POPULATION DYNAMICS, REPRODUCTION AND GROWTH OF *UPOGEBIA PUSILLA* (DECAPODA, THALASSINIDEA) IN THE EVROS DELTA (NORTH AEGEAN SEA)

BY

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ABSTRACT

Monthly samples of *Upogebia pusilla* were collected from February 1983 to February 1984 in an area of the Evros Delta located close to the sea, where salinity and temperature of the water ranged from 4 to 25‰ and 4.3° to 24.5°C, respectively. Population density and wet weight biomass varied greatly, being higher in summer. Young shrimps appeared in August and had a maximum life span of approximately three years. Ovigerous females were found from April to August. The frequency of females among the collected individuals was 0.393. The smallest ovigerous female had a total length (TL) of 39 mm, while the maximum TL for females was 82 mm and for males 106 mm. Growth in age classes I and II was greater in the period from July to August. Mean growth of carapace length (CL) was described by the Von Bertalanffy function. A positive correlation existed between total length and CL or wet weight (W).

RÉSUMÉ

Des échantillons mensuels d'*Upogebia pusilla* ont été recueillis de février 1983 à février 1984 dans une zone du delta d'Evros localisée près de la mer, où salinité et température de l'eau s'échelonnaient de 4 à 25‰ et de 4,3° à 24,5°C respectivement. La densité de population et le poids humide de la biomasse variaient fortement, étant plus élevés en été. Les jeunes apparaissaient en août et avaient une durée de vie maximale de trois ans environ. Des femelles ovigères ont été trouvées de février à août. La fréquence des femelles parmi les individus collectés était de 0,393. Les plus petites femelles ovigères avaient une longueur totale (TL) de 39 mm, tandis que la TL maximale était de 82 mm pour les femelles et de 106 mm pour les mâles. La croissance dans les classes d'âge I et II était plus grande de juillet à août. La croissance moyenne de la longueur de la carapace (CL) a été décrite par la fonction de Von Bertalanffy. Une corrélation positive a été observée entre la longueur totale et CL ou le poids humide (W).

INTRODUCTION

Upogebia pusilla (Petagna, 1792) is a burrowing species of thalassinid decapods living in littoral and sublittoral soft sediments, exclusively in sheltered environments with euhaline to mixomesohaline waters (Dworschak, 1987a; Thessalou-Legaki, 1987). This decapod is known from the Eastern Atlantic, where it ranges from Mauretania to Brittany and occasionally to Norway, and from the Mediterranean Sea up to the Black Sea and Red Sea (Monod, 1937; Bulgurkov, 1938; Bouvier, 1940; Lewinsohn & Holthuis, 1964; Saint Laurent & LeLoeuff, 1979). In the Mediterranean Sea, where it is the most common species of the family Upogebiidae, it is sometimes found in high densities (Dworschak, 1987a). The species of this family are known to be food resources for a variety of fishes and birds, while they are used as bait by man as well (e.g., Tunberg, 1986; Hanekom & Baird, 1992).

Although some aspects of the biology and ecology of *U. pusilla* have been studied in the past (Popovici, 1940a, b, c; Daguerre de Hureaux, 1970; Ott et al., 1976; Dworschak, 1981, 1983, 1987a, b, 1988; Chaud, 1984a, b, c; etc.) very little information exists on its population dynamics and growth. The present study describes and compares the dynamics, breeding period and growth of an *U. pusilla* population.

The study area

The Evros Delta is located at the NE end of the Aegean Sea. In the NW part of the Delta, the streams Mikri Maritsa and Loutron discharge their waters. However, from July to October, freshwater reaches the Delta area only through the eastern branch of Evros. Several relatively small lagoons are formed near the sea and are connected with it to some extent. Besides the small streams and the canals in which there is a constant flow of water, there are areas in the upper part of the Delta, where the water remains stagnant continuously or over long periods of time due mainly to the construction of embankments. The sampling area is located in the western part of the estuary, quite near the mouth of the eastern branch, very close to the open sea, from which is protected by the island Karaviou. Thus, the sampling area is well protected from wave action, but directly influenced, all year round, by the river water which is physically diverted to this direction under the influence of the Coriolis effect.

MATERIALS AND METHODS

Monthly sampling of the *Upogebia pusilla* population was carried out from February 1983 to February 1984. Every month, 2 or 3 samples were taken, using a metal frame which was designed by the authors and had a surface of 1 m^2 and a height of 40 cm. The sediment in the frame was removed to a depth of 30 cm, and sieved through a sieve with a 2 mm opening. In addition, all the shrimps swimming in the water, were collected with a net of the same opening.

All animals were preserved in a 5% formalin. During each sampling, a sediment sample was taken with a small corer for particle size analysis and estimate of organic matter. The depth, salinity and temperature of the water near the bottom, as well as the temperature of the sediment at depths of 1 cm and 5 cm were measured.

In the laboratory, the animals were counted and the following parameters were determined for each animal: sex, based on the presence (female) or absence (male) of the first pair of pleopods; presence or absence of eggs in the females; total length (TL) in mm from the tip of the rostrum to the end of telson and carapace length (CL) in mm from the tip of the rostrum to the end of the carapace using sliding calipers; wet weight (W) in g, after drying on laboratory tissue. Sediment analysis and estimate of organic mater were made according to the method described by Buchanan (1984).

RESULTS

Monthly variation of the physicochemical parameters

In the study area bottom water temperature ranged from 4.3° to 24.5°C, while in the sediment from 4.1° to 23.0°C (at 1 cm depth) and from 3.8° to 23.2°C (at 5 cm depth) (fig. 1). Salinity near the bottom was 4.0-25‰ (fig. 1). The depth of the water was 15-40 cm. Mean [granule] diameter (Md) of the sediment varied between 147 and 208 μm and QD between 0.25 and 0.50 φ. Organic matter of the sediment was 0.374-1.319%.

Monthly variation in population density and biomass

The variation of density and wet weight biomass of the population is given in fig. 2. Population density was higher during June-July (41-43 ind./m^2) while no individuals were found from November to January, at least down to a depth of 30 cm. The same variation pattern is followed by the biomass values. A positive correlation exists between population density and the temperature of the water

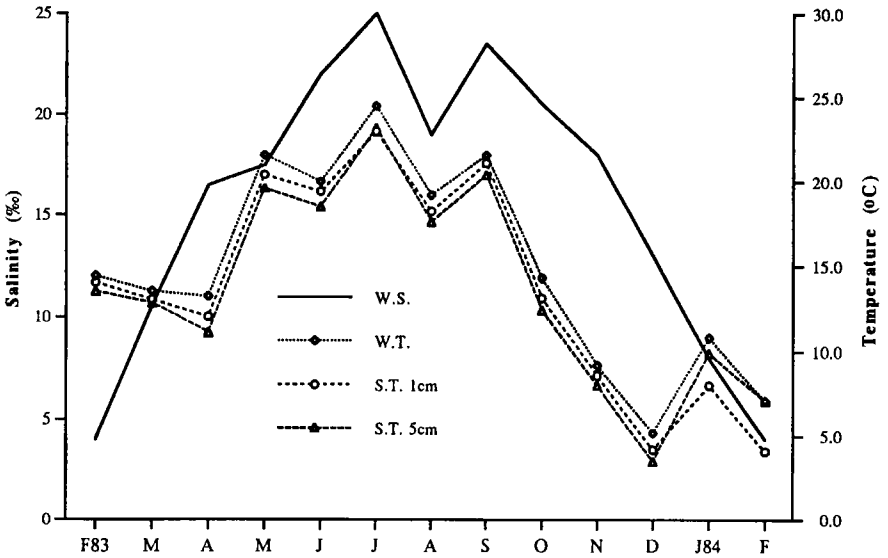

Fig. 1. Water and sediment (at 1 cm and 5 cm depth) temperature and salinity fluctuations during the sampling period; W.S. = water salinity; W.T. = water temperature; S.T. 1 cm = sediment temperature at 1 cm depth; S.T. 5 cm = sediment temperature at 5 cm depth.

($r = 0.769$, $N = 13$), the sediment at 1 cm depth ($r = 0.793$, $N = 13$) and the sediment at 5 cm depth ($r = 0.790$, $N = 13$).

Monthly variation in population structure

A total of 383 individuals of *U. pusilla* were examined during this study. The population composition of samples with an adequate number of individuals (from April to August) is illustrated in fig. 3. The size class interval of 1 mm was selected according to Goulden's method (Cancela da Fonceca, 1965).

By means of the graphic analysis of polymodal frequency distributions (Harding, 1949), we delimited four size groups (A, B, C and D) during the period April-August (fig. 4). These size groups can be characterized as age groups O, I, II, and III, respectively. Size group A occurs only in August. Size group B, which makes up the 39.0-56.2% of the population, is divided into two sub-groups in April-June. Size group C constitutes 34.4-51.7% of the population. Size group D also seems to be divided in two sub-groups, in May. This separation may be attributed to the death of some individuals of the intermediate (21-22 mm) size class (fig. 3). No females were found in size class D. From fig. 4 we can see that young shrimps appear for the first time in August and have a maximum life span of about three years.

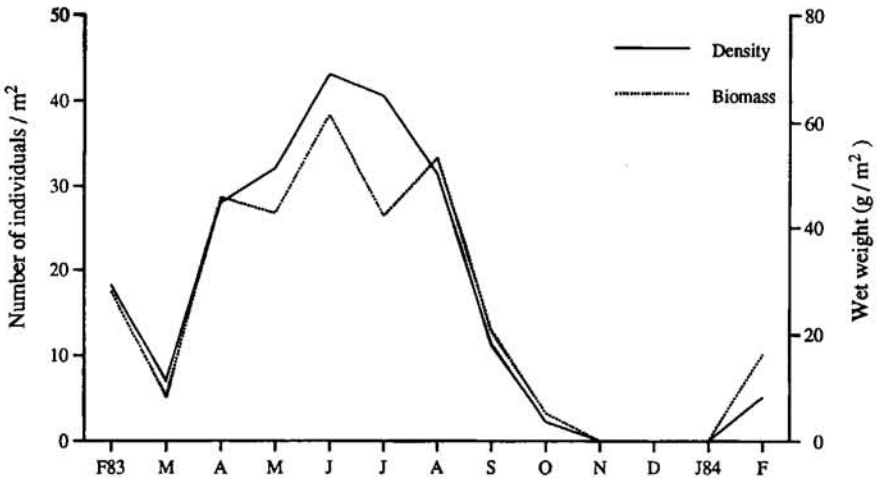

Fig. 2. Seasonal variation of the population density and wet weight biomass of *Upogebia pusilla* (Petagna, 1792) in the Evros Delta.

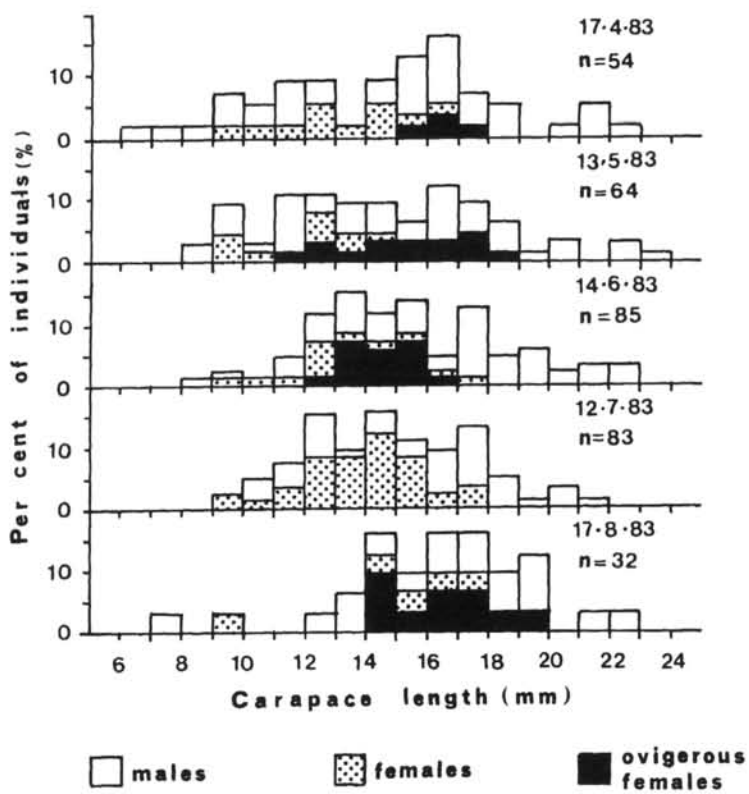

Fig. 3. Size frequency histograms of *Upogebia pusilla* (Petagna, 1792) from 17.iv.83 to 17.viii.83, in the Evros Delta.

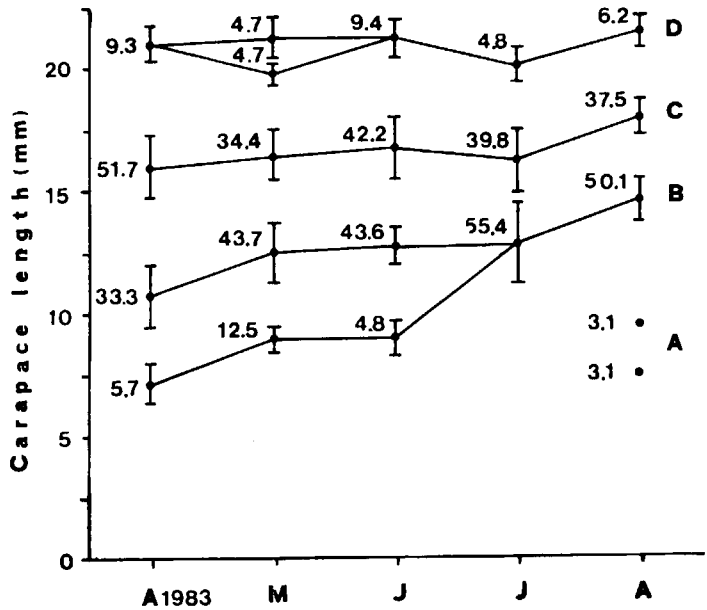

Fig. 4. Development from 17.iv.83 to 17.viii.83 of the size groups of *Upogebia pusilla* (Petagna, 1792); dots = mean carapace length; bar lines = standard deviation; numbers = percentages of size groups in the whole population.

The sex ratio (frequency of females in the total of individuals) throughout this research was 0.393, a value significantly different from 0.5 ($P < 0.0001$). During April-August, males were more numerous than females only in size classes C and D. The sex ratio was 0.525 for size class B, 0.336 for size class C and 0 for size class D. However, the sex ratio was significantly different from 0.5 only in size classes C ($P < 0.001$) and D ($P < 0.000001$).

Reproduction

Breeding period. — Ovigerous females were found from April to August but not in July. The proportion of ovigerous females in the total number of adult females (CL $\geqslant$ 11.5 mm), was higher in May (73.7%) and August (75.0%) (table I).

Size at maturity. — The smallest ovigerous female had a CL of 11.5 mm. The mean carapace length of ovigerous females ranged from 14.7 (in June) to 16.6 mm (in April) (table I). The ovigerous females belong to one size class (size class C) in April, and in two size classes in May, June and August (size classes B and C).

TABLE I

Monthly variation in the percentage of ovigerous females in the total number of adult females and in the mean (± standard deviation) carapace and total length of ovigerous females

		April	May	June	August
%		28.6	73.7	65.5	75.0
CL (in mm)	mean	16.6	15.4	14.7	16.3
	± SD	± 0.9	± 2.3	± 1.1	± 1.7
TL (in mm)	mean	62.3	55.4	51.1	56.1
	± SD	± 11.5	± 10.7	± 4.8	± 8.8

Growth

Absolute growth. — Fig. 4 shows that growth in carapace length for B and C size classes is nearly constant from April to August being greater during July-August. Mean monthly growth was 1.0-1.9 mm for size class B and 0.6 mm for size class C. Carapace length of size class D remains almost unchanged during this period.

Mean growth in carapace length of the population can be described by the equation of Von Bertalanffy (Crisp, 1984). In order to form that equation for males we used as carapace length at zero age (L_0) the value of 5 mm; as maximum possible carapace length (L_∞), the value of 24 mm, since only few individuals were longer than 20 mm and the maximum observed carapace length was 23.2 mm; we used as K, the value 0.715, which was estimated by the Ford-Walford method. For the females, the values used were $L_0 = 5$ mm, $L_\infty = 20$ mm and $K = 1.161$. So, the equation is $Lt\ (mm) = 24 - 19 \cdot e^{-0.715.t}$ for males, and $Lt\ (mm) = 20 - 15 \cdot e^{-1.161.t}$ for females. The theoretical growth curves of males and females predicted by these equations are given in fig. 5.

Size. — Throughout the study period, males reached larger sizes than females. The maximum carapace length for the males was 23.2 mm and the maximum total length 106 mm compared to 19.1 and 82 mm respectively for the females. The smallest individual collected had a TL of 17 mm, while the smallest CL recorded measured 5.6 mm.

Relative growth. — Total length (TL)-carapace length (CL) relationship: The scatter diagram of CL in relation to TL for the whole population is illustrated in fig. 6. Searching for the best description of the relation between CL and TL we came to the linear relation $CL = b + \alpha \cdot TL$ (where α represents the slope and b the intercept) which additionally showed the highest positive coefficient of correlation.

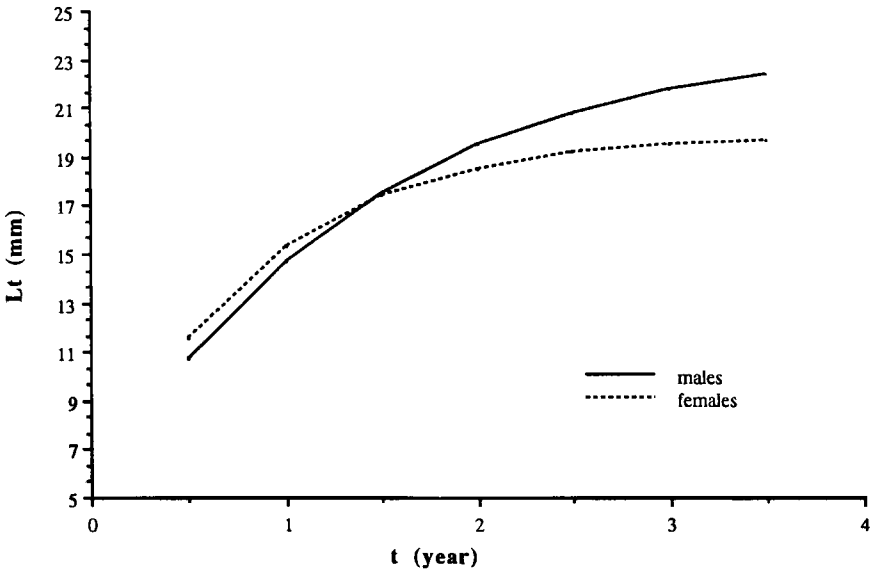

Fig. 5. Theoretical growth of males and females of *Upogebia pusilla* (Petagna, 1792) predicted by the Von Bertalanffy equation.

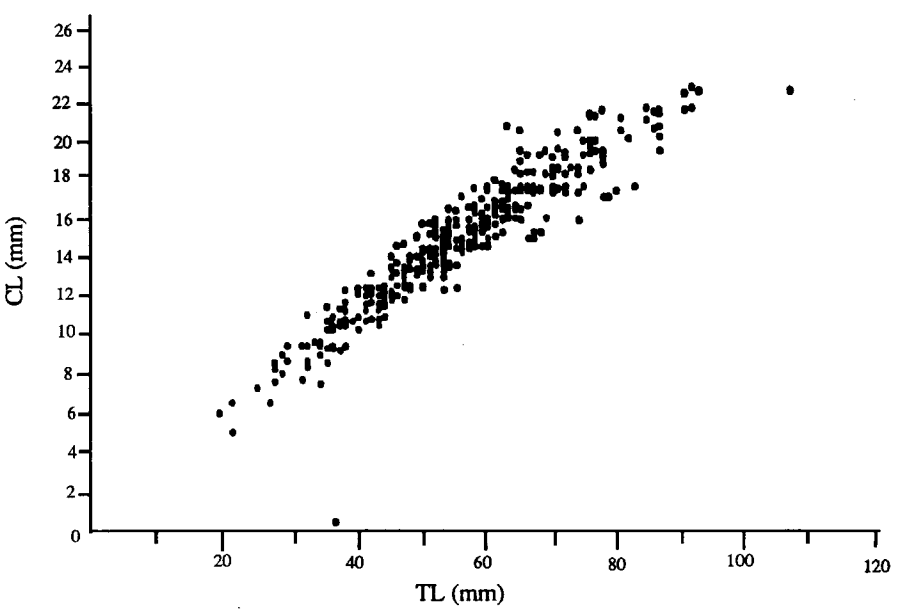

Fig. 6. Dispersion diagram of carapace length in relation to total length in 383 individuals of *Upogebia pusilla* (Petagna, 1792).

TABLE II

Estimate of statistical parameters of the population of *Upogebia pusilla* (Petagna, 1792). α, b = constants; TL = total length in mm; CL = carapace length in mm; s = standard deviation; r = coefficient of correlation; N = number of animals

	Whole population	Males	Females	Ovigerous females
α	0.221	0.226	0.198	0.188
b	3.299	3.033	4.321	5.203
$\overline{TL} \pm sTL$	54.859 ± 14.451	57.418 ± 16.238	49.419 ± 10.203	54.370 ± 8.688
$\overline{CL} \pm sCL$	15.409 ± 3.389	15.991 ± 3.876	14.129 ± 2.246	15.398 ± 1.785
r^2	0.886	0.894	0.813	0.833
N	383	232	105	46

A positive correlation existed between CL and TL ($r = 0.941$; $N = 383$) (table II) for the whole population (fig. 6); a negative allometry was found for the relation CL, TL since $\alpha < 1$ ($\alpha = 0.221$) (table II), which means that the carapace length increases more slowly than the total length.

Tests were carried out for any statistical differences in relative growth of CL, TL between males, females and ovigerous females; in all these cases CL, TL showed a negative allometry ($\alpha < 1$) (table II). Comparing the slopes of males and females and those of females and ovigerous females (table II) using the method of Mayrat (1965), no statistical differences were found. A difference was only found between the slopes of males and ovigerous females (at the level of $P < 0.05$). Those slopes intercept at CL = 15.9 mm and TL = 57.1 mm.

Total length (TL)-wet weight (W) relationship. — The scatter diagram of W in relation to TL for the whole population is given in fig. 7. Searching for the best description of the above relation we came to the equation $W = b(TL)^{\alpha}$ (where α, b are constants) which additionally showed the highest positive coefficient of correlation. This formula was transformed to $\log_{10} W = \alpha(\log_{10} TL) + \log_{10} b$.

There was a positive correlation between $\log_{10}W$ and $\log_{10}TL$ ($r = 0.945$; $N = 383$) (table III) for the whole population (fig. 7). Wet weigth increases more slowly than length (or a shrimp becomes lighter for its length as it grows larger) since $\alpha < 3$ ($\alpha = 2.618$) (table III).

It was tested if there existed a statistical difference of the relative growth of $\log_{10}W$ in relation to $\log_{10}TL$ between males, females and ovigerous females (in all three cases $\alpha < 3$) (table III). Comparing the slopes of males and females, those of males and ovigerous females, and those of females and ovigerous females (table III) using the method of Mayrat (1965), no statistical differences were found.

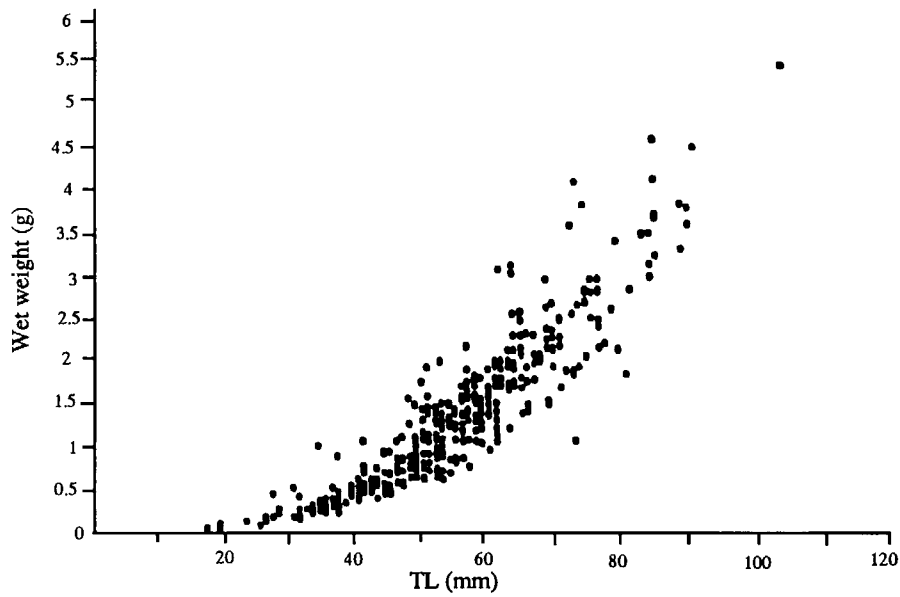

Fig. 7. Dispersion diagram of wet weight in relation to total length in 383 individuals of *Upogebia pusilla* (Petagna, 1792).

TABLE III

Estimate of statistical parameters of the population of *Upogebia pusilla* (Petagna, 1792). α, b = constants; log = $\log_{10}$; TL = total length in mm; WW = wet weight in g; s = standard deviation; r = coefficient of correlation; N = number of animals

	Whole population	Males	Females	Ovigerous females
a	2.618	2.612	2.586	2.428
log b	−4.488	−4.479	−4.453	−4.118
$\overline{\log TL} \pm s \log TL$	1.723 ± 0.122	1.739 ± 0.138	1.684 ± 0.092	1.730 ± 0.068
$\overline{\log WW} \pm s \log WW$	0.022 ± 0.339	0.065 ± 0.376	−0.098 ± 0.270	0.083 ± 0.188
r^2	0.892	0.921	0.780	0.764
N	383	232	105	46

DISCUSSION

In the Evros Delta the high values of the density of *Upogebia pusilla* population during the warm period, coincide with the reproductive period and, in our opinion, they should be attributed to the migration of a large number of individuals, from the open sea to this area for reproduction; at the end of the reproductive period they leave the area.

The reproductive period of *U. pusilla* started in April, with the appearence of ovigerous females, and lasted until the end of August (5 months). According to Popovici (1940c) and Dworschak (1988), in the Mediterranean and the Black Sea, the beginning and the duration of the reproductive period (which seem to depend mainly on temperature) change locally and temporally between March and October. In the Atlantic French coasts (Biscay Bay), however, this period starts later (in June) and lasts 3 months (till August) according to Chaud (1984c). In other species of the genus *Upogebia*, the period of time during which ovigerous females are present in the population is variable; for *U. deltaura* (Leach, 1815), in NW Sweden (Gøteborg) it is between May and August (Tunberg, 1986); for *U. pugettensis* (Dana, 1852), on the Pacific coasts of the U.S.A., it is between October and June (Dumbauld et al., 1989); for *U. africana* (Ortmann, 1894), on South African coasts, it was found that some populations have well defined spring and summer breeding cycles, while in other populations, the spring and summer breeding cycles tend to merge, forming a longer breeding season (Hill, 1977; Hanekom & Erasmus, 1989).

The presence of one and two year-old ovigerous females, in high percentages during May and August, shows that they can breed in the Evros Delta more than once in the same reproductive period. The absence of ovigerous females during July, could be attributed to a release of larvae before the last breeding. Dworschak (1988) reported that the females of *U. pusilla* carry three separate batches during the breeding season. Two to four broods of eggs are produced per adult female per year also for the species *U. africana* (cf. Hanekom & Erasmus, 1989). The females of *U. pusilla* in the Evros Delta seem to breed every year, from the first year of their life. The same observation was made by Thessalou-Legaki (1987) for *Callianassa tyrrhena* (Petagna, 1792).

In the Evros Delta, young shrimps appeared for the first time in August and had a maximum life span of about three years. It is estimated that young individuals appear in the Evros Delta between July and November. This estimate is based on the calculation of incubation time (Wear, 1974; Hill, 1977) and larval development time (Dworschak, 1988). The separation of age group I in to two subgroups during the period April-June could be attributed to the different recruitment time of the various individuals, due to the long duration of the reproductive period, resulting in a lack of homogeneity in the structure of this size class at the start. Thessalou-Legaki (1987) reported the appearance of young individuals of *U. pusilla* in the Aegean, during July and August. A life span of at least three years (resulting from size frequency distribution) was suggested by Tucker (1930, in Dworschak, 1988) and Popovici (1940c) for *U. pusilla*; the same life span was suggested by Gustafson (1934, in Dworschak, 1988) for *U. deltaura* and another

of 4 years (resulting from cohort analysis) for *U. africana* by Hanekom & Baird (1992). Chaud (1984b) estimated that *U. pusilla* lives mostly two years in the French coasts of the Atlantic. Dworschak (1988) showed that under laboratory conditions *U. pusilla* individuals, with a total length of 40-50 mm, lived over three years and calculated a life span of over five years, which is the longest ever reported for Upogebiidae. According to Hanekom & Baird (1992) this observation shows that cohort analyses probably underestimate longevity, possibly due to difficulty in the separation of the older year classes.

In the Evros Delta males prevail. Sex ratio varied between the various populations of *U. pusilla*; in some of them, males prevail, in others, females (Dworschak, 1988). Variations in sex ratio have been reported among different populations of other *Upogebia* species, as well; in these cases, however, females were never less numerous (Hill, 1977; Tunberg, 1986; Hanekom & Erasmus, 1989).

The size of *U. pusilla* individuals in our study area is very large in comparison with other populations. The maximum total length was 106 mm, and 13% of the population had a total length larger than 70 mm. In other Mediterranean and Black Sea areas, maximum total length was less than 70 mm (e.g., Popovici, 1940c; Dworschak, 1988). This large size is probably due to the fast growth rate, which is, in its turn, a result of adequate food supply of the population. The greater growth recorded during July-August should be attributed to the relatively high temperatures and salinities in this period. According to Dworschak (1988) the optimal salinities for *U. pusilla* seem to lie around 26‰, because the respiration rates in small animals at temperatures 15-17.5°C and in large animals at temperatures 20-22.5°C are lowest at this salinity value.

In the Evros Delta, carapace length increases more slowly than total length. The same has been reported for *U. pusilla* by Dworschak (1988). In the Evros Delta population, the growth rate in males was greater than in ovigerous females. In various species of the genus *Upogebia*, females reach a 1-4 mm smaller maximum carapace length than males (e.g., Hill, 1977; Dworschak, 1988; Hanekom & Erasmus, 1989; Hanekom & Baird, 1992; the present study). The difference in the relative growth between males and ovigerous females, concerning the relation TL/CL, was found to start when the carapace length of ovigerous females is 15.9 mm and the total length 57.1 mm. This size corresponds to the size of the individuals of age group II, in the beginning of their second reproductive period, namely to the size of individuals which have already bred. Finally, in the Evros Delta population, the shrimps (males, females, ovigerous females) increase faster in length than they do in mass (relative weight), which implies that length is not a good indicator of actual size.

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