# Predation of invasive crayfish on aquatic vertebrates: the effect of Procambarus clarkii on fish assemblages in Mediterranean temporary streams

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## INTRODUCTION

Non-indigenous species (NIS) have various effects on indigenous communities. In some cases, species invasion can result in substantial loss of biodiversity through competitive interactions and predation (e.g. Diamond and Case 1986, Ashton and Mitchell 1989, Brown 1989, Vitousek *et al.* 1996). In freshwater, in particular, the extinction of indigenous species is becoming common as

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aggressive species invade degraded ecosystems. The loss of biodiversity has often been caused by the spread of species assisted by man. Endemic fish and amphibians are among the taxa most vulnerable to intentional introductions throughout the world. As a result of introductions of NIS, several species have disappeared or have been subject to major reductions in their numbers to the extent that they are now threatened with extinction (Lloyd 1990, Arthington 1991, Minckley and Douglas 1991, Townsend and Crowl 1991, Witte *et al.* 1992).

Typically, successful invaders are characterized by a tolerance to wide environmental conditions, omnivory, rapid growth, dispersal, breeding in ephemeral habitats, and other traits associated with opportunism. The high predation efficiency and the lack of predators frequently make them the originators of important changes to the original biota.

Crayfish are among the most notorious invasive aquatic species in freshwater ecosystems and have been reported not only to displace indigenous crayfish but also to impact a number of other aquatic organisms (Chapter 28). Crayfish feed omnivorously on detritus, algae, plants, invertebrates (including other crayfish), and vertebrates (e.g. Ilhéu and Bernardo 1993a, 1995, Momot 1995, Smart *et al.* 2002, Chapter 30). Low-protein resources such as plants, detritus, and algae are important energy sources for maintenance (e.g. Ilhéu and Bernardo 1995, Rudnick and Resh 2005) but they might be expected to feed predominantly on macroinvertebrates when these are available (Ilhéu and Bernardo 1993b, Correia 2003, Nyström 2005). A large number of studies have shown that, because of their omnivorous character, introduced crayfish can profoundly modify the trophic structure of freshwater communities at several levels, often acting as keystone species (e.g. Lodge *et al.* 1994, Nyström *et al.* 1996, 2001, Covich *et al.* 1999, Dorn and Wojdak 2004, Usio and Townsend 2004).

Crayfish display a wide plasticity in their feeding behaviour, switching from detritivore/herbivore to scavenger/carnivore habits in response to food availability (Ilhéu and Bernardo 1993a, 1993b, 1995, Nyström 2002, Alcorlo *et al.* 2004). This is in accordance with previous studies which produced evidence of the crayfish predation effects of crayfish particularly on benthic invertebrates (Ilhéu *et al.* 2002, Smart *et al.* 2002, Dorn and Wojdak 2004, Wilson *et al.* 2004, Correia *et al.* 2005, Geiger *et al.* 2005, McCarthy *et al.* 2006, Roth *et al.* 2006), including bivalves (e.g. Perry *et al.* 1997, 2000, Reynolds and Donohoe 2001), amphibian species (e.g. Renai and Gherardi 2004, Cruz and Rebelo 2005), and fish (e.g. Savino and Miller 1991, Guan and Wiles 1997). The aim of this chapter is to review the predation effects of invasive crayfish on indigenous vertebrates, both amphibians and fish, and present a case study on the impact of the red swamp crayfish, *Procambarus clarkii* (Girard), on fish assemblages in dry-season pools of temporary streams in southern Portugal.

### CRAYFISH PREDATION ON VERTEBRATES

## Crayfish predation on amphibians

There are numerous reports of crayfish impact on amphibians (reviewed in Nyström 1999) but few studies focus on the effect of crayfish predation on amphibian populations.

Recently, both experimental studies and correlative field surveys implicated non-indigenous predators, such as crayfish, as major contributors to amphibian population decline and, in some instances, to local extinction (Kats and Ferrer 2003). The introduction of the American signal crayfish, *Pacifastacus leniusculus* (Dana), in Sweden produced a negative impact on the embryos and larvae of the indigenous amphibians (Axelsson *et al.* 1997, Nyström and Abjörnsson 2000, Nyström *et al.* 2002). The effects of this species on the breeding habitat selection by anurans were also reported (Nyström *et al.* 2001).

Laboratory studies showed *P. clakii* preying upon tadpoles of several indigenous species of *Rana* from Italy (Gherardi *et al.* 2001, Renai and Gherardi 2004), along with embryos and tadpoles of *Bufo bufo* (Linnaeus) and larvae of *Triturus vulgaris* (Linnaeus) (Renai and Gherardi 2004). The introduction of this species into Californian mountain streams was a cause of the decline of the newt *Taricha torosa* (Rathke) as a result of predation by the crayfish on embryos and larvae (Gamradt and Kats 1996).

Many amphibians from the south of Portugal reproduce mainly in temporary ponds where typical aquatic predators, such as fish, are absent. However, these habitats are now occupied by the red swamp crayfish, and a negative correlation between the distribution of some amphibian species and the presence of the crayfish was found (Beja and Alcazar 2003). After the introduction of this crayfish into a lagoon in NW Spain, five amphibian species previously reproducing in the lagoon eventually disappeared (Rodríguez *et al.* 2005). In the Paul de Boquilobo, a wetland in central Portugal, apparently for no other reason than the impact of the red swamp crayfish, there was a collapse of the amphibian community, with drastic reductions of the populations of *Pleurodeles waltl* (Michahelles), *Triturus marmoratus* (Latreille), and *Rana perezi* (Seoane), and the probable extinction of previously abundant species, such as *Hyla arborea* (Linnaeus) and *Pelodytes punctatus* (Daudin) (Cruz 2006).

There are numerous reports of crayfish consuming amphibian eggs. Cruz and Rebelo (2005) found a very high consumption rate of amphibian egg masses by the red swamp crayfish in mesocosm experiments, even when alternative vegetable food items were available. Cruz *et al.* (2006b) assessed the effects of the presence of *P. clarkii* presence in the breeding site distribution of 13 amphibian species in SW Portugal. Amphibian species richness was lower in places where crayfish presence was a negative predictor of the breeding probability of all urodeles [*P. waltl, Salamandra salamandra* (Linnaeus), *Triturus boscai* (Lataste), and *T. marmoratus*] and of two anurans [*Pelobates cultripes*]

(Cuvier) and *B. bufo*]. In the temporary ponds of Doñana Natural Park, red swamp crayfish had a strong effect on the reproductive success of *Bufo calamita* (Laurenti), the survival of its embryos being strikingly reduced when they were directly exposed to crayfish (Cruz *et al.* 2006a).

Dorn and Wojdak (2004) studied the effects of the virile crayfish, *Orconectes virilis* (Hagen), on the development and structure of littoral communities in newly established freshwater ponds in south-western Michigan (USA) and found no bullfrog (*Rana catesbiana* Shaw) tadpoles in any of the crayfish ponds although tadpoles were abundant in the control ponds.

In response to indigenous predators, amphibians frequently develop adaptive mechanisms, such as toxic or unpalatable eggs and larvae (e.g. Eklöv and Werner 2000). Behavioural or morphological features may also be effective to escape predators (e.g. Rödel 1999, Lardner 2000, Nyström and Abjörnsson 2000). When no co-evolutionary process takes place, prey species may lack suitable responses to crayfish predation. However some crayfish species, such as *P. clarkii*, are apparently resistant to certain amphibian toxic compounds and are able to predate eggs with highly protective gelatine layer (Gamradt and Kats 1996, Renai and Gherardi 2004).

In general, invasive crayfish are efficient predators and a significant threat to amphibians. Furthermore, in several instances, habitat degradation caused by crayfish (e.g. Ilhéu *et al.* 2002, Geiger *et al.* 2005, Rodríguez *et al.* 2005) may severely affect the amphibian populations as well.

## **Crayfish predation on fish**

Crayfish have been implicated in the decline of fish populations mainly indirectly due to competition for food and shelter (Guan and Wiles 1997, Miller *et al.* 1992, Gherardi 2002, Nyström 2002, Light 2005) and through the destruction of macrophyte beds, which are important habitats for juvenile fish (Rubin and Svensson 1993, Scheidegger and Bain 1995, Shoup *et al.* 2003).

However, several studies also suggest that crayfish readily prey on all the life stages of fish but the effects and mechanisms of predation are less well-studied than the crayfish-fish competitive interactions (reviewed in Dorn and Mittlelbach 1999). Even though the number of studies involving the role of crayfish as an omnivorous predator is increasing, most knowledge is based on experimental work and the magnitude of these effects is very much dependent on the particular environmental context.

In northern Wisconsin lakes (USA), the decline of game fish populations has been attributed to the invasions of the crayfish *Orconectes rusticus* (Girard) (Hobbs *et al.* 1989). Egg predation by crayfish has been suggested to cause declines in bass *Micropterus dolomieu* Lacépède, pumpkinseed sunfish *Lepomis gibbosus* (Linnaeus), walleye *Stizostedion vitreum* (Mitchill), and lake trout *Salvelinus namaycush* (Walbaum). Savino and Miller (1991) report the predation of *O. rusticus* on lake trout eggs in experimental conditions. Egg consumption

(2–5 eggs/crayfish/day) was dependent upon temperature, substrate, and crayfish species. They concluded that, in conditions of high crayfish density and/or low egg density in cobble habitats, crayfish predation may affect trout recruitment. Similar effect may occur with bass and pumpkinseed sunfish, as the crayfish potential to consume eggs of warm-water species is greater (Horns and Magnunson 1981). Further, most bass and pumpkinseed sunfish concentrate their nests in shallow littoral zones, which make eggs more vulnerable to crayfish predation. In experimental ponds, Dorn and Mittlebach (2004) and Dorn and Wojdak (2004) observed virile crayfish preving heavily on fish eggs and found that a crayfish presence significantly affected the successful reproduction of bluegill sunfish, Lepomis macrochirus Rafinesque, reducing the recruitment of young-of-the-year. Fitzsimons et al. (2002) estimated a crayfish (O. virilis) consumption of 82% of the potential egg numbers at lake trout spawning reefs based on both the published literature (Miller et al. 1992) and experimental work, concluding that high crayfish density and low egg abundance ( $<100 \text{ eggs m}^{-2}$ ) may also limit natural recruitment of trout in Lake Ontario. Corkum and Cronin (2004) also found that consumption of rainbow trout eggs by crayfish depended on several factors, including crayfish density, food levels, and habitat complexity. Other studies report that O. virilis, in its native range, is a significant egg predator of the fathead minnow, *Pimephales* promelas Rafinesque. Matity et al. (1994) found that breeding male fathead minnows had significantly more scars from crayfish pinches than non-breeding males or females, which may be due to their involvement in nest defence. The fathead minnows exposed to chemical cues from these cravitsh presented variations in hatching time, egg morphology, and fry size (Kusch and Chivers 2004). They suggested that the recognition of crayfish as an egg predator is innate in fathead minnows. However, Rubin and Svensson (1993) studied predation by the indigenous crayfish Astacus astacus (Linnaeus) on trout eggs and fry and found no evidence of A. astacus ability to consume trout eggs laid in reeds.

Evidence for crayfish predation on juvenile or adult fish is scarce and few data are available to judge their importance. Light (2005) noted that sculpin *Cottus beldingi* (Linnaeus) and signal crayfish may be considered as intraguild predators (*sensu* Polis and Holt 1992) based on observations of each species consuming the young-of-the-year of each other. Guan and Wiles (1997) found evidence of predation by signal crayfish on sculpin as well as on bullhead *Cottus gobio* (Linnaeus) and stone loach *Noemacheilus barbatulus* (Linnaeus). Nevertheless, because such predation was rare, it seems unlikely that it has significant population consequences.

In fact, only in high crayfish densities is the impact more perceptible. Rogowski and Stockwell (2006) assessed the potential impacts of non-indigenous crayfish on the threatened white sands pupfish, *Cyprinodon tularosa* (Miller and Echelle), and found that fish biomass was significantly lower at high densities of *O. virilis*. On several occasions virile crayfish were seen consuming adult pupfish in a high density crayfish experiment.

Other studies are not so conclusive on predation rates. Xinya (1995) studied the effect of crayfish *P. clarkii* on the survival of fry and fingerlings of cultivated fishes in China [carp, *Cyprinus carpio* (Linnaeus); grass carp, *Ctenopharyngodon idella* (Valenciennes); silver carp, *Hypophthalmichthys molitrix* (Valenciennes); and tilapia, *Oreochromis niloticus* (Linnaeus)] and found no significant negative impacts; fry grew well with or without crayfish. Stenroth and Nyström (2003) studied the effect of signal crayfish on brown trout using enclosures in a Swedish stream and found no impact on growth or survival of juvenile trout. Virile crayfish were found to reduce the activity rate and movement in and out of shelter of the Little Colorado spinedace, *Lepidomeda vittata* Cope, a threatened indigenous minnow of the south-western USA, but the predation rate was not significant (Bryan *et al.* 2002).

Several studies reported the presence of fish in the crayfish diet (e.g. Lorman and Magnuson 1978, Ilhéu and Bernardo 1993a, Gutiérrez-Yurrita *et al.* 1998, Correia 2003, Pérez-Bote 2005). In experimental laboratory studies, Ilhéu and Bernardo (1993b) demonstrated that crayfish predation success is very much dependent on the ability of the prey to escape. The choice of the feeding strategies may be interpreted in terms of cost-benefit analysis. In spite of a preference for animal food items, such as fish, the high costs involved in active predation may explain the low consumption of high mobility animals. This conclusion leads us to the hypothesis that crayfish feeding on fish occurs mainly when prey is vulnerable and thus low costs of predation are involved. This situation only happens in strongly confined conditions, which is the case of the temporary aquatic systems during the drying period.

## PREDATION EFFECTS OF INVASE CRAYFISH (*Procambarus clarkii*) ON FISH OF DRY-SEASON STREAM POOLS IN SOUTHERN PORTUGAL

Lowland streams in Mediterranean-climate regions are shaped by predictable seasonal events of flooding and drying over an annual cycle. During the summer and early autumn, streams show a marked pattern of zero flow. When the flow ceases, and because of the high temperatures and evaporation, many rivers show long dry reaches and the surface waters are reduced to isolated pools (Bernardo and Alves 1999). Throughout the dry months, the wet area and volume of the summer pools decrease, and environmental conditions become more critical to the biota (Ilhéu 2004). Many receding pools will eventually dry and the remaining ones are important refuges for the aquatic organisms. During the following run-off period, streams start to flow again and longitudinal connectivity is re-established (Bernardo and Alves 1999, Ilhéu 2004).

During the drying phase, the combination of nutrients, organic detritus, shallow waters, favourable temperature, and dense populations of algae and water plants form the basis of a highly productive food web capable of

supporting large populations of aquatic consumers. Throughout the summer period, the aquatic biota, namely fish and invertebrates including the red swamp crayfish, become progressively more concentrated in the receding pools.

The red swamp crayfish is an example of a successful invader in the temporary stream of the Mediterranean region. This species is very well adapted to the natural flow variation of this type of stream and frequently develops high density populations (Ilhéu 1994, Ilhéu and Bernardo 1996). Moreover, these waterbodies show no indigenous crayfish species and thus *P. clarkii* occupies a vacant niche.

The potential impacts of NIS on temporary aquatic systems are of special concern because such systems can have relatively high levels of endemism (e.g. Williams *et al.* 1985, Doadrio 2001, Cabral 2005). Many fish extinctions have been associated with the introduction of NIS (Miller *et al.* 1989, Richter *et al.* 1997, Minckley *et al.* 2002). The potential impact of NIS is apparently higher when endemic fish evolved in an environment with few aquatic predators and competitors (Minckley and Douglas 1991). Moreover, regions with Mediterranean climate are especially susceptible to invasions, as suggested by Macdonald *et al.* (1988).

Assessing the impact of NIS in the rivers of southern Portugal is of extreme importance because of the high conservation value of the indigenous fish fauna, which show a high proportion of endemism most of which are threatened (Cabral 2005). This fauna is mostly composed of cyprinids and no indigenous piscivorous species exists. Fish assemblages are dominated by indigenous species, although NIS, such as pumpkinseed sunfish *L. gibbosus* and mosquitofish *Gambusia holbrooki* Girard, also occur very frequently (Ilhéu 2004).

Crayfish predation on fish was studied in 17 isolated pools in the south of Portugal (Degebe stream, 2nd and 3rd orders) during the summer of 2002. Crayfish and fish were collected with electrofishing. In the shallow pools crayfish were also captured by hand.

Pool volumes were highly variable, ranging from 0.06 to 700 m<sup>3</sup>, with mean water depth from 0.03 to 0.7 m. Very shallow pools showed a high percentage of aquatic vegetation, mainly filamentous algae. Many pools presented critical conditions for the aquatic fauna because of the extreme temperature and low dissolved oxygen (DO). Maximum water temperature was  $28.6 \pm 2.9$  °C. Minimum oxygen concentrations were lower than 1 mgL<sup>-1</sup> in 41% of pools and very large daily ranges were observed in 53% of the pools, mostly shallow ones.

Fish density in the pools ranged from 1.9 to 80.0 fish m<sup>-2</sup>. Shallow pools (<0.15m mean water depth) had high fish densities, ranging from 20.1 to 80.2 fish m<sup>-2</sup>, with a mean value of 50.7 fish m<sup>-2</sup>  $\pm$  19.5 (SD). Fish density was inversely correlated to pool depth (after Spearman correlation: r = -0.82, P < 0.001) which may be interpreted as an effect of fish concentration as pools shrink.

The most abundant species in the pools were mosquitofish (33.6%) and the Iberian roach *Squalius alburnoides* (Steindachner) (30.4%), with the former more

abundant in the very shallow pools (<0.15 m water depth), reaching up to 60% of total fish specimens. Lower frequencies were observed for pumpkinseed (10.1%), arched-mouth nase *Chondrostoma lemmingii* (Steindachner) (5.1%), Iberian dace *Squalius pyrenaicus* (Günther) (3.2%), stoneloach *Cobitis paludica* (De Buen) (2.6%), barbels *Barbus* spp. (1.1%), Guadiana nase, *Chondrostoma willkommii* Steindachner (0.3%), and largemouth bass *Micropterus salmoides*, Lacépède (0.03%). Specimens with 0–30 mm total length were dominant in shallow pools (<40 cm depth) where no fish larger than 50 mm occurred. In the deeper pools, very small fish were less representative and larger fish (50–80 mm) were observed.

Crayfish density in the pools ranged from 0 to 39.3 crayfish m<sup>-2</sup> and, as for fish, was inversely correlated to the water depth (after Spearman correlation: r = -0.46, P < 0.05). Apparently, crayfish concentrate in the pools where fish are more abundant and vulnerable because of the spatial confinement. In fact, choice tests showed that fish is the preferred food type if the costs involved in the capture are relatively low (Bernardo and Ilhéu 1993b).

A total of 409 crayfish stomach contents were analysed. For fish specimens, the identification was based on skeleton remains, skin, and scales. The number of eaten organisms was estimated by the skeleton parts. The food types in the crayfish diet for each pool were characterized through a Modified Main Food Index: MFI = (frequency of occurrence × proportion of each food item to the total volume of the gut content)<sup>1/2</sup> (Bernardo 1990).

Crayfish consumed a broad diversity of food items, the most common being vegetal detritus, invertebrates, and fish. Vegetal detritus was dominant in 76% of the pools. Overall, invertebrates were the second most important item in the crayfish diet. Fish was the third most consumed item, present in 24% of crayfish stomach contents; this type of food was dominant in 24% of the pools.

Consumption of animal material was negatively correlated with water depth (after Spearman correlation: r = -0.63, P < 0.01; Fig. 1) and pool area (after Spearman correlation: r = 0.69, P < 0.01). Fish consumption by crayfish increased significantly with fish density in pools (after Spearman correlation: r = 0.68, P < 0.05) (Fig. 2). This fact clearly supports the hypothesis that crayfish concentrate in the shallow pools because of the high availability and vulnerability of the fish. The most abundant prey, mosquitofish, was also the more consumed, representing 76% of total fish, thus corroborating the opportunistic character of *P. clarkii*. Pumpkinseed sunfish represented only 9% of fish prey and some indigenous species such as Iberian roach and barbel juveniles were also observed in the stomach contents but in very low frequencies and volumes.

As the larger proportions of fish in the crayfish diet were observed in the shallower (< 0.15 m water depth) and densely populated pools (both by crayfish and fish), the predation pressure of crayfish on fish was estimated on the basis of the conditions of those pools. For the evaluation of the predation pressure, values from this and previous studies on crayfish ecology were used.

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**Fig. 1** Proportion of total animal items and of fish consumed by crayfish in each studied pool and pool water depth. MFI = Main Food Index. (After Bernardo 1990)



**Fig. 2** Relation between fish consumption by crayfish and fish density in the studied pools.

To estimate crayfish predation pressure on fish, crayfish food consumption rate and the proportion of fish in the stomach contents were used. Total crayfish biomass per area was assessed using the crayfish density and crayfish mean weight. The consumption rate of fish by crayfish (CONS, g of fish  $m^{-2}$ ) was calculated as:

$$CONS = DENS \times CW \times DCR \times PF$$

in which DENS is the crayfish density (N m<sup>-2</sup>), CW is the mean crayfish weight (g), DCR is the daily consumption rate (g food/g crayfish per day), and PF is the proportion of fish in the crayfish stomach contents. Weights are wet weights.

A crayfish density of 10 crayfish m<sup>-2</sup> was adopted; this density was observed in some pools in this study and is a mean value for these stream types (Ilhéu 1994). Crayfish size was homogenous, the average weight being 30.0 g ( $\pm$ 5.3 SD).

The mean proportion of fish observed in the stomach contents was 69.7%. The consumption rate was based on the experimental assessment in ad libitum conditions by Bernardo and Ilhéu (1994), was 0.088 g/g crayfish per day, i.e. 8.8% of the crayfish weight per day. Based on these values, the estimated consumption of fish in the conditions of the shallow summer pools is 18.4 g fish m<sup>-2</sup> per day.

In order to have a relative measure of the magnitude of this consumption rate, this value was compared to the fish density. The estimated mean biomass of fish in the shallow and densely populated pools was 126.3 g m<sup>-2</sup>. Based on this value and on the consumption rate of fish, a prediction of the approximate time for crayfish to consume all fish present in pools at the time of sampling would be 6.9 days.

Results clearly demonstrate that the crayfish performs a significant role in the removal of fish but only in the last phase of the vanishing summer pools. As pools recede, confinement and concentration of the aquatic fauna causes the intensification of biological interactions, in particular predation. High vulnerability of fish makes them the ideal prey only during the low-water conditions associated with the temporary character of these streams. As the surface water disappears, in the extreme confinement of the very shallow pools, fish are totally predated (M. Ilhéu and J. Bernardo, unpublished data).

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## CONCLUDING REMARKS

Crayfish have been described as an opportunistic species feeding on various types of animal and vegetal food items (e.g. Ilhéu and Bernardo 1993a, 1995, Gherardi *et al.* 2001, Nyström 2002, Correia 2003). As the crayfish grow, diet shifts from a more zoophagous to an almost exclusively phytophagous-detritophagous one (Ilhéu and Bernardo 1993a, Pérez-Bote 2005). Usually, fully grown adults feed almost entirely on vegetal matter, either fresh or detritic (Ilhéu and Bernardo 1995).

As previous experimental laboratory studies predicted (Ilhéu and Bernardo 1993b), when prey face confined conditions, as in shallow pools, crayfish profit from their vulnerability and in such an advantageous cost–benefit ratio crayfish behave as opportunistic predators. In the large pools, fish display strong escape ability, and predation efficiency by crayfish is low. Moreover, large persistent

pools tend to show higher habitat complexity, which is also reflected in the crayfish predation success.

Both invasive and indigenous crayfish generally are well adapted for dispersal and can move from habitats with low prey availability to other locations where prey densities are higher and foraging success is greater. They often occupy "ephemeral home ranges" and move from one location to another (Ilhéu *et al.* 2003). The short-term movement is well studied in crayfish (e.g. Gherardi *et al.* 1998, Gherardi 2002, Bubb *et al.* 2006).

In general, the cost-benefit analysis – the basic principle of theories of optimal foraging strategies (Schoener 1971) – is consistent with the opportunistic character of the red swamp crayfish. To consume a certain quantity and quality of food (i.e. the benefit) the forager has to spend a cost involved in food searching, pursuit, handling or catching, and eating. The balance of costs and associated benefits will determine the choice among the available options. Thus, depending on the availability and ease of capture of the food categories, crayfish may be a phyto/detritophagous or a predator.

When highly populated receding pools reach very low water depths, crayfish face the ideal conditions of prey availability/vulnerability to perform an easy and rewarding predation. This pattern is likely to be found in other temporary, ephemeral, or intermittent aquatic systems of temperate or tropical regions where the dramatic circumstances of the vanishing waterbodies provide a feast for the predators.

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## **Author Queries**

#### [AQ1] Not in reference

- [AQ2] Pl. provide the year of unpubl. data
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