# Energy maximization and foraging strategies in *Potamon fluviatile* (Decapoda, Brachyura)

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SUMMARY. 1. Foraging of the freshwater crab *Potamon fluviatile* was studied by recording the activity of seventy-eight specimens in a 50 m$^2$ pool in a Tuscan stream during early summer. Foraging was related both to the organic content of the substrate and to the crabs' oxygen consumption. During this period, adult females underwent 'second vitellogenesis', with abundant deposition of yolk in oocytes.

2. A dispotic distribution (not accompanied by agonistic interactions, but 'peacefully' based on size) was observed within the foraging area. Larger animals (mostly males) fed on the rare patches of vegetable debris, which presented the highest organic content. Conversely, smaller specimens were relegated to the poorer substrates, such as the stream banks.

3. The females extended and diversified their foraging areas by also venturing into terrestrial habitats, in contrast to the more sedentary and aquatic males. This behaviour (which was not accompanied by a different energetic output) resulted in a more proteinaceous diet (even when the N-content of vegetable debris fell drastically), and in a significant increase in fats and the hepatopancreas index.

4. The reserves of energetic substances are presumed to sustain the highly expensive vitellogenesis, with the production of macrolecithal eggs. The females' behaviour as 'energy maximizers' seemed to be under a strong selective pressure, since their reproductive success is directly related to the efficient harvesting of food.

## Introduction

Decapods dominate the macroinvertebrate biomass of many streams. Because of their utilization of energy from diversified trophic levels, they play a primary role in the structure of aquatic communities and significantly contribute to

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material cycling and energy flow. With the exception of crayfishes, where an extensive literature exists (reviewed by Momot, 1984), only a few, scattered records report the feeding habits of other freshwater decapods (in prawns, Ruello, 1973; Marte, 1980; in crabs, Williams, 1961, 1962; Kabish, 1968; Schneider, 1971; Gherardi, Guidi & Vannini, 1987).

*Potamon fluviatile* Herbst is a common brachyuran living in many hill streams in south-

ern and central Italy. In its feeding habits, this species shows a great plasticity, extending its foraging area to the terrestrial habitat (Gherardi & Vannini, 1989). It behaves like a generalist, and exploits food items most available at the time (Gherardi, 1987). In water, the crabs forage freely on the substratum, feeding on vegetable debris, scraping on algal-covered surfaces, or actively preying on frogs, tadpoles and various invertebrates (Gherardi *et al.*, 1987). Except in colder months, when the animals are mostly diurnal, foraging is concentrated during the night (Gherardi *et al.*, 1988a, b).

The objective of the present study was to examine the foraging activity of this species in the field, and to relate it to (i) the quality of the substrate, (ii) the crabs' metabolism, and (iii) organic content of the hepatopancreas, gonads and stomach. Effects of size, sex, reproductive phase, population density, and neighbours are also investigated.

## Materials and Methods

### The study animal

Amphibious habit, burrow occupation and high vagility are peculiar aspects of this species' behavioural ecology (Gherardi *et al.*, 1987, 1988b). Reproductive patterns follow an annual cycle at least in the adult females (>35 mm carapace length). Oocytes begin to grow in the gonads in November–March ('first vitellogenesis' according to Adiyodi, 1985; phase 1), while the more energetically expensive 'second vitellogenesis' (characterized by the abundant deposition of yolk in the oocytes; phase 2) occurs in April–mid July, followed by ovulation. In the post-ovulatory phase (mid July–October; phase 3), eggs (which are macrolecithal) are incubated for about 40 days inside the chamber limited by the sternum and abdomen. Embryonic development is direct, and hatchlings remain under the female abdomen for at least 10 days before
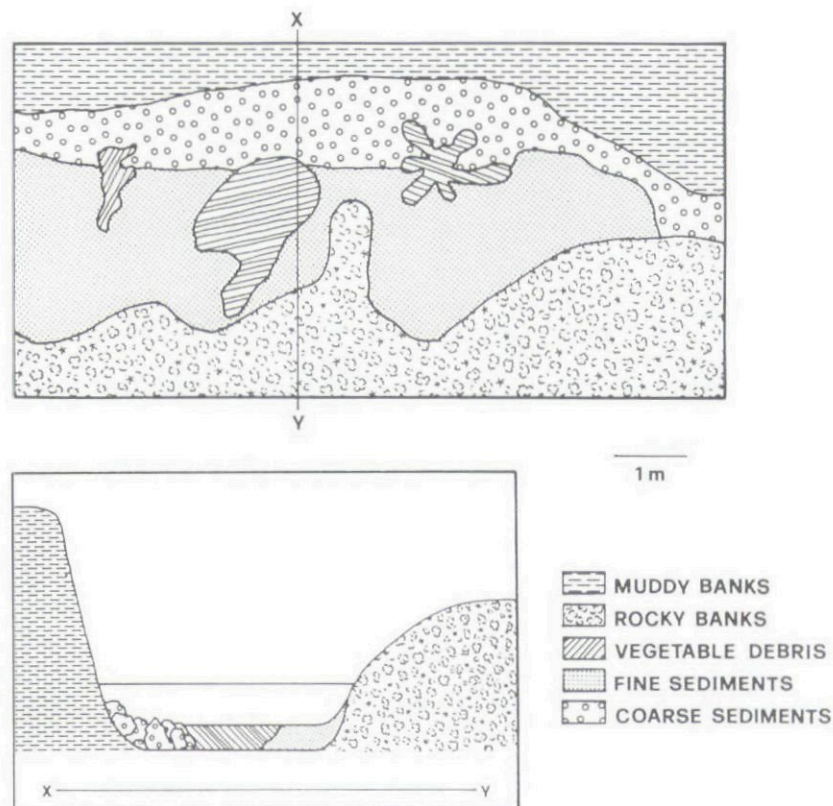


FIG. 1. Map of the pool under study (upper) and its section (lower) along the *X–Y* axis. Types and distribution of substrates are represented.

dispersing along the stream. At least in adults, ecdysis occurs only once a year in September. Copulations were observed in the field from June to October, when male spermatogenesis was also more active (Delpino, 1934) (phase 2 of the males' reproductive cycle).

*Methods in the field*

The study area was a 50 m² pool on a hill stream near Florence, Italy (Fig. 1). Observations were made in eleven sessions of 1.5 h each, beginning at 21.00 hours during the period 3 June to 11 July 1986. The pool was illuminated by a dim incandescent light, which did not alter the crabs' behaviour. Two observers on opposite sides of the stream, at about 5 m above water level (where they could not be seen by the animals), recorded the positions of the crabs every 2 min with respect to a grid system, their behaviour, and the type of substratum they occupied. We observed forty males, twenty-five females, and thirteen others which could not be sexed. Fig. 2 shows the frequency distribution of size. Only in a few cases was the same crab followed for more than one session. The number



FIG. 2. Size (carapace length) distributions of males (upper) and females (lower) which were observed during their foraging activity in June–July.

of specimens simultaneously present in the pool ranged from three to nine individuals. At the end of each session, any animals which had not previously been marked were caught when possible, their sex and size recorded, marked with a water-proof paint, and then released.

Behaviour was classified as: immobile, walking, searching for food (when the animals, either still or on the move, scraped the substratum with one or both of their chelipeds), feeding (when they brought their chelipeds with pieces of food to their buccal cavity) and aggression. Aggressive interactions were defined as avoidance, threat, strike, and fight (Bovbjerg, 1953). Avoidance occurred when one of the two opponents simply avoided the other by changing its direction of movement. Threat consisted of agonistic posturing, such as raising one or both chelae. Strikes involved only brief encounters ($<2$ s), while fights involved longer interactions, with highly aggressive patterns (pushes, grasps and strikes) (Vannini & Sardini, 1971). We considered the winner as the opponent which did not flee at the end of a contest.

*Methods in the laboratory*

Among the various substrates, we were able to distinguish muddy banks, rocky banks, coarse sediments (particles larger than 16 mm), fine sediments (comprising silt and clay), and vegetable debris.

For the analysis of organic content of the substrates, surface soil 2–3 mm deep was sucked up with a pump (three samples for each substrate every 2 months). For the rocky banks, epilithic algae and mosses were taken. Samples were dried at 110°C, and triturated in a mortar. Organic carbon was estimated by the Walkley & Black's (1934) method and then determined by tritroprocessor. For nitrogen content, Kjeldahl's (1883) method was used.

Oxygen consumption was evaluated with an Oxygen Meter YSI mod. 57 fitted with polarographic electrodes mod. 5700 (for further details, see Gherardi *et al.*, 1988a). Animals were collected from the stream under study in June–July, and kept unfed for a few days in the laboratory at room temperature (18–20°C) before testing. Hourly consumption per animal (at 20°C) was considered the average resulting from a 3-h-long experiment.
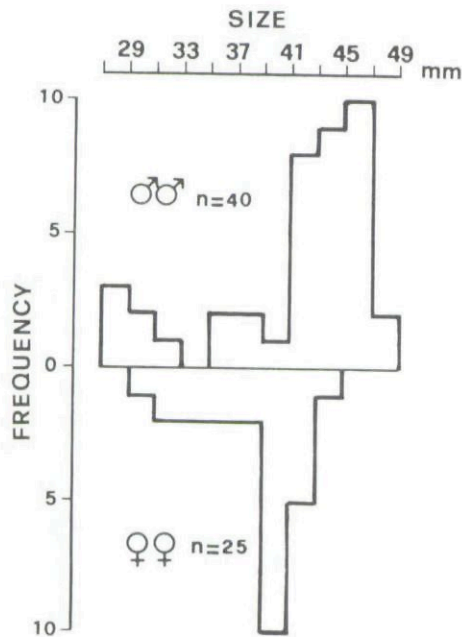
Over an annual cycle, approximately fifty

adult animals were killed for gravimetric and chemical analyses. All specimens were frozen on capture and brought to the laboratory on dry ice. The hepatopancreas and female gonads were removed and weighed with an analytical balance to give, respectively, the hepatopancreas (HPI), and gonadic (GI) index (i.e. the ratio between the fresh weight of the organ and the fresh weight of the crab per cent). Their organic concentrations were evaluated through the methods described by Heath & Barnes (1970) for lipids, and Keppler & Decker (1984) for glycogen. The percentage of nitrogen in the stomachs (only specimens with full stomachs were used) was determined by Kjeldhal's method.

## Results

### Substrates

Table 1 gives the organic content of the stream substrates over an annual cycle. These differed in their richness of both carbon (after arcsin square transformation, ANOVA: F=27.49, df=4 and 79, $P<0.001$), and nitrogen (ANOVA: F=16.26, df=4 and 79, $P<0.001$). Vegetable debris were obviously the richest substrate in organic carbon. Nitrogen was also more abundant in detritus, but it changed drastically over the year, reaching a minimum in June.

### Behaviour

Fig. 3 shows the time spent on each substrate by males and females during their foraging activity. The two sexes differed in their choice of substrate, the females more often preferring sand and stones, and spending less time on vegetable
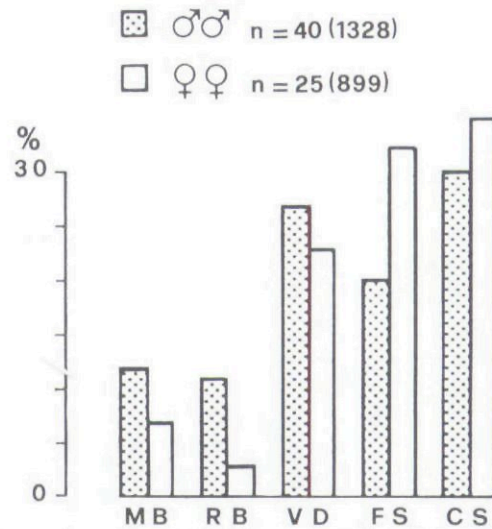
FIG. 3. Frequency distribution of the time spent on each substratum by the foraging crabs (in parentheses the number of records), compared between sexes. For abbreviations, see Table 1.

TABLE 1. Organic content (dry weight) of substrates (averaged from three samples). MB=muddy banks; RB=rocky banks; VD=vegetable debris; FS=fine sediments; CS=coarse sediments; M=mosses.

|  | MB | RB | VD | FS | CS | M |
|---|---|---|---|---|---|---|
| A. Carbon (cg g$^{-1}$) |  |  |  |  |  |  |
| February | 2.4 | 4.6 | 15.4 | 0.7 | 5.3 | 13.8 |
| April | – | 4.0 | 12.3 | 0.3 | 3.8 | 8.1 |
| June | – | 2.1 | 28.3 | 0.8 | 2.1 | 12.5 |
| August | – | 3.3 | 29.2 | 2.5 | 2.3 | 11.3 |
| October | – | 2.6 | – | 0.5 | 0.3 | 6.0 |
| December | – | 7.1 | 22.7 | 11.3 | 2.8 | 22.3 |
| Yearly average (±SE) | 2.4 | 3.9±2.3 | 21.8±13.1 | 2.3±3.6 | 2.7±2.3 | 12.4±7.8 |
| n | 2 | 17 | 15 | 18 | 18 | 18 |
| B. Nitrogen (mg g$^{-1}$) |  |  |  |  |  |  |
| February | 2.0 | 3.4 | 5.0 | 1.3 | 2.7 | 8.8 |
| April | – | 4.8 | 5.9 | 1.5 | 1.1 | 5.7 |
| June | – | 2.1 | 2.1 | 1.7 | 1.6 | 1.3 |
| August | – | 1.8 | 9.5 | 1.2 | 0.9 | 5.8 |
| October | – | 2.0 | 5.7 | 1.3 | 1.4 | 4.3 |
| December | – | 2.3 | 7.0 | 1.5 | 1.3 | 8.7 |
| Yearly average (±SE) | 2.0±0.8 | 2.8±1.3 | 5.9±3.7 | 1.5±0.3 | 1.5±1.0 | 5.4±3.2 |
| n | 3 | 18 | 18 | 13 | 17 | 18 |

debris and banks than males ($\chi^2=99.771$, df=4, $P<0.001$). Males especially spent relatively more of their time on vegetable debris which, although scarce in the pool, was the richest substrate in organic content. In males, size was positively correlated with the time spent on vegetable debris (after semi-logarithmic transformation: $r=0.332$, df=37, $P<0.025$), and negatively with that spent on the banks ($r=0.439$, df=37, $P<0.005$).

The occurrence of behavioural patterns (Fig. 4) differed significantly between sexes, females searching for food more often than males ($\chi^2=15.417$, df=4, $P<0.01$). A positive correlation between size and percentage of time spent in searching for food and feeding was discovered only in the females ($r=0.37$, df=23, $P<0.05$), while immobility was negatively correlated with size ($r=-0.463$, df=23, $P<0.01$).

Aggression was a rare behaviour, in spite of the fact that the density of the crabs could often
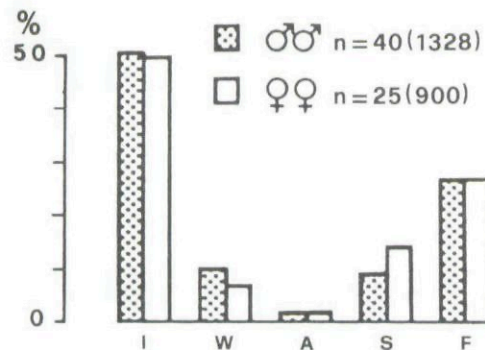


FIG. 4. Frequency distribution of the behaviour patterns performed by the foraging crabs (in parentheses the number of records), compared between sexes. For abbreviations, see Table 2.

be high, and the areas inspected by different animals were often superimposed. Only eighteen interactions were observed, and they were mostly of low aggressive value (56% of threat and 28% of avoidance *v.* 16% of strikes and fights). Males and females won equally, while in 67% of the interactions the winner was the larger crab. Animals reacted aggressively when the two opponents were at an average distance of 28.7 cm (SE=4.1 cm; minimum 5 cm, maximum 70 cm).

Table 2 shows the frequency of behaviour patterns on the different substrates. Considering the overall time an animal spent on each substratum, aggression occurred more often when at least one animal was grazing on vegetable debris (comparing the frequency distribution of aggression on two categories of substrates, vegetable debris and others, with the same distribution of non-agressive patterns: $\chi^2=4.266$, df=1, $P<0.05$). The occurrence of searching for food and feeding in animals moving on detritus also differed significantly from its frequency on other substrates ($\chi^2=372.173$, df=1, $P<0.001$).

## Locomotory speed and size of the foraging area

The frequency distribution of locomotory speed every 2 min is shown in Fig. 5. Females were significantly faster than males while foraging in the pool ($\chi^2=27.4$, df=8, $P<0.001$). In females, the distance covered after 1 h was positively correlated with size ($r=0.575$, df=15, $P<0.01$). Movement was randomly oriented, being the directions followed uniformly distributed in the plane (Rayleigh test, Batschelet, 1981; males: $z=1.099$, $n=377$, ns; females: $z=2.064$, $n=224$, ns), with no difference

TABLE 2. Time budget (in %) on each substrate while foraging. In parentheses the percentage of one behaviour pattern with respect to its frequency on the other substrates. The total behavioural patterns and occupied substrates are indicated, respectively, at the final column and row. I=immobile; M=moving; A=aggression; S=searching for food; F=feeding. For the other abbreviations, see Table 1.

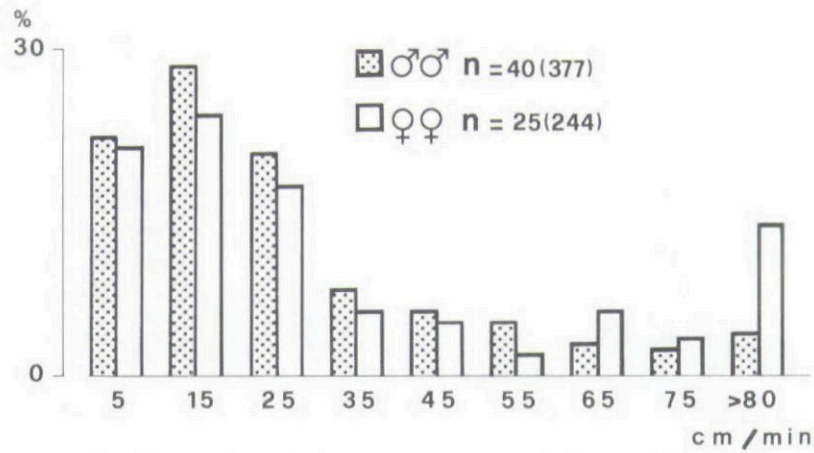| | MB | RB | VD | FS | CS | Behaviour patterns |
|---|---|---|---|---|---|---|
| I | 88.6 (16.2) | 47.0 (7.3) | 20.4 (10.0) | 67.7 (46.3) | 44.4 (20.2) | 1292 |
| M | 10.2 (10.5) | 11.5 (10.0) | 6.0 (16.6) | 10.2 (39.3) | 9.2 (23.6) | 229 |
| A | 0.0 (0.0) | 3.0 (13.9) | 2.7 (39.5) | 1.4 (27.9) | 1.4 (18.6) | 43 |
| S | 0.8 (0.7) | 6.5 (4.8) | 13.8 (31.9) | 7.6 (24.5) | 17.7 (38.1) | 273 |
| F | 0.4 (0.1) | 32.0 (9.1) | 57.1 (51.3) | 13.2 (16.6) | 27.4 (22.9) | 704 |
| Occupied substrates | 236 | 200 | 632 | 885 | 588 | |

FIG. 5. Frequency distribution of locomotory speed recorded every 2 min (in parentheses the number of records), compared between sexes.

between sexes ($\chi^2=13.467$, df=17, ns). Considering the mean vector length '$r$' as a straightness index (Batschelet, 1981), both sexes followed a path with pronounced detours and

deviations (in males, average=0.26, $n=18$; in females, average=0.22, $n=10$; males $v$. females: Mann-Whitney $U$ test: $U=81$, ns).
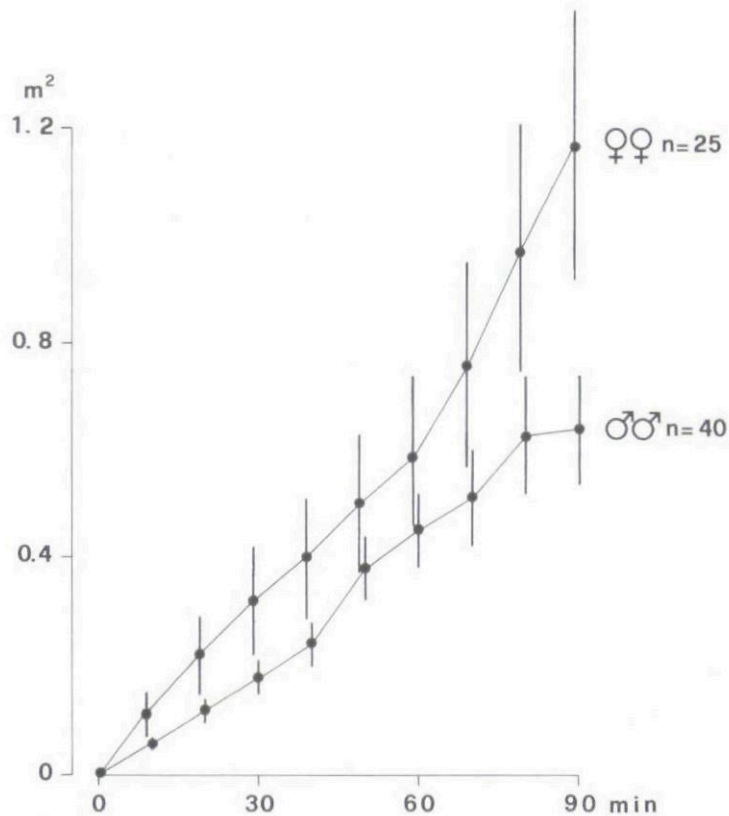
The area occupied by crabs while foraging



FIG. 6. Increase of the foraging area with time (mean values ±SE). For the method of computation of the area, see the text.

increased with time (Fig. 6). This is calculated here as the sum of the 1 dm² quadrats in which the animal was seen every 2 min, plus the sum of minimum number of quadrats the animal would have had to traverse in order to reach disjunct quadrats (grid cell methods: Siniff & Tester, 1965). Area grew faster in females (in males: $b=0.766$; in females: $b=1.209$; males $v$. females: $t=6.695$, df=2197, $P<0.001$). In addition, the size of the area traversed in 1 h was positively correlated with size only in the females ($r=0.494$, df=18, $P<0.025$).

No correlation was discovered between area and density of foragers ($r=0.122$, df=47, ns), while the extent of superimposition of the area occupied by the crabs simultaneously present in the pool increased as the number of crabs increased ($r=0.259$, df=166, $P<0.005$).

Relationships between contiguous animals (Fig. 7) were studied in terms of the extent of superimposed areas, comparing the couples of the same or of different sexes with respect to increasing densities: no difference was found between these two categories (ANOVA: $F=-3.7$, df=152 and 1, ns), while a significant difference in the degree of superimposition resulted from different densities (F=5.19, df=4 and 152, $P<0.01$), and replications (F=3.17, df=9 and 152, $P<0.01$).

The same aspect was analysed in couples of equal and different size, discriminating 'small' (<42 mm carapace length), and 'large' (≥42 mm carapace length), and thus considering the three possible combinations (small–small, large–large and small–large). No difference was found among size classes (ANOVA: $F=-0.37$, df=153 and 2, ns), while the density of foragers did influence the extent of superimposition (F=3.76, df=4 and 153, $P<0.01$).

*Oxygen consumption*

A positive correlation between size and hourly oxygen consumption existed for both
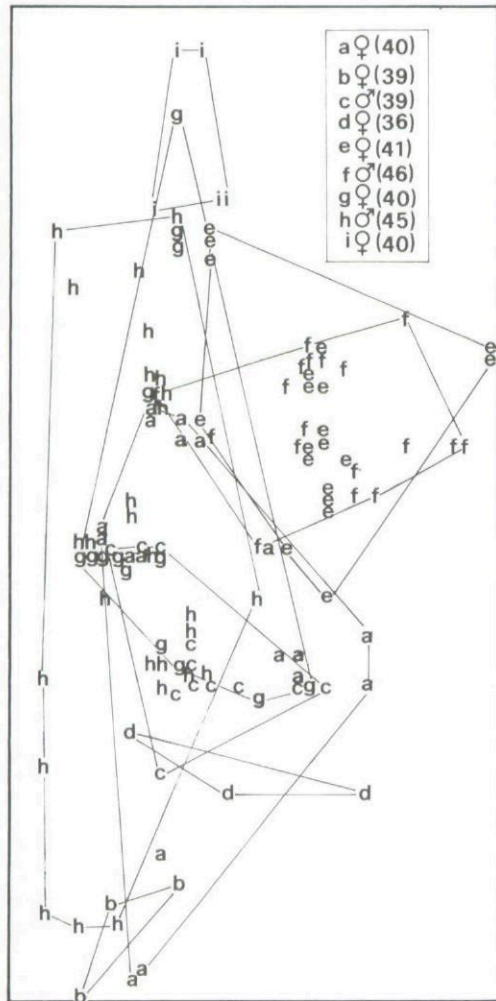


FIG. 7. Areas occupied during one hour by nine specimens which were foraging in the pool during one session of observation. Letters indicate locations of stops for feeding. For each animal, sex and size (carapace length in mm, in parentheses) are also shown.
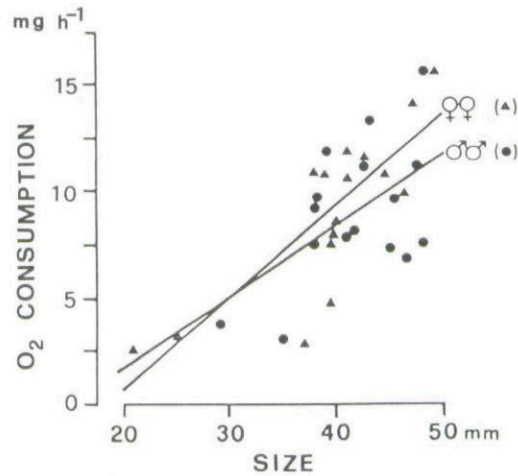


FIG. 8. Oxygen consumption plotted against size (carapace length) for male and female crabs tested in June–July. All measurements were made at 20°C.

TABLE 3. Relative size and organic content (dry weight) of gonads (G), hepatopancreas (HP), and stomachs (average ±SE), compared (by $t$-test, after arcsin square transformation) among reproductive phases (see the text) ($^*P<0.05$, $^{**}P<0.01$).

A. Females

| | Phase 1 | Phase 2 | Phase 3 | 1 v. 2 | 1 v. 3 | 2 v. 3 |
|---|---|---|---|---|---|---|
| GI (g g$^{-1}\times10^2$) | 0.82±0.15 | 1.05±0.18 | 0.43±0.06 | 0.43 | 1.36** | 2.59** |
| $n$ | 11 | 14 | 12 | | | |
| G lipids (g g$^{-1}$) | 0.12±0.01 | 0.18±0.01 | 0.07±0.01 | 1.86 | 1.59 | 4.59** |
| $n$ | 8 | 8 | 5 | | | |
| HP I (g g$^{-1}\times10^2$) | 3.56±0.34 | 5.50±0.50 | 3.42±0.27 | 3.36** | 0.25 | 3.11** |
| $n$ | 10 | 11 | 13 | | | |
| HL lipids (g g$^{-1}$) | 0.06±0.01 | 0.13±0.03 | 0.05±0.01 | 6.04** | 0.47 | 2.64* |
| $n$ | 10 | 14 | 6 | | | |
| HP glycogen (mg g$^{-1}$) | 1.17±0.31 | 1.38±0.44 | 0.46±0.17 | 0.21 | 1.43 | 1.26 |
| $n$ | 7 | 9 | 5 | | | |
| Stomach nitrogen (cg g$^{-1}$) | 8.72±0.96 | 12.12±1.19 | 10.65±3.12 | 2.19* | 0.47 | 0.88 |
| $n$ | 15 | 8 | 5 | | | |

B. Males

| | Phase 1 | Phase 2 | 1 v. 2 |
|---|---|---|---|
| GI (g g$^{-1}\times10^2$) | 2.91±0.31 | 3.13±0.19 | 0.83 |
| $n$ | 16 | 18 | |
| HP I (g g$^{-1}\times10^2$) | 3.50±0.32 | 3.68±0.22 | 0.70 |
| $n$ | 12 | 19 | |
| HP lipids (g g$^{-1}$) | 0.10±0.01 | 0.13±0.03 | 0.34 |
| $n$ | 12 | 12 | |
| HP glycogen (mg g$^{-1}$) | 0.89±0.34 | 0.78±0.27 | 0.09 |
| $n$ | 10 | 8 | |
| Stomach nitrogen (cg g$^{-1}$) | 10.70±1.65 | 8.43±0.90 | 0.72 |
| $n$ | 8 | 11 | |

sexes (males: $y=0.33x-4.99$, $r=0.546$, df=14, $P<0.025$; females: $y=0.43x-7.95$, $r=0.795$, df=14, $P<0.005$) (Fig. 8). The regression coefficient does not differ significantly between sexes ($t=0.145$, df=30, ns), i.e. a male and female of the same size consumed oxygen to the same extent, thus having the same aerobic energy demands.

*Analyses of gonads, hepatopancreas, and stomach content*

Table 3 summarizes the results obtained from the analysis of gonad, hepatopancreas and stomach content in the different reproductive phases. In the females, GI is significantly higher during April–mid July when histological analysis also revealed the occurrence of the second vitellogenesis, which is accompanied by a con-

sistent deposition of fats in the gonads. During this phase, HPI (Fig. 9) and the lipid content of hepatopancreas (Fig. 10) were also higher, while glycogen (Fig. 11) did not change significantly. Conversely, in males all these measurements were constant throughout the year. Fat concentration is significantly correlated with HPI in both males ($r=0.434$, $b=0.005$, df=20, $P<0.05$), and females ($r=0.479$, $b=0.008$, df=24, $P<0.02$), suggesting that the increment in the relative size of this organ depends largely on the deposition of fats.

ANOVA test (after arcsin square transformation) was used to compare HPI, and hepatopancreas content of fats and glycogen between sexes and at different periods. Although being in overall equal in both sexes (HPI: F=2.43, df=1 and 59, ns; fats: F=0.12, df=1 and 48, ns), at least fats were not constant throughout the year
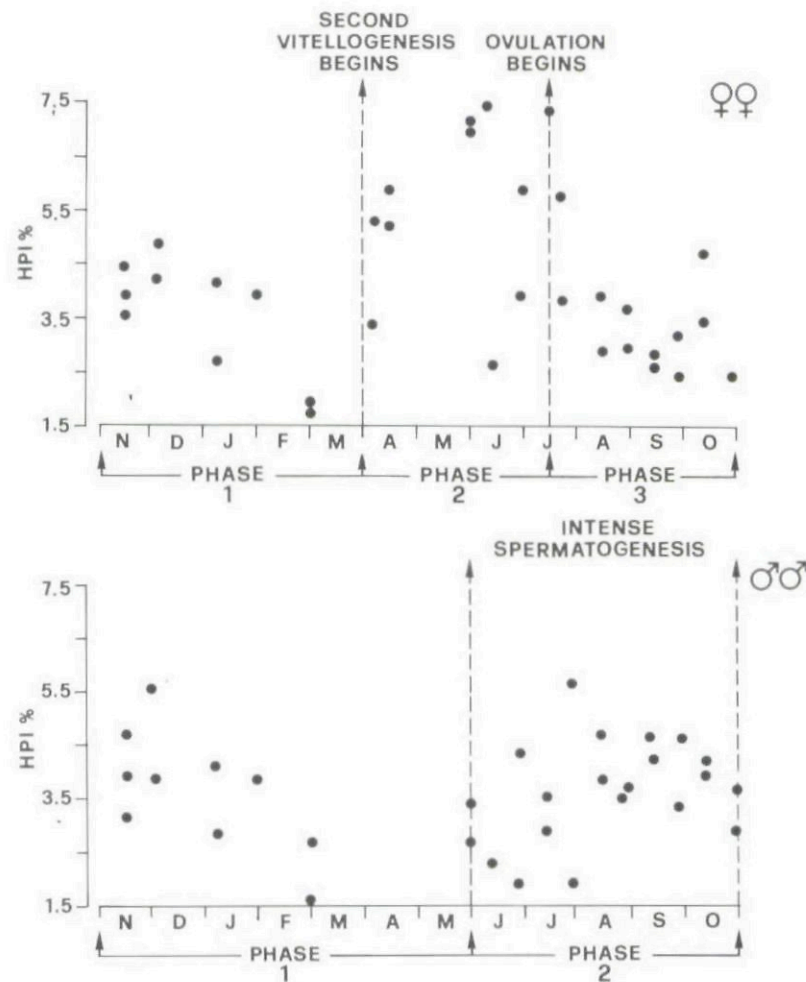
FIG. 9. Hepatopancreas index during a yearly cycle in thirty-four females (upper) and thirty-one males (lower).

($F=4.66$, df=2 and 48, $P<0.05$; on the contrary: HPI: $F=2.67$, df=2 and 59, ns), but it was significantly higher in the phase 2 in females ($F=6.07$, df=2 and 48, $P<0.01$). The interaction between sexes and periods was also significant for HPI ($F=8.24$, df=2 and 59, $P<0.01$). On the contrary, no significant difference was revealed for glycogen content between sexes ($F=0.62$, df=1 and 33, ns), in reproductive phases ($F=0.22$, df=2 and 33, ns), and in the interaction between these latter two factors ($F=1.16$, df=2 and 33, ns).

During the second vitellogenesis, females also had a more protein-rich diet than males during the same period (after arcsin square transformation: $t=2.3$, $P<0.05$), although the N-content of the stomachs did not differ over the whole

annual cycle between sexes (ANOVA after arcsin square transformation: $F=0.18$, df=41 and 1, ns), neither did it change in the whole population throughout the year ($F=0.53$, df=41 and 2, ns).

## Discussion

Plant debris, broken down into more or less amorphous detritus, mixed with small mineral particles and diatom frustules, is one of the main sources of energy for many members of the stream community. It constitutes the principal foodstuff of a wide range of invertebrates, including most orders of insects, most of the smaller Malacostraca, most oligochaetes, and
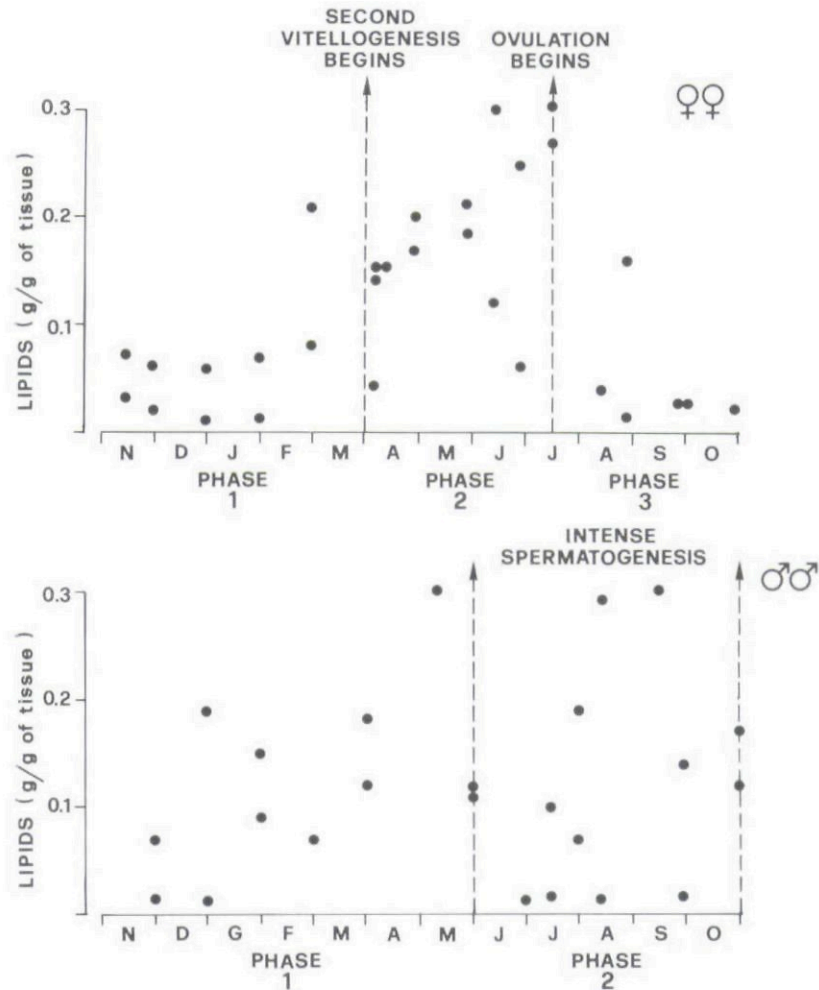
FIG. 10. Lipid content of hepatopancreas during a yearly cycle in thirty females (upper) and twenty-four males (lower).

some molluscs (see, e.g., Chapman & Demory, 1963; Hynes, 1963; Jones, 1950). For a food generalist like *P. fluviatile*, heaps of vegetable debris patchily distributed along the stream are a rich deposit of organic substances, which are more frequently explored than other substrates during its aquatic foraging, and where the animal spends most time feeding.

In addition to the spatial instability of these patches (depending on current intensity), their quality also drastically changes over the year, due to a seasonal pattern in the abundance of the micro-fauna occurring in them: in early summer, most insects, the aquatic larvae of which forage and refuge within debris, emerge from the stream, causing a drastic reduction in the protein

content of these substrates (Gherardi, unpublished). This decrease was reflected in the diet of the sedentary and aquatic males, while the females maintained a relatively high protein content in their stomachs, probably because of their frequent and long-lasting excursions onto land (Gherardi & Vannini, 1989), where there is abundant prey (Gherardi, 1987).

Aggression occurred more often on vegetable debris than on other substrates, as has been observed in the crayfish *Orconectes rusticus* Girard, whose aggressive activity in the laboratory was affected by the quality of food (Capelli & Hamilton, 1984). However, at least in the field, aggression seldom occurred in this species, notwithstanding the sometimes high animal den-
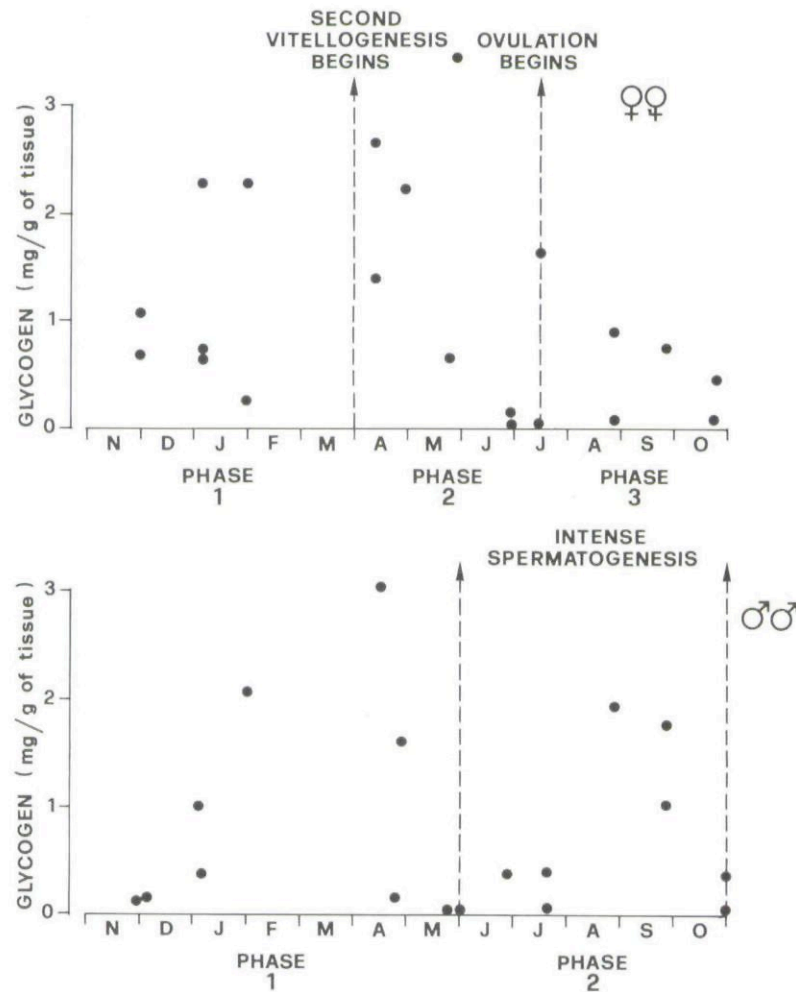
FIG. 11. Glycogen content of hepatopancreas during a yearly cycle in twenty-one females (upper) and eighteen males (lower).

sity in the pool and the paucity of patches of debris. The area inspected by the animals while foraging was not actively defended by them, nor was its size related to animal density, contrary to what is observed in territorial animals (Grant, 1968; Barlow, 1974). Conversely, there was a large extent of superimposition of contiguous foragers (independent of sex and size), which increased with the crabs' density.

Moreover, the few agonistic interactions seldom escalated, and were limited to low aggressive patterns, such as avoidance and threats. Because of the low fidelity of crabs to any particular area, and their dispersal along the stream (Gherardi & Vannini, 1989), this weak and rare aggression can only in part be due to a pre-

existing hierarchy maintained in time on the basis of individual recognition (even if in the laboratory *P. fluviatile* proved capable of learning some physical characteristics of a conspecific in a hierarchy; Vannini & Gherardi, 1981). The winner, either a male or female, was more often the larger individual, in accordance with observations in many other decapods, where size appears to be the most important factor in determining a hierarchy (see, e.g., Lowe, 1956; Bovbjerg, 1956). In *P. fluviatile*, cheliped length, which shows a positive allometry (more marked in the males) with respect to carapace length (Gherdardi *et al.*, 1987), has a strong aggressive value (Vannini, Gherardi & Pirillo, 1983). The function of chelipeds as 'resource holding poten-

tial' (*sensu* Maynard Smith & Parker, 1976) could explain the 'peaceful' behaviour of the crabs observed here: on the basis of this non-ambiguous asymmetry, with no expenditure of surplus energy in fighting, larger animals have easy access to the patches of vegetable debris, while smaller specimens are relegated to the poorer substrates such as the stream banks. For these latter animals, feeding on debris does not pay for the risks of dangerous injuries inflicted in escalated contests where the opponent is better armed, i.e. for small size classes these patches do not represent economically defendable resources. However, this dispotic distribution over the foraging area matches the difference in energetic requirements revealed in the population, smaller specimens significantly consuming less oxygen than bigger ones (however, they have a higher weight-relative oxygen consumption than adults; Gherardi *et al.*, 1988a).

A different feeding strategy between sexes seemed to occur: males moved more slowly than the females, and occupied a smaller area, minimizing the time required to search for food, but maximizing the rate of energy intake while feeding, as they prevalently grazed on vegetable debris ('time minimizers', Schoener, 1971). On the contrary, females were frequently excluded from the richer sources of energy because they were normally smaller than males and had relatively shorter chelipeds, were faster in their movements, inspected a wider foraging area, and searched for food mostly on sand and stones. The size of the inspected areas was positively correlated with carapace length in females, probably because larger crabs have higher energy requirements. As shown by radio-telemetry (Gherardi *et al.*, 1988b), in this sex these short movements over an area where organic matter accumulates are intercalated, at least in early summer, with long displacements along the stream or into the surrounding terrestrial habitat ('nomadic' movements), in contrast to the sedentary behaviour of the males. Much evidence, such as the consistent increase of both gonad index and its fat content, as well as histological analysis, suggest that in early summer second vitellogenesis (Adiyodi, 1985) occurs. In other phases of the reproductive cycle, radio-tracked females appeared less vagile and more aquatic in their habits (Gherardi & Vannini, 1989).

This sexual diversity in spatial strategy associ-ated with the reproductive phases was not related to differences in energy expenditure in the sexes (oxygen consumption was the same for males and females of equal size), but was accompanied by a consistent increase in the female hepatopancreas index. The hepatopancreas, which in Crustacea functions as an indicator organ of the general energy flow affecting an individual (Aldrich, 1975), mainly accumulates lipids (glycogen on the contrary is scanty and almost constant over the yearly cycle), which could measure the actual energetic input.

The rationale here is that increased locomotion, in spite of its costs in terms of risks of predation, furnishes an energetic reward to females, allowing them to extend and diversify their foraging area and thus to maximize food intake in terms of quantity and/or quality. The alimentary input which exceeds metabolic requirements is stored in the hepatopancreas as long-term lipid reserves to sustain the highly expensive vitellogenesis, resulting in the production of macrolecithal eggs. In this species, where female parental investment is high, the behaviour of 'energy maximizers' (Schoener, 1971) seems to be subject to a strong selective pressure in females, whose reproductive success is directly related to the efficiency of harvesting food.

## Acknowledgments

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