RELATIVE GROWTH AND POPULATION STRUCTURE OF THE FRESHWATER CRAB, *POTAMON POTAMIOS PALESTINENSIS*, IN THE DEAD SEA AREA (ISRAEL)

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ABSTRACT

Morphological and ecological studies have been carried out on three populations of the crab *Potamon potamios palestinensis* inhabiting freshwater springs in the Dead Sea area of Israel. To a certain extent, relative growth patterns followed those already described for other Brachyura. In the males, the chelipeds showed a positive allometry with respect to carapace length, which was probably related to their function in intra- and/or intersexual competition. Righthandedness has been associated with the distribution of scars and mutilations over the body. The wider abdomen is a female sexual character, the allometric growth of which decreases after the puberty moult. Males were on the average bigger than females; it is advantageous for them to grow faster to the size at which they are more likely to copulate successfully. On the contrary, the optimal size of females seems to be conditioned by energetic expenditure for reproduction.

INTRODUCTION

Potamon potamios (Olivier, 1804) is a freshwater crab occurring in Anatolia, in several southern islands of the Aegean Sea, in Syria, northern Iran, Lebanon and Israel (Pretzmann, 1961, 1983a,b, 1984; Bott, 1967). In Israel, the subspecies *P. potamios palestinensis* (Bott, 1967) is widely represented in aquatic habitats throughout most of the country, including the arid Negev, and its distribution extends as far as the northemmost corner of Sinai (Flower, 1931). Rich populations of this species dwell in the freshwater springs of the Dead Sea area, where the density can exceed 0.1 specimens per m^2 (Mr. Ran Levi, The Hebrew University of Jerusalem, pers. comm.). The animals are active all year round and are prevalently nocturnal. Reproductive activity occurs over a long period during which females may spawn (May–October), while copulation does not seem to be seasonable (Mr. Ran Levi, pers. comm.).

Similar to other Potamoidea, eggs are incubated in the chamber limited by the sternum and abdomen, and the hatchlings remain under the female abdomen for a certain period before dispersing. The animals are amphibious, and especially the males spread over the

surrounding terrestrial habitats, straying up to 40 m away from the stream at night. In its feeding habits this species behaves as a generalist, actively preying on frogs, fishes and various invertebrates, and scraping alga-covered surfaces or grazing on vegetable debris, mainly consisting of dead leaves and stalks of *Phragmites australis* (Reice & Herbst, 1982). Its main predators are considered to be birds, especially kingfishers and herons.

This study was conducted in the desert streams of Israel with the purpose of examining the differences in population structure and allometry between this species which inhabits an arid zone and *P. fluviatile* of temperate areas, whose biology and behavioural ecology have been the object of extensive studies (Gherardi, 1987). The paper also provides some data on the general ecology and behaviour of the populations under study.

MATERIALS AND METHODS

The research was carried out in two streams, Nahal David (ND) and Nahal 'Arugot (NA) ('En Gedi Nature Reserve), and in the streams and pools of 'Ein Fashkha (EF) (Enot Zukim Nature Reserve), all on the western shore of the Dead Sea (Fig. 1). At 394 m below sea level, these streams are among the lowest in the world. Some data on the water chemistry are provided by the 'En Gedi Nature Reserve Authority for ND and NA streams (Dr. Eli Geffen, pers. comm.), and by Reice and Herbst (1982) for some EF water bodies. For the cations, calcium content was 49–112 mg/lt in ND and NA, and 199–671 mg/lt in EF, while, for the anions, chloride measured 63.2–150.5 mg/lt in ND and NA, and 1418–6390 in EF. Conductivity ranged from 0.57 to 1.31 mΩ/cm in ND and NA, and from 4.41 to 18.98 mΩ/cm in EF. During the year, water flow was always higher than 100×10^3 m^3 per month, at least in ND and NA (no flow data were available for EF). However, these streams are subject to autumnal floods, when rain water drains into the catchment areas above the canyons. Floods can quickly change the aspects of canyons, especially in NA, whose catchment area measures up to 210 km^2 (compared to 60–70 km^2 in ND).

The climate in this area is arid, annual precipitation being 50–80 mm in the Dead Sea Valley and 100–200 mm in the nearby mountainous area (Margalit et al., 1973). The mean daily air temperature along the Dead Sea shore is approximately 20°C from September to April, and 30°C from May to August, with extremes of 3°C (in January) and 48°C (in August) also recorded (Ashbel, 1939). Relative humidity ranges from 38% during daytime hours in summer to 75% during the night in winter. July is the driest month (daily average 54%), whereas January is the dampest (daily average 72%).

In September 1988, a 300 m strip was inspected during daytime and nighttime hours along ND and NA, and a similar strip along EF only in daytime. During this period, hourly air temperature and relative humidity ranged from 27–36°C and 46–66% respectively for daytime hours to 25–34°C and 51–66% at night. Crabs were caught by hand and marked with waterproof nail varnish to avoid remeasuring. The following information was recorded for each capture: date, time of day, some body dimensions, sex, egg state if female, moult state, scars and mutilations, type of microhabitat, and behaviour. For body dimensions we measured, in mm, carapace length (CL) (from the median frontal notch to the posterior carapace margin), carapace width (across the carapace just
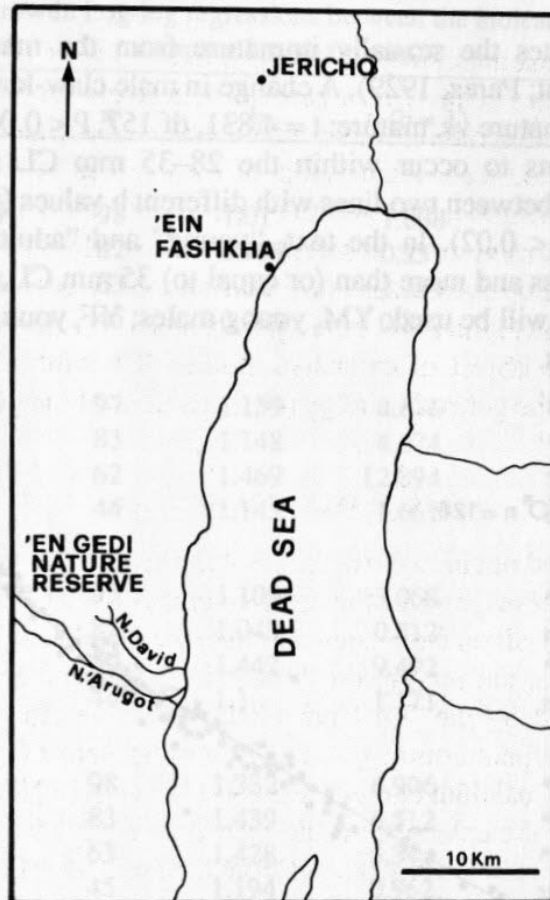
Fig. 1. Map of the northern Dead Sea, Israel, showing the geographical locations of the streams under study.

anterior to the antero-lateral tooth), maximum length, width and height of the propodite of each cheliped, and abdomen width (at the largest abdominal segment in females, and at the 5th in males).

In studying relative growth we used CL as an indicator of body size, since in crabs this is the least susceptible to growth variation with sexual maturation (Hartnoll, 1982). Relative growth patterns are represented by the logarithmic transformation ($\log y = \log a + b \log x$) of the exponential function $y = a x^b$. The values of b define the type of allometry ($b = 1$: isometry; $b > 1$: positive allometry; $b < 1$: negative allometry).

The text gives mean values ± standard error. Statistical methods were parametric (Student's t-test) when distribution seemed to be normal, and nonparametric (chi-square test) for "distribution-free" and independent samples (Siegel, 1956).

RESULTS

Relative Growth

Log-log plots of the major claw length in males and of abdomen width in females compared to CL (Fig. 2 and Table I) show the size when the puberty moult occurs, i.e the

ecdysis which demarcates the sexually immature from the mature phases (from a morphological standpoint; Perez, 1929). A change in male claw-length allometry occurs at about 35 mm CL (immature vs. mature: t = 4.831, df 157, P < 0.001), while in females, the puberty moult seems to occur within the 28–35 mm CL size range, where a superposition is evident between two lines with different b values (immature vs. mature: t = 2.424, df = 121, P < 0.02). In the text, "young" and "adult" will refer to those specimens measuring less and more than (or equal to) 35 mm CL, respectively, and the following abbreviations will be used: YM, young males; YF, young females; AM, adult males; AF, adult females.
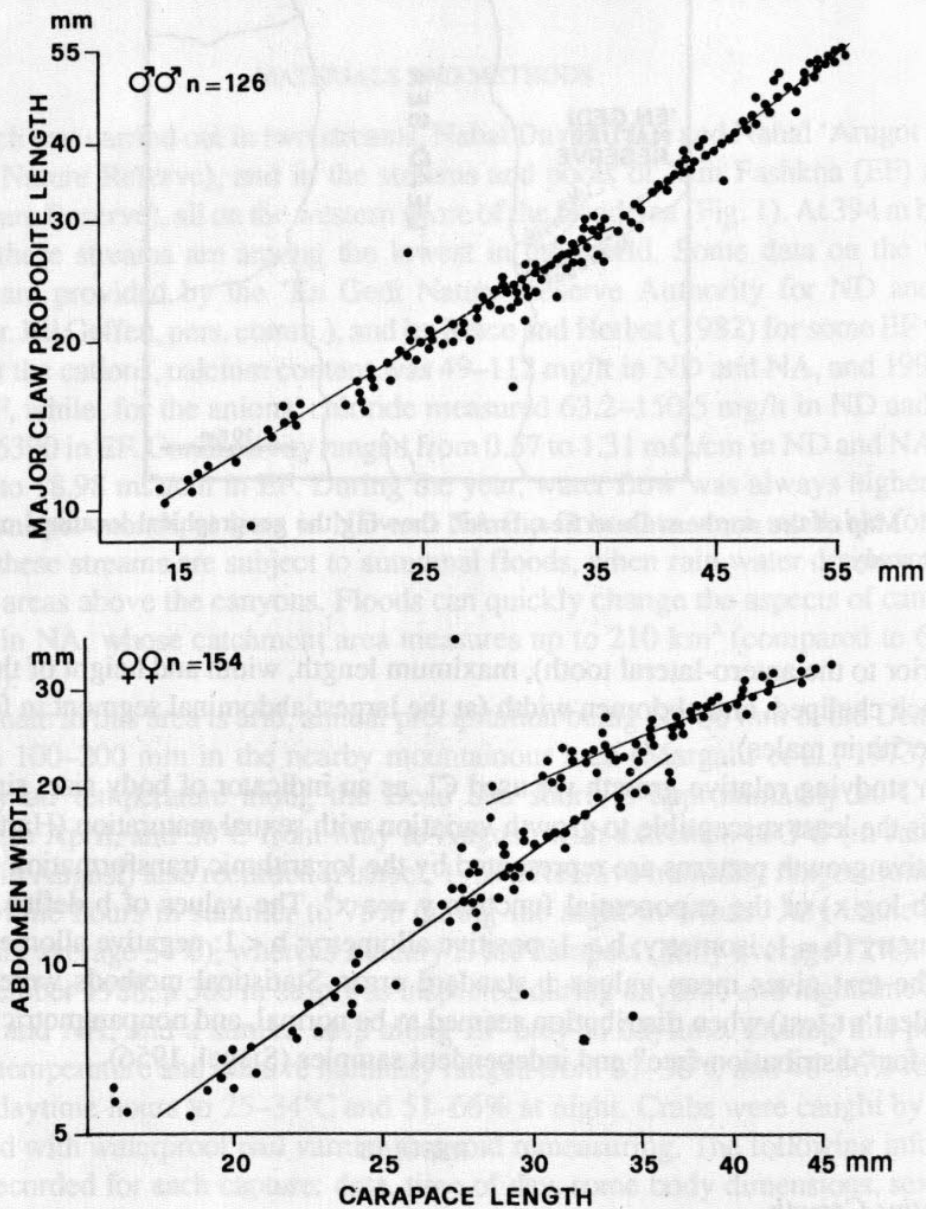

Fig. 2. Allometric growth of the major claw length in males (top) and of abdomen width in females (bottom) vs. carapace length. The discontinuities of the curves mark the pubertal moult.

TABLE I

Patterns of relative growth. Log-log regressions between the indicated characters and the carapace length (in mm)

Characters	n	b	t (b ≠ 1)	p	Allometry level
Carapace width					
YM	98	1.01	1.008	ns	=
YF	82	0.997	0.231	ns	=
AM	63	1.02	1.159	ns	=
AF	45	0.992	0.247	ns	=
Major chela length					
YM	97	1.159	4.676	**	+
YF	83	1.148	4.874	**	+
AM	62	1.469	12.894	**	+
AF	44	1.145	1.661	ns	=
Minor chela length					
YM	95	1.109	3.068	**	+
YF	81	1.043	0.812	ns	=
AM	60	1.442	9.492	**	+
AF	44	1.1	1.171	ns	=
Major chela width					
YM	98	1.332	6.906	**	+
YF	83	1.439	6.512	**	+
AM	63	1.428	5.34	**	+
AF	45	1.194	0.962	ns	=
Minor chela width					
YM	96	1.15	4.724	**	+
YF	80	1.145	4.121	**	+
AM	60	1.36	5.117	**	+
AF	44	1.827	2.644	*	+
Major chela height					
YM	98	1.368	8.588	**	+
YF	83	1.395	6.057	**	+
AM	63	1.335	4.455	**	+
AF	45	1.283	1.906	ns	=
Minor chela height					
YM	96	1.295	6.74	**	+
YF	80	1.337	6.944	**	+
AM	60	1.311	3.894	**	+
AF	44	1.027	0.15	ns	=
Abdomen width					
YM	99	1.019	0.43	ns	=
YF	51	1.409	3.291	**	+
AM	63	0.646	2.242	*	–
AF	72	0.98	0.168	ns	=

YM = young males; YF = young females; AM = adult males; AF = adult females; n = number of animals; b = regression coefficient; t = result of the Student's t-test of the slope against 1, i.e., it reveals the existence of negative, –, or positive, +, allometry or of isometry, =. ns $P > 0.05$; * $P < 0.05$; ** $P < 0.01$.

Growth patterns of *P. potamios* are shown in Table I. In both sexes carapace width is always isometric in its growth. In males, both claws become longer, wider, and higher relative to CL, and also the growth of minor chela length is faster in adults than in young specimens (YM vs. AM: $t = 4.678$, df = 153, $P < 0.001$). In AF, all the measurements of both chelae (with the exception of minor chela width) maintain a constant relationship with CL, while in YF they are all positively allometric (excluding minor chela length), with no difference from YM. Among adults, the speed of growth of the length in both claws differs significantly between sexes (major chela: $t = 3.472$, df = 104, $P < 0.001$; minor chela: $t = 3.143$, df = 102, $P < 0.01$). The abdomen shows a positive allometry in its width among YF, while it is isometric in AF. In the males, the abdomen becomes relatively narrower in adults, its growth significantly differing from that in young specimens, where it is isometric ($t = 2.772$, df = 160, $P < 0.01$).

Asymmetry of chelae is shown by all individuals and increases significantly with size, in both males (plotting the ratio between major and minor cheliped lengths vs. CL: $r = 0.239$, df = 146, $P < 0.005$) and females ($r = 0.165$, df = 122, $P < 0.02$). Its growth rate does not differ between sexes ($t = 0.261$, df = 266, $P > 0.05$).

Righthandedness occurs in 79% of the population ($n = 291$; vs. 50%: $X^2 = 98.148$, df = 1, $P < 0.001$), with no difference between sexes (males: 75%, $n = 152$; females: 83%, $n = 125$; males vs. females: $X^2 = 2.284$, $P > 0.05$). However, the frequency of righthanded individuals is significantly higher among the young (84%, $n = 190$ vs. 70%, in the adults, $n = 101$, $X^2 = 6.348$, df = 1, $P < 0.02$). Righthandedness was also more frequent in the EF population (ND: 65%, $n = 49$; NA: 76%, $n = 116$; EF: 87%, $n = 124$; $X^2 = 11.476$, df = 2, $P < 0.01$).

Population Structure

In total, 299 individuals were captured in the three study areas. Fig. 3 represents the size-frequency distribution of these specimens for males and females. The smallest animal found measured 5.5 mm CL. Most specimens under 14 mm CL could not be sexed on morphological grounds only, probably because they undergo the pre-puberty moult at approximately this size. Because small specimens are difficult to find (due to their cryptic life-style) and the size of the larger instars varies greatly, the study of peaks in size-frequency distributions cannot give much information on the number of instars, on the growth rate or on age (Hartnoll, 1982).

Males (average CL = 33.88 ± 0.91 mm, $n = 157$) were significantly larger than females (average CL = 31.95 ± 0.62 mm, $n = 129$) ($X^2 = 34.037$, df = 7, $P < 0.001$), reaching 57 mm CL in size (the largest female measured 46 mm CL). Considering daytime sampling only, no difference in the size-frequency distributions was revealed among the study areas either for males ($X^2 = 2.258$, df = 1, $P > 0.05$) or females ($X^2 = 0.078$, df = 1, $P > 0.05$).

Average sex-ratio was 55.09%, which does not differ from 50% ($X^2 = 2.951$, df = 1, $P > 0.05$). Nor was a significant difference revealed among the study areas (ND: 61.54%; NA: 51.40%; EF: 55.56%; $X^2 = 1.473$, df = 2, $P > 0.05$). But the frequency of males changes with size-class; all individuals over 50 mm CL were males ($n = 22$, vs. 50%: $X^2 = 22$, df = 1, $P < 0.001$).
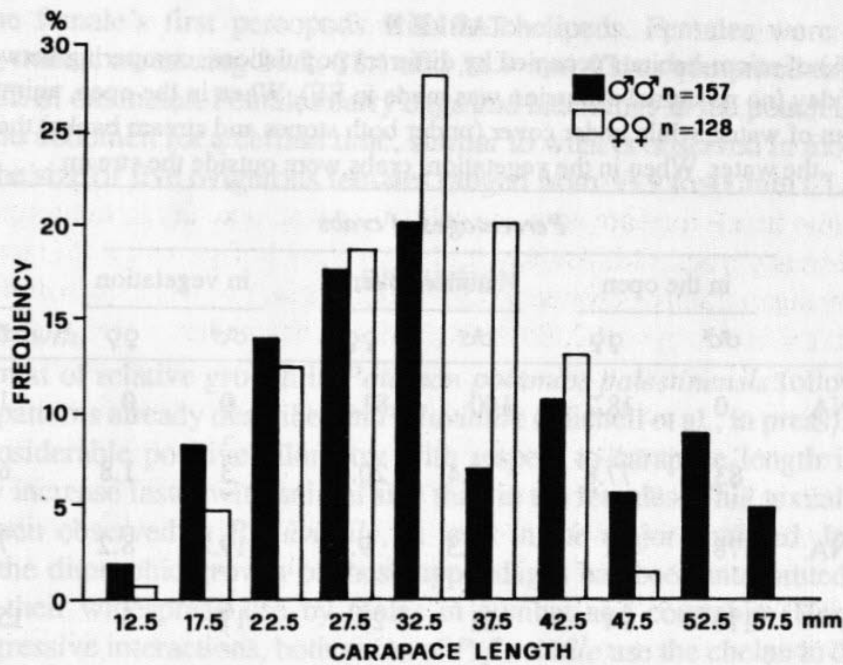
Fig. 3. Size-frequency (%) distribution of the populations under study, comparing between sexes calculated separately.

Ecology and Behaviour

Micro-habitat distribution for sex and time of day is shown in Table II. The two sexes occurred out of water to the same extent (males: 11.04%; females: 9.60%; $X^2 = 0.038$, df = 1, P > 0.05), but the females were more often under cover ($X^2 = 5.351$, df = 1, P < 0.05). Considering only the animals recorded in ND and NA, where nighttime transects were also performed, a significant difference was revealed between night and day hours, the animals being more often found during the night both out of water (23.36%, vs. 0% during the day: $X^2 = 6.419$, df = 1, P < 0.02) and in the open (80.88%, vs. 9.37% during the day: $X^2 = 116.819$, df = 2, P < 0.001). Young specimens were found prevalently under stones or other cover (in males: 17.90% vs. 5.17% in the adults, $X^2 = 9.646$, df = 1, P < 0.01; in females: 38.71% vs. 12.83% in the adults, $X^2 = 7.531$, df = 1, P < 0.01).

The animals were prevalently nocturnal (in ND and NA, average captures along the same transects: in the day 14.67 ± 2.96, n = 3; at night 30.25 ± 8.35, n = 4). Activity (estimated here as the number of animals caught along the same transect) over the 24 h cycle differs among the size-classes, young animals of both sexes being more diurnal than adults (in males, 64.95% of young vs. 28.81% of adults, $X^2 = 17.754$, df = 1, P < 0.001; in females 69.88% of young vs. 20% of adults; $X^2 = 27.138$, df = 1, P < 0.001). No difference in sex-ratio was revealed between night and day hours ($X^2 = 0.062$, df = 1, P > 0.05).

Indirect signs of intraspecific aggression are scars and mutilations; their frequency on the body surface is represented in Table III. No sexual difference was revealed in their location over the body ($X^2 = 7.24$, df = 6, P > 0.05). In the populations examined, 32%

TABLE II

Frequency (%) of micro-habitats occupied by different populations, comparing between sexes and time of day (no nocturnal excursion was made in EF). When in the open, animals were either in or out of water; while under cover (under both stones and stream banks) they were in the water. When in the vegetation, crabs were outside the stream

		Percentages of crabs						Number of crabs	
		in the open		under cover		in vegetation			
		♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀
Day	ND+NA	0	18.2	100	81.8	0	0	11	11
	EF	83.6	77.8	13.4	20.4	3	1.8	67	54
Night	ND+NA	78.9	82	1.3	9.8	19.8	8.2	76	61
Total numbers		116	94	21	26	17	5	154	126
% of habitats occupied by each sex		75.3	74.6	13.6	20.6	11.1	4.8		

of males and 37% of females had at least one scar or mutilation, with no difference between sexes ($X^2 = 0.496$, df = 1, P > 0.05), while males had a larger number of injuries per individual (2 on the average, as compared to 1.39 in females; t = 2.66, df = 91, P < 0.01). Left pereopods and chelipeds were significantly more often injured than right ones (84 vs. 51; $X^2 = 8.067$, df = 1, P < 0.01), probably associated with the righthandedness of these specimens and with the crabs' fighting technique.

Three matings were observed during the study. The couples were in the open, and both partners had hard integuments. They kept their ventral surfaces in contact, the male

TABLE III

Frequency (%) of scars and mutilations over body surface (males: n = 97; females: n = 59)

Location	♂♂	♀♀
Chelipeds	20.6	22.0
1st pereopods	14.4	16.9
2nd pereopods	10.3	16.9
3rd pereopods	19.6	13.6
4th pereopods	24.7	11.9
Carapace	6.2	10.2
Others	4.2	8.5

holding the female's first pereopods with its chelipeds. Females were smaller than copulating males, measuring 31.2, 38.1 and 38.9 mm CL as compared to 45, 54.6 and 51.2 mm CL of the males. Females carry eggs and hatchlings in the pouch limited by the sternum and abdomen for a certain time, similar to what is observed in most freshwater species. The size of five ovigerous females ranged from 33.9 to 41 mm CL.

DISCUSSION

Relative Growth

The format of relative growth in *Potamon potamios palestinensis* follows to a great extent the patterns already described in *P. fluviatile* (Micheli et al., in press). Both chelae exhibit considerable positive allometry with respect to carapace length in the males, where they increase faster with animal size than in the females. This sexual dimorphism has also been observed in *P. fluviatile*, at least in the major cheliped. In brachyuran literature, the dimorphic growth of these appendages has been interpreted as a consequence of their widespread use by males in combat and courtship (Hartnoll, 1982). During aggressive interactions, both sexes of *P. fluviatile* use the chelae to display to the opponent, to touch, push, grasp and fight (Vannini & Sardini, 1971). The chelae have a highly aggressive value in this species (Vannini et al., 1983) and their large size, which means a better-armoured animal, increases the probability of winning a contest (Gherardi, 1979). However, the frequency of mutilations is higher (Gherardi et al., 1987), and the aggressive repertoire is stronger in males (Vannini & Sardini, 1971). Similarly, the males of *P. potamios* have a higher number of scars and mutilations per individual than the females, suggesting that the former venture more easily on escalated contests than the other sex and/or that combats are mostly between males.

In the males of *P. potamios*, chela length undergoes a dramatic change in allometry level when the animal reaches a size of 35 mm CL. The puberty moult (i.e., the critical ecdysis when the animals attain their morphological maturity; Perez, 1929) seems to occur at this size, in accordance with observations in *P. fluviatile* (Micheli et al., in press). Our albeit limited data collected on mating seem to suggest that functional maturity, i.e., the ecdysis when they are first able to copulate successfully (Hartnoll, 1969), is attained at a larger size in this species too, since copulating males of *P. potamios* were larger than 35 mm. It is likely that the delay between morphological and functional maturity depends on the low probability of succeeding in the intra- and/or intersexual contests. In the xanthid *Eriphia smithi*, small crabs cannot defend or conquer suitable burrows where copulation takes place (Vannini & Gherardi, 1988), which are strong limiting factors in the cliff where this species lives (Vannini, 1987).

Handedness is widespread among Brachyura (Hartnoll, 1982), occurring in many freshwater crabs, such as *Geotelphusa dehaani* (Yamaguchi & Takamatsu, 1980), *P. gedrosianum* (Schneider, 1971), and *P. fluviatile* (Gherardi et al., 1987). About 80% of individuals in *P. potamios* populations are righthanded, and asymmetry increases with animal size. However, the frequency of righthanded specimens is lower among adults, where the reversal of handedness may be induced by the loss of the original master chela in agonistic contests. No difference has been revealed between the sexes, unlike the

Japanese *Geotelphusa dehaani* where only the males have an enlarged right cheliped, the crusher, which also differs morphologically from the left cutter (Yamaguchi & Takamatsu, 1980). In *P. fluviatile*, handedness has been related to different roles played by the chelipeds in agonistic interactions, the master chela inflicting over 60% of blows during a contest (Vannini, unpublished data); similarly, in *P. potamios*, scars and mutilations are significantly higher on the left side of the body, suggesting a more intense use of right chelipeds during aggression in this species too.

A second sexual character is the abdomen, the growth of which follows the general brachyuran trend in this species (Hartnoll, 1982). In the males, where it only functions as a protective cover for the gonopods, its growth is isometric with respect to the carapace length in pre-pubertal specimens, whereas it becomes negatively allometric at puberty. In the females, on the contrary, it produces an incubatory chamber together with the sternum, which holds the eggs and hatchlings. Here, abdomen width has a highly positive allometry, which decreases after the puberty moult (to the point of becoming isometric in *P. potamios*), when it would no longer be advantageous to carry such a disproportionate structure, also in terms of efficiency of locomotion (Hartnoll, 1982).

The analysis of the growth of abdomen width has revealed that the female puberty moult in *P. potamios* occurs within 28–35 mm CL; also copulating and ovigerous females exceeded 30 mm CL. The females of *P. fluviatile* attain morphological and anatomical maturity at the size of 35 mm, when ovigerous specimens are also found, but they can copulate at a smaller size, preserving spermatozoa within the seminal receptacles for one or more ecdyses (Gherardi, 1987). For these solitary species, sperm is precious because the opportunities of mating are limited to casual meetings along the stream, perhaps induced at a short distance by an aquatic pheromone emitted by the receptive female, similar to *Paratelphusa hydrodromus* (Sundara et al., 1973). However, in *P. fluviatile* the probability of intercepting a male may be low after puberty, because, especially during summer when crabs are most active (Gherardi et al., 1988a), they disperse over the surrounding terrestrial habitat (Gherardi et al., 1988b) for energetic requirements (Gherardi et al., 1989), straying up to 100 m away from the stream and staying out of water for over two weeks (Gherardi & Vannini, 1989). Thus, the best strategy for this species is to copulate as soon as possible, and eventually to store the sperm and wait to spawn until the optimal size is reached when fecundity (i.e., the size of brood) outweighs the energetic costs of reproduction, since, as in other brachyurans, clutch size is a function of female size.

Habitat Preferences

Post-pubertal females of *P. potamios* seem to be more aquatic, at least in September, when the sex-ratio along the stream is balanced. This species is physiologically equipped to cope with hot spells even if water is scarce, surviving, at least in the laboratory, up to 21% water loss and remaining alive even at 37.5°C in dry air for 24 h (Warburg & Goldenberg, 1984). However, the extremes of temperature and relative humidity of the surrounding terrestrial habitat prevent the females from leaving the stream for long periods. As these crabs are active all year round, it would, moreover, be unadaptive for them to risk dehydration when they can collect a good store of energy reserves for growth

and reproduction at a lower cost even if they only forage along the stream. Due to their more aquatic behaviour, it could be easier for adult females to intercept a male, in which case it would be useless for them to copulate when still immature. However, males seem to be more amphibious, wandering up to 40 m away from the stream and staying under the terrestrial vegetation more often than the females, who were instead found under cover in the water. This tendency to diffuse into terrestrial habitats could lead adult males to colonize new streams after the drastic changes in their original one after autumnal floods (Mr. Ran Levi, pers. comm.), thus assuring a certain gene flow among otherwise isolated populations.

Activity

Population structure exhibits an evident asymmetry, the older age classes being represented more than the younger ones. As in *P. fluviatile* (Gherardi et al., 1987), this can be explained on the basis of the more cryptic life style of younger specimens, who tend more to hide under stones and rocks, especially during nighttime hours, and are more active in the day. Conversely, animals over 35 mm were found in the open during nighttime hours, wandering along the stream and foraging. Escape from extremes of temperature and relative humidity, avoiding possible diurnal predators, or copying the nocturnal habit of their principal prey organisms, are all factors which press the crabs to concentrate their activity at night. Nocturnal habits have also been observed in *P. fluviatile* all year round (apart from the coldest months, when the few animals still active concentrate their foraging during the day) (Gherardi et al., 1988a), and in *P. gedrosianum* of Afghanistan, which leaves its daytime shelter at sunset to forage in the water at night (Schneider, 1974). Probably the observed prevalence of diurnalism in the young results from the active competition exerted on them by adults, who will even cannibalize small conspecifics, as observed in *P. fluviatile*. Staggering of daily activity in different size classes has been revealed in *P. potamios* in the Yizre'el Valley, where medium-sized crabs were nocturnal, but the larger ones diurnal (Warburg et al., 1982), and in *P. fluviatile* under extreme environmental conditions at 5°C in the laboratory, where nocturnalism was negatively correlated with size (Gherardi et al., 1988a).

General Biology

As in *P. fluviatile* (Gherardi et al., 1987), males are larger than females, probably because their best strategy for increasing their fitness is to grow quickly and reach the size which gives them most probability of winning in intra- and/or intersexual competition and consequently copulating successfully. Female growth, on the contrary, is subject to two contrasting tendencies. On the one hand, rapid growth could maximize their reproductive output because clutch size increases with animal size. On the other hand, energetic constraints make growth incompatible with reproduction. This latter consideration is particularly important in temperate populations of *P. fluviatile*, where ecdysis and oviposition occur simultaneously in the annual cycle in September, and thus females must choose between the two alternatives, mobilizing the stored energy for either growth or reproduction (Micheli et al., 1989). The reproductive period of *P. potamios* in the Dead Sea area ranges from May to October, and adult specimens were found moulting even in

February. Certainly, more data are required on the frequency of spawning and moulting, mortality rate, and the values of absolute growth in these arid zone populations. However, females in this area may well both grow and reproduce in the same annual cycle, since energetic input is not a strong limiting factor, given the constant activity of these populations throughout the year. Optimal size in females is thus subject to different selective pressures from those in *P. fluviatile*, and is probably related to the high energy costs of sustaining a cumbersome and heavy body which, above a certain size, could overweigh any increase in fecundity.

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