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ITALIAN FRESHWATER DECAPODS : EXCLUSION BETWEEN THE CRAYFISH *AUSTROPOTAMOBIUS PALLIPES* (FAXON) AND THE CRAB *POTAMON FLUVIATILE* (HERBST).

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ABSTRACT

In Italian freshwater systems, the crayfish *Austropotamobius pallipes* and the crab *Potamon fluviatile* mainly occur in different geographic areas and, when they are in sympatry, in different streams. Four issues are raised : **(1)** the two species once coexisted, **(2)** the two species share the same resources, **(3)** river crab is behaviorally dominant over crayfish, and **(4)** crab influences the habitat occupied by crayfish. These issues suggest a scenario of competitive exclusion in these two species, which is the result of past interspecific competition for common resources. The winner was *P. fluviatile* which had higher levels of aggression and strength than *A. pallipes* ; the latter was forced to migrate to other regions or, when still in sympatry, to remain in less favorable habitats, characterized by a lower temperature regime.

Key-words : competitive exclusion, freshwater decapods, *Austropotamobius pallipes*, *Potamon fluviatile*.

DÉCAPODES D'EAU DOUCE ITALIENS : EXCLUSION ENTRE L'ÉCREVISSE *AUSTROPOTAMOBIUS PALLIPES* (FAXON) ET LE CRABE *POTAMON FLUVIATILE* (HERBST).

RÉSUMÉ

Dans le réseau d'eau douce italien, l'écrevisse *Austropotamobius pallipes* et le crabe *Potamon fluviatile* sont présents dans différentes aires géographiques et, quand ils sont en sympatrie, ils vivent dans des cours d'eau différents.

Quatre points sont relevés : **(1)** les deux espèces ne coexistaient qu'à une seule occasion, **(2)** les deux espèces partagent les mêmes ressources, **(3)** le crabe d'eau douce présente un comportement dominant sur l'écrevisse, **(4)** le crabe influence l'habitat occupé par l'écrevisse. Ces observations suggèrent un scénario d'exclusion compétitive entre ces

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deux espèces, résultant de la compétition interspécifique pour les ressources communes. *Potamon fluviatile*, qui a un niveau d'agressivité plus élevé et qui est plus fort qu'*Austropotamobius pallipes*, a été le vainqueur ; l'écrevisse a été forcée d'émigrer dans d'autres régions, ou, quand les deux espèces sont encore en sympatrie, elle reste reléguée dans les habitats caractérisés par un régime plus bas de températures.

Mots-clés : exclusion compétitive, décapodes d'eau douce, *Austropotamobius pallipes*, *Potamon fluviatile*.

INTRODUCTION

In crustacean decapods, intraspecific competition has been extensively cited as the main factor conditioning both the access to limited resources and the spatial distribution of populations (BOVBJERG, 1953, 1956 ; LOWE, 1956 ; BOVBJERG and STEPHEN, 1975 ; HAZLETT, 1974 ; HAZLETT, RUBENSTEIN and RITTSCHOF, 1975 ; GHERARDI, GUIDI and VANNINI, 1987 ; GHERARDI, TARDUCCI and MICHELI, 1989). However, only scattered information is available about interspecific competition (exceptions are : BOVBJERG, 1970 ; CAPELLI and MUNJAL, 1982 ; ALMAÇA, 1988 ; SÖDERBÄCK, 1991, 1995), and the mechanisms influencing species segregation and replacement have often been neglected.

The two most abundant native decapod species inhabiting Italian freshwater systems are the crayfish *Austropotamobius pallipes* (Faxon) and the river crab *Potamon fluviatile* (Herbst).

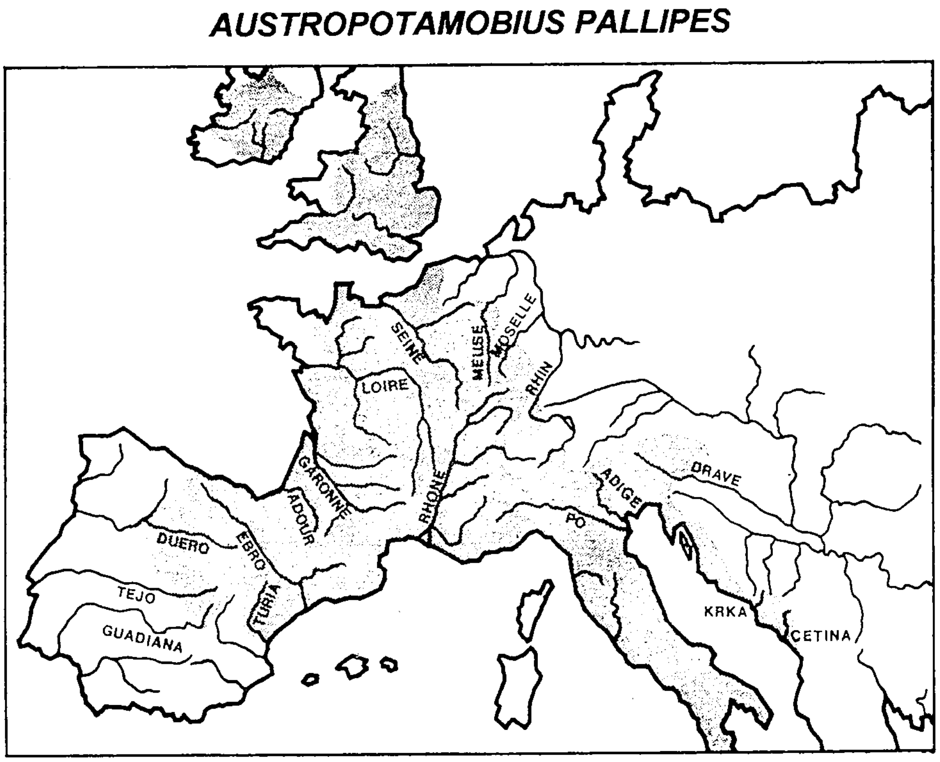
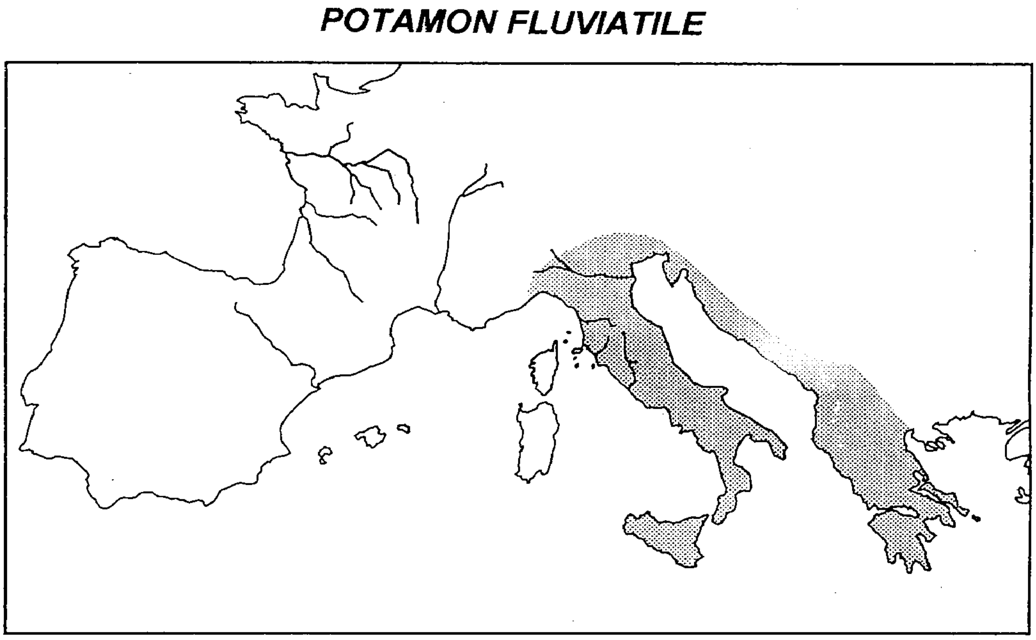


Figure 1a
General distribution of *Austropotamobius pallipes* (LAURENT, 1988) in Europe.

Figure 1a
Distribution générale d'*Austropotamobius pallipes* (LAURENT, 1988) en Europe.



POTAMON FLUVIATILE

Figure 1b
General distribution of *Potamon fluviatile* (PRETZMANN, 1987) in Europe.

Figure 1b
Distribution générale de *Potamon fluviatile* (PRETZMANN, 1987) en Europe.

Figure 1 shows the general distribution of *A. pallipes* (a) (LAURENT, 1988) and *P. fluviatile* (b) (PRETZMANN, 1987) in Europe. In Italy *A. pallipes* is present from Piedmont to Calabria and Venezia Giulia and *P. fluviatile* in Liguria and in central and southern parts of the country, including Sicily.

The two species occur, respectively, on the northern and southern sides of the Apennine (CAPRA, 1953 ; PRETZMANN, 1987 ; SALVIDIO, CRESTA and DORIA, 1993 ; DARDI, 1994). On the southern side of the Tuscan-Emilian Apennine, *A. pallipes* and *P. fluviatile* live in sympatry, but never share the same stream or pond.

PRETZMANN (1987) hypothesized that the present geographical distribution of these two species resulted from the interaction of various biotic and abiotic factors, including competitive exclusion and climatic changes. The two species converged in Italy along two different migration routes originating in eastern Europe. During the last glaciation, river crabs survived in small refuges in southern Italy (Calabria and Sicily) while Astacidae occupied the other regions. After the end of Pleistocene, *P. fluviatile* migrated northwards up to the Tuscan-Emilian Apennines. In the area of sympatry, they entered into competition and the prevalence of one species over the other led to the present distribution.

Within the framework of PRETZMANN's theory, the purpose of this study is to explain the sharp geographical segregation of these two species on the basis of climatic analysis, preliminary observations on agonistic competition between the two species and the effect of different temperatures on their locomotor, and thus general, activity.

MATERIAL AND METHODS

Field surveys

In the years 1988-1992 a total of 66 streams was explored, 28 on the southern side and 38 on the northern side of the Tuscan-Emilian (T-E) Apennine (Figure 2). For each stream, we recorded the altitude where the species were found.

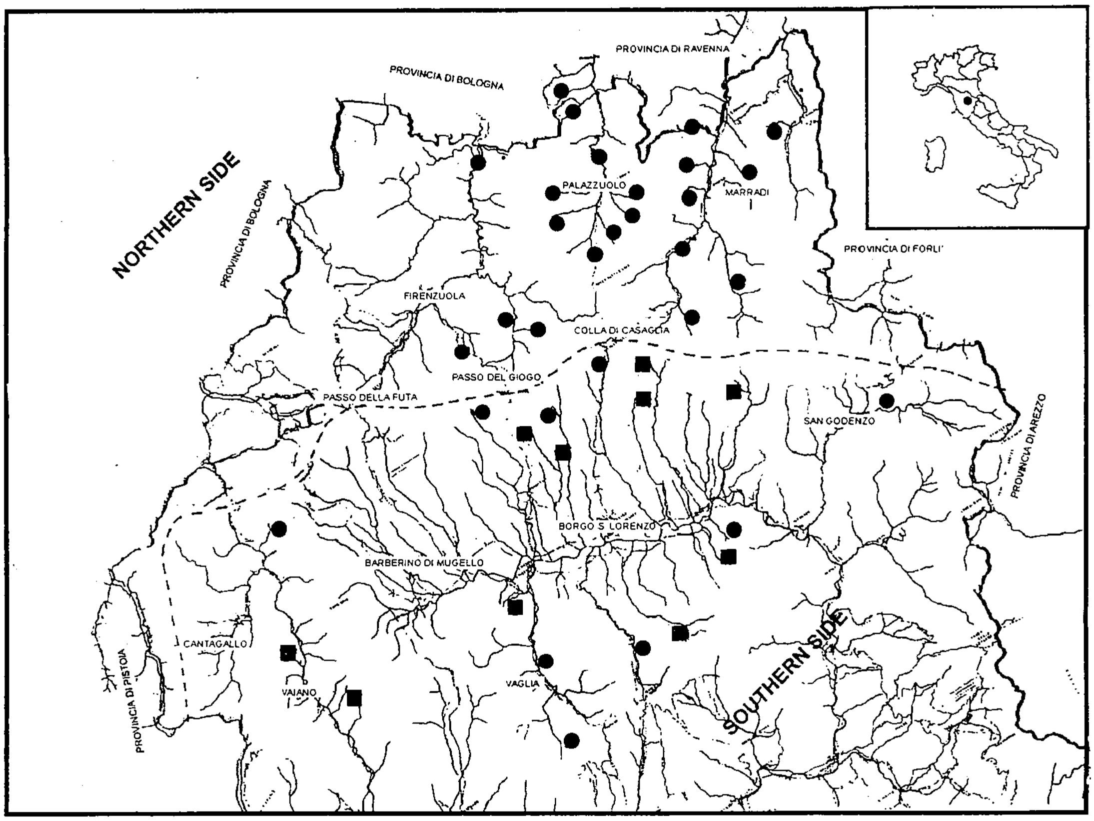


Figure 2

Map of the area under survey (Tuscan-Emilian Apennine, Italy) with main localities and streams where *A. pallipes* (circles) and *P. fluviatile* (squares) occur.

Figure 2

Carte de la zone étudiée (Apennin Tosco-Emilien, Italie) comprenant les principales localités et les torrents où *A. pallipes* (cercles) et *P. fluviatile* (carrés) se trouvent.

The 5-year averages of mean minimum and maximum temperatures in the coldest and warmest months and of the mean annual rainfall were provided by 6 meteorological stations (3 located on the northern and 3 on the southern side of the T-E Apennine).

Laboratory studies

Laboratory studies were carried out in 1990 and 1991. The two decapods were collected by hand near Florence, from Torrente Carza (*A. pallipes*) and Borro S. Giorgio (*P. fluviatile*). For at least a week before testing, the animals were kept in a room where the natural L/D cycle and ambient temperature were maintained. Crayfish were reared in mass in plastic tanks where the water was filtered by a pump. Crabs were kept individually in perspex tanks (16 x 40 cm) because of their strong intraspecific aggression. Both species were fed on Tetramin fish flakes and earthworms every third day.

Competition

Before the experiment, each specimen's carapace length (CL) was measured with a vernier caliper to the nearest 0.05 mm. The specimens were then individually marked and divided on the basis of size, which ranged from 16.5 to 50 mm CL for crayfish and from 8.8 to 43.35 mm CL for crabs. In order to compare the two species by size, we assigned the values of 0 and 10 to the minimum and maximum size measurements in both species and all intermediate sizes were calculated according to this new scale. Since males show a higher aggressive behavior than females, at least in *P. fluviatile* (VANNINI and SARDINI, 1971), only specimens of this sex were tested.

Before testing, the specimens were isolated in 2 tanks in the dark and starved for 24 hours. Experiments were carried out in round plastic basins (diameter 45 cm), containing 6 l of water. Each pair was observed for 30 min, either early in the morning or late in the evening. This time schedule corresponded to the peak activity periods, as indicated by previous observations (ROBERTS, 1944 ; BOVBJERG, 1956, 1970 ; HECKENLIVELY, 1970 ; FLINT, 1977 ; GHERARDI *et al.*, 1988).

For each interaction, the agonistic behavioral pattern was recorded according to the description by BOVBJERG (1953) for crayfish and VANNINI and SARDINI (1971) for crabs. On the basis of the behavior of the two opponents, the level of aggression was scored as +2 if fight was followed by the crayfish death, +1 if fight was followed by the crayfish flight, 0 if the opponents were still or avoided each others, -1 if fight was followed by the crab flight, and -2 if fight was followed by the crab death.

Locomotor activity

Experiments were carried out in a thermostatic cell where 5 adult crabs and 5 adult crayfish of both sexes were tested at the same time for 4 days. Before testing, animals were starved for 2 days and acclimated for 24 h to the experimental temperature. During the experiment, each specimen was kept in a transparent tank measuring 10 x 40 cm, and its locomotor activity was recorded by infrared photo-cell interruptions.

Temperature was maintained at a constant level, with a margin of ± 0.5°C ; the light cycle had a 12:12 L/D regime (06.00 lights on and 18.00 lights off). Specimens were tested at : 2, 4.5, 10, 13.5, 15.5, 19.5 and 25°C. Crabs were not tested at 2°C because previous observations had shown that their survival was highly reduced at this temperature. Activity is expressed as the number of events (equal to photo-cell interruptions) per hour.

To exclude the effect of different oxygenation on specimens' activity, it has been measured the oxygen concentration in the water at different temperatures. It ranged on average from 4.95 mg/l at 23°C to 9.1 mg/l at 4.5°C.

RESULTS

Field surveys

Local and altitudinal ranges

On the southern side of the T-E Apennine, *A. pallipes* and *P. fluviatile* coexist, particularly in tributaries of the Sieve and Bisenzio Rivers, but never share the same stream. In contrast, *A. pallipes* is the only decapod occurring in several streams (*e.g.* Santerno, Lamone and Accerreta Rivers) located on the northern side of the T-E Apennine (Figure 2).

Figures 3 and 4 show the distribution of crayfish and river crabs within streams at different altitudes on, respectively, the northern and the southern side of the T-E Apennine. There is an obvious difference in the distribution of *A. pallipes*. On the northern side, *A. pallipes* (which is the only decapod) is quite uniformly distributed between 200 and 700 m above sea-level, although more abundant at 250-300 m and 550 m. On the southern side, the overall distribution of the two decapods is between 550 and 150 m above sea-level ; however, while *A. pallipes* is distributed between 500 and 750 m, *P. fluviatile* always occupies the lowest altitudes.

NORTHERN SIDE OF THE TUSCAN-EMILIAN APENNINE

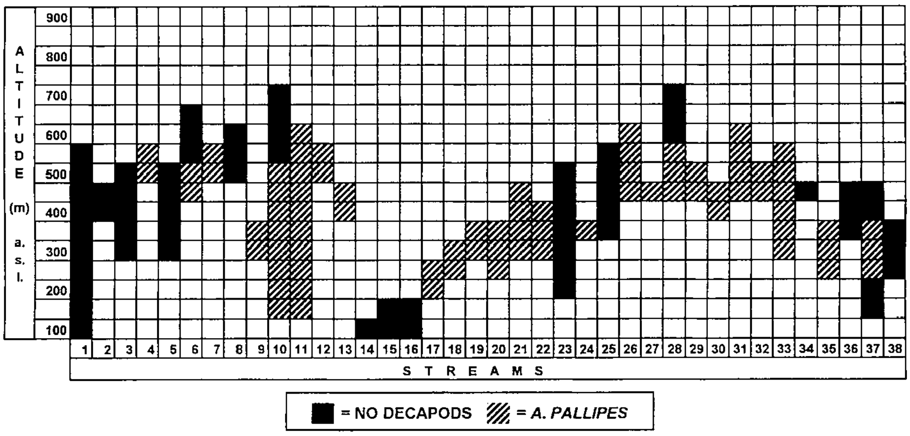


Figure 3

Occurrence of *Austropotamobius pallipes* at various altitudes (columns) and in different streams (rows) on the northern side of the Tuscan-Emilian Apennine.

Figure 3

Présence d'*Austropotamobius pallipes* à différentes altitudes (colonnes) et dans des torrents différents (lignes) sur le versant nord de l'Apennin Tosco-Emilien.

SOUTHERN SIDE OF THE TUSCAN-EMILIAN APENNINE

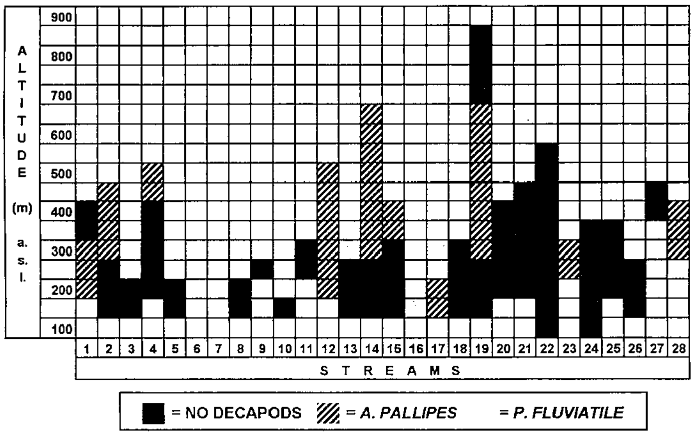


Figure 4

Occurrence of *Austropotamobius pallipes* and *Potamon fluviatile* at various altitudes (columns) and in different streams (rows) on the southern side of the Tuscan-Emilian Apennine.

Figure 4

Présence d'*Austropotamobius pallipes* et de *Potamon fluviatile* à différentes altitudes (colonnes) et dans des torrents différents (lignes) sur le versant sud de l'Apennin Tosco-Emilien.

Physical parameters.

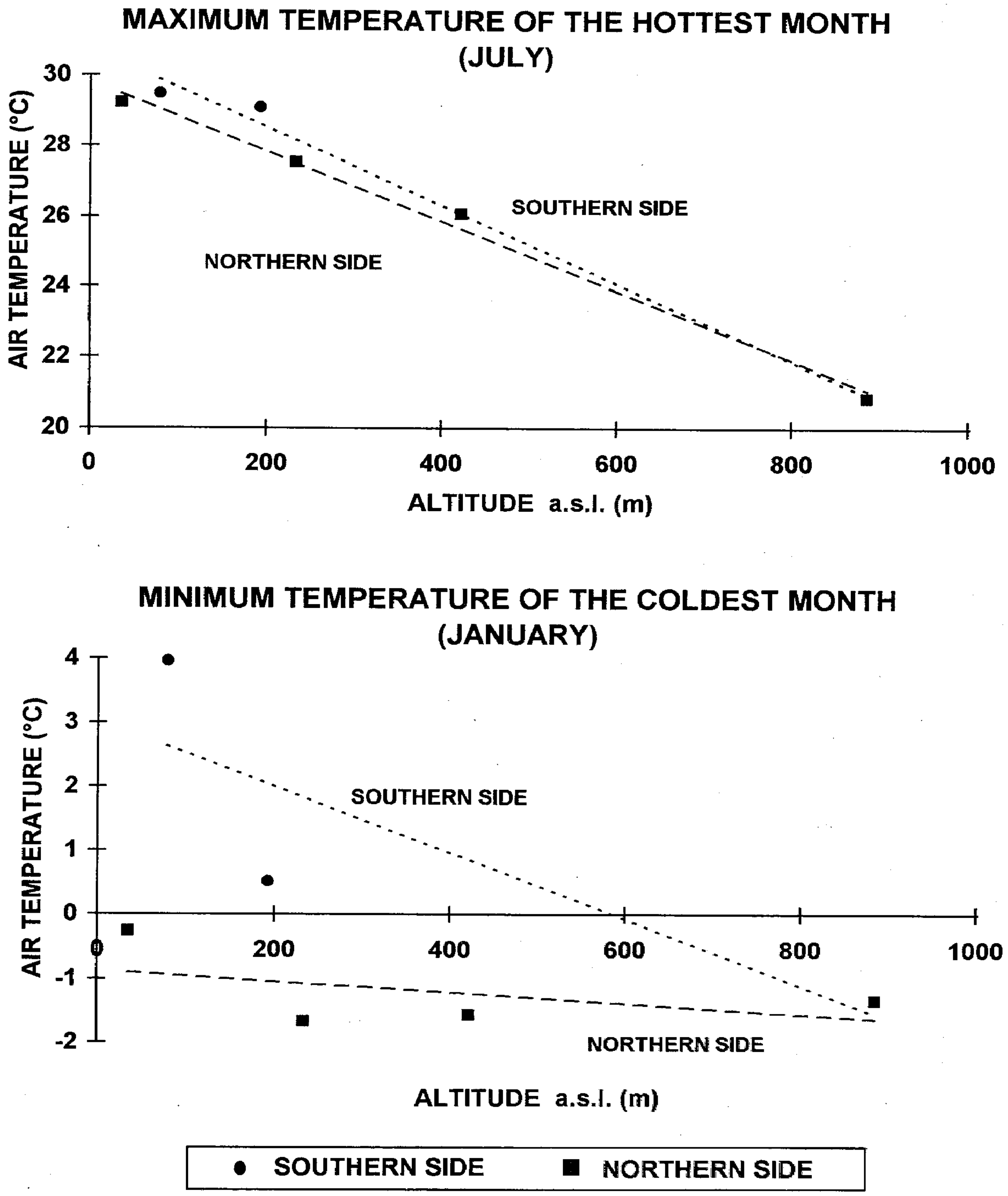


Figure 5

Relationships between altitude and the 5-year average of the maximum temperatures of the hottest month (top) and the minimum temperatures of the coldest month (bottom), compared between the northern and southern sides of the Tuscan-Emilian Apennine.

Figure 5

Relations entre l'altitude et la moyenne sur cinq années de la température maximum au cours du mois le plus chaud (en haut) et de la température minimum au cours du mois le plus froid (en bas), comparées entre les versants nord et sud de l'Apennin Tosco-Emilien.

There was no significant difference between the two sides of the T-E Apennine in the correlation between altitude and maximum temperature (b : t = 1.139, df = 3, ns ; a : t = 1.231, df = 4, ns) (Figure 5, top). However, the northern side reached lower temperatures (under 0°C) in the coldest month at all altitudes ; indeed on the southern side the minimum temperature was under 0°C only above 800 m (b : t = 2.064, df = 3, ns ; a : t = 2.612, df = 4, P<0.002) (Figure 5, bottom). There was higher annual rainfall on the northern side (b : t = 2.064, df = 3, ns ; a : t = 2.612, df = 4, P<0.05) (Figure 6).

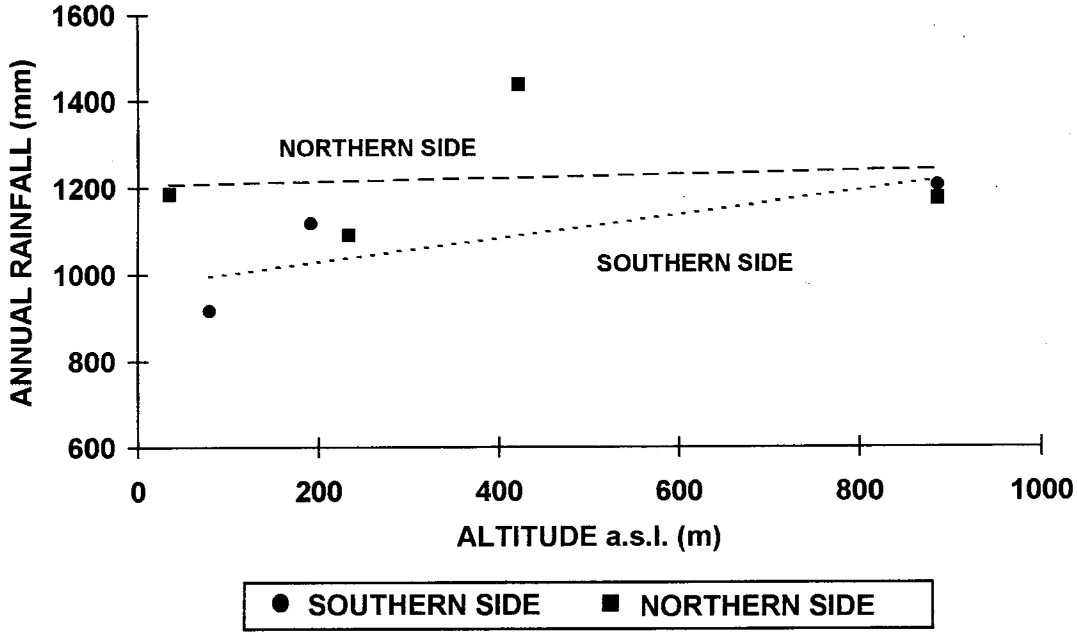


Figure 6

Relationships between altitude and the 5-year average of annual rainfall, compared between the northern and southern sides of the Tuscan-Emilian Apennine.

Figure 6

Relations entre l'altitude et la moyenne sur cinq années des pluies annuelles comparées entre les versants nord et sud de l'Apennin Tosco-Emilien.

A previous chemical analysis conducted in the same area revealed no difference between streams populated by either *A. pallipes* or *P. fluviatile* in oxygen concentration, nitrate, ammonium and chloride (TARDUCCI, 1987).

Laboratory studies

Competition

The agonistic behavior recorded in both species during interspecific contests did not differ much from the agonistic repertoire performed in intraspecific competition. The only pattern that crayfish performed exclusively with crabs as opponents was «pushing» ; the crayfish pushed the crab with both its chelae, trying to hide itself under the crab's abdomen. Usually, the crab allowed the crayfish to push it along a few centimeters, a behavior also performed by dominant individuals during intraspecific competition (VANNINI and SARDINI, 1971), and then walked over the crayfish, sometimes pinching it.

In both species, the intensity of aggression depended on the size of the performer. The most aggressive patterns were recorded for the largest individuals (in sequence : approaching, threatening and fighting), as in intraspecific aggression (see BOVBJERG, 1956, for crayfish, and VANNINI and SARDINI, 1971, for crabs).

The average levels of aggression for pair categories are given in Table I. Six size classes were distinguished for each species, and, for each class, an average level of aggression was calculated from the scores given in Material and Methods. Crabs with a carapace longer than 37.9 mm usually won against crayfish of all sizes, gaining an average score of +2. In this size class, the crabs exhibited a predatory behavior towards the crayfish. Small or medium-sized individuals (from 22 to 42 mm CL for crayfish, and from 14 to 37 mm CL for crabs) were more tolerant towards their opponent (exhibiting patterns of avoidance or pushing and touching) ; crabs simply pushed larger crayfish away with their chelae, raised their chelae in aggressive displays (threatening) or showed displacement activities (self-cleaning, defecating or performing a series of chewing movements). *A. pallipes* did not manifest predatory activities towards crabs of any size class, with the exception of adults over 45.7 mm CL towards small crabs of only 13.7 mm CL.

Table I

Levels of aggression (mean scores ± SE, n in brackets) scored during the interactions between the crayfish, *Austropotamobius pallipes* (columns), and the crab, *Potamon fluviatile* (rows), of different size classes (CL = carapace length).

Tableau I

Niveaux d'agressivité (moyenne des points ± écart type, n entre parenthèses) obtenus lors des interactions entre l'écrevisse, *Austropotamobius pallipes* (colonnes), et le crabe, *Potamon fluviatile* (lignes), de classes de taille différentes (CL = longueur de la carapace).

		CRAYFISH						
	size classes (CL in mm)	<25	25-30	30-35	35-40	40-45	45-50	overall score
CRABS	<20	- 0.35 ± 0.17 (20)	-0.18 ± 0.10 (28)	-0.27 ± 0.12 (15)	-0.75 ± 0.25 (16)	-0.83 ± 0.30 (12)	-1.13 ± 0.35 (8)	-0.58
	20-25	+0.45 ± 0.18 (20)	-0.14 ± 0.07 (28)	0.00 ± 0.00 (16)	-0.25 ± 0.11 (16)	-0.08 ± 0.08 (12)	-0.14 ± 0.14 (7)	-0.03
	25-30	+1.00 ± 0.45 (5)	0.00 ± 0.38 (7)	-0.17 ± 0.17 (6)	-0.35 ± 0.15 (17)	-0.38 ± 0.18 (8)	-0.20 ± 0.11 (10)	-0.02
	30-35	+2.00 ± 0.00 (10)	+0.93 ± 0.24 (14)	+0.43 ± 0.30 (7)	-0.09 ± 0.01 (11)	+0.25 ± 0.25 (4)	-0.17 ± 0.17 (6)	+0.56
	35-40	+2.00 ± 0.00 (7)	+1.55 ± 0.85 (11)	+0.88 ± 0.35 (8)	+0.48 ± 0.19 (21)	+0.56 ± 0.29 (9)	0.00 ± 0.25 (12)	+0.91
	40-45	+2.00 ± 0.00 (13)	+2.00 ± 0.00 (17)	+1.71 ± 0.29 (7)	+2.00 ± 0.00 (7)	+2.00 ± 0.00 (3)	+2.00 ± 0.00 (4)	+1.95
	overall score	+1.18	+0.69	+0.43	+0.17	+0.25	+0.06	

There was a positive correlation between the relative size difference of the two opponents (ranging from -10 to +10, *e.g.* -10 when the smallest crab was opposed to the largest crayfish and +10 for the opposite situation) and the score at the end of the battle (Spearman rank correlation test : t = 4.914, df = 8, P<0.01), suggesting that a main factor in agonistic contests was the relative size difference between the opposing species (Figure 7). However, when the relative size was the same, the absolute score for the crabs (average = 0.717, SE = 0.078, n = 187) was significantly higher than that for the crayfish (average = 0.004, SE = 0.063, n = 235 ; Mann-whitney U test : z = 5.353, P<0.001).

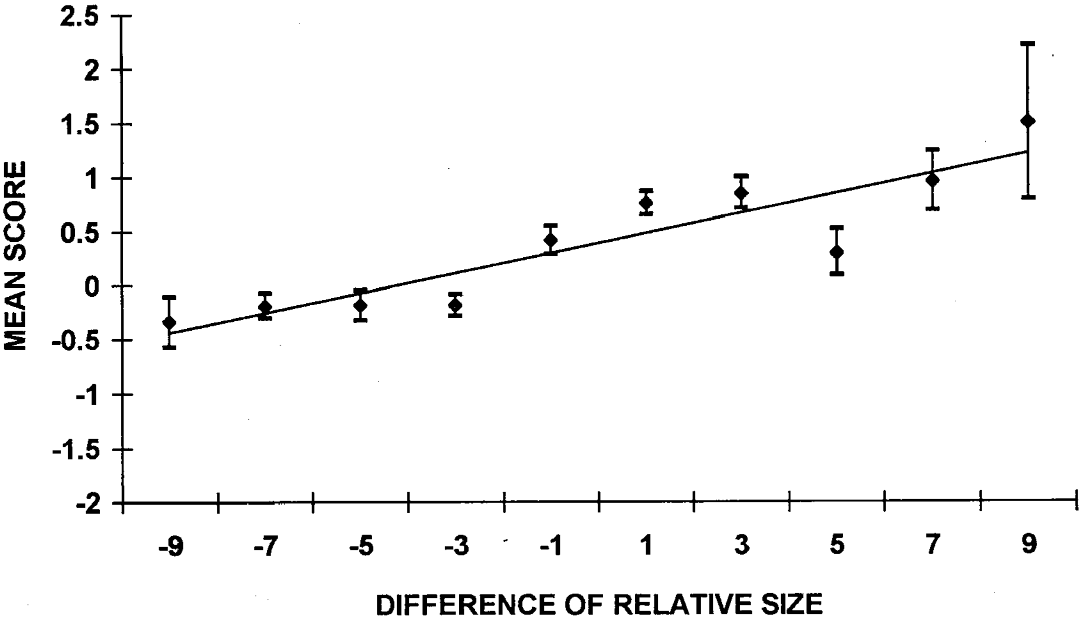


Figure 7

The score (mean ± SE) acquired at the end of competition between the crab, *Potamon fluviatile*, and the crayfish, *Austropotamobius pallipes*, plotted against the difference in relative size of the two opponents (see text for details).

Figure 7

Points obtenus (moyenne ± écart type) à la fin de la compétition entre le crabe, *Potamon fluviatile*, et l'écrevisse, *Austropotamobius pallipes*, représentés par un graphique contre la différence en taille relative des deux espèces (détails : voir texte).

Locomotor activity at different temperatures

Figure 8 shows the relative locomotor activity of the two species (averaged for the 4 days of testing and for the 5 tested specimens) at different experimental temperatures. The relative locomotor activity was computed in order to exclude the effect of specific differences in activity level ; we assigned the values of 0 and 100 to the minimum and maximum values for each species, and all intermediate values were then calculated according to this new scale. ANOVA (after arcsine transformation) revealed that the relative locomotor activity of the two species did not significantly differ (crayfish 31.31 % *vs* crabs 34.80 % : F = 0.66, df = 1 & 48, ns), while the average activity at the various temperatures did differ (4.5°C 15.72 % *vs* 10°C 27.10 % *vs* 13.5°C 33.61 % *vs* 15.5°C 42.03 % *vs* 19°C 30.6 % *vs* 25°C 49.27 % : F = 9.21, df = 5 & 48, P<0.01 ; the Tukey test revealed differences between the lowest temperature and all the others and between 10 and 25°C).

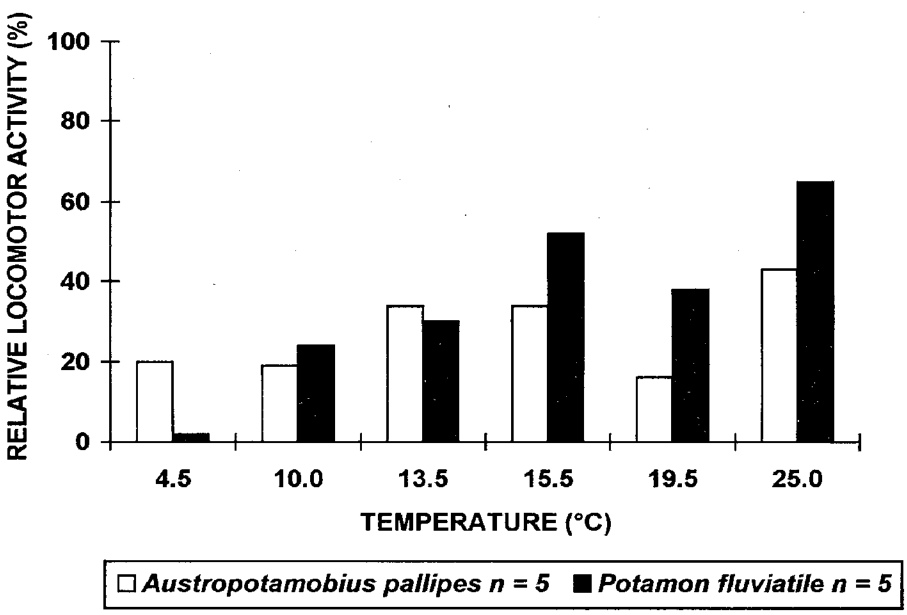


Figure 8

Relative locomotor activity per day (average of 5 specimens per species averaged over 4 days of testing) at different temperatures, compared between the two species.

Figure 8

Comparaison de l'activité journalière relative (moyenne de 5 individus par espèce sur quatre jours d'expérience) à différentes températures, entre les deux espèces.

In both species there was a positive correlation between temperature and relative locomotor activity (crayfish : $r = 0.474$, $df = 33$, $P<0.01$; crabs : $r = 0.697$, $df = 28$, $P<0.01$) (Figure 9a and b), with a significant difference between the two species in the regression coefficients (0.963 *vs* 2.167 : $t = 2.236$, $df = 56$, $P<0.02$). Crabs increased their activity more than crayfish with the rise in temperature.

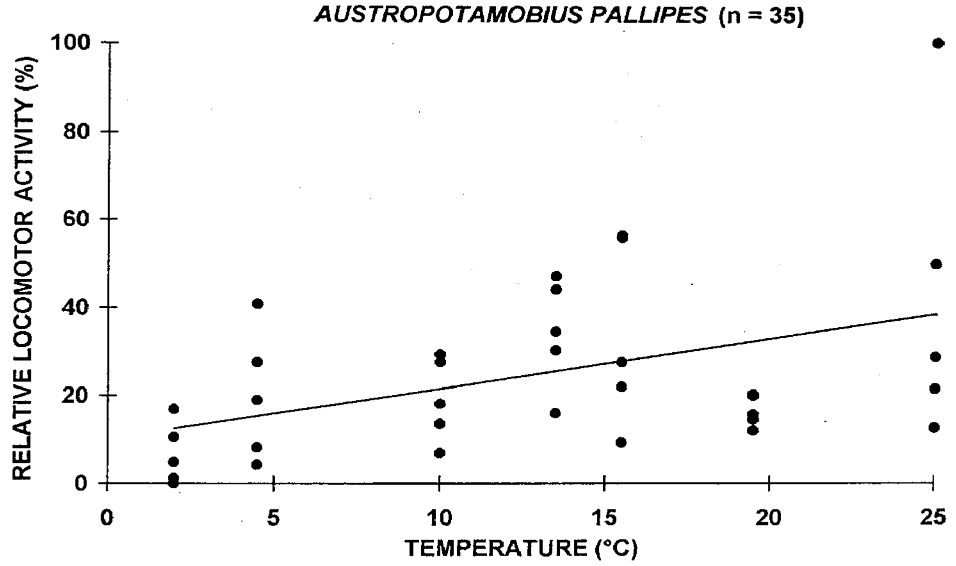


Figure 9a

Relationships between temperature and relative locomotor activity in *Austropotamobius pallipes*.

Figure 9a

Relations entre la température et l'activité locomotrice relative d'*Austropotamobius pallipes*.

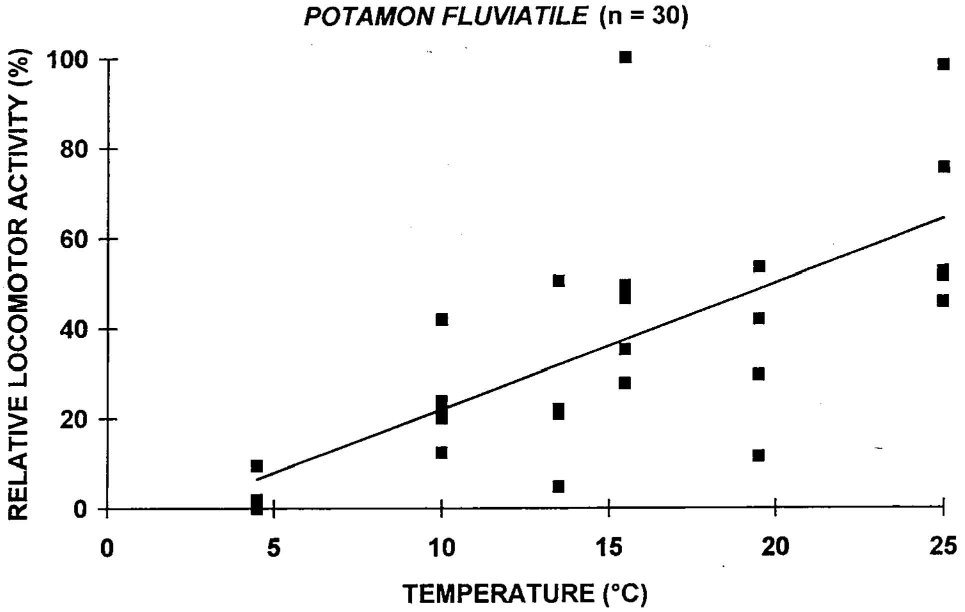


Figure 9b

Relationships between temperature and relative locomotor activity in *Potamon fluviatile*.

Figure 9b

Relations entre la température et l'activité locomotrice relative de *Potamon fluviatile*.

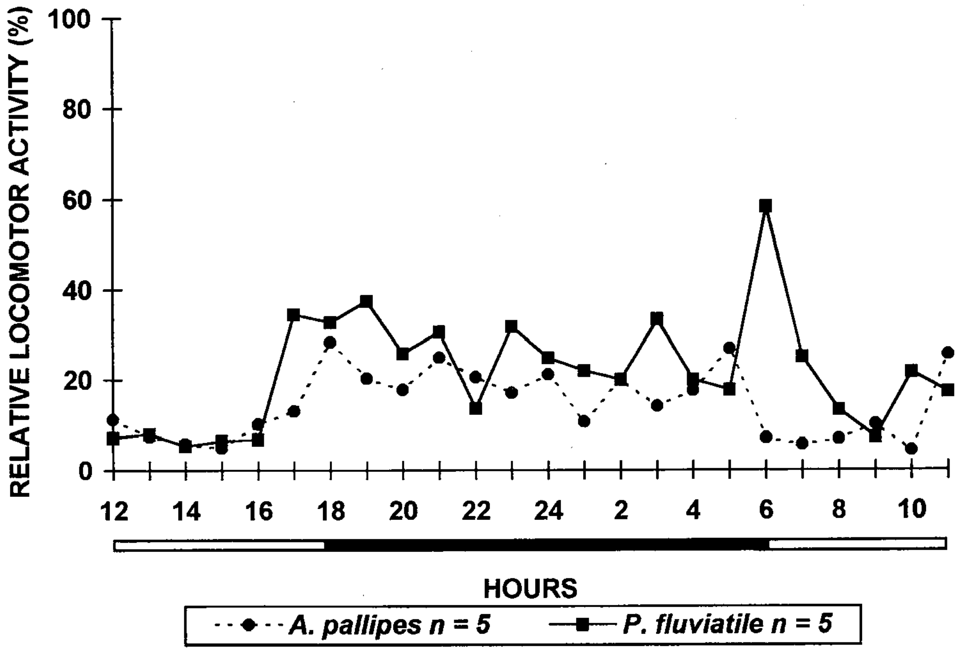


Figure 10

Relative locomotor activity (average of 5 specimens per species averaged over 4 days of testing) plotted against the different hours of the day, compared between the two species.

Figure 10

Comparaison de l'activité locomotrice relative (moyenne de 5 individus par espèce pendant quatre jours d'expérience) aux différentes heures du jour, entre les deux espèces.

Hourly activity at 25°C

Since the two species showed maximum relative locomotor activity at 25°C, we carried out an analysis of activity during a 24-hour cycle at this temperature (Figure 10). The two species did not differ in their overall activity (ANOVA : crayfish 21.73 % *vs* crabs 26.79 % : F = 1.91, df = 1 & 23, ns). However, there were significant differences in activity at various hours of the day (F = 6.94, df = 23 & 23, P<0.01), both species concentrating their activity during night-time (day 20.24 % *vs* night 27.97 % : F = 5.41, df = 1 & 16, P<0.05).

DISCUSSION

Interspecific dominance has been investigated in laboratory only for a few freshwater decapods species (*e.g.* BOVBJERG, 1970 ; CAPELLI and MUNJAL, 1982 ; BUTLER and STEIN, 1985). Generally, the results have been consistent with the observed distribution patterns, one species thought to competitively exclude another by its dominance (SÖDERBÄCK, 1995). Competitive exclusion, involving a variety of mechanisms, has often been invoked as an explanation for observed replacements (SÖDERBÄCK, 1995), while other authors have assumed that direct aggression is the main factor (PENN and FITZPATRICK, 1963 ; BOVBJERG, 1970 ; CAPELLI and MAGNUSON, 1975 ; CAPELLI, 1982 ; FLYNN and HOBBS, 1984).

Crayfish and crabs rely on aggressive behavior to procure resources, such as food and shelters (BUTLER and STEIN, 1985). The importance of competitive interaction should depend on the availability of these resources ; when these are limiting, subordinate species may be restricted to suboptimal habitats or diets (HIXON, 1980 ; BERGLUND, 1982). However, as BUTLER and STEIN (1985) pointed out, evidence for competition in laboratory studies has been largely circumstantial and partial. Other mechanisms that do not arise in the laboratory, such as differential susceptibility to predation or reproductive interference, might explain displacement in many cases. In our case, predation does not seem to be a factor that might cause displacement. In fact, the two species share same predators as rats, foxes, weasels, nocturnal and diurnal birds of prey and obviously man.

In the study of *A. pallipes* and *P. fluviatile*, behavioral analysis must be integrated with ecological and historical evidence in order to elaborate a hypothesis for the present distribution of the two species. Four issues provide insight for the solution of the puzzle.

1. The two species once coexisted

At present, the two species are found in different distribution ranges, with the exception of an overlap area where they never share the same stream or pond. The historical reconstruction provided by PRETZMANN (1987) suggests that the two species lived in sympatry during the Pleistocene.

2. The two species share the same resources

Eco-ethological studies of these and other closely related species suggest that crayfish and river crabs are similar in food choice, habitat use and temporal pattern of activity. In feeding behavior, both crayfish and river crabs show an omnivorous and opportunistic habit which changes with the seasonal food supply (REYNOLDS, 1978 ; GHERARDI, GUIDI and VANNINI, 1987). The effects of feeding have been detected in intraspecific aggression in crayfish, *e.g. Orconectes* spp. (HAZLETT, RUBENSTEIN and RITTSCHOF, 1975 ; MAGNUSON *et al.*, 1975 ; CAPELLI and HAMILTON, 1984), and in the river crab *P. fluviatile* (GHERARDI, TARDUCCI and MICHELI, 1989). The latter species manifests more intense aggression towards an opponent when it feeds on patches of vegetable debris, which proved to be the richest energy source along the inhabited stream (GHERARDI, TARDUCCI and MICHELI, 1989).

Territoriality has been poorly documented in these species ; when territories were claimed, they appeared to be transient and partly overlapping. Competitive intraspecific interactions were limited to patterns of low-level aggression (either avoiding or approaching and threatening) (BOVBJERG, 1956 ; LOWE, 1956 ; VANNINI and SARDINI, 1971). One resource which is defended from competitors is shelter, which provides protection from the water current and a refuge from extreme temperatures, low humidity and predators (especially during molting) (WARNER, 1977). Both species burrow in loose soil and packed clay along the stream or live in natural holes or crevices (GHERARDI, GUIDI and VANNINI, 1987). However, neither crayfish nor crabs seem faithful to one permanent hiding place. *Cambarellus shufeldtii* did not consistently remain in the same shelter for long periods of time (LOWE, 1956). After «nomadic» displacement (GHERARDI, TARDUCCI and VANNINI, 1988), but also after shorter foraging excursions (GHERARDI, TARDUCCI and MICHELI, 1989), *P. fluviatile* occupied the first free cavity at hand, often restoring it (GHERARDI, 1987). However, hiding places might be a limiting factor in the inhabited area, *e.g.* the ability of *O. virilis* to occupy and defend crevices determined the exclusion of *O. immunis* (BOVBJERG, 1970 ; BOVBJERG and STEPHEN, 1975).

Our laboratory experiments, which have been supported by field observations (for crayfish : VILLANELLI, 1996 ; for river crabs, GHERARDI *et al.*, 1988), proved that the two species share a similar 24-h rhythmicity. Both are prevalently nocturnal in their locomotion (and thus in their general activity).

3. River crabs are behaviorally dominant over crayfish

The experiments on aggression demonstrated that *P. fluviatile* is dominant over *A. pallipes*, as it can outcompete the latter in situations where direct aggressive interactions are important.

Relative size conditions the probability of victory in interspecific contests. However, large freshwater crabs strongly dominated all sizes of *A. pallipes*, showing a high level of agonism and even performing predatory behavior. In crabs smaller than 38 mm carapace length, the outcome of a contest mainly depended on the relative size of the two opponents. Besides, the observed interspecific differences in aggressive ability, size has been extensively reported to govern both intra- and interspecific dominance (in crayfish : BOVBJERG, 1953, 1956 ; BUTLER and STEIN, 1985 ; RABENI, 1985 ; in river crabs : VANNINI and SARDINI, 1971 ; GHERARDI, GUIDI and VANNINI, 1987).

In both species, juveniles have some defensive behavior against predation. *P. fluviatile* specimens of carapace length <30 mm have a cryptic behavior hiding under little rocks or in the mud (GHERARDI, 1987). Hatchlings of *Austropotamobius* remain under female abdomen till stage 3 when juveniles become independent. Only at this moment, the risk of predation becomes higher.

4. Crabs influence the habitat occupied by crayfish

The analysis of abiotic parameters showed that crayfish live at higher altitudes (that is lower temperatures) in the overlap area with crabs on the southern side of the Tuscan-Emilian Apennine, while they extend to lower altitudes when they are the only decapod species occupying the freshwater systems. However, the minimum temperature of the coldest month is significantly lower on the northern than on the southern side even at lower altitudes, which possibly limits the diffusion of the less cold-resistant crab.

In the laboratory, it was proved that crayfish are more active at lower temperatures than crabs, maintaining a consistent locomotor activity at temperatures less than 10°C, when crabs are nearly inactive.

Annual rainfall seems to influence the distribution of the two species to a lesser extent. Both *A. pallipes* and *P. fluviatile* inhabit streams with a constant water supply and high oxygen concentration. A more amphibious behavior of the river crab could explain its presence in areas where rainfall is generally lower.

CONCLUSION

These issues suggest the following scenario for the competitive exclusion of *A. pallipes* by *P. fluviatile*. The present distribution of the two species in Italy is the result of their past interspecific competition for the acquisition of common resources, such as food and shelter. Competitive interactions began during the Pleistocene, when the two species converged in Italy after migrating from eastern European regions (PRETZMANN, 1987). The winner was *P. fluviatile*, which had higher levels of aggression and strength than *A. pallipes*, and was therefore able to supplant the latter in their overlapping ranges. The crayfish were thus forced to migrate to other regions or, when still in sympatry, to remain in less favorable habitats, characterized by a lower temperature regime.

Certainly, we urge caution in accepting the influence of competition on species distribution, especially in situations where such hypotheses are mainly based on laboratory studies in simplified environments. However, our hope is that the here hypothesized greater competitive ability of *P. fluviatile* as instrumental in the exclusion of *A. pallipes* will help to direct more attention towards the effects of the deliberate (*e.g. Procambarus clarkii*) or accidental (*e.g. Orconectes limosus*) introduction of alien freshwater decapods into areas inhabited by native species.

BIBLIOGRAPHY

ALMAÇA C., 1988. Competition, available space, and speciation in Mediterranean crabs. *Monit. Zool. Ital.*, *22*, 477-486.

BERGLUND A., 1982. Coexistence, size overlap and population regulation in tidal *vs* non-tidal *Palaeomon* prawns. *Oecologia*, *54*, 1-7.

BOVBJERG R.V., 1953. Dominance order in the crayfish *Orconectes virilis* (Hagen). *Physiol. Zool.*, *24*, 173-178.

BOVBJERG R.V., 1956. Some factors affecting aggressive behaviour in crayfish. *Physiol. Zool.*, *26*, 173-178.

BOVBJERG R.V., 1970. Ecological, isolation and competitive exclusion in two crayfish (*Orconectes virilis* and *Orconectes immunis*). *Ecology*, *51*, 225-236.

BOVBJERG R.V., STEPHEN S.L., 1975. Behavioural changes with increased density in the crayfish *Orconectes virilis*. *Freshwater crayfish*, *2*, 429-441.

BUTLER M.J., STEIN R.A., 1985. An analysis of the mechanism governing species replacement in crayfish. *Oecologia*, *66*, 168-177.

CAPELLI G.M., 1982. Displacement of native crayfish by *Orconectes rusticus* in northern Winsconsin. *Limnol. Oceanogr.*, *27*, 471-475.

CAPELLI G.M., MAGNUSON J.J., 1975. Reproduction, molting, and distribution of *Orconectes propinquus* (Girard) in relation to temperature in a northern mesotrophic lake. *Freshwater crayfish*, *2*, 415-428.

CAPELLI G.M., MUNJAL B.L., 1982. Aggressive interactions and resource competition in relation to species displacement among crayfish of the genus *Orconectes. Crustacean Biol., 2*, 486-492.

CAPELLI G.M., HAMILTON P.A., 1984. Effects of food and shelter on aggressive activity in the crayfish *Orconectes rusticus* (Girard). *Crustacean Biol., 4*, 252-260.

CAPRA F., 1953. Il granchio di fiume, *Potamon edule* (Latr.) in Liguria. *Doriana, 44*, 1-7.

DARDI P., 1994. Studio causale della distribuzione dei decapodi d'acqua dolce in Italia. Master thesis, University of Florence, Italy, 116 p.

FLINT R.W., 1977. Seasonal activity, migration and distribution of the crayfish, *Pacifastacus leniusculus*, in Lake Tahoe. *Am. Midl. Nat., 97*, 280-292.

FLYNN M.F., HOBBS III H.H., 1984. Parapatric crayfishes in southern Ohio : evidence of competitive exclusion ? *Crustacean Biol., 4*, 382-389.

GHERARDI F., 1987. Eco-etologia del granchio di fiume *Potamon fluviatile* (Crustacea, Decapoda, Brachyura). Doctoral dissertation, University of Florence, Italy, 265 p.

GHERARDI F., GUIDI S., VANNINI M., 1987. Behavioural ecology of the freshwater crab, *Potamon fluviatile* : preliminary observations. *Invest. Pesq., 51*, 389-402.

GHERARDI F., MESSANA G., UGOLINI A., VANNINI M., 1988. Studies on the locomotor activity of the freshwater crab, *Potamon fluviatile. Hydrobiologia, 169*, 241-250.

GHERARDI F., TARDUCCI F., VANNINI M., 1988. Locomotor activity in the freshwater crab *Potamon fluviatile* : the analysis of temporal patterns by radio-telemetry. *Ethology, 77*, 300-316.

GHERARDI F., TARDUCCI F., MICHELI F., 1989. Energy maximization and foraging strategies on *Potamon fluviatile* (Decapoda, Brachyura). *Freshwater Biol., 22*, 233-245.

HAZLETT B.A., 1974. Field observation on interspecific agonistic behaviour in hermit crabs. *Crustaceana, 26*, 133-138.

HAZLETT B., RUBENSTEIN D., RITTSCHOF D., 1975. Starvation, energy reserves, and aggression in the crayfish *Orconectes virilis* (Hagen, 1870). *Crustaceana, 28*, 11-16.

HECKENLIVELY D.B., 1970. Intensity of aggression in the crayfish *Orconectes virilis* (Hagen). *Nature, 225*, 180-181.

HIXON M.A., 1980. Competitive interactions between California reef fishes of genus *Embriotica. Ecology, 61*, 918-931.

LAURENT P.J., 1988. *Austropotamobius pallipes* and *A. torrentium*, with observations on their interactions with other species in Europe. *In* HOLDICH D.M. and LOWERY R.S. (eds.), Freshwater crayfish, 341-364, University Press, Cambridge.

LOWE M.E., 1956. Dominance-subdominance relationships in the crawfish *Cambarellus shufeldti. Tulane Stud. Zool., 4*, 469-480.

MAGNUSON J.J., CAPELLI G.M., LORMAN J.G., STEIN R.A., 1975. Consideration of crayfish for macrophyte control. BERZONIK P.L and FOX J.L. (eds.), Proc. Symp. Water Quality Mgmt. through Biol. Control. Univ. Florida, 66-74, Gainesville.

PENN G.H., FITZPATRICK J.F., 1963. Interspecific competition between two sympatric species of dwarf crawfishes. *Ecology, 44*, 793-797.

PRETZMANN G., 1987. A contribution to a historic analysis of Mediterranean freshwater decapods chorology. *Invest. Pesq., 51 (Supl. 1)*, 17-25.

RABENI C.F., 1985. Resource partitioning by stream-dwelling crayfish : the influence of body size. *Am. Midl. Nat., 113*, 20-29.

REYNOLDS J.D., 1978. Crayfish ecology in Ireland. *Freshwater crayfish, 4*, 215-220.

ROBERTS T.W., 1944. Light, eyestalk, and certain other factors as regulators of the comunity activity for the crayfish, *Cambarus virilis* Hagen. *Ecol. Monogr., 14*, 359-392.

SALVIDIO S., CRESTA P., DORIA G., 1993. Preliminary survey on the distribution of the freshwater crayfish *Austropotamobius pallipes* in Liguria, N.W. Italy. *Crustaceana, 65*, 218-221.

SÖDERBÄCK B., 1991. Interspecific dominance relationship and aggressive interactions in the freshwater crayfish *Astacus astacus* (L.) and *Pacifastacus leniusculus* (Dana). *Can. J. Zool., 69*, 1321-1325.

SÖDERBÄCK B., 1995. Replacement of the native crayfish *Astacus astacus* by the introduced species *Pacifastacus leniusculus* in a Swedish lake : possible causes and mechanisms. *Freshwater Biol., 33*, 291-304.

TARDUCCI F., 1987. Aspetti dell'eco-etologia del granchio di fiume *Potamon fluviatile* (Herbst). Master thesis, University of Florence, Italy, 71 p.

VANNINI M., SARDINI A., 1971. Aggressivity and dominance in river crab *Potamon fluviatile* (Herbst). *Monit. Zool. Ital., 5*, 173-213.

VILLANELLI, F. 1996. Eco-etologia del gambero di fiume *Austropotamobius pallipes.* Master thesis, University of Florence, Italy, 91 p.

WARNER G.F., 1977. The biology of crabs. Elek Science, London, 202 p.