

Spatial and temporal patterns in the movement of *Procambarus clarkii*, an invasive crayfish

Francesca Gherardi*, Silvia Barbaresi and Gabriele Salvi

Dipartimento di Biologia Animale e Genetica “Leo Pardi”, Università di Firenze,
Via Romana 17, 50125 Firenze, Italy

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ABSTRACT

Introduced in Italy in the 1980s for aquaculture enterprises, the red swamp crayfish, *Procambarus clarkii*, has invaded many water bodies, giving rise to breeding populations that now threaten freshwater ecosystems. An understanding of the spatial behaviour of this crayfish could be the baseline for future research aimed at control and management. Following the same pattern as other freshwater decapods, *P. clarkii*, studied in an irrigation ditch system in Florence, Tuscany, displayed stationary phases (several marked individuals were recaptured in the area) interposed with nomadic bursts of movement (many marked crayfish disappeared). With a few exceptions, nocturnal activity prevailed in almost all the seasons in two different analysed habitats (irrigation ditches and the Massaciuccoli Lake, Lucca). However, in the laboratory, locomotion occurred mostly at daytime. Although still prevailing, *P. clarkii*'s nocturnal activity appeared puzzling, because some of its major predators are nocturnal and this species is mostly herbivorous. The intercalation between stationary and wandering phases leaves open further promising studies on social structures in the field.

Introduction

Within the literature on freshwater decapods, the use of space and the dispersal in the habitat have been investigated in depth exclusively in river crabs. After anecdotal reports on *Potamon gedrosianum* Alcock (Schneider, 1971), radio-tracking has been applied in *Potamon fluviatile* (Herbst) (Gherardi et al., 1988; Gherardi and Vannini, 1989) and seasonal movements of this species were related to its biological cycle (Gherardi et al., 1989). The movement of crayfish inhabiting streams, ditches and ponds was described by several authors (Henry, 1951; Camougis and Hichar, 1959; Black, 1963; Momot, 1966; Mobberly and Pfrimmer, 1967; Merkle, 1967, 1969; Momot and Gowing, 1972; Fast and Momot, 1973; Hazlett et al., 1974, 1979; Flint, 1977; Guan and Wiles, 1997; Gherardi et al., 1998), while others, working in the

* Corresponding author, e-mail: gherardi@dbag.unifi.it.

laboratory, referred to the relationship between movement and population density (Bovbjerg, 1953, 1956, 1959, 1964, 1975; Mobberly and Owens, 1972). Although provisional, these studies have indicated that a number of factors, such as density pressure, availability of burrows, reproductive condition, sediment types, water level and other physical parameters (e.g. light) are responsible for the distribution of crayfish in their habitat.

In the analysis of locomotor rhythms, freshwater decapods were classical objects of study by electrophysiologists, with the result that a great deal of information is available about details of nerve activity. The most extensive studies dealing with the possible sites of the controlling clocks and processes involved in coupling clock and environment and between clock and overt rhythmic processes have been done on crayfish (see references in Webb, 1983). Only a few authors have examined the timing of locomotor activity under an eco-ethological perspective (in crabs: Schneider, 1971; Warburg et al., 1982; Gherardi et al., 1988; Barbaresi et al., 1997; in crayfish: Page and Larimer, 1972, 1975).

In the present study, field and laboratory data were collected with the basic aim to describe the spatial and temporal patterns of movement of the red swamp crayfish, *Procambarus clarkii* (Girard). This species, native to the north-eastern Mexico and the south-central USA (Huner, 1988), once escaped from aquaculture enclosures, is well established in northern and central Italy with breeding populations. It is undergoing a great expansion in some sectors of the Po and Reno River drainage basins, in Tuscany, Umbria, the Marches, Latium and Abruzzo (Gherardi et al., 1999a). An understanding of the spatial behaviour of this invasive crayfish could be the baseline for future research aimed at its control and management (Barbaresi and Gherardi, 2000).

Materials and methods

Spatial patterns

Fieldwork was conducted along two parallel 200 m long by 2 m wide canals (5 m apart) of an irrigation ditch system at the neighbourhood of Florence (Osmannoro), Italy, between June 1996 and May 1997. Crayfish were captured during 32 field excursions (once every second week) using five cylindrical baited traps (80 cm long, 28 cm in diameter and 4 mm in mesh size) placed at a reciprocal distance of 100 m (Fig. 1). At their first capture, crayfish were sexed, their cephalothorax length (CL) was measured and their moulting condition and ovigerous state (if females) were recorded. We classified three categories of individuals on the basis of CL (small CL < 34 mm, medium CL = 34–52 mm, and large CL > 52 mm). Immature specimens were clearly distinguished because they did not manifest evident secondary sexual characters. Before being released, each crayfish was individually marked with a numbered plastic tag glued to the first half of the cephalothorax; although innocuous and quickly applied, this mark does not persist after ecdysis. No doubt, this is a weak point of this study, because it may (at least in part) explain the large number of disappeared crayfish.

In those individuals that have been captured at least twice, we analysed their spatial behaviour. Three complementary parameters were used to describe move-

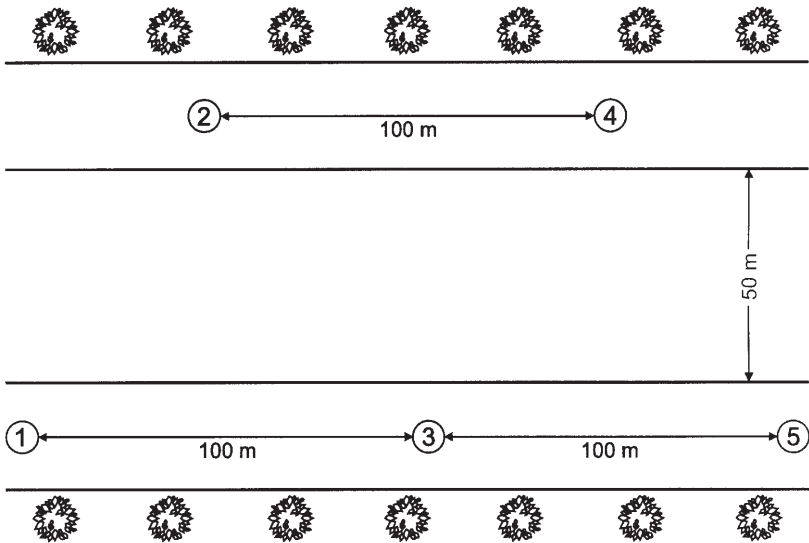


Figure 1. The study area at Osmannoro (Florence, Italy). Five baited traps were placed at a reciprocal distance of 100 m along two canals in an irrigation ditch system lined with poplar trees

ment: (1) the displacement from the point of the first capture (point 0), (2) the maximum distance travelled (i.e., the sum of distances travelled from the preceding and the following places of capture) and (3) the locomotor speed (i.e., the maximum distance travelled divided by the time passed from the first to the last capture). Obviously, none of these parameters gives an exact measure of displacement, distance or speed, since we did not have control over what was occurring between twice-weekly sampling efforts, but certainly provided a good estimate of movement.

Temporal patterns

For the study of the temporal activity of locomotion in the field, we placed 5 baited traps as described above at a reciprocal distance of 100 m along the irrigation ditch system of Osmannoro and, for comparison, along a 400 m long transect of Massaciuccoli Lake. *Procambarus clarkii*'s activity was evaluated from the number of captured crayfish once every fourth hour for a 24 h cycle. Sex and size of the collected specimens were also recorded. This procedure was repeated once for each season, that is May 19–20, 1997, August 28–29, 1997, November, 5–6, 1997 and January, 20–21, 1998 at Osmannoro and May, 21–22, 1997, August 27, 1997, December, 11–12, 1997 and February, 17–18, 1998 at Massaciuccoli. During each record, the air temperature and the water height were also measured. Air temperature was preferred over water temperature because of the large part spent by this crayfish outside water (F. Gherardi, unpublished data).

For the laboratory experiments, crayfish were collected from Osmannoro and maintained isolated in the laboratory at room temperature (18–20°C) with a

natural L/D cycle for at least a week before testing. The crayfish were fed earthworms once a week, but they were always starved while testing. During the experiments, each specimen was kept in a rectangular aquarium measuring $16 \times 28 \times 15$ cm, where its locomotor activity was recorded by infra-red photo-cell interruptions (more details in Barbaresi et al., 1997). Thirty-five adult specimens were tested. Experiments were conducted under the following five constant temperatures (with a margin of $\pm 0.5^\circ\text{C}$): 5°C , 10°C , 15°C (without and with an artificial shelter), 20°C and 25°C . The light cycle had a 12:12 L/D regime (06:00 lights on and 18:00 lights off). Experiments lasted 5 days, but we did not compute recordings of the first day. For each individual, activity is expressed as the average for 4 days of number of events (equal to photo-cell interruptions) per hour.

Statistical analysis

Parametric statistical techniques were used following Zar (1984), when the scores appeared to be drawn from a normally distributed population. Otherwise, statistical inference was made through nonparametric tests (Siegel, 1956). Statistical tests included: Wilks, Pearson, Wilcoxon-Mann-Whitney, Binomial, Fisher tests and the two-way ANOVA. The level of significance at which the null hypothesis was rejected was $\alpha = 0.05$.

Results

Spatial patterns

Recaptures

As shown in Table 1, the number of recaptures was low over the study period in both sexes without any difference (Wilks test: $G = 0.407$, $df = 2$, ns). Individuals of medium and large size and mature specimens were more often recaptured than small ($G = 26.515$, $df = 4$, $P < 0.001$) and immature ($G = 17.251$, $df = 2$, $P < 0.001$) ones, possibly because the latter moult more frequently, thus they more often lose their tags.

Displacement

The displacement from the location of the first capture was not correlated with the length of time the crayfish was followed in any sex (females: $r = 0.326$, $df = 21$, ns; males: $r = -0.110$, $df = 20$, ns). The same results were obtained analysing size classes (medium crayfish: $r = 0.307$, $df = 34$, ns; large crayfish: $r = -0.216$, $df = 10$, ns). All of the recaptured crayfish changed the original canal, a fact that supports our occasional observations of crayfish moving outside the water.

Maximum distance travelled

The computation of the maximum distance travelled by each crayfish depends on the number of records taken and on the length of time passed from the first to the

Table 1. Number of marked and recaptured crayfish, compared between sexes, size-classes and maturation stages (in brackets, frequency in percent)

	Marked	First recapture	Second recapture	N
Females	289 (93.7)	19 (6.1)	2 (0.6)	310
Males	287 (92.9)	21 (6.8)	1 (0.3)	309
Small	192 (100)	0 (0)	0 (0)	192
Medium	344 (92.0)	27 (7.2)	3 (0.8)	374
Large	118 (90.7)	12 (9.2)	0 (0)	130
Immature	204 (99.0)	2 (1.0)	0 (0)	206
Mature	437 (91.4)	38 (8.0)	3 (0.6)	478

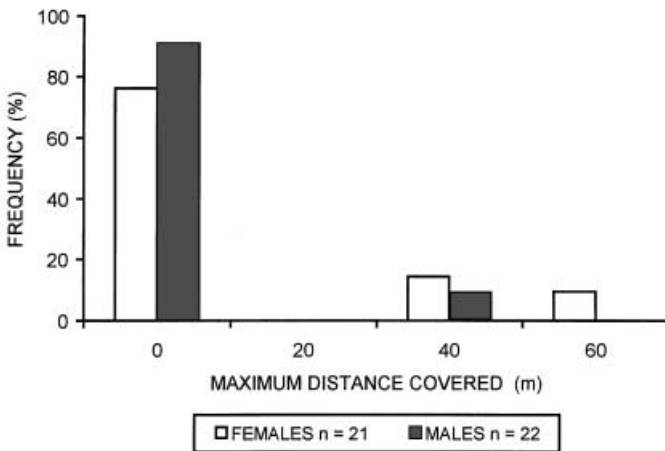


Figure 2. The maximum distance covered (in m) compared between sexes

last capture; thus it underestimates the actual movement of the crayfish. In this case (Fig. 2), the most frequent class is 0 m, that is most crayfish were recaptured in the same location (83.72 % of the overall crayfish recaptured). No significant difference in the frequency distribution of covered distance was obtained between the two sexes ($G = 2.887$, $df = 2$, ns). Considering only those crayfish moving after one year of observation, movement averaged 44 m ($SE = 3.89$, $N = 7$).

Locomotor speed

The measurement of locomotor speed confirmed the above results. No significant differences were shown between either sex (females: 1.51 md^{-1} , $SE = 0.81$, $N = 21$; males: 0.61 md^{-1} , $SE = 0.57$, $N = 22$; Wilcoxon-Mann-Whitney test: $U = 198.5$, $N = 22$, $z = 0.789$, ns) or size class (medium crayfish: 0.78 md^{-1} , $SE = 0.52$, $N = 30$; large crayfish: 1.81 md^{-1} , $SE = 1.17$, $N = 40$; $U = 158.5$, $N = 12, 30$, $z = 0.599$, ns).

Temporal patterns

Field studies

Figure 3 shows the number of captured crayfish per hour-class within a 24 h cycle for each season at Osmannoro, compared to air temperature and L/D regimes. The overall number of animals captured in 24 h was positively correlated with the mean air temperature ($r = 0.965$, $df = 2$, $P < 0.05$), but not with the mean water height ($r = 0.734$, $df = 2$, ns).

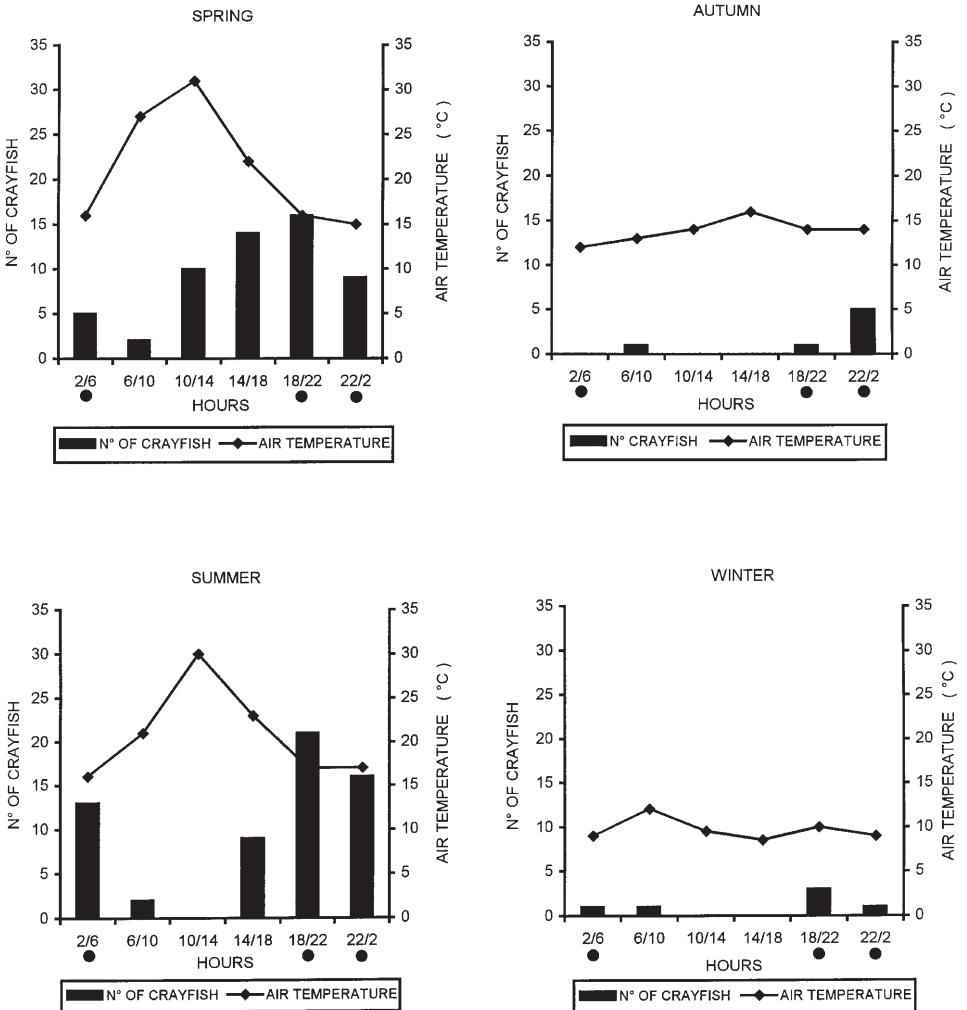


Figure 3. The number of crayfish captured at different hour intervals at Osmannoro, compared among seasons. Air temperature is also indicated. Dots under x-axis mark dark hours

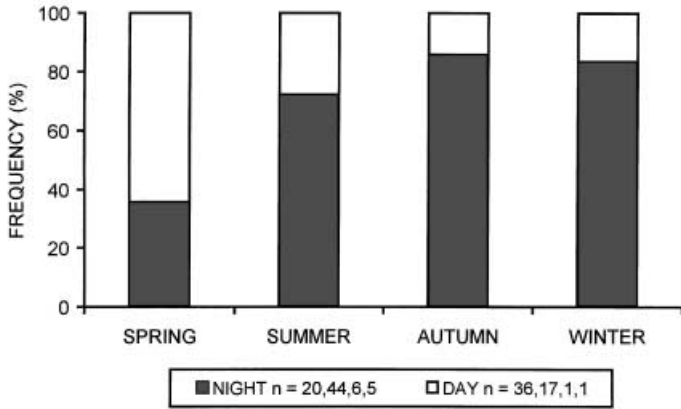


Figure 4. The percentage of nocturnal activity in the four seasons at Osmannoro

Activity is mostly nocturnal (summer: $G = 12.275$, $df = 1$, $P < 0.05$; autumn: after Binomial test $P = 0.062$; winter: after Binomial test $P = 0.109$), with the only exception of spring, when crayfish are more often active during daytime ($G = 4.595$, $df = 1$, $P < 0.001$) (Fig. 4). No difference in the frequency of catches between diurnal and nocturnal hours was found either among size classes (spring: $G = 2.52$, $df = 2$, ns; summer: $G = 2.788$, $df = 2$, ns; autumn: Fisher test $P = 0.444$; winter: Fisher test $P = 0.444$) or between sexes (spring: $G = 0.028$, $df = 1$, ns; summer: $G = 0.639$, $df = 1$, ns; autumn: Fisher test $P = 0.5$; winter: Fisher test $P = 0.75$).

At Massaciuccoli, three seasons were analysed (in summer the transect was dried) (Fig. 5). Contrary to the other habitat, the overall number of animals captured in 24 h was positively correlated with the mean water level ($r = 0.990$, $df = 2$, $P < 0.001$), and not with the mean air temperature ($r = 0.976$, $df = 1$, ns).

Activity (Fig. 6) is prevalently nocturnal in spring ($G = 13.134$, $df = 1$, $P < 0.001$) and autumn ($G = 10.984$, $df = 1$, $P < 0.001$), but not in winter ($G = 1.072$, $df = 1$, ns). Large crayfish were more often active during nocturnal hours in spring ($G = 6.77$, $df = 2$, $P < 0.05$), small ones in winter (Fisher test $P = 0.026$), while no difference between size classes was found in autumn ($G = 0.076$, $df = 2$, ns). The two sexes were equally found in nocturnal and diurnal hours (spring: $G = 1.884$, $df = 1$, ns; autumn: $G = 1.729$, $df = 1$, ns; winter: Binomial test $P = 0.344$).

A comparison between the irrigation ditch system at Osmannoro and the Massaciuccoli Lake shows a higher number of catches in summer in the former and in autumn and winter in the latter ($G = 138.938$, $df = 3$, $P < 0.001$) (Fig. 7). The hourly activity did not differ between the two habitats in both spring ($G = 3.750$, $df = 5$, ns) and autumn ($G = 6.732$, $df = 5$, ns), while at Massaciuccoli crayfish reached a peak at 14–18 h in winter ($G = 8.338$, $df = 4$, P ca. 0.05).

Air temperature did not differ between the two habitats (ANOVA: $F = 1.18$, $df = 1, 30$, ns), but obviously it did among seasons ($F = 21.53$, $df = 2, 30$, $P < 0.01$).

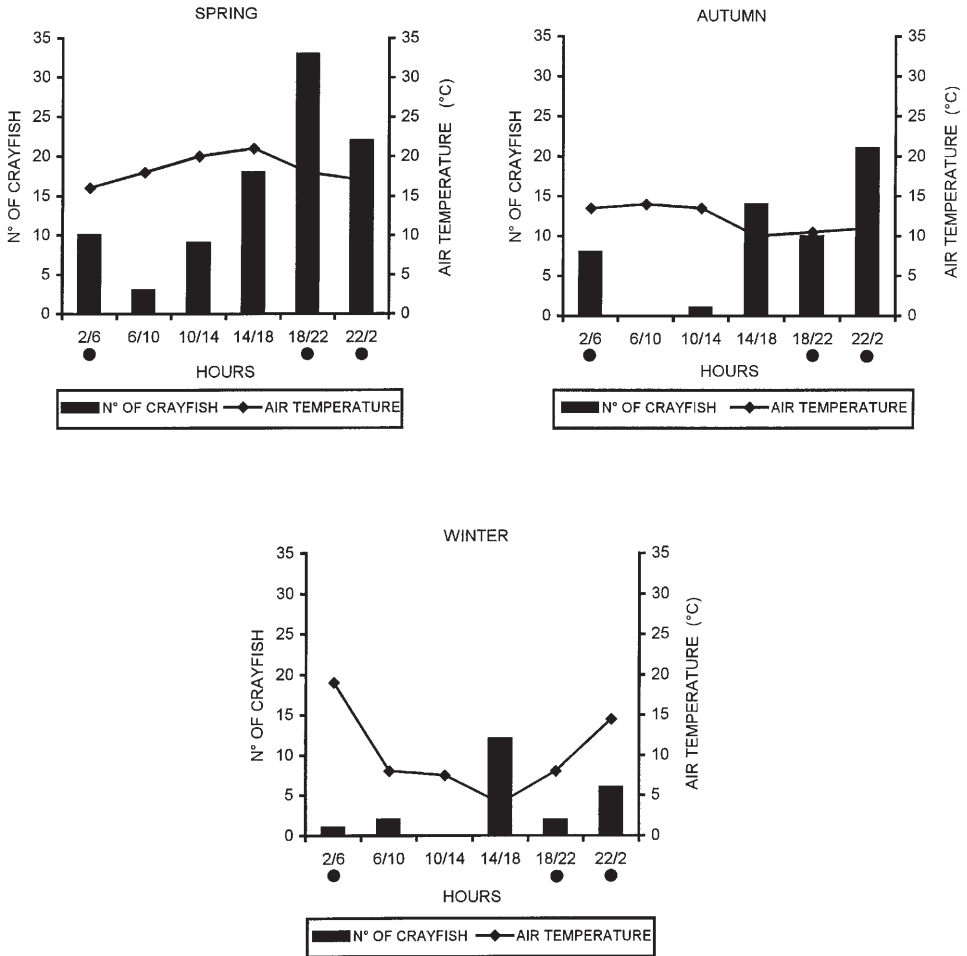


Figure 5. The number of crayfish captured at different hour intervals at Massaciuccoli Lake (Lucca, Italy) compared among three seasons. Air temperature is also indicated. Dots under x-axis mark dark hours

Laboratory studies

Hourly activity during each experiment is given in Figure 8. The total activity, but not the pattern of locomotor rhythm, was influenced by the rise of temperature (two-way ANOVA: $F = 56.29$, $df = 4$, 480 , $P < 0.001$). A comparison was made at 15°C between crayfish kept in boxes with and without a shelter, that revealed a difference in both the overall activity ($F = 7.09$, $df = 1$, 192 , $P < 0.01$) and the pattern of locomotion ($F = 2.19$, $df = 23$, 192 , $P < 0.01$) (Fig. 9).

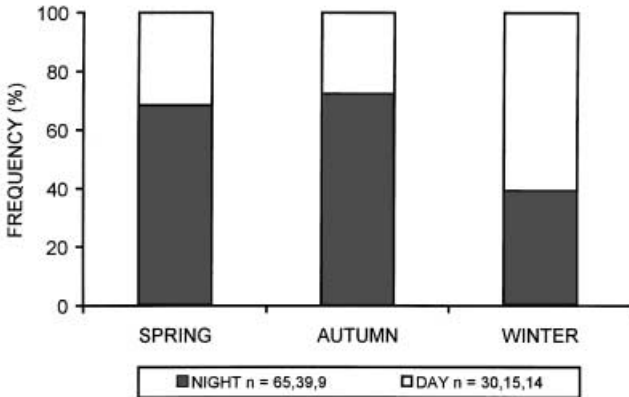


Figure 6. The percentage of nocturnal activity in three seasons at Massaciucoli

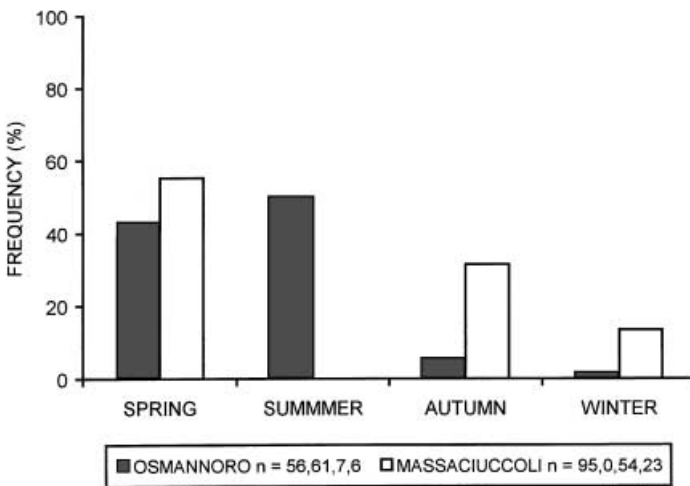


Figure 7. The frequency of crayfish captured in 24 h in the four seasons compared between Osmannoro and Massaciucoli

Discussion

Spatial patterns

The methods used to collect information on the movement of crayfish seem crucial in understanding the adaptive value of spatial and temporal patterns. Merkle (1969) utilised radioactive tags in *Orconectes juvenalis* [= *O. rusticus* (Girard)], while Black (1963) collected groups of *Procambarus* (= *Pennides*) *penni* Hobbs and *Procambarus bivittatus* Hobbs using electroshocking equipment. Camougis and Hichar (1959), Momot (1966), Momot and Gowing (1972) and Fast and Momot (1973)

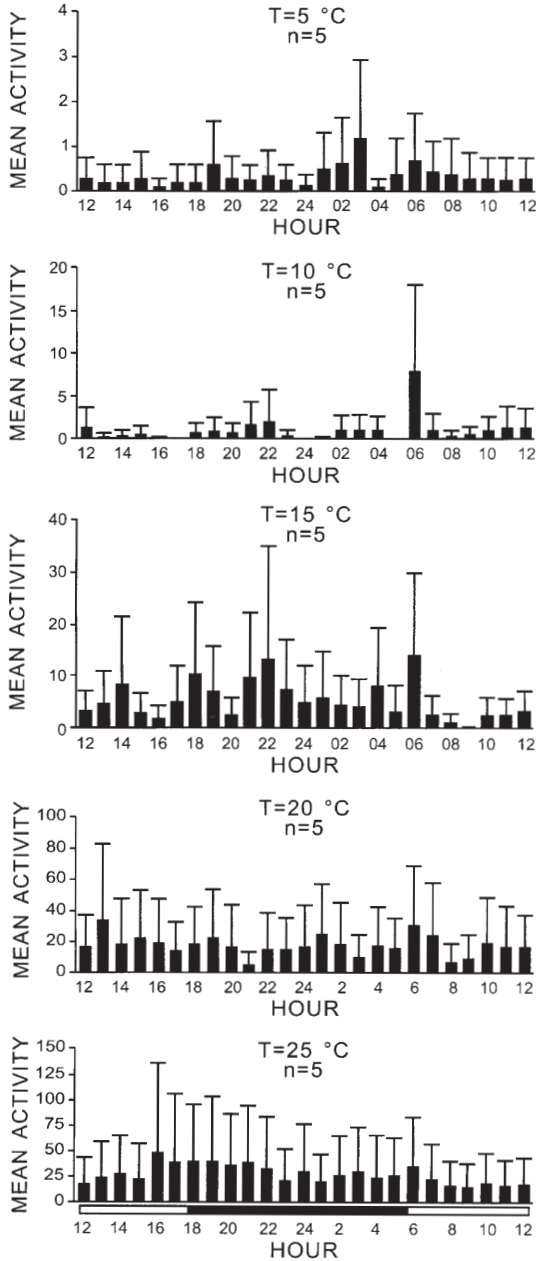


Figure 8. The mean hourly activity in actographic boxes during a 24 h cycle for each tested temperature

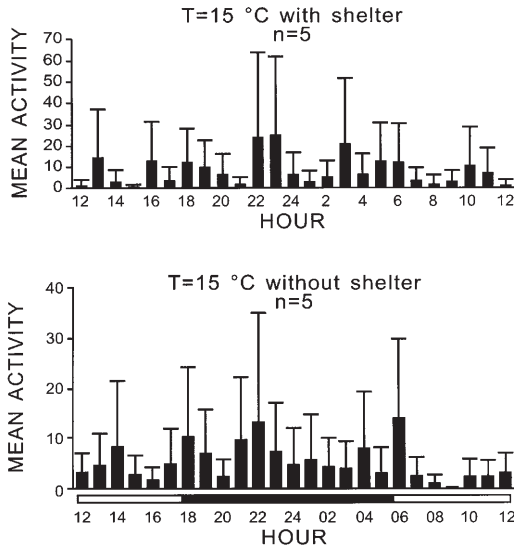


Figure 9. The mean hourly activity in actographic boxes during a 24 h cycle at 15°C compared between the presence and the absence of a shelter

employed minnow traps. Wiles and Guan (1993) used coded microchips, inserted into the cephalothorax of the signal crayfish, *Pacifastacus leniusculus* (Dana). Skurdal and Taugbøl (1995) did a study of the post-stocking movements of noble crayfish, *Astacus astacus* (Linnaeus), by SCUBA-diving in southeastern Norway. Recently, radiotelemetry was applied to crayfish by Schütze et al. (1999), who followed 13 adult male *Astacus astacus* in a river north of Munich, Germany, and by Gherardi and Barbaresi (2000) who radiotracked 5 adult male *P. clarkii* in the rice fields of the Guadalquivir River, Spain.

However, even the more sophisticated method confirmed the overall complexity of freshwater decapod movement and the coexistence of opposing spatial strategies within the same population (Gherardi et al., 1998). In the river crab, *Potamon fluviatile*, Gherardi et al. (1988) distinguished foraging movements, i.e. less than 2 m displacements, mostly occurring at night, which were performed to graze vegetable debris, scrape algae-covered surface, or prey, and a wandering phase, when crabs move without any overall directional tendency and do not return to their starting point. Similarly, *Orconectes juvenalis* (= *O. rusticus*) showed a tendency to reside in a very limited area for some days and then abruptly move to a new area (Merkle 1969). Hazlett et al. (1974) observed that many specimens of *Orconectes virilis* (Hagen) inhabited the same pond for a number of weeks. A longer sample showed that some individuals are stationary for a while and then move, while others are not stationary, at least during any part of the period they were followed. Using microchip implantation, Guan and Wiles (1997) estimated a range of movement within 190 m and a mean home range area exceeding 3000 m². This is relatively high compared with other North American crayfish, *Orconectes inermis inermis* Cope (Hobbs, 1978) and *O. virilis* (Black, 1963). A number of specimens made

long-distance excursions away from their home area. Due to the failure of intensive restocking activities, radiotelemetry was used to assess individual migratory movement in *Astacus astacus* (Schütze et al., 1999). That study showed that after stocking, crayfish manifested a high motion activity, followed first by 3–9 days of sedentary phase and then large-scale movements. The study by Gherardi and Barbaresi (2000) revealed a massive use of the habitat by *P. clarkii* in Guadalquivir rice fields.

Thus, if these results are extended to *P. clarkii* in the irrigation ditch system at Osmannoro, the population (without any difference of sex and size) can be divided into two components: the crayfish during their nomadic phase (those specimens captured only once) and those spending a stationary phase in the stretch under study (as revealed through the analysis of the displacement from the first capture, the maximum distance covered and the locomotor speed), a phase which can last up to one year.

Temporal patterns

In *P. clarkii*, movement is ruled by a nycthemeral rhythm, which is the prevailing pattern in freshwater decapods (e.g., in *Orconectes virilis*, Roberts, 1944, Hazlett et al., 1974; in *Austropotamobius pallipes* (Lereboullet), Arrignon, 1996, Barbaresi et al., 1998a; in *Potamon gedrosianum*, Schneider, 1971; *Potamon fluviatile*, Gherardi et al., 1988). At both Osmannoro and Massaciucoli, in spring and summer, crayfish activity increases at dusk, reaches a maximum at 18–22 h and continues until the early hours of the morning.

However, at Osmannoro more than 50% of the animals collected in spring were active during daytime and the few crayfish active in winter at Massaciucoli were diurnal. In addition, in actographic boxes, the activity of *P. clarkii* was more diffused within 24 h without a substantial difference between day- and night-time. These data confirmed observations performed in the rice fields of the Guadalquivir River (Gherardi and Barbaresi, 2000), where a large number of crayfish appeared active also during daytime. However, the presence of shelter inside the actographic boxes reduced diurnal activity and concentrated locomotion during the midnight.

Field and laboratory studies showed a correlation between activity and temperature, i.e. the number of either captured crayfish or photo-cell interruptions increased at higher temperatures. However, neither in field nor in the laboratory the temperature at which the crabs' activity might decline was reached (in *Potamon potamios* Olivier, locomotion dropped at 37.5°C, Warburg et al., 1982).

Conclusion

Some of the life history traits of *P. clarkii*, i.e. adaptability to burrow environments, resistance to air exposure, polytrophism, rapid growth, high fecundity and disease resistance (Huner and Lindqvist, 1995), can explain the extensive success of this species. As well, *P. clarkii* displays a surprisingly high plasticity in its biological cycle, appearing well adapted to both permanent and fluctuating aquatic systems (Gherardi et al., 1999c).

A further aspect of its biology, that might justify its potential of invader, is this species' use of space. First, we found that nomadic movements were interposed with a stationary behaviour. This eco-ethological aspect, that seems to be shared by other freshwater decapods, opens a multitude of questions, especially when the environment is uniform (in the irrigation ditch system of Osmannoro and in the rice fields in the Guadalquivir River, Gherardi and Barbaresi, 2000). In freshwater decapod literature, one explanation for the nomadic habit was given in *Potamon fluviatile* females (Gherardi et al., 1988): Gherardi et al. (1989) interpreted as proximate causes of this spatial strategy their energetic demands and the need for a more proteic diet required during vitellogenesis. Another explanation is offered by Peay and Rogers (1999), who suggested a pulsed expansion rather than a uniform spread of a signal crayfish population related to the availability of suitable habitats.

During the stationary phase, with slight differences among seasons and areas of study, individuals refuge inside burrows at daytime, while at night they emerge to forage into the canal bed to come back to the burrows at sunrise. This pattern appears puzzling in view of (1) the nocturnal habit of some of their major predators (birds of prey and rats at Osmannoro, largemouth bass (*Micropterus salmoides*), eel (*Anguilla anguilla*) and pike (*Esox lucius*) at Massaciuccoli) and (2) the mostly herbivorous feeding habits of *P. clarkii* (Barbaresi et al., 1998b).

The intercalation between stationary and wandering phases leaves open further promising studies on this species' social structure. Whether individuals show transient territoriality (are they faithful to the burrow they had dug? One species where individuals restore already excavated burrows, is *Potamon fluviatile*, Gherardi et al., 1987) and/or form hierarchies, as reported for laboratory situation in a number of crayfish (e.g., Bovbjerg, 1953 in *Orconectes virilis*; Gherardi et al., 1999b in *P. clarkii*), can be elucidated only by additional field observations.

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