

## Growth and reproduction in the freshwater crab, *Potamon fluviatile* (Decapoda, Brachyura)

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**SUMMARY.** 1. The patterns of relative and absolute growth and the reproductive biology of the freshwater crab *Potamon fluviatile* were studied in a natural population inhabiting a hill stream close to Florence, Italy, over an annual cycle. Periodical inspections of a stretch of the stream were made and morphological and anatomical analysis carried out.

2. As in other decapods, the females are smaller than the males (they can however occasionally reach larger dimensions). This may be determined by a lengthening of the moulting interval in the females, by their higher energetic cost of reproduction (since reproduction occurs simultaneously with moulting, at least in this habitat) and/or by a higher mortality rate resulting from the risks associated with carrying eggs and vagility.

3. The analysis of relative growth in secondary sexual characters (abdomen width and major chela length) with respect to carapace length, shows that the pre-puberty and puberty ecdysis occur at 15 and 35 mm carapace length respectively, which was also confirmed by the gonad weight, vas deferens in males, and the onset of vitellogenesis in females.

4. A delay between anatomical and functional (i.e. the ability to copulate successfully) maturity was observed in the males. Being larger may be an advantage in intra-sexual competition for mating, but larger males, being more vagile, are also more likely to meet receptive females. The females may mate before their puberty moult and store sperms in their seminal receptacles for when they attain full maturity; this could be adaptive since opportunities of encountering males are few and far between in their adult phase, characterized by their vagile and amphibious habits.

### Introduction

If the study of relative growth (that is the change of shape as animals grow) throws light on the life history of a given species, information on the absolute growth patterns (determined by the

moult increment or growth factor and the inter-moult period or moult interval; Hartnoll, 1982) can undoubtedly help analysis of the population structure. Though relative growth is obviously not an exclusive feature of crustaceans, the presence of a rigid integument and thus the possibility of accurate measurements, together with the discontinuous growth pattern, make this group an ideal object for allometric studies (Teissier, 1960; Hartnoll, 1982).

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The most relevant changes in shape (apart from those connected with larval life) take place with the attainment of sexual maturity, often accomplished at one particular moult, the puberty moult (Perez, 1928), after which chelae, abdomen and pleopods (the secondary sexual characters) are seen to follow differential growth rates (Hartnoll, 1978).

In some cases, predictions of the attainment of sexual maturity made on the basis of morphometrical analysis have been confirmed by anatomical (Finney & Abele, 1981) or histological (Haley, 1969, 1973) examinations. Only a few works examine growth patterns as well as reproductive cycles (Haley, 1969; Finney & Abele, 1981; Vannini & Gherardi, 1988).

Scattered references exist on population structure and allometry of the secondary sexual characters for river crabs, in *Potamon gedrosianum* Alcock from Afghanistan (Schneider, 1971), and *Geotelphusa dehanni* White from Japan (Yamaguchi & Takamatsu, 1980), or to the attainment of sexual maturity, in *Barytelphusa guerini* Milne Edwards from India (Gangotri, Vasantha & Venkatachari, 1978). Data on the population structure of *Potamon fluviatile* Herbst have already been published (Gherardi, Guidi & Vannini, 1987). In the present work, the patterns of absolute and relative growth are considered, together with gravimetric and histological analysis of the gonads, which allows identification of the puberty moult. The interaction between moult and reproductive cycles and their effects on the population structure are also discussed.

## Materials and Methods

*Potamon fluviatile* is the only representative of the Potamoidea in Italy, occurring from Liguria and Tuscany southwards, Sicily included (Gherardi *et al.*, 1987). Fieldwork was conducted along a hill stream near Florence (170 m above sea level, mean width approximately 2 m, depth ranging from 10 to 90 cm, though greatly variable with the seasons).

In order to determine the timing of the main events of the life cycle, a 150 m stretch of the stream was periodically inspected from July to October 1986. No breeding females or moulting animals (except some juveniles) were seen during all the other periods of the year.

During these inspections, the following morphometrical data were taken: carapace length (CL) and width, width of the sixth abdominal segment, and length, width and height of chelae (Fig. 1). Measurements were also made of newly moulted individuals, including exuviae, when they were found near the moulted animal. Ovigerous females and mating pairs were also recorded. Other morphometrical data, i.e. abdomen and gonopod lengths, were taken from animals sacrificed for gonad examination.

About thirty-five specimens for dissection were collected from the stream once a month during 1986–87 and transferred to the laboratory, where they were killed with chloroform within a few hours and weighed. The weight of the gonads from males and females, the colour of the ovaries and mean oocyte diameter (calculated from the measurements of about ten randomly chosen oocytes under the binocular microscope) were recorded. Samples of ovaries and seminal receptacles were fixed in Carnoy's fluid and embedded in polystyrene resin. Sections (7  $\mu\text{m}$  thick) were stained using the haemalum–eosin technique in order to check for the presence of sperm in the seminal receptacles or of yolk inside the oocytes. As a criterion of anatomical sexual maturity in males, the presence of sperm in the vas deferens was adopted. Deferens tubules (from either freshly dissected or fixed gonads) were dipped in distilled water and broken with forceps, then examined under the microscope.

Sex-ratio at birth was determined in five broods. About 50% of specimens from each brood were examined under a binocular microscope: buds of four pairs of pleopods are visible in newly hatched females, whilst there are only two in males.

The text gives mean values  $\pm$  standard error.

## Results

### *Absolute growth*

Ecdysis was principally restricted to early autumn (Fig. 2); animals in the early instars probably moult more frequently (soft individuals smaller than 20 mm CL were found all year round, especially in autumn and spring).

The correlation between per cent increment at moult (i.e. the percentage by which the post-moult length exceeds the pre-moult length;

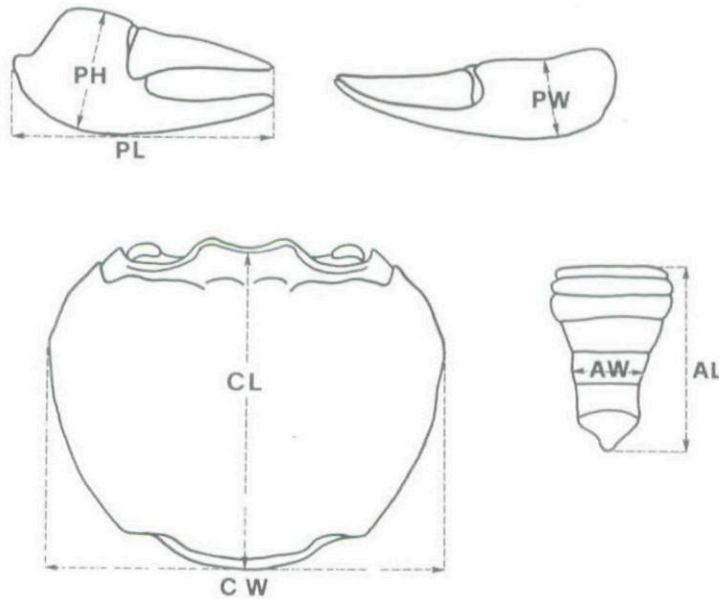


FIG. 1. A diagram of *P. fluviatile* showing some of the measurements taken (CL=carapace length; CW=carapace width; AL=abdomen length; AW=abdomen width; PL=claw propodite length; PW=claw propodite width; PH=claw propodite height).

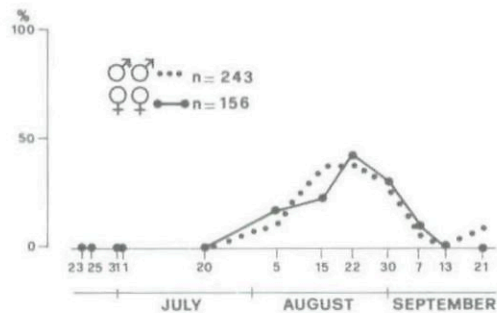


FIG. 2. Time of moulting (per cent of moulting animals) found in transects along the stream from June to September.

Mauchline, 1976) and CL was not quite significant (males: mean value =  $16.1 \pm 1.5\%$ ;  $r=0.466$ ,  $df=10$ , ns; females: mean value =  $15.5 \pm 1.12\%$ ;  $r=0.338$ ,  $df=11$ , ns; males v. females:  $t=0.32$ ,  $df=23$ , ns).

A significant difference existed between the size of moulting and hard animals (Fig. 3), males of the former more frequently being smaller than 25 mm CL ( $\chi^2=9.757$ ,  $df=2$ ,  $P<0.01$ ), whilst moulting females fell more in the range of 25–35 mm CL ( $\chi^2=34.127$ ,  $df=2$ ,  $P<0.001$ ). Mould frequency dropped dramatically after 35 mm CL, with no difference between the

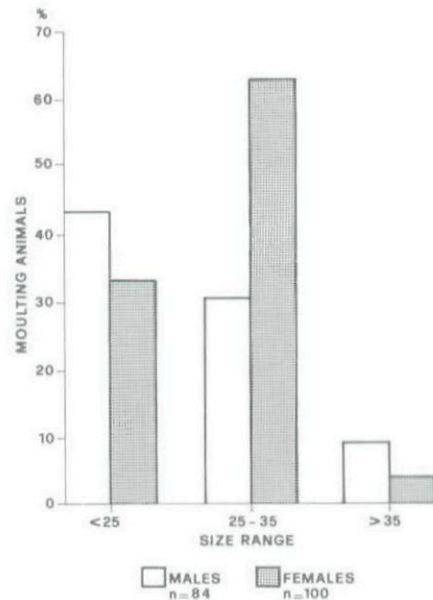


FIG. 3. Size-frequency distribution of moulting males and females.

sexes ( $\chi^2=1.24$ ,  $df=1$ , ns). The difference between sexes was not significant for animals smaller than 25 mm CL either ( $\chi^2=0.104$ ,  $df=1$ , ns), although it was so in the size range 25–35 mm ( $\chi^2=5.247$ ,  $df=1$ ,  $P<0.05$ ).

TABLE 1. Patterns of relative growth.  $b$ =regression coefficient ( $*P<0.05$ ;  $**P<0.01$ ). (CL=carapace length; CW=carapace width; MPL=major claw propodite length; mPL=minor claw propodite length; MPW=major claw propodite width; mPW=minor claw propodite width; MPH=major claw propodite height; mPH=minor claw propodite height; AL=abdomen length; AW=abdomen width; BWt=body weight.)

ln (CL) v:	Males			Females			
	$N$	$b$	$t$ ( $b \neq 1$ )	$N$	$b$	$t$ ( $b \neq 1$ )	$t$ ( $\sigma \neq \varphi$ )
ln (CW)	343	1.023	10.97**	305	1.025	6.88**	0.37
ln (MPL)	229	1.262	35.79**	153	1.217	15.39**	2.90**
ln (mPL)	228	1.176	25.11**	155	1.152	4.09**	0.81
ln (MPW)	231	1.364	32.48**	155	1.411	17.73**	1.95
ln (mPW)	231	1.205	16.80**	155	1.179	7.39**	1.02
ln (MPH)	231	1.314	31.57**	154	1.354	10.16**	1.36
ln (mPH)	231	1.140	14.72**	154	1.11	5.66**	1.43
ln (AL)	8	1.570	6.84**	11	1.014	0.26	5.70**
ln (AW)	206	0.935	4.63**	235	1.928	32.27**	32.36**
ln (BWt)	16	2.836	38.22**	15	2.693	17.60**	1.25

ln (CL) v:	$N$	$b$	$t$ ( $b \neq 0$ )	$N$	$b$	$t$ ( $b \neq 0$ )	$t$ ( $\sigma \neq \varphi$ )
MPL/mPL	226	0.085	16.35**	153	0.066	1.82	0.68

TABLE 2. Relative growth of pleopods

ln (CL) v:	df	$b$	$t$ ( $b \neq 1$ )
ln (female pleopods)			
1st endopod.	8	1.385	3.169**
exopod.	8	2.112	11.644**
2nd endopod.	8	1.617	5.268**
exopod.	8	2.182	11.491**
3rd endopod.	7	1.513	2.952*
exopod.	8	1.806	2.650*
4th endopod.	7	1.563	3.545**
exopod.	8	1.980	10.741**
ln (male pleopods)			
1st pleopod.	19	1.161	2.101
2nd pleopod.	15	0.897	1.253

The total number of moulting animals, compared with that of the non-moulting ones, did not differ significantly between the sexes (males: 27.38%; females: 31%; males v. females:  $\chi^2=0.14$ ,  $df=1$ , ns).

Adults do not moult every year: of the animals marked in autumn 1985, by gluing plastic tags onto their carapaces (see Gherardi *et al.*, 1987) and captured the following year still carrying their markers, 8% of males and 10% of females had not moulted in autumn (all of them were larger than 30 mm CL).

#### Relative growth

Carapace width, length, width and height of both chelae, degree of heterochely, abdomen length and width, total body weight, and length of female pleopods all showed allometric growth relative to CL (Tables 1 and 2). Bilogarithmic transformation was used (Huxley, 1932; Hartnoll, 1974), and CL was referred to as the independent variable (Gray & Newcombe, 1938).

Positive allometric growth of carapace width versus CL was revealed with no difference

TABLE 3. Growth rate of major claw length (v. ln of carapace length) in different instars (\* $P < 0.05$ ; \*\* $P < 0.01$ )

ln (major claw length)							
	<i>N</i>	<i>b</i>	<i>t</i> ( <i>b</i> ≠1)				
Juveniles (<15 mm)	42	1.075	2.27*				
	Males			Females			
	<i>N</i>	<i>b</i>	<i>t</i> ( <i>b</i> ≠1)	<i>N</i>	<i>b</i>	<i>t</i> ( <i>b</i> ≠1)	<i>t</i> (♂≠♀)
Sub-adults (15–35 mm)	53	1.231	17.71**	35	1.159	5.17**	2.45*
Adults (>35 mm)	159	1.541	17.76**	113	1.471	7.56**	1.11
	Males			Females			
		<i>t</i>	df		<i>t</i>	df	
Juv. v. Sub-ad.		4.85**	93		1.81	75	
Sub-ad. v. Ad.		9.31**	210		4.46**	146	

between males and females, and in the length of the minor chela, the width and height of both chelae, and body weight (Table 1). On the contrary, the length of the major chela differed significantly in its level of allometry in the sexes (Table 3), growing more rapidly in males ( $t=2.90$ ,  $P < 0.01$ ), with no difference between the growth rate for right- (over 90% of the entire population; Gherardi *et al.*, 1987) or left-handed individuals ( $t=0.076$ ,  $df=148$ , ns).

The allometric growth of the major chela was not constant (Fig. 4 and Table 3): the slope of the regression line increases at 15 and 35 mm CL in males, and at 35 mm in females. The ecdyses occurring at these sizes are assumed to correspond to the pre-puberty (only shown in the males) and puberty moults, respectively, thus demarcating three phases: juvenile (CL <15 mm), when individuals are still sexually undifferentiated; sub-adult (CL  $\geq 15$  mm and <35 mm), when sexual dimorphism becomes apparent; and adult (CL  $\geq 35$  mm), when the animals attain sexual maturity. The abbreviations J, SM, SF, AM and AF will be used in the text to refer to juveniles, sub-adults and adults, males and females respectively.

The abdomen showed the most evident growth differences between the sexes (Fig. 5 and Table 4). The female abdomen began to widen faster at 15 mm CL, its growth rate slowing down after 35 mm. In males, a variation in slope was seen at 15 mm, with no difference in the

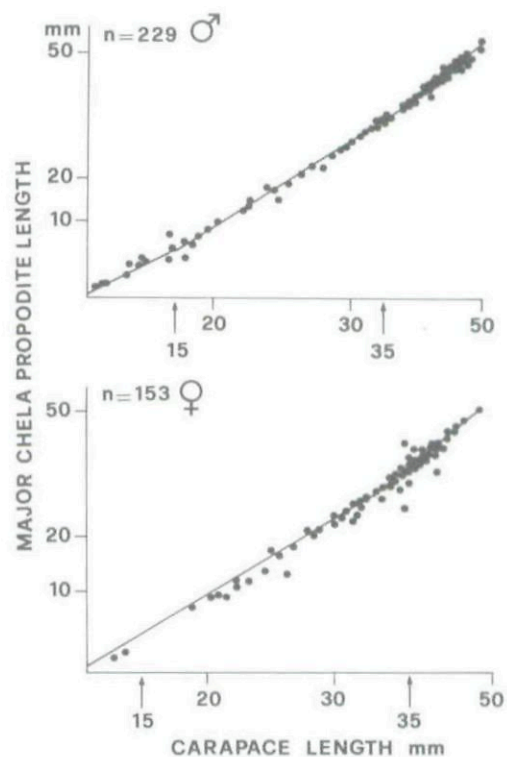


FIG. 4. Allometric growth of major claw length in males (top) and females (bottom) versus carapace length. The discontinuities of the curve mark the pre-pubertal (males, at 15 mm CL) and pubertal (males and females, at 35 mm (CL) moults). Plotted on logarithmic scale.

TABLE 4. Growth rate of abdomen width (v. ln of carapace length) in different instars (\* $P < 0.05$ ; \*\* $P < 0.01$ )

ln (abdomen width)							
	<i>N</i>	<i>b</i>	<i>t</i> ( <i>b</i> ≠1)				
Juveniles (<15 mm)	27	1.126	0.90				
	Males			Females			
	<i>N</i>	<i>b</i>	<i>t</i> ( <i>b</i> ≠1)	<i>N</i>	<i>b</i>	<i>t</i> ( <i>b</i> ≠1)	<i>t</i> (♂≠♀)
Sub-adults (15–35 mm)	80	0.871	3.13*	90	2.058	20.18**	16.82**
Adults (>35 mm)	148	0.951	1.05**	145	1.363	3.16**	3.54**
	Males			Females			
			<i>t</i>			<i>t</i>	df
Juv. v. Sub-ad.			2.02*			7.97**	115
Sub-ad. v. Ad.			1.13			5.66**	233

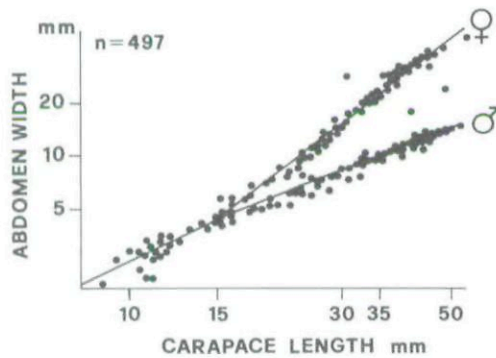


FIG. 5. Allometric growth of abdomen width versus carapace length. Male and female curves separate in correspondence to pre-pubertal moult (15 mm CL), while discontinuity in the female curve (top) marks the pubertal moult (35 mm CL). Plotted on logarithmic scale.

level of allometry between the S and A instars. In females, the abdomen length exhibited a positive allometry both in S and A instars (S:  $t=5.341$ ,  $df=5$ ,  $P<0.01$ ; A:  $t=4.988$ ,  $df=55$ ,  $P<0.001$ ), though in the latter growth became significantly slower (S v. A:  $t=2.654$ ,  $df=55$ ,  $P<0.02$ ). In males, abdomen length is isometrical in S, while in A it showed a negative allometry, but the change in slope was not significant (S:  $t=1.935$ ,  $df=2$ , ns; A:  $t=5.156$ ,  $df=42$ ,  $P<0.001$ ; S v. A:  $t=0.516$ ,  $df=42$ , ns).

The growth of male gonopods (both first and second pairs) did not differ from isometry (Table

2). Gonopods of the first pair, which are positively allometric in immature crabs of other species (Hartnoll, 1974), were isometric in both S ( $t=1.317$ ,  $df=2$ , ns) and A males ( $t=1.274$ ,  $df=15$ , ns), and no change occurred at the puberty moult (S v. A:  $t=0.346$ ,  $df=15$ , ns). Female pleopod exopodites (considering the average length of the four pairs) grew faster, relative to CL, in S ( $t=8.823$ ,  $df=4$ ,  $P<0.001$ ) and isometrically in A ( $t=0.905$ ,  $df=13$ , ns), with a significant difference between these two categories ( $t=8.588$ ,  $df=13$ ,  $P<0.001$ ).

With respect to abdomen length (as a structure, the abdomen carries and covers pereopods), the exopodites showed a positive allometric growth in S ( $t=5.593$ ,  $df=4$ ,  $P<0.01$ ) and an isometric one in A ( $t=1.506$ ,  $df=12$ , ns; S v. A:  $t=5.147$ ,  $df=12$ ,  $P<0.001$ ). Pleopod endopodites (mean values) grew isometrically with respect to abdomen length, with no change at the puberty moult. Male first pleopods showed a fairly positive allometry with respect to abdomen length ( $t=2.146$ ,  $df=19$ ,  $P<0.05$ ), while the growth of the second male pleopods was isometrical ( $t=0.614$ ,  $df=15$ , ns).

#### Anatomical sexual maturity

**Gonad weight.** Fig. 6 shows the net weight of the reproductive tract of males and females as a function of CL. In both sexes there was an abrupt change in the slope of the regression line at about 35 mm CL (SM:  $r=0.894$ ,  $b=0.052$ ,

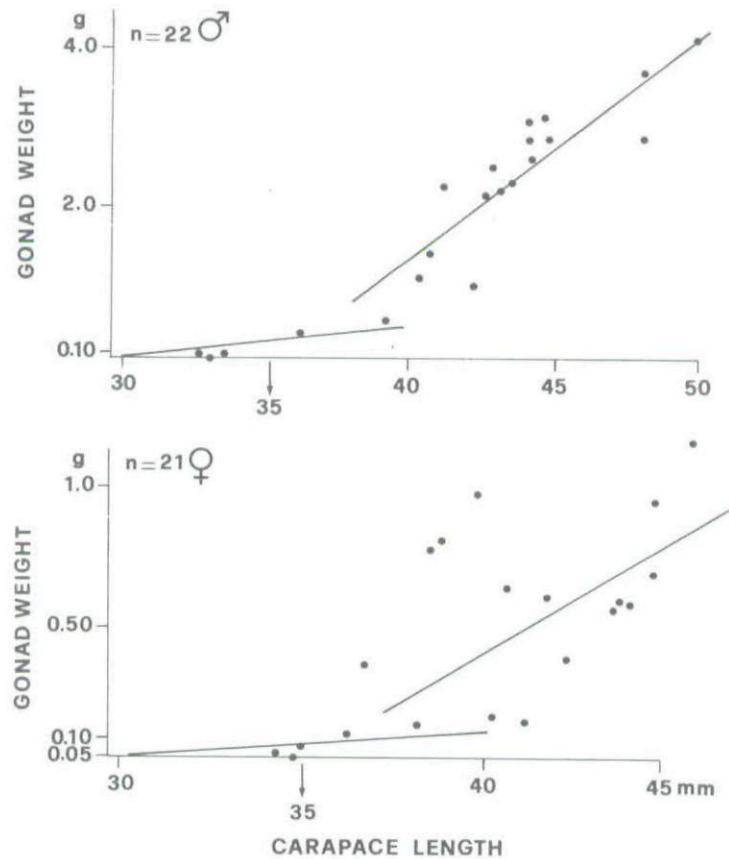


FIG. 6. Correlation between body size (carapace length) and gonad weight (wet) in males (top) and females (bottom).

df=4,  $P<0.02$ ; AM:  $r=0.861$ ,  $b=0.26$ , df=14,  $P<0.001$ ; SM v. AM:  $t=2.706$ , df=14,  $P<0.02$ ; SF:  $r=0.724$ ,  $b=0.013$ , df=3, ns; AF:  $r=0.643$ ,  $b=0.088$ , df=13,  $P<0.01$ ; SF v. AF:  $t=2.652$ , df=13,  $P<0.02$ ). In S, gonad weight exhibited a slight positive allometry in males, while female ovaries were inconspicuous until the onset of sexual maturity. Weight increased rapidly in both sexes in the larger classes.

*Vas deferens.* The anatomical subdivision proposed by various authors (Cronin, 1947; Ryan, 1967; Hinsch & Walker, 1974) of vas deferens into anterior, medial and posterior portions was adopted. Classification was made on the basis of the external appearance and position of the deferential tracts without histological examination. The presence of sperms was checked in the anterior and medial regions.

Examination of the vasa deferentia from six-

teen males (ranging from 25.4 to 50.5 mm CL) revealed the constant presence of sperms in animals over 35 mm, while they were never found in S individuals.

#### *Vitellogenesis*

At the onset of vitellogenesis, the originally white, thin ovaries acquire a creamy colour and start to grow as a consequence of the deposition of yolk inside the oocytes. As this process continues, the ovary turns yellow in colour and, finally, bright orange. Oocytes on the external surface of the ovary started to colour at about 0.5 mm diameter. This agrees with the classification of vitellogenic stages proposed by Adiyodi (1968). In our histological sections of ovaries, minute eosinophilic granules were present at the periphery of the oocytes over 0.5 mm in dia-

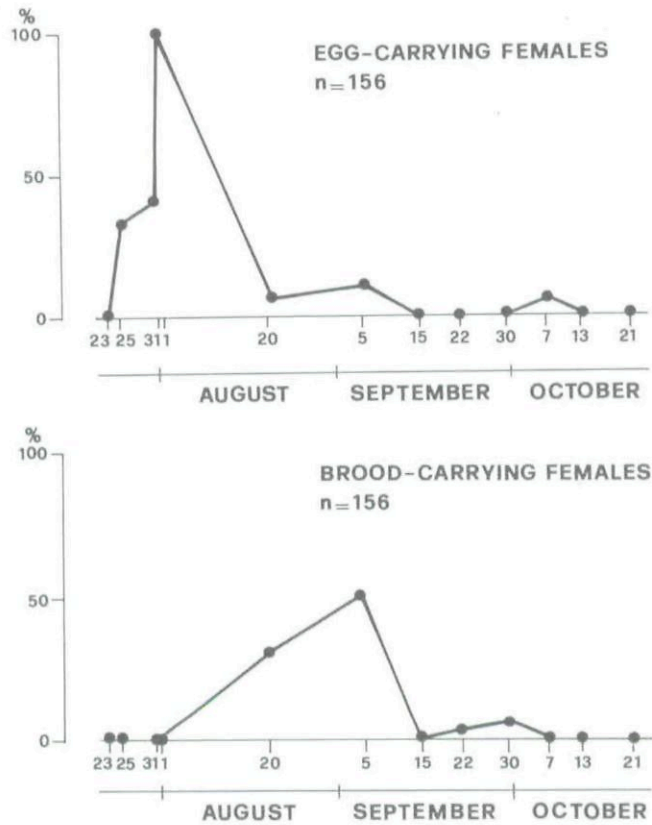


FIG. 7. Time of spawning (top) and hatching (bottom) (per cent of egg- and brood-carrying females, respectively, founded in transects along the stream from July to October).

meter and acidophily increased with cell size. Ovaries with oocytes larger than 0.5 mm on average were thus considered as vitellogenic.

All of the ten females measuring 26–35 mm CL examined had immature gonads, whilst only one of the sixty-six adults (ranging from 35 mm to 46 mm) had a non-vitellogenic ovary.

*Functional sexual maturity*

*Oviposition and hatching.* Egg-bearing females were found in the stream from late July to early August (Fig. 7). Like all freshwater crabs studied to date (Koba, 1936; Schneider, 1971; Minei, 1976; Yamaguchi & Takamatsu, 1980; Pillai, 1982), and as already reported for this species (Mercanti, 1885; Pace, Harris & Jaccarini, 1976), hatching occurs in the pouch limited by the mother's abdomen. Brood-carrying females were found in the second half of August

and the first half of September. The distance between the peaks of the diagram in Fig. 7 corresponds to 1 month approximately but no direct measurement of the incubation period was made. Pace *et al.* (1976) indicated a duration of 45±2 days at 23°C for this species in Malta. All breeding females found at stream inspections (26.4% of total number of females) were in the instar indicated here as A, and the size distributions of breeding and non-breeding individuals

TABLE 5. Size frequencies of breeding and non-breeding females found along stream transects from July to September 1986

Size range (CL, mm)	No. of females	
	Breeding	Non-breeding
<35	0	41
≥35 and <40	8	12
≥40	20	25



were significantly different ( $\chi^2=24.0$ ,  $df=2$ ,  $P<0.001$ ; Table 5).

Although on the basis of morphometrical and anatomical analysis it could be inferred that animals are already sexually mature at about 35 mm CL, no breeding female under 38 mm was ever found and larger ones were more common (average CL of breeding females  $41.99 \pm 0.28$  mm,  $n=45$ ).

The number of hatchlings for each female, counted in seven different broods, ranged from 55 to 157 (average 103.7). No correlation seemed to exist between CL of these females and the number of hatchlings ( $r=0.23$ ,  $df=5$ , ns), i.e. fecundity does not seem to increase with size. The fecundity of twenty-four females was evaluated by classifying the numerical consistency of

chilipeds with his, or with his first pereopods and grasping her with his pereopods.

The most striking feature was the difference in size between the partners, the females always being smaller than the males (females: CL from 29.7 to 42 mm, average  $35.74 \pm 0.87$  mm; males: CL from 41.2 to 50.5 mm, average  $45.37 \pm 0.76$  mm). Size frequencies (Table 7) of mating and non-mating animals (comparing data gathered over the same period) were significantly different in both sexes (males:  $\chi^2=19.624$ ,  $df=1$ ,  $P<0.001$ ; females:  $\chi^2=12.794$ ,  $df=2$ ,  $P<0.01$ ), which suggests that the difference in size of mating males and females is not simply a reflection of the size composition of the population.

The mechanisms of sex-recognition are still unknown. In two matings observed in the laboratory (male CL: 47.9 and 45.7 mm; female CL: 34.5 and 34.7 mm) the first phases showed all the signs of an aggressive interaction, with the male grasping the female by the chelipeds, then, after a few minutes, turning her over with the aid of his pereopods and pushing her under himself, at the same time inserting his abdomen under his partner's. In both cases, mating lasted about 3 h. Minei (1976) gave a similar description of mating behaviour in the river crab *Geotelphusa dehaani* White.

Seminal receptacles from eighteen females were examined histologically. Out of fourteen animals with CL  $>35$  mm, captured in all months of the year, only one had empty spermathecae. Two adult, post-moult ('soft') females also had masses of sperms in their receptacles, indicating that sperms are kept over ecdysis. Sperms were also present in one YF (34 mm CL), while other three YFs had not yet copulated.

## Discussion

The analysis of the population structure (con-

TABLE 6. Female fecundity relative to size

Size range (CL, mm)	Egg masses		
	Small	Medium	Large
38-42	3	2	4
42-46	6	6	3

the egg masses in three categories, i.e. small, medium and large (Table 6), and this confirmed the previous results (Fisher test: ns).

Sex-ratio at birth (determined in 293 crablets) did not differ significantly from 1:1; 47.4% ( $\chi^2=0.577$ ,  $df=1$ , ns) of the crablets were male.

## Mating

Fourteen mating pairs were observed in nature, from May to October. In all cases both partners had hard integuments and were found free in the water, in the open; only in two cases were they found at a burrow entrance. The partners remained motionless for a period varying from 30 min to 21 h, with their ventral surfaces in contact, the male holding the female's

TABLE 7. Size frequencies of mating and non-mating individuals during the breeding season (CL=carapace length)

Size range (CL, mm)	Males		Females	
	Mating	Non-mating	Mating	Non-mating
<35	0	32	4	33
$\geq 35$ and <40	0	8	8	12
$\geq 40$ and <45	4	19	2	34
$\geq 45$	9	7	0	0

ducted on the same population as the present study; Gherardi *et al.*, 1987), showed that the size classes were not equally represented in the sexes, individuals over 40 and under 30 mm CL more often being males, whereas females were represented more in the 35–40 mm CL range. In other decapods too, especially brachyurans (Adams, Edwards & Emberton, 1985), females are smaller than males, as a consequence of an increase in the intermoult interval, e.g. in *Cancer pagurus* Linnaeus (Bennet, 1974) and in *Pachygrapsus crassipes* Randall (Hiatt, 1948), and/or of a reduction of the growth rate (as in the case of *Cancer magister* Dana, Cleaver, 1949). *P. fluviatile* does not exhibit any sexual difference in carapace growth rate, contrary to the freshwater crab *Paratelphusa hydrodromus* Herbst from India, where a differential growth rate between sexes was detected during sexual maturity (Kurup & Adiyodi, 1981).

Though in most decapods the increment at moult declines with size, some exceptions do exist, e.g. *Carcinus maenas* Linnaeus (Crothers, 1967; Hogarth, 1975), *C. mediterraneus* Czerniavsky (Veillet, 1945), *Maja squinado* Herbst (Carlisle, 1957) and *Pisa tetraodon* Pennant (Vernet-Cornubert, 1958). All of these have a definite terminal anecdyosis, which, however, must be excluded in our case because large females were also found, though only rarely (the biggest animal found in the stream was in fact a female measuring 51.9 mm CL).

A second possible mechanism limiting female size could be a lengthening of the moult interval compared with males, caused by the onset of reproductive activity, which, at least in Anomura and Brachyura (Adiyodi, 1985), is restricted to the intermoult period. Furthermore, both moulting and reproduction entail considerable energy demands (Passano, 1960; Yamaguchi & Takamatsu, 1980; Adiyodi, 1985; Gherardi, Tarducci & Micheli, 1989). Since, in the populations of *P. fluviatile* Herbst in temperate areas, the breeding and moulting seasons almost coincide, it is unlikely that an animal would undergo both events in the same annual cycle. In terms of optimization strategies, the size range of mature females could represent a compromise between the advantages to be had from spawning every year, and from reaching a larger size before maturity, and thus higher fecundity (i.e. the number of eggs produced per animal per breeding season) with the onset of

reproductive activity. However, while a positive relation between female size and number of eggs spawned has been shown in many crustacean species (e.g. *Pseudocalanus minutus* Krøyer, McLaren, 1965; *Heterozius rotundifrons* Milne Edwards, Jones, 1978; *Homarus americanus* Milne Edwards, Aiken & Waddy, 1980; *Eriphia smithi* MacLeay, Vannini & Gherardi, 1988), this was not the case in *P. fluviatile*, though ovary weight does exhibit a positive allometry with respect to body size.

An alternative hypothesis explaining the smaller size of females could be their higher mortality rate, caused by the high cost of egg production (especially if compared to the low cost of spermatogenesis; Pillay & Nair, 1971), and/or by the intense vagility exhibited during the pre-ovulatory period (Gherardi, Tarducci & Vannini, 1988), bringing exposure to risks of both predation and dehydration as a consequence. The evidence that the sex-ratio calculated in this population (58.6% males) during the winter months (i.e. in the period of the lowest vagility in both sexes), differs significantly from 50% (Gherardi *et al.*, 1987), contrary to the sex-ratio at birth, could possibly support the hypothesis of a higher mortality rate amongst females.

During the breeding season the sex-ratio changes, shifting in favour of the females in September, i.e. when they carry the brood under their abdomens, so that their locomotor activity is limited and they crowd into the stream (Gherardi *et al.*, 1988a). A similar seasonal variation in sex-ratio has also been observed in *Geotelphusa dehaani* White (Yamaguchi & Takamatsu, 1980). The lowering of moult frequency with the onset of sexual maturity (over 35 mm CL) is not surprising, because the same phenomenon is widely observed in all Crustacea, and is probably connected to the energy cost of reproduction (Hartnoll, 1982).

The different distribution of moulting animals in the two sexes observed in smaller classes (in particular for CL >25 and <35 mm, where there were more moulting females than males) indicates that females grow faster than males as they approach the puberty moult, anticipating the onset of their reproductive activity. The acceleration of moult frequency prior to sexual maturity could explain the large number of adult females in the population (Gherardi *et al.*, 1987). The length and frequency of oogenic

cycles seem to be characteristic for each crustacean species in a given environment, because oviposition is timed by some environmentally correlated mechanism is such a way that it takes place when conditions are likely to be favourable for the release of the young. For instance, in *Paratelphusa hydrodromus* Herbst, a freshwater crab with a wide geographical distribution in India, oviposition occurs from March to October in South Kerala, where rains are scattered, while in North Kerala, where rains are more seasonal, it only occurs in March, so that release of the young coincides with the beginning of the monsoon. In the first case, multiple spawning over a single annual cycle seem to be the rule, while the northern populations spawn once only (Adiyodi, 1985).

The patterns of relative growth by chelae, heterochely, and abdomen follow those already shown in most species studied so far (Hartnoll, 1974), and the adaptive value of the allometry exhibited by these organs has already been largely discussed (Hartnoll, 1974, 1982; Finney & Abele, 1981; Vannini & Gherardi, 1988).

*P. fluviatile* males do not adhere to the general branchyuran trend of positive allometry of the first pleopods versus carapace length in the instars preceding puberty, as their growth is isometric relative to carapace and abdomen lengths in both S and A. According to Hartnoll (1974), allometric growth of male gonopods brings them to an operative size at puberty. Their growth is correlated with the size of the genital openings of the females. Large male gonopods would be disadvantageous, as they would limit the size range of possible partners. In most species this is prevented by the negative allometry exhibited by these structures in adult males (Hartnoll, 1974). However, in *P. fluviatile* mating is accomplished only by large males with small females. This could justify the absence of a positive allometry in the male gonopods, because by the time a male begins its reproductive activity its gonopods are probably already of the effective size with no need for accelerated growth.

Allometry of female pleopods is a feature not generally observed in brachyurans. Female pleopod endopodites are slightly allometric relative to carapace length, but isometric with abdomen length, which in turn is positively allometric with carapace length; endopodite growth could simply follow abdomen growth. On the

contrary, exopodites grow faster relative both to carapace and abdomen length prior to the puberty moult, while they become isometric in the adult phase. Female exopodites protect eggs and brood, preventing them from loss and dehydration. A positive allometry of these structures before puberty would therefore grant an adequate protective structure as soon as the female is ready to spawn for the first time. Protection of the brood is particularly important for this species in relation to the long time the young stay under the mother's abdomen and the risks arising from the environment (newly hatched crabs could be carried away by the current or become dehydrated).

No difference was observed between the sexes in the level of allometry of carapace width versus CL, which in many species is related to the ovary development (Hines, 1982; Vannini & Gherardi, 1988). However, in male *P. fluviatile*, gonads are very voluminous, especially the deferens portion, ranging from 1.5% to 5% of the total body wet weight in adult animals, while in the females gonad weight only exceptionally exceeds 2% (Micheli, 1988). The considerable development of the male reproductive system in this species does not seem to be a general feature of freshwater brachyurans: in the river crab *Barytelphusa guerini* Milne Edwards, for example, female gonads are heavier than those of males (Gangotri *et al.*, 1978).

Both sexes of *P. fluviatile* undergo the puberty moult at approximately the same size (35 mm CL), but functional maturity (which in females means the capability of producing eggs, and in males corresponds to the phase when they are first able to copulate; Hartnoll, 1969) is in both cases delayed, though to a different extent. The long gap between the onset of sperm production and their effective transfer observed also in *Portunus sanguinolentus* Herbst (Ryan, 1967) and in the superfamily Oxyrhyncha (Hartnoll, 1963), might be adaptive either because larger males have an advantage in agonistic encounters with conspecifics (Vannini, Gherardi & Pirillo, 1983), or because large animals inspect wider areas and meet more females; a positive correlation exists between locomotor activity and body size (Gherardi *et al.*, 1988a).

A deeper knowledge of reproductive behaviour, and sex-recognition mechanisms in particular, is of course necessary. In the case of females, mating is usually coincident or even

precedent to the pubertal moult, so that sperms are kept in the seminal receptacles until ovulation – all adult females had sperms in their spermathecae. Storage of sperms occurs in many crustacean species (Sastry, 1983). In *Chionoecetes bairdi* Rathbun, sperms stored in the receptacles are still viable after 2 years (Paul, 1984). In some cases, sperms received during a single copulation may fertilize eggs for several ovipositions (Hartnoll, 1963; Ryan, 1967).

In *P. fluviatile*, mating of pre-pubertal females could be advantageous, due to the vagile and largely terrestrial habits characterizing their adult phase, which reduce the possibility of encountering males, and/or to the considerable overlap of the mating and breeding season, so that, by the time mating does occur, most females over 38 mm CL already carry a brood.

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