  | Montes et al. (1993) |
| *Anguilla anguilla* | 66.7 |  |  |  | Montes et al. (1993) |
| Birds |  |  |  |  |  |
| *Gelochelidon nilotica* |  | 40.1 |  | 70.1 | Costa (1984) |
| *Nycticorax nycticorax* |  | 70 | 71 |  | Correia (2001) |
| *Egretta garzetta* |  | 52 | 86 |  | Correia (2001) |
| *Ardea cinerea* |  | 21 | 40 |  | Correia (2001) |
| *Ardea purpurea* |  | 30 | 31.5 |  | Correia (2001) |
| *Ciconia ciconia* |  | 67 | 86 |  | Correia (2001) |
| Mammals |  |  |  |  |  |
| *Lutra lutra* |  | 67 | 85 |  | Correia (2001) |
|  | 80.3 |  |  |  | Adrián and Delibes (1987) |
|  |  | 22.7 | 42.2 |  | Ruiz-Olmo et al. (2002) |
| *Herpestes ichneumon* |  | 26 | 49 |  | Correia, (2001) |
|  | 5.6 |  |  | 1.7 | Palomares and Delibes (1991a) |
| *Vulpes vulpes* |  | 14 | 27.5 |  | Correia (2001) |
|  |  | 5 | 10 |  | Correia (2001) |
| *Genetta genetta* | 0.8 |  |  | 0.1 |  |

whether the reduction in crayfish numbers observed in the past years is due to increased bird predation or to other factors such as reduced hydroperiods induced by droughts.

Amongst fish, eels (*Anguilla anguilla*) are known to be the most important predators of crayfish (Svardson 1972). In the natural marshlands of the Lower Guadalquivir (Spain), the eels considerably reduced their food spectrum after the red swamp crayfish was introduced, (Table 3). Before introduction, it mainly fed on other fish species such as mosquito fish (*Gambusia affinis*) or carp (*Cyprinus carpio*) which occurred in more than 50% of the stomach contents. After introduction, in 1992, only 16.7% of eel stomachs contained other fish species, and the dominant prey item was *P. clarkii* with a 66.7% occurrence (Montes et al. 1993).

As they readily feed on *P. clarkii*, eels were proposed as effective biological control organisms in a Swiss lake (Mueller and Frutiger 2001). However, eels are also efficient predators of fish eggs and fry as well as of amphibians and reptiles, and therefore, their use to control crayfish populations should be considered with caution.

The other two fish species which include *P. clarkii* in their diet – the northern pike and the largemouth bass (*Micropterus salmoides*) – are both introduced exotics. Crayfish became the dominant prey item of all size classes of pike throughout the year in the Spanish lake system of Ruidera. Crayfish substituted the natural prey species which were reduced near to extinction after the introduction of the pike (Elvira et al. 1996). Without *P. clarkii,* the pike population would have become extinct, as the rest of the fish fauna, mainly composed of other introduced species, could not support self-maintaining pike populations in these lakes. Pike prey on crayfish of a similar size than do birds and mammals (7–9 cm total length).

The largemouth bass (Hickley et al. 1994) readily accepted crayfish as a prey item. In the Guadalquivir marshlands of south-western Spain, it was found to feed exclusively on *P. clarkii* (Montes et al. 1993). In the Spanish lake of Banyoles, dominated by an assemblage of exotic fish, larger size classes of this species (>250 mm) feed predominantly on crayfish except in winter (García-Berthou 2002) (Table 3), a situation typical for water bodies with a low fish diversity (García-Berthou 2002). A similar scenario was described by Hickley et al. (1994) in Lake Naivasha (Kenya), which is also a lake characterised by its low richness in native fish species.

Other species such as perch are known to prey on *P. clarkii*. Perch are able to efficiently reduce densities of *P. clarkii* in mesocosm experiments (Neveu 2001). However, the quantitative impact of the predation of this species on *P. clarkii* populations is not known.

## Impact of *P. clarkii* on ecosystem energetics

Besides the impact on structural components of the invaded communities described above, the presence of crayfish might alter to a large degree the pattern of energy flow, especially in systems where detritivores are rare and which are dominated by autotrophs as in temporary freshwater marshes. In such systems, crayfish put the detritus energy pool directly at the disposal of higher trophic levels. This greatly shortens the energy pathways and simplifies their structure (Figure 2). Without crayfish, macrophytes and the associated periphyton are the dominant primary producers in freshwater marshlands from which only a small part of the energy is transmitted to herbivores. Most of the energy is lost to the detritus pool which accumulates high amounts of organic matter. Detritivores, mainly macroinvertebrates (oligochaetes, chironomids) and meiofauna (nematodes, ostracods) are supposed to use only a small fraction of the deposited material. The detritus food chain gains in importance only during drought and refilling of the system in early summer and late autumn, when macrophytes are absent. These systems are characterised by a high diversitiy of herbivores and consist of a minimum of four levels of consumers. Due to the large number of trophic levels and losses of energy to the detritus pool, the energy transferred to top predators such as birds and mammals is comparatively low (Figure 2).

After crayfish introduction, much of the detritus is consumed by this species (Gutiérrez-Yurrita 1997), and the energy gained is directly transferred to the top predator level (fish, birds and mammals). The consequence is a reduction in the number of trophic levels, a decreased importance of macrophytes, herbivores and primary

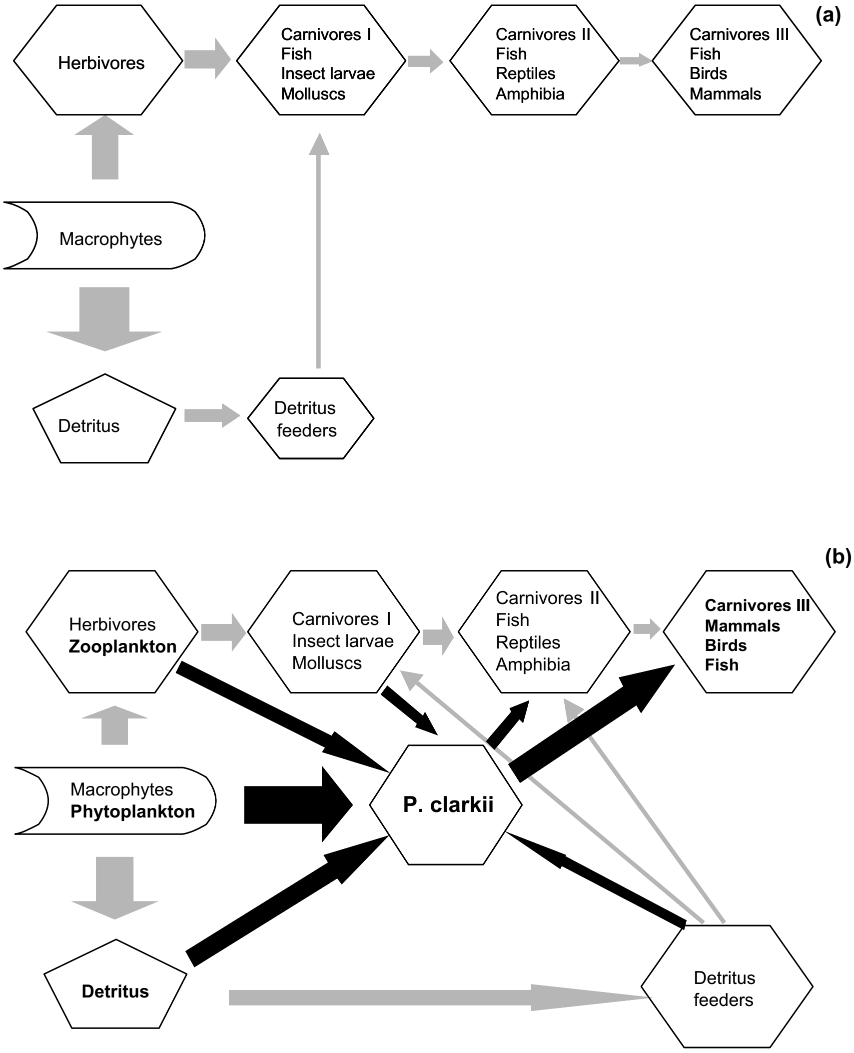

*Figure 2.* Simplified representation of the energy flow in waterbodies of a freshwater marshland: (a) before the introduction of crayfish and (b) after the introduction of crayfish.

carnivores, but more energy is available for vertebrate predators.

In summary, alien crayfish change both the structure and the functional links of the trophic web in wetlands by opening new resource pathways (detritus food chain), reducing the number of trophic levels, and thus providing more energy to the highest trophic levels.

## *P. clarkii* as a vector of diseases

Introduced crayfish are vectors of several diseases for native crayfishes thus contributing to their decline. One of the most widespread diseases is the ‘Crayfish plague’, produced by *Aphanomyces astaci* (Schikora), a parasitic saprolegniaceous fungus especially adapted to live in the cuticule of freshwater crayfish (Unestam 1972). This disease has devasted many native European crayfish populations since the 1890s, and the problem became more acute through the massive introductions of American crayfish during the 1960s and 1970s (Persson and Söderhäll 1983; Diéguez-Uribeondo et al. 1995). In Europe, three North American species of crayfish have been shown to carry the infectious fungus in their cuticule: *Pacifastacus leniusculus* (Unestam 1972; Persson and Söderhäll 1983), *Orconectes limosus* (Vey et al. 1983) and

*Procambarus clarkii* (Diéguez-Uribeondo and Söderhäll 1993). Recent studies using RAPD-PCR have demonstrated the existence of species-specific strains of this fungus. The strain isolated from *P. clarkii* was shown to be the most temperature tolerant (Huang et al. 1994; Diéguez-Uribeondo et al. 1995). The introductions of alien species such as *P. clarkii* also introduced a new *A. astaci* strain with a different genotype and unknown levels of virulence adapted to warm waters (Diéguez-Uribeondo et al. 1995). Recent genetic studies have linked *P. leniusculus* to many recent plague outbreaks in Great Britain (Lilley et al. 1997), Sweden, Finland, Germany and Spain (Diéguez-Uribeondo et al. 1997; Diéguez-Uribeondo 1998).

Other diseases for native species carried by introduced crayfish such as *P. leniusculus*, are the Psorospermiasis, produced by *Psorospermium haeckeli* (Hilgendorf) (Cerenius and Söderhäll 1992; Gydemo 1992; Henttonen et al. 1997), protists which have their phylogenetic roots near the animal–fungal divergence (Ragan et al. 1996).

A question still open for debate is the role of *P. clarkii* in transmitting diseases to humans. An outbreak of tularemia, normally transmitted by small rodents and caused by the bacterium *Francisella tularensis*, in a contaminated stream in central Spain was recently related to *P. clarkii* as a mechanical transmitter (Anda et al. 2001).

## *P. clarkii* – a transmitter of heavy metal contamination

Crayfish have frequently been considered as biological indicators of heavy metal pollution in aquatic environments (Rincón-León et al. 1988). There have been numerous studies on the accumulation of heavy metals in crayfish living in polluted environments (Evans and Edgerton 2002). Most field studies involved chemical analysis of the metal content of crayfish tissues and provided little information on the pathology of heavy metal exposure (Dickson et al. 1979; Finerty et al. 1990; King et al. 1999; MacFarlane et al. 2000; Rowe et al. 2001). There are also many laboratory studies that provide data on the toxicity of metals to freshwater crayfish, the concentrations of metals causing mortality and the pathological effects arising from heavy metal exposure (Bagatto and Alikhan 1987; Naqvi and Flagge 1990; Naqvi et al. 1990; Naqvi and Howell 1993; Reddy et al. 1994; Maranhao et al. 1995; Anderson et al. 1997a, b; Bollinger et al. 1997; Naqvi et al. 1998; Antón et al. 2000). Little attention has been paid to the sublethal pathology of such exposures and how pathological changes could influence the survival of crayfish living in polluted water systems or contaminated culture systems. These kinds of studies is needed for the implementation of adequate restoration and management plans for contaminated areas such as the Guadiamar river basin, which was affected by a toxic spill of approximately 5 $Hm^3$ of untreated acid fresh water with a high content of metals (especially zinc, copper, cadmium, lead, iron and arsenic) in April 1998 during an accident in Aznalcóllar mine (southwestern Spain). Crayfish captured in this area, have higher heavy metal contents in their tissues compared to those captured outside the contaminated area (Figure 3). They can transfer contaminants to their consumers through bioaccumulation processes (e.g. heavy metals or pesticides enrichment in organs and tissues) (Otero et al. 2003). Other well documented examples of bioaccumulation of heavy metals by red swamp crayfish in Mediterranean wetlands are the studies performed in the rice fields of Albufera Lake in Valencia (eastern Spain) by Díaz-Mayans et al. (1986) and Pastor et al. (1988). These rice fields are surrounded by waters, which received for the last four decades high loads of sewage and toxic industrial residues including heavy metals and pesticides.

Indeed, crayfish are able to effectively regulate the concentration of heavy metals in their tissues (Rainbow and White 1989) and to remove some contaminants from their internal organs and muscles depending on their physiological needs. This is achieved through excretion (faeces) and/or storage in the hepatopancreas – considered the organ of metal storage and detoxification (Alikhan et al. 1990; Anderson et al. 1997a, b; Naqvi et al. 1998) – gills and exoesqueleton (Anderson and Brower 1978; Naqvi et al. 1990; Wright et al. 1991). Consequently, their predators absorb the contaminants immobilised in these crayfish tissues when they ingest them. Measurements of accumulation of heavy metals in waterfowl and other wetland birds living and feeding in the toxic spill area showed that Zn, Cu and As from the spill have entered the food

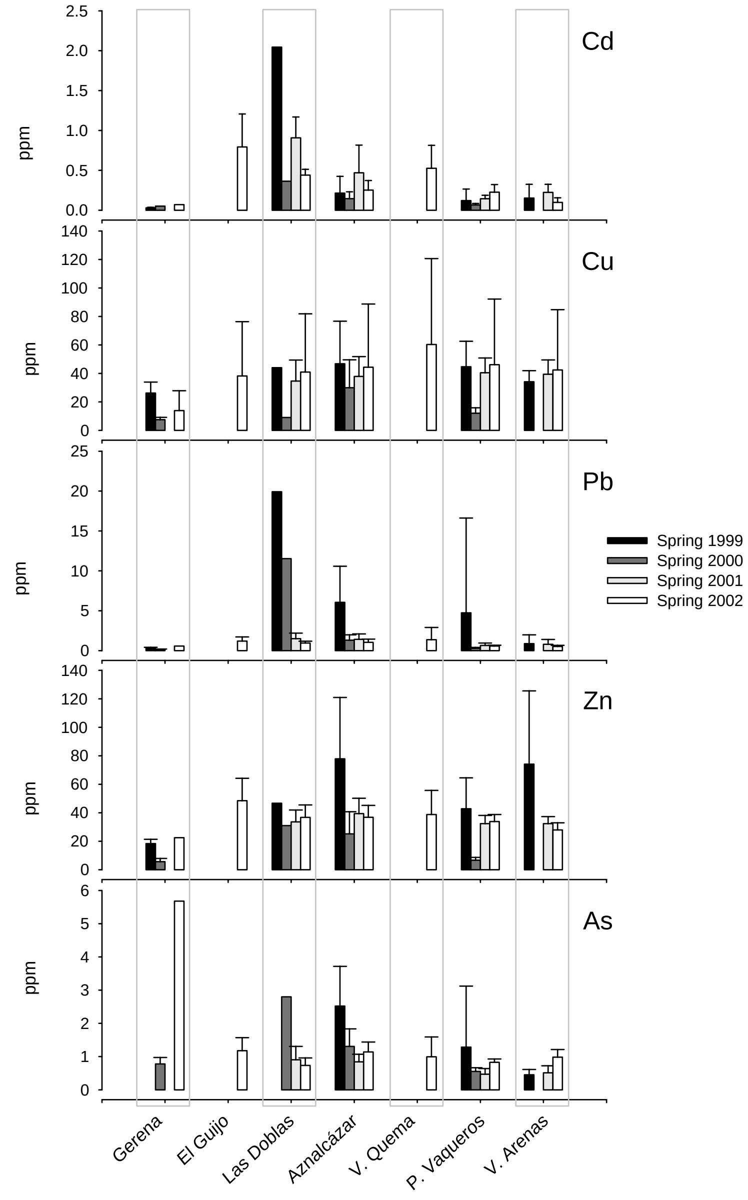

*Figure 3. P. clarkii* as a vector of contamination for higher trophic levels. Temporal evolution of heavy metal concentrations in crayfish from different sites in the Guadiamar Guadalquivir Basin, southwestern Spain). Bars: mean values; whiskers: standard deviations. Units are in ppm of fresh weight (from Otero et al. 2003).

chain and can be detected in some bird species, such as white stork (*Ciconia ciconia*), spoonbill (*Platalea leucorodia*), or grey heron (*Ardea cinerea*). All these species are fish and crayfish predators (Benito et al. 1999; Hernández et al. 1999). Further studies quantifying the extent of vertebrate contamination through crayfish ingestion are urgently needed.

## Impacts derived from the commercial exploitation of *P. clarkii*

In contrast to the significant increase in the attention devoted to the impact that crayfish have on invaded habitats (see above), much less attention is paid to the environmental impact derived from the economic activity which is promoted by the presence of dense crayfish populations or to the socio-economic benefits related to crayfish exploitation. Both kinds of interactions have to be properly considered in any integrative approach to crayfish management.

One important issue to bear in mind is the nature of crayfish exploitation. Extensive crayfish production is not common and is restricted to some areas in the USA and, on a limited basis, in Spain, France, Italy and Zambia (Huner 2002). The most widespread method is the direct use of wild stocks of *P. clarkii* grown in ricefields, irrigation systems, natural marshlands, reservoirs and river deltas. The main crayfish (*P. clarkii*) producer is China, a country that exceeds the production of the USA with 70,000 Tm/year. Spain has developed a much smaller industry (2000–3000 Tm/p year) but of great regional importance (Figure 4a).

Commercial crayfish exploitation in Spain is mainly concentrated in the southwest, in the Lower Guadalquivir Basin. There, *P. clarkii* stocks were intentionally introduced in the early 1970s and immediately developed dense populations within the ricefields. Nowadays, the red swamp crayfish is distributed over almost the whole country with a significant effect on most ecosystems it inhabits. However, exploitation in most places is but recreational with almost no incidence in local economy. Although in these areas the impact of crayfishing should be low, the role of man as a vector of transportation is of major concern. Some areas important for amphibians or fish reproduction can be severely endangered with a single inoculation of just a few animals.

In the area where crayfish exploitation has developed into a growing industry, environmental impact derived from this activity is mainly caused by fishermen during their fishing activity. This impact refers to

(1) physical alteration of the habitat produced by the continuous roaming of the fishermen –

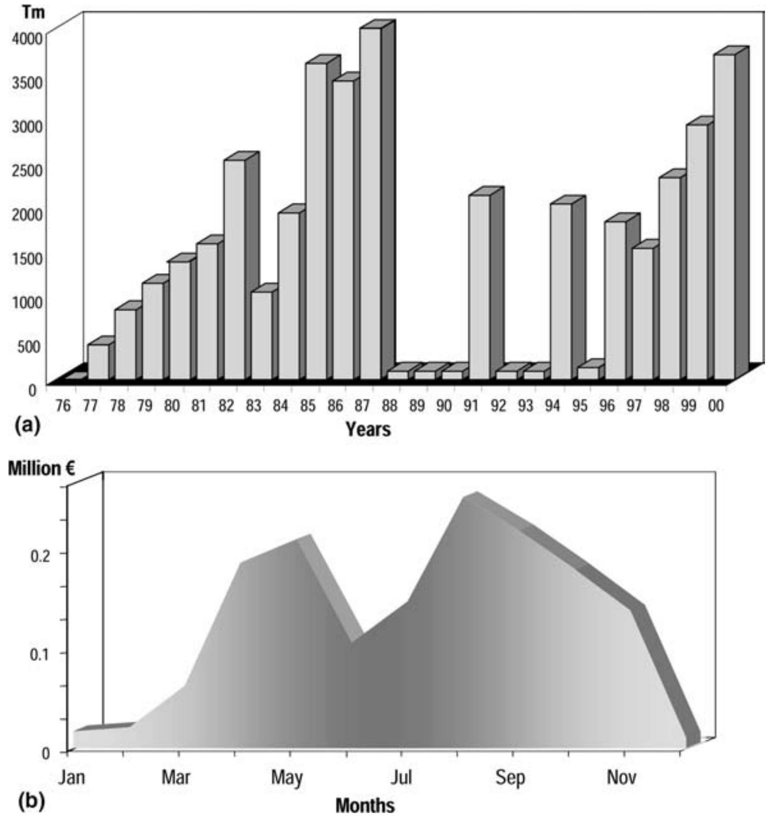

*Figure 4*. (a) Crayfish commercial captures in Lower Guadalquivir marshlands and (b) commercial value of captured crayfish in 1999.

from 100 to 300 traps/fishermen can be installed simultaneously over large areas; and

(2) the capture of non-target organisms within the crayfish traps.

Fishing activities in natural habitats might severely affect not only habitat structure but also many organisms' reproductive activities. Crayfish exploitation is highly seasonal (Figure 4b) with maxima in late spring and late summer. That first period clearly overlaps with the nesting period of many birds in the area. Intense wandering of people is likely to interfere with reproduction, although no quantitative data are available up to now.

The second kind of impact has been evaluated several times, and results have shown to be relevant for management policies. The traps traditionally used for crayfish were modified eel traps. This kind of trap is not selective for crayfish and, when baited, attracts many different kinds of organisms. Early studies performed in the area (Coronado 1982; Molina and Cadenas 1983; Molina 1984; Domínguez 1987; Asensio 1989) demonstrated the large impact of these traps on birds, amphibians and reptiles. This led to regulation of fishing activities in the area, now strictly forbidden during nesting periods. The impact level on native communities lowered significantly wherever fishing activity was forbidden during the breeding season (Figure 5). Still, a sensible number of non-target organisms die every year in crayfish traps. Some turtle species are of special concern. Most of the victims of this 'collateral damage', however, belong to non-endangered, highly abundant species (Figure 5). Far from being ideal, management of fishing activities – including timing, trap design, and selected locations – can severely reduce the negative impact of crayfishing.

It has to be reminded that crayfish exploitation supports, at least partially, the economy of many families in a poorly developed area and that socio-economic aspects have to be integrated if any management policy is to be developed in order to minimise the negative environmental impact of this alien species.

## Conclusions

In the 30 years of invasion history, *P. clarkii* changed the structure and functioning of the invaded ecosystems where it readily occupied a central position in the food webs.

Its success as an invader is mainly due to its adaptation to the main characteristics of Mediterranean wetlands: the frequent periods of drought.

The impact caused by *P. clarkii* affects both lower and higher trophic levels, including grazing

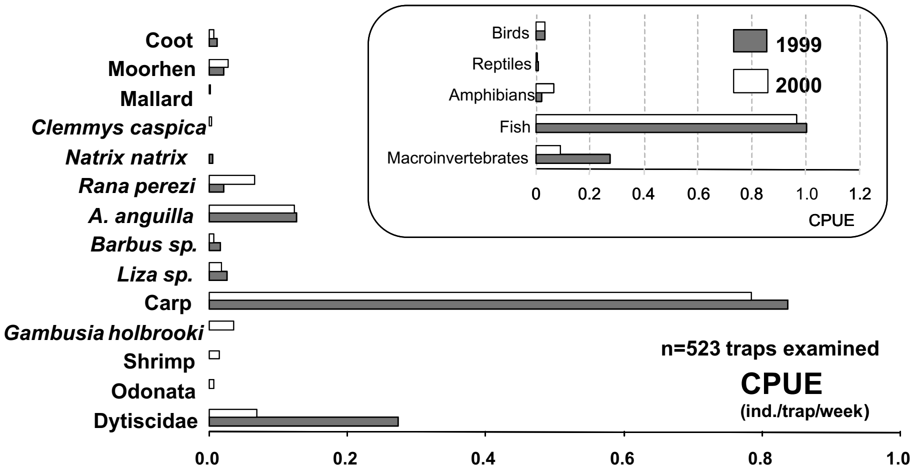

*Figure 5.* Organisms captured by crayfish traps.

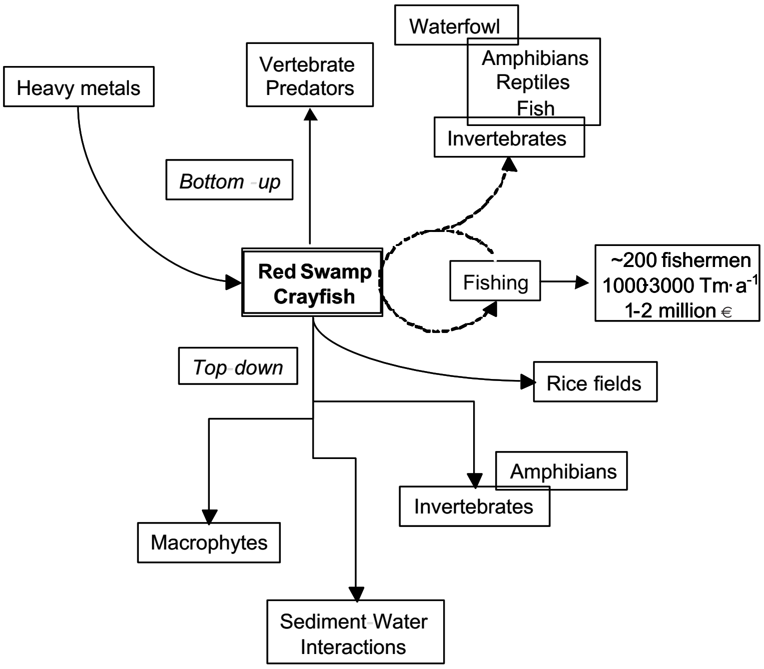

*Figure 6.* Scheme representing the manyfold impacts of introduced crayfish in Mediterranean wetlands.

on macrophytes, predation on macroinvertebrates and its role as an important food source for numerous vertebrate species (Figure 6).

From a socio-economic point of view, crayfish represent, at least in some areas, an additional, although temporary source of income but cause, on the other hand, serious damage on rice field infrastructure and crayfishing negatively affects vertebrate and invertebrate species.

The numerous and tight links between the invader and the native communities render a successful eradication unlikely. Therefore, control measures to minimise the negative impact should be established. They should include, where possible, a return to natural hydroperiods (salinity limits the distribution of *P. clarkii*) and the implantation of fishing plans with the aim to change the age and size structure of the population. Favouring low density populations dominated by large-sized adults with lower metabolic demands will minimise the impacts caused by this crayfish species. This measurements should be accompanied by a strict control of large herbivore grazing such as cattle and flamingos, water quality and anthropogenic disturbances. All these measures should also favour the recovery of autochthonous crayfish populations.

Prevention is as necessary as control to avoid a further widespread of the species to presently unaffected areas, although most of the suitable habitats seem to be already occupied. We urgently need to protect the remaining areas from being invaded by *P. clarkii* in order to preserve them as ecological reference sites.

## Acknowledgements

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## Appendix 1

| Effect | Impact on | Habitat type | Location | Source | Comments |
|---|---|---|---|---|---|
| Bioturbator | *Tilapia zilli* | Lake | Naivasha (Kenia) | Lowery and Mendes (1977) | Only comments, destroys nesting ground of bottom living *Tilapia* |
| Bioturbator | Nutrient release | Stream | Degebe stream, Alentejo (Portugal) | Bernardo and Ilhéu (1994) | |
| Bioturbator | Nutrient release | Ponds | Tablas de Daimiel (Spain) | Angeler et al. (2001) | *P. clarkii* enhances nutrient release from sediment and increases primary production |
| Bioturbator | Sediment resuspension | Lake | Lago Chozas, León Province (Spain) | Rodríguez et al. (2002) | *P. clarkii* enhances nutrient release from sediment and increases primary production |
| Competition | Prawns (*Macrobrachium rosenbergii*), Channel catfish (*Ictalurus punctatus*) | Aquaculture ponds | Louisiana (USA) | Huner et al. (1983) | Competition favours large prawns, no effect on catfish fingerlings |
| Competition | *Austropotamobius pallipes* | Streams and rivers | Province of Granada (Spain) | Gil-Sánchez and Alba-Tercedor (2002) | *P. clarkii* causes regression of *A. pallipes*; cites factors limiting the distribution of *P. clarkii* (altitude, temperature, nutrients, substrate); similar results as in studies of Diéguez-Irubeondo et al. (1997) in Navarra and Bolea-Berné (1995) in Aragon somewhat contradictory as densities of *P. clarkii* are far below those of *A. pallipes* ('not adapted to environment') |
| Herbivory | Nymphae species | Lake | Naivasha (Kenia) | Lowery and Mendes (1977) | No data, disappearance coincides with introduction of *P. clarkii* |
| Herbivory | *Elodea* | Laboratory crayfish cultures | Louisiana (USA) | Wiernicki (1984) | Fresh and as detritus; 15-day detritus best assimilated |
| Herbivory | Macrophytes (*Potamogeton pectinatus*) | Pond | Fremont, California (USA) | Feminella and Resh (1989) | With crayfish exclusion: six-fold macrophyte biomass and higher *Anopheles* densities |
| Herbivory | Macrophytes (*Potamogeton pectinatus*) | Experimental mesocosms in marsh | Coyote Hills Marsh, California (USA) | Feminella and Resh (1987) | Enclosure experiments showed a strong positive relationship between crayfish density and macrophyte clearance |
| Herbivory | Macrophytes | Laboratory crayfish cultures | North Carolina (USA) | Bolser et al. (1998) | Preference experiments, defense mechanisms of plants decide about preferences |
| Herbivory | Macrophytes | Laboratory crayfish cultures | | Cronin (1998) | Preference experiments among nine species of submersed, floating, emergent, and shoreline macrophytes |
| Herbivory | Macrophytes | Laboratory crayfish cultures | North Carolina (USA) | Cronin et al. (2002) | Preference experiments among 14 species of freshwater macrophytes (including macroscopic algae) |
| Herbivory | Macrophytes, detritus | Stream | Degebe stream (Portugal) | Ilhéu and Bernardo (1995) | Preference experiments: prefer high organic matter contents, high protein and low fibre, prefer 'fresh' detritus to macrophytes |

| | | | | | |
|---|---|---|---|---|---|
| Predator | *Corbicula* sp. (Asiatic clam) | Laboratory ponds | Oklahoma (USA) | Covich et al. (1980) | *P. clarkii* feeds on damaged *Corbicula*, cites also predation of *Orconectes limosus* on *Dreissena* in Poland (Piesik, 1974), not as efficient as *O. limosus* due to different shape of prey and that it is not used to prey |
| Predator | Amphibia (eggs and tadpoles) | Freshwater marsh | Doñana National Park, Arroyo Rocina, Lucio Bolín (Spain) | Delibes and Adrián (1987) | |
| Predator | Two high pelletised diets and a third one formulated with fishmeal, | Laboratory crayfish cultures | Baja California, Mexico | Cordero and Voltolina (1990) | *P. clarkii* responds better to two of the diets at lower temperatures (20 °C) |
| Predator | *Rana perezi* (eggs and tadpoles) and other macroinvertebrates | Freshwater marsh, rice fields | Ebro Delta (Spain) | Ibañez et al. (2000) | |
| Prey | Black bass (*Micropterus salmoides*) | Lake | Naivasha (Kenia) | Lowery and Mendes (1977) | Pers. comm.: 70% of the food of black bass |
| Prey | Dragonfly (*Anax junius*) | laboratory crayfish cultures | Louisiana (USA) | Witzig et al. (1986) | Max 1. 16 crayfish/day; depends on temperature and crayfish size. Do not coincide temporally in the field |
| Prey | Gull-billed tern (*Gelochelidon nilotica*) | Freshwater and saline marsh, rice fields | Guadalquivir basin (Spain) | Costa (1984) | *P. clarkii* represents 70% of the biomass of the diet |
| Prey | Otter (*Lutra lutra*) | Freshwater marsh | Doñana National Park: Arroyo Rocina, Lucio Bolín (Spain) | Adrian and Delibes (1987) | *P. clarkii* occurred in 80% of the faeces from Arroyo de la Rocina |
| Prey | Otter (*Lutra lutr*a L.) Mentions also (without data): Red fox (*Vulpes vulpes*), Polecat (*Mustela putorius*), Common genet (*Genetta genetta*), Egyptian mongoose (*Herpestes ichneumon*), Badger (*Meles meles*). Birds, Ciconiiformes: Night heron (*Nycticorax nycticorax* L.), Grey heron (*Ardea cinerea* L.), Purple heron (*Ardea purpurea* L.), Little egret (*Egretta grazetta* L.), White stork (*Ciconia ciconia* L.) Raptors: Black kite (*Milvus migrans*), Tawny owl (*Strix aluco*) | Freshwater marsh | Doñana National Park | Delibes and Adrián (1987) | Adaptation to new food within five years. Most important prey after five years. Increasing importance of insects is an indirect effect of crayfish hunting. Emphasises on the negative consequences of a possible eradication for otters but need of control |

**Appendix 1. Continued.**

| Effect | Impact on | Habitat type | Location | Source | Comments |
|---|---|---|---|---|---|
| Prey | Black-backed Gull (*Larus fuscus*) | Freshwater marsh, rice fields, streams, channels, ponds | Guadalquivir basin (Spain) | Amat and Aguilera (1988) | All attacks performed by the Gulls were done on birds carrying *P. clarkii* in their mouth |
| Prey | Egyptian mongoose (*Herpestes ichneumon*), Common genet (*Genetta genetta*). | Freshwater marsh | Doñana National Park (Spain) | Palomares and Delibes (1991a, b) | Appear in 5.6% of the mongooses and in 0.8% of the genets |
| Prey | Otter (*Lutra lutra*) | Torgal stream | Alentejo (Portugal) | Beja (1996) | Crayfish and eels were particularly important in the diet from April to October. For the rest of the year, crayfish accounted for <10% of the monthly energetic intake, and cyprinids and toads were the most important prey. |
| Prey | Pike (*Esox lucius*) | Lakes | Ruidera lakes (Spain) | Elvira et al. (1996) | Exotic–exotic interaction; *P. clarkii* the dominant prey item under all conditions (frequency of occurrence 72. 55%, rel. importance 70%) |
| Prey | Waterfowls | Freshwater marsh, rice fields | Ebro Delta (Spain) | Ibañez et al. (2000) | |
| Prey | Mammals, Carnivora: Red fox (*Vulpes vulpes L.*), Otter (*Lutra lutra L.*), Common genet (*Genetta genetta L.*), Egyptian mongoose (*Herpestes ichneumon L.*). Birds, Ciconiiformes: Night heron (*Nycticorax nycticorax* L.), Grey heron (*Ardea cinerea* L.), Purple heron (*Ardea purpurea* L.), Little egret (*Egretta grazetta* L.), White stork (*Ciconia ciconia* L.) | Freshwater marsh, ponds, reservoirs, rice fields | Tejo river basin (Portugal) | Correia (2001) | Most predators prey on *P. clarkii* more in spring summer and autumn than in winter; *L. lutra* (67% of diet); mongoose (26%), genet (5%). Follows abundance pattern of *P. clarkii*. Prey size below mean size at reproduction, mature females are in burrows, feeding on sub-adults leads to larger size at maturity, reduces intra-specific competition. |
| Prey | Black stork (*Ciconia nigra*) | Rice fields and drainage channels | Las Cabezas de San Juan, Guadalquivir Basin (Spain) | Parkes et al. (2001) | *P. clarkii* is the major contribution to the diet of black storks in this area |
| Prey | Otter (*Lutra lutra*) | Rivers | Pyrenees, Ebro basin (Spain) | Ruiz-Olmo et al. (2002) | Timing of breeding with availability of *P. clarkii*, 46% of diet |
| Secondary effects | Amphibia, reptiles | Freshwater marsh | Doñana National Park, Arroyo Rocina, Lucio Bolín (Spain) | Delibes and Adrián (1987) | No direct results but mentions egg and tadpole predation and secondary effects by getting trapped in fishing nets |
| Secondary effects | Marbled teal (*Marmaronetta angustirostris*) | Rice fields, channels, freshwater marsh | Guadalquivir basin (Spain) | Aguayo and Ayala (2002) | Endangered avian species; gets trapped in crayfish nets |

|  |  |  |  |  |  |
|---|---|---|---|---|---|
| Secondary effects | Native crayfish species | Laboratory crayfish cultures | North Carolina (USA) | Antonelli et al. (1999) | Juvenile *P. clarkii* and adults prefer different shelter, *Orconectes* the same, advantage for *P. clarkii* |
| Secondary effects | Native crayfish species | Commercial cultures | Laboratory | Figler, Cheverton and Blank (1999) | Competition for shelter might expose native crayfish species to increased predation |
| Secondary effects | White stork (*Ciconia ciconia*) | Freshwater marsh, rice fields | Doñana National Park, Guadalquivir basin (Spain) | Negro and Garrido-Fernández (2000) | Astaxanthin: red colour of skin and tarsi – potential negative effects on mating behaviour |
| Secondary effects | Native crayfish species (*Austropotamobius pallipes*) | Streams and rivers | Zamora province (Spain) | Palacios and Rodríguez (2002) | *P. clarkii* acts as an afanomicosis vector infecting native crayfish |
| Secondary effects | Native crayfish species (*Austropotamobius pallipes*) | Streams and rivers | Granada province (Spain) | Gil and Alba-Tercedor (1998) | *P. clarkii* acts as an afanomicosis vector infecting native crayfish |
| Secondary effects | Native crayfish species (*Austropotamobius pallipes*) | Streams and rivers | Valencia province (Spain) | Monzó et al. (2001) | *P. clarkii* acts as an afanomicosis vector infecting native crayfish |
| Secondary effects | Native crayfish species (*Austropotamobius pallipes*) | Streams and rivers | Spain | Diéguez and Rueda (1994) | *P. clarkii* and *Pacifastacus leniusculus* act as afanomicosis vectors infecting native crayfish |
| Secondary effects | Waterfowls | Lake | Lago Chozas, León Province (Spain) | Rodríguez et al. (2002) | The density of waterfowls has diminished because of the lack of food consequence of the activity of *P. clarkii* that has destroyed submersed macrophytes |
| Economic losses | Destruction of fishnets and damage on fish yield in nets | Lake | Naivasha (Kenia) | Lowery and Mendes (1977) | 30% damage on fish yield |
| Economic losses | Rice field structures | Rice fields, freshwater marsh | Guadalquivir basin (Spain) | Algarín (1980) | Damages on rice field installations – no data |
| Economic losses | Rice field structures | Rice fields, freshwater marsh | Guadalquivir basin (Spain) | Gaudé (1984) | Damage to dams and irrigation structures due to deeper and more complicated burrows in semi-permanent water bodies |
| Economic losses | Rice field structures | Rice fields, freshwater marsh | Guadalquivir basin (Spain) | Serres, González and Parrondo (1985) | Damages on rice field installations – no data |
| Economic losses | Rice field structures | Rice fields, freshwater marsh, reservoirs | Portugal | Correia and Ferreira (1995) | Damage to dams and irrigation structures due to deeper and more complicated burrows in semi-permanent water bodies |
| Economic losses | Rice field structures | Rrice fields, irrigation channels | Guadalquivir basin (Spain) | Cano and Ocete (1997) | Damage to dams and irrigation structures due to deeper and more complicated burrows in semi-permanent water bodies |
| Economic losses | Rice field structures | Rice fields, irrigation channels | Guadalquivir basin (Spain) | Aguayo and Ayala (2002) | Damage to dams and irrigation structures due to deeper and more complicated burrows in semi-permanent water bodies |

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