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Relative growth and secondary production of the Amphipod *Gammarus aequicauda* (Martynov, 1931) in the Evros Delta (N. Aegean sea)

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Résumé : Il existe une très bonne corrélation entre la longueur céphalique (Lc) et la longueur du corps (Lb) ou le poids sec du corps (W) chez *Gammarus aequicauda.* La longueur céphalique croît plus lentement que les critères Lb et W. A partir de ces critères morphométriques, on a déterminé les stades juvéniles (Lc < 16 unités microscopiques = 616 μm) et adultes (mâles ou femelles indifféremment). Les femelles ovigères croissent plus vite que les non-ovigères. Le taux de croissance chez les mâles est plus rapide que chez les femelles.

La production secondaire de *G. aequicauda* à Evros Delta avec la méthode de Hynes a donné une densité annuelle moyenne de 3 127.7 individus/m^2, une biomasse moyenne (B) de 4.24 g poids sec m^{-2} a^{-1}, une production (P) de 22.40 g m^{-2} a^{-1} et un taux de renouvellement de la biomasse (P/B) de 5.28.

Abstract : There exists a positive correlation between the cephalic length (Lc) and the body length (Lb) or dry body weight (W) in *Gammarus aequicauda.* Lc grows slower than Lb and W. Using the above criteria, the juvenile stage (Lc < 16 microscopic units = 616 μm) and the adult one (males or females indifferently) were determined. Ovigerous females grow faster than non ovigerous and males grow faster than females.

Secondary production in *G. aequicauda,* living in Evros Delta (Northern Greece) calculated by Hynes's method, gave a mean annual density equal to 3 127.7 individuals/m^2, a mean biomass (B) of 4.24 g dry weight m^{-2} yr^{-1}, a production (P) of 22.40 g.m^{-2} yr^{-1} and an annual turnover ratio (P/B) of 5.28.

INTRODUCTION

Very little is known about the relative growth of gammaridean Amphipoda. Some aspects of it have been studied (Kaim-Malka, 1969 ; Morand, 1974 ; Bulnheim, 1977 ; Sagar, 1980 ; Collie, 1985). Few estimates of secondary production for marine amphipod species are also available in the literature ; especially for *Gammaridae,* only one publication is known to us concerning *Gammarus mucronatus,* by La France and Ruber (1985). So in this paper, the relative growth and the estimate of secondary production of the amphipod *Gammarus aequicauda* (Martynov, 1931) are studied.

Gammarus aequicauda is one of the most abundant and widely distributed amphipods in the coast of the Mediterranean Sea and a major food organism for commercially exploited fish species in its lagoons (Stock, 1967 ; Bellan-Santini *et al.,* 1982 ; Cottiglia *et al.,* 1983 ; Diviacco, 1983 ; Porcu & Tagliasacchi Masala, 1983 ; etc.). Especially, in the biologically important Evros Delta (N. Aegean Sea), *G. aequicauda* and *Corophium orientale* Schellenberg, 1928 are the most common amphipods. The biology and ecology of *G. aequicauda* have been studied in the Evros Delta from February 1983 to February 1984 (Kevrekidis & Koukouras, in press).

Study area

The sampling area is located in a natural channel representative for the inner regions of the Evros Delta. That landward ended channel is isolated due to the construction of an embankment at its seaward end; this embankment prevents the direct communication of channel water with that of the adjacent lagoon. The channel has a length of about 2 km, an average width of 60 m and maximum depth of about 3 m.

Along the banks of the channel and in depths, seasonally varying from 0.3 m to 1 m, formations of the polychaete *Ficopomatus enigmaticus* (Fauvel) existed. The polychaete zone on the southeastern bank was denser. Throughout the year on that zone, was almost exclusively found the channel population of *Gammarus aequicauda*. Three species, the polychaete *Hediste diversicolor* (O.F. Müller), the bivalve *Abra ovata* (Philippi) and the gastropod *Hydrobia salaria* (Radoman), were the most abundant macrobenthic organisms associated with that amphipod on the *F. enigmaticus* formations. During the sampling period, the temperature and the salinity of the channel water near the bottom fluctuated from 4°C to 27°C and from 24 ‰ salinity to 36 ‰ respectively; the values of the dissolved O_2 varied between 5.3 ppm and 8.4 ppm and the pH values between 7.3 and 8.3.

Some aspects of the biology of *Gammarus aequicauda*.

According to the study of biology and ecology of *Gammarus aequicauda* in the Evros Delta, this amphipod presents two generations per year (Kevrekidis & Koukouras, in press). *G. aequicauda* population was sexually active throughout the year and two reproductive maxima-periods were distinguished. The first one appeared in May, showed its quickest growth during summer and autumn and disappeared the following April, approximately 12 months later. The second generation appeared in October, showed its quickest growth during spring and disappeared in August, about 12 months later (Fig. 1). The sex ratio was characterized by a slight dominance of the male individuals. The average cohort production interval from hatching to the attainment of the largest cephalic size class was about 335 days (Kevrekidis & Koukouras, in press).

TABLE 1 - Mean monthly density variation (± standard error) per 400 cm^2 of *Gammarus aequicauda* population in Evros Delta between 12 February 1983 to 29 February 1984.

F	M	A	M	J	J	A	S	O	N	D	J	F
2.8 ±1.2	3.0 ±1.6	5.2 ±1.5	1.4 ±0.9	3.4 ±2.5	36.0 ±8.3	335.8 ±10.2	334.0 ±20.9	258.6 ±29.4	348.2 ±64.6	107.4 ±19.6	97.1 ±19.0	93.2 ±19.2

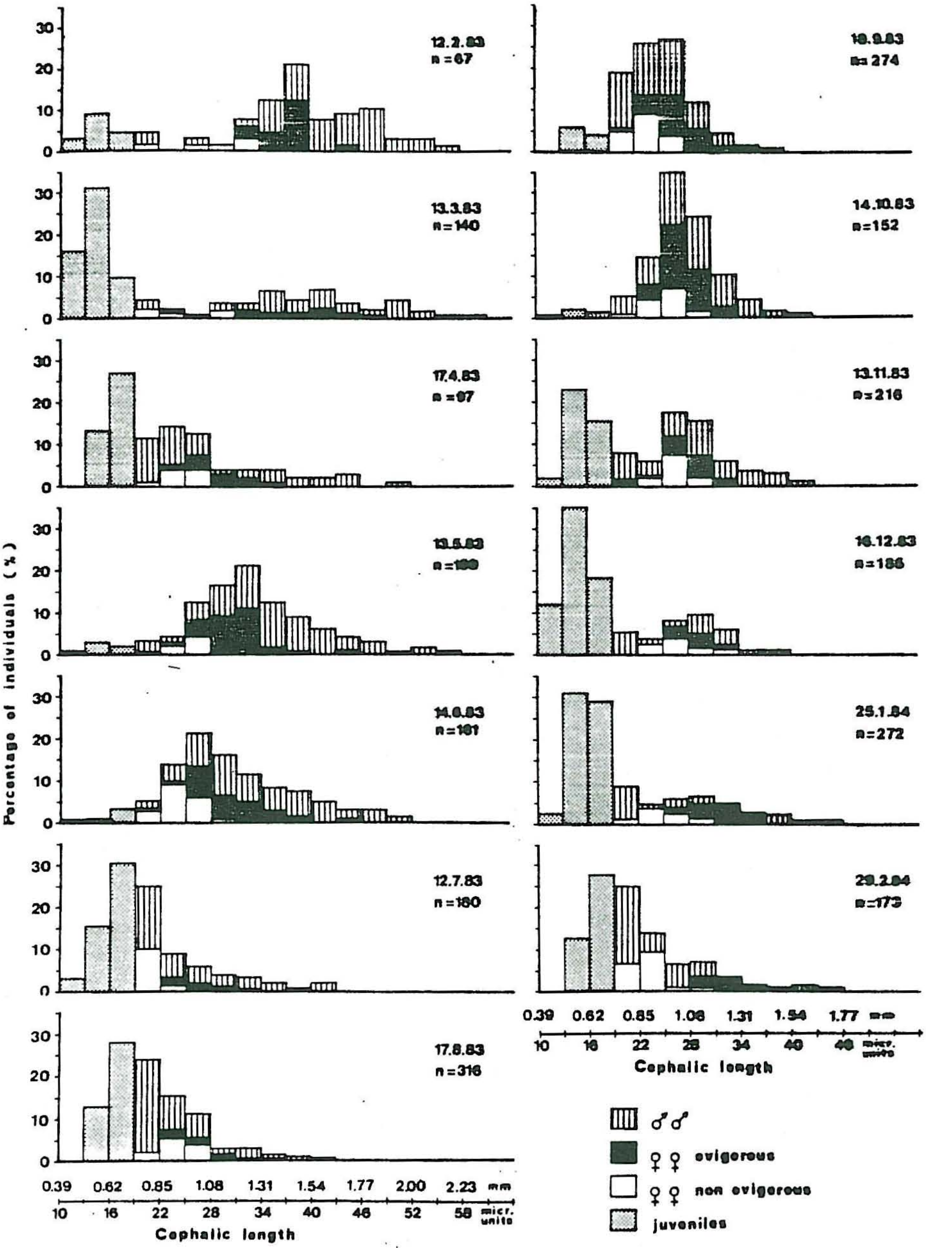

Fig. 1 - Size frequency histograms of *Gammarus aequicauda*, from the 12/2/83 to the 29/2/84 in the Evros Delta (N. Greece) (from Kevrekidis and Koukouras, in press).

In the study area, *G. aequicauda* density varied markedly throughout the year (Table 1). More precisely, in September 1983, *G. aequicauda* showed approximately 12 % wet weight of the total macrobenthic fauna, while the wet biomass of *Abra ovata* (Philippi) represented about 80 %, and that of *Hydrobia salaria* (Radoman) represented about 8 % of the total biomass.

MATERIALS AND METHODS

Monthly samples of *Gammarus aequicauda* were collected from 12 February 1983 to 29 February 1984. A special Petersen type sampler with handles and a sampling area of 20 x 20 cm^2, was used. Five random sampling units were taken from the southeastern zone of the *F. enigmaticus* formations. Samples were sieved in a sieve having a mesh of 1 mm and the collected animals were preserved in a formalin solution 5 %.

Body length (Lb) was measured with the aid of a stereoscope in mm. Cephalic length (Lc) of the individuals was measured in the laboratory under a compound microscope with the aid of an eye-piece micrometer and was expressed in µm, knowing that each of those units (microscope unit) corresponded to 38.5 µm. All individuals were placed in 17 size classes ; it was selected a class interval of 3 microscope units according to Goulden's method (*in* Cancela da Fonseca, 1965). After the above measurements, the animals were placed in an oven at 60°C and the dry body weight (W) was taken in mg after 48 hours.

G. aequicauda individuals were separated in juveniles and adults according to Vlasblom (1969) ; so, since the smallest ovigerous female had a cephalic length (Lc) of 20 microscope units (m.u.) (=770 µm), it was considered that all amphipods having a cephalic length smaller than 19 m.u. (=731.5 µm) were juveniles. The rest individuals (having a Lc $\geqslant$ 19 m.u.) have been distinguished to be males, non-ovigerous females or ovigerous females (i.e. females with setose oostegites).

A. Relative growth.

For the study of relative growth, the morphometric criterions of Lc, Lb and W were used. Searching for the best description of the relation Lc/W and Lc/Lb (curvilinear regression), we arrived at the equations $W = \alpha\ (Lc)^b$ and $Lb = \alpha\ (Lc)^b$ which additionally showed the highest positive coefficients of correlation ; this is clearly shown in the dispersion diagrams (Fig. 2). So the simple allometry formula was used according to Huxley et Teissier (1936), which was transformed as following : $Log_{10}W = \alpha\ Log_{10}Lc + Log\ _{10}b$ and $Log_{10}Lb = \alpha\ Log_{10}Lc + Log\ _{10}b$ respectively (where α, b : constants and W, Lc and Lb : the morphometric criterions described above).

B. Secondary production.

Annual production was calculated by the size-frequency Hynes's method. This method was chosen for two reasons in spite of the possible limitation that it may produces an overestimate because a) it shows promise in being capable of accomplishing the estimation of annual production (Waters & Crawford, 1973) and b) it has an important advantage that single cohorts within the data need not to be identified for the calculation of production (Krueger & Martin, 1980). Waters and Crawford (1973) suggest that the possible overestimate by Hynes's method may be caused by the very low number of individuals in the largest size groups. So the 17 size classes were grouped into 13 by combining the four last classes which had a mean number of individuals/m² less than 0.5. The formula used was Hynes's formula after being modified by Hamilton (1969), converted by Benke (1979) and given by Menzie (1980). The formula is as following :

$$P = [i\sum_{j=1}^{i}(nj - nj+1) \,.\, (Wj\ Wj+1)^{1/2}] \,.\, 365/CPI$$

where i : the number of size classes or "times loss" factor,
where nj : the mean number of individuals in size class j,
where Wj : the mean weight of an individual in the j^{th} size class,
where $(Wj\ Wj+1)^{1/2}$: the geometric mean weight between two size classes, and
where CPI : the cohort production interval in days.

RESULTS

A. Relative growth.

There exists a positive correlation between the criterions $Log_{10}W$ and $Log_{10}Lc$ (r = 0.848 ; N = 429) (Table 2) and $Log_{10}Lb$ and $Log_{10}Lc$ (r = 0.891 ; N = 655) (Table 3) for the whole population of *G. aequicauda* (Fig. 2).

It is also found that there exists a positive allometry for the relation $Log_{10}W$, $Log_{10}Lc$ for the whole population since $\alpha > 1$ (α = 3.691) (Table 2), which means that the body weight increases faster than the cephalic length. A positive allometry is also found for the relation $Log_{10}Lb$, $Log_{10}Lc$, since $\alpha > 1$ (α= 1.237) (Table 3), that is the body length increases faster than the cephalic length.

Having noticed that juveniles had a cephalic length between 16-19 microscope units (= 616-731.5 μm), it was tested if there existed a statistical difference of the relative growth of $Log_{10}W$, $Log_{10}Lc$ between juveniles ($Lc \leqslant$ 17.5 m.u. or 673.8 μm) and adults ($Lc >$ 17.5 m.u.). Having also noticed that the majority of non-ovigerous females was in the size class of 26 microscope units (= 847 μm) (Fig. 1) it was tested if there existed a statistical difference in the relative growth of W in relation to Lc between ovigerous ($Lc >$ 25 m.u. or 962.5 μm) and non-ovigerous females ($Lc \leqslant 25$). The individuals were separated in juveniles, adults, males or females and in ovigerous and non-ovigerous females (Table 2, 4) according to the above observations. In non-ovigerous females and in ovigerous females the linear and not the exponential relation was used (Table 4) because it showed the highest coefficient of correlation.

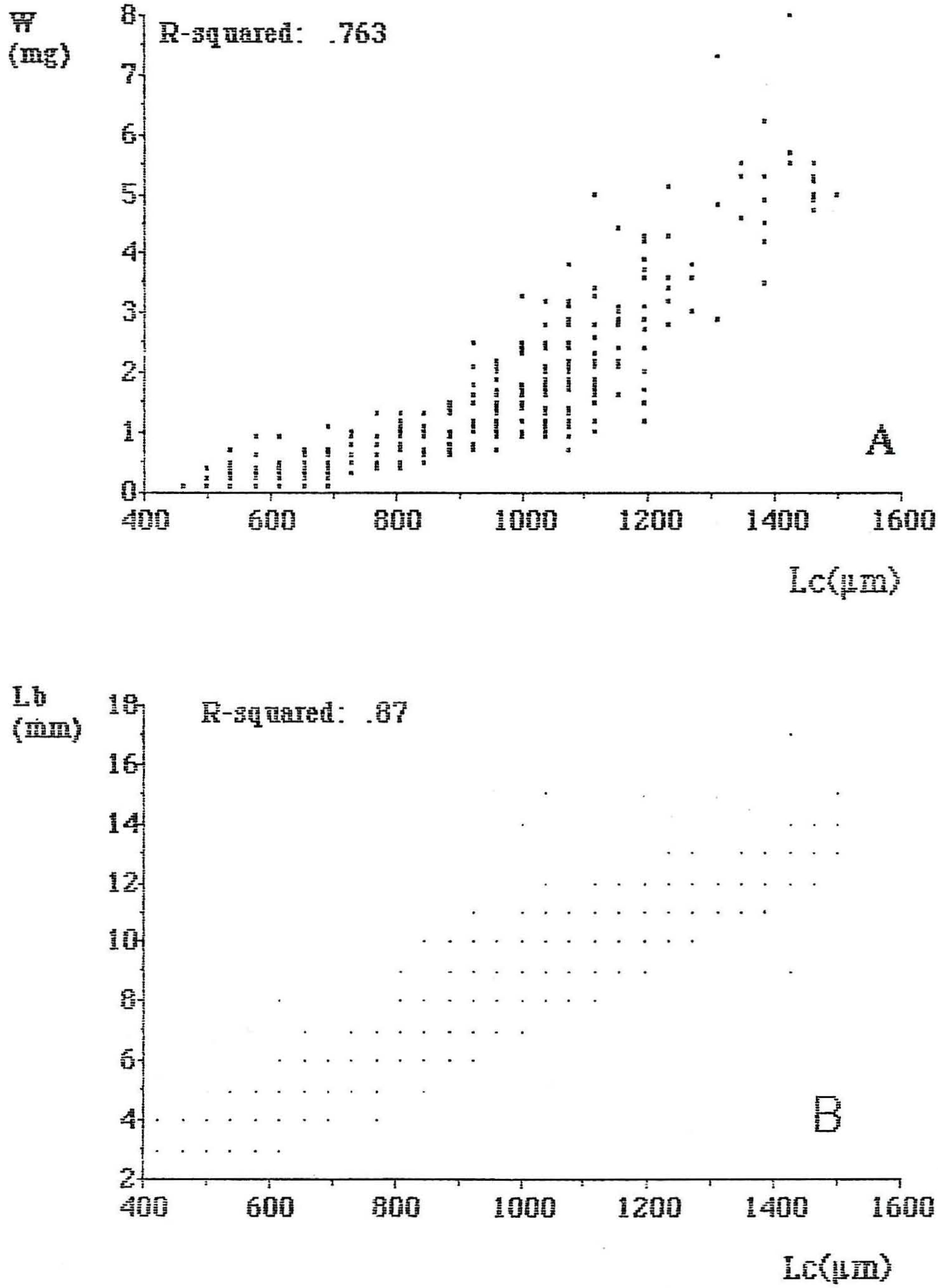

Fig. 2 - A) Dispersion diagram of W (dry body weight in mg) in relation to Lc (cephalic length in μm) in 429 animals of *Gammarus aequicauda*, and B) Dispersion diagram of Lb (body length in mm) in relation to Lc (cephalic length in μm) in 655 animals of *G. aequicauda*.

TABLE 2 - Estimate of statistical parameters of the population of *Gammarus aequicauda* (where a, b : constants ; Log : Log_{10} ; Lc : cephalic length in µm ; W : dry body weight in mg ; s : standard error ; r : coefficient of correlation ; N : number of animals).

	WHOLE POPULATION	JUVENILES	ALL ADULTS	MALES	ALL FEMALES
a ± sa	3.691 ± 0.245	3.581 ± 0.460	3.202 ± 0.126	3.580 ± 0.300	3.208 ± 0.207
Logß ± sLogß	-10.891 ± 0.221	-10.603 ± 1.290	-9.409 ± 0.381	-10.591 ± 0.276	-9.385 ± 0.624
LogLc ± sLogLc	2.925 ± 0.129	2.778 ± 0.045	3.011 ± 0.071	2.888 ± 0.134	3.009 ± 0.056
LogW ± sLogW	-0.097 ± 0.516	-0.655 ± 0.310	0.232 ± 0.272	-0.253 ± 0.528	0.266 ± 0.221
r^2	0.848	0.273	0.704	0.825	0.655
N	429	159	270	301	126

TABLE 3 - Estimate of statistical parameters of the population of *Gammarus aequicauda* (where a, b : constants ; Log : Log_{10} ; Lc : cephalic length in µm ; Lb : body length in mm ; s : standard error ; r : coefficient of correlation ; N : number of animals).

	WHOLE POPULATION	JUVENILES	MALES	ALL FEMALES	NON-OVIGEROUS FEMALES	OVIGEROUS FEMALES
a ± sa	1.237 ± 0.017	1.009 ± 0.084	3.080 ± 0.095	1.104 ± 0.055	0.901 ± 0.105	0.918 ± 0.071
Logß ± sLog ß	-2.773 ± 0.045	-2.149 ± 0.239	-4.651 ± 0.176	-2.363 ± 0.164	-1.777 ± 0.313	-1.785 ± 0.210
LogLc ± sLogLc	2.942 ± 0.123	2.762 ± 0.055	1.813 ± 0.033	2.996 ± 0.055	2.963 ± 0.046	3.022 ± 0.048
LogLb ± sLogLb	0.866 ± 0.161	0.638 ± 0.081	0.934 ± 0.115	0.946 ± 0.078	0.893 ± 0.066	0.988 ± 0.058
r^2	0.891	0.463	0.806	0.620	0.401	0.560
N	655	161	245	249	111	138

It was found that in all the above cases, the morphometric criteria $Log_{10}W$/ $Log_{10}Lc$ and $Log_{10}Lb/Log_{10}Lc$ showed a positive allometry (Table 2, 3) since $\alpha > 1$. For the case of non-ovigerous females/ovigerous females, the above criteria showed a negative allometry (Table 3, 4). Growth is faster in juveniles than in adults (Table 2). In the latter case where growth is slower, standard errors of W (which grows faster than Lc) is less, too (Table 2).

Comparing the slopes of juveniles and adults (males or females) (Table 2) with the covariance analysis (Snedecor & Cochran, 1976) and the method of Mayrat (1965), it was found that: a) the two slopes of juveniles and adults intercept at Lc = 15.47 (= 596.2 μm) and W = 0.30 mg ($P < 0.001$) (Table 2); the slopes of juveniles and males intercept at Lc = 15.19 (= 584.8 μm) and W = 0.21 mg ($P < 0.001$) (Table 2); and the slopes of juveniles and females intercept at Lc = 15.75 (= 606.7 μm) and W = 0.34 mg ($P < 0.001$) (Table 2). Additionally, the slopes of non-ovigerous and ovigerous females intercept at Lc = 26.84 (= 1033.4 μm) and W = 2.06 mg ($P < 0.001$) (Table 4).

Comparing the slopes of the relative growth of Lc, Lb in juveniles, adult males or females, there was found no statistical difference. A difference was only found between the slopes of ovigerous and non-ovigerous females (at the level of $P < 0.001$). Those slopes intercept at Lc = 30.38 m.u. (= 1169.5 μm) and Lb = 9.71 mm (Table 3).

The comparison between the relative growth of W in relation to Lc and Lb in relation to Lc in males and females shows that the rate of growth in males is slightly quicker than in females (Table 2, 3).

TABLE 4 - Estimate of statistical parameters of the population of *Gammarus aequicauda* (where a, b : constants ; Lc : cephalic length in μm ; W: dry body weight in mg ; s : standard error ; r : coefficient of correlation ; N : number of animals).

	NON-OVIGEROUS FEMALES	OVIGEROUS FEMALES
a ± sa	0.004 ± 0.001	0.007 ± 0.001
b ± sb	-2.072 ± 0.664	-5.530 ± 0.725
Lc ± sLc	939.69 ± 94.46	1095.20 ± 117.70
W ± sW	1.42 ± 0.59	2.58 ± 1.09
r^2	0.350	0.637
N	53	73

Intersection point at Lc = 26.84m.u. = 1033.4 μm

B. Secondary production.

The calculations of the size-frequency method are listed in Table 5. The mean number of individuals in each size class is shown in the second column. The mean weight of each size class is expressed in dry weight on the basis of linear relations used between cephalic length and body dry weight (Table 2), for the juveniles ($Log_{10}W = 3.581 Log_{10}Lc - 10.603$) and for the adults ($Log_{10}W = 3.202 Log_{10}Lc - 9.409$). The values of $\bar{n}$ (mean annual density), $\bar{B}$ (mean annual crop) and P (annual production) are equal to 3127.7 individuals per m^2, 4.24 $g.m^2$, and 22.40 $g.m^{-2}$ (after the CPI correction) (Table 5). Additionally, the annual turnover ratio ($P/\bar{B}$) is equal to 5.28.

DISCUSSION

A. Relative growth.

The difference found between juveniles, males and females showed that juveniles had a cephalic length less than 16 m.u. (= 616 μm) which corresponded to our observations that the smallest non-ovigerous female measured 19 m.u. (= 731.5 μm) and that the largest juveniles belonged to the size class 16-19 (Fig. 1). The difference also found between non-ovigerous and ovigerous females in the relation W/Lc showed that ovigerous females had a cephalic length greater than 27 m.u. (= 1040 μm) (Table 4). However, the difference in the relative growth of non-ovigerous and ovigerous females, concerning the relation $Log_{10}Lb/Log_{10}Lc$, was found to start when the cephalic length of females is equal to 30 m.u. (= 1155 μm) (Table 3). Both of the above findings correspond with our field and laboratory data, according to which the largest non-ovigerous females belonged from 26.5 to 32.5 m.u. (1020.3-1251.3 μm) cephalic size class according to the examined month of the year (Fig. 1).

Finally, it was found that the rate of growth of males was greater than in females, which was in opposition with the results of Sagar (1980).

B. Secondary production.

Gammarus aequicauda productivity at the Evros Delta (22.40 g dry wt . m^{-2} . yr^{-1}) is among the highest productivity estimates reported elsewhere for marine amphipods. It was only found the annual production of *Corophium insidiosum* (3.00 - 60.00 g dry wt . m^{-2} . yr^{-1}) in a mediterranean lagoon (Casabianca, 1975) and of *C. volutator* (1.5 - 30 g dry wt . m^{-2} . yr^{-1})* in the Swedish coast (Moller & Rosenberg, 1982), both exceeding our estimates. The higher values for *Eogammarus confervicolus* (6.12 - 21.65 g dry wt . m^{-2} . yr^{-1}) in Squamish estuary (Stanhope & Levings, 1985) and for *Gammarus mucronatus* (12.4 - 15.8 g dry wt . m^{-2} . yr^{-1}) in a northern Massachusetts salt marsh (La France & Ruber, 1985) are slightly near those reported in our paper. It must be mentioned that all the previous records were reported on estuarine or littoral amphipod populations. Several

* These values have been calculated by Collie (1985) after a conversion of wet weight in dry weight.

TABLE 5 - Computation of secondary production of *Gammarus aequicauda* by the size-frequency method. Annual production based on 13 sets of samples from 12 February 1983 to 29 February 1984 (where nj = mean number of animals at the size class j ; W = mean dry body weight ; G = geometric mean ; B = biomass (mean annual crop) : P = annual production ; P/B = annual turnover ratio ; i = number of size classes ; CPI = cohort production interval in days).

Size group cephalic length in microscope units (= μm)	nj/m^2	$(nj-nj+1)/m^2$	Wj(mg)	Gj $(Wj \cdot Wj+1)^{0.5}$ (mg)	B $[nj/m^2 \cdot Wj(mg)]$ $(mg.m^{-2})$	P' (nj-nj+1)(Gj) $(mg.m^{-2})$
10-13(442.8)	48.7		0.075		3.653	
		- 401.3		0.113		-45.347
13-16(558,3)	450.0		0.171		76.950	
		- 36.3		0.240		- 8.712
16-19(673,8)	486,3		0.336		163.397	
		40.4		0.498		20.119
19-22(789.3)	445.9		0.738		329.074	
		16.0		0.918		14.688
22-25(904.8)	429.9		1.142		490.946	
		- 153.3		1.384		- 212.167
25-28(1020.3)	583.2		1.678		978.610	
		218.1		1.993		434.673
28-31(1135.8)	365.1		2.366		863.827	
		193.7		2.763		535.193
31-34(1251.3)	171.4		3.226		552.936	
		92.8		3.716		344.845
34-37(1366.8)	78.6		4.280		336.408	
		33.5		4.874		163.279
37-40(1482.3)	45.1		5.550		250.305	
		27.5		6.258		172.095
40-43(1597.8)	17.6		7.057		124.203	
		13.9		7.892		109.699
43-46(1713.3)	3.7		8.825		32.653	
		1.5		11.852		17.778
46-61(2059.8)	2.2		15.916		35.015	
		2.2		15.916		·35.015
	3127.7				4237.977	1581.158

or $4.24 g \cdot m^{-2}$

$P = i \cdot P' \cdot 365/CPI = 13 \cdot 1581.158 \cdot 365/335 = 22395.805 mg/m^2 = 22.40 g/m^2$

$P/B = 22.40/4.24 = 5.28$

productivity estimates of marine amphipod populations are lower than ours; indeed, most of them are much lower (never exceeding 5 g dry wt . m^{-2} . yr^{-1}) (Klein *et al.*, 1975; Ankar & Elmgren, 1976; Cederwall, 1977; Glémarec & Menesguen, 1980; Hastings, 1980; Hastings, 1981; Wildish & Peer, 1981; Albright & Armstrong, 1982; Carlsson, 1983; Carrasco & Arcos, 1984; Wildish, 1984; Collie, 1985; Kemp *et al.,* 1985).

The annual turnover ratio of *Gammarus aequicauda* at the Evros Delta is 5.28. Comparing our $P/\bar{B}$ ratios with $P/\bar{B}$ ratios of marine amphipods, we found that our $P/\bar{B}$ ratio was lower than the ones found for *Gammarus mucronatus*, similar to the higher values of those recorded for *Eogammarus confervicolus* and similar to the lower values of those found for corophiid amphipods. However, they are higher than that obtained for many other marine species of gammaridean Amphipoda. The above information was drawn from table 1 in Kemp *et al.* (1985), and from Moller and Rosenberg (1982), from Collie (1985), La France and Ruber (1985), and Stanhope and Levings (1985). Thus, annual $P/\bar{B}$ ratios are of 12.4 to 15.8 for *Gammarus mucronatus* and of 3.28 to 6.01 for *Eogammarus confervicolus*; the $P/\bar{B}$ ratio for corophiid amphipods ranges from 5.1 to 19.5, for ampeliscid amphipods from 1.29 to 4.45, for haustoriid amphipods from 0.78 to 4.78, for phoxocephalid amphipods from 1.29 to 3.14, and finally for other amphipod species from 2.46 to 4.4.

The values found for *Gammarus aequicauda* secondary production and turnover ratio are within or greater than the ones found for freshwater *Gammarus* species. Thus, a secondary production from 2.94 g dry wt . m^{-2} . yr^{-1} to 44.9 g dry wt . m^{-2} . yr^{-1} and $P/\bar{B}$ ratio from 4.65 to 7.3 have been recorded for populations of *G. pseudolimnaeus* (Waters & Hokenstrom, 1980; Marchant & Hynes, 1981; Waters, 1984); secondary production of 3.81 g dry wt . m^{-2} . yr^{-1} to 12.9 g dry wt . m^{-2} . yr^{-1} and $P/\bar{B}$ ratios from 2.03 to 2.6 have been also reported for populations of *G. pulex* (Iversen & Jessen, 1977; Welton, 1979; Mortensen, 1982).

CONCLUSIONS

1. There exists a positive correlation between W, Lc and Lc, Lb in *Gammarus aequicauda.*

2. The body length and body weight increase more than the cephalic length.

3. There is a difference in the relative growth of W, Lc in: a) juveniles and adults (males and females); b) juveniles and males; c) juveniles and females and d) non-ovigerous and ovigerous females.

4. Juveniles grow quicker than adults.

5. The rate of growth in males is slightly quicker than in females.

6. With the size-frequency method mean annual density is equal to 3127.7 individuals per m^2, mean annual biomass is equal to 4.24 g dry weight . m^{-2} . yr^{-1},

annual production is equal to 22.40 g . m^{-2} . yr^{-1} and annual turnover ratio is equal to 5.28.

7. *G. aequicauda* productivity at the Evros Delta is among the highest productivity estimates reported elsewhere for marine amphipods. As for the annual turnover ratio, it is among the highest ones found for other gammaridean Amphipoda.

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