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Global Importance of Local Experience

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CHARACTERISATION OF THE *Echinogammarus marinus* (LEACH) (AMPHIPODA) POPULATION IN THE MONDEGO ESTUARY

Abstract

A benthic sampling program was carried out in 1985/86, in winter and summer periods, to characterise the intertidal community structure in the Mondego estuary (Portugal). *Echinogammarus marinus* (Amphipoda, Gammaridae) was considered a key species in rocky substrates, particularly in association with *Fucus spp*, and consequently a study on its life cycle and population dynamics was carried out. *E. marinus* showed an aggregated spatial distribution, and the population density changed seasonally, with peaks during spring and summer. No migratory patterns were detected between the estuary and the sea, but migrations inside the estuary might occur. An analysis of the population structure and dynamics was carried out based on the assumption that, although sexual activity was continuous through out the year, it would be possible to recognise and track population groups from their origin up to their total disappearance. Growth was continuous through life, although growth rates were higher during the early phases, and females were morphologically recognisable at smaller sizes than males. In addition, males became larger than females. Females reached sexual maturity before males, producing a succession of broods during the rest of their life. Fecundity increased with the size of females. Life span was estimated to be 10 to 12 months, but females showed higher mortality rates than males. This was probably due to higher costs of reproduction, which might cause a decrease in female survival. Sexual activity showed an increase in spring and summer. In the Mondego estuary, *E. marinus* is a semi-annual species, with three or four generations per year. Reproduction through the year, iteroparous females, high fecundity, and a multivoltine life cycle clearly suggest an r adaptive strategy. Production of *E. marinus* in the algal cover of *Fucus spp*. was estimated. Growth production (P) ranged from 6.36 to 8.81 $g.m^{-2}.y^{-1}$ (AFDW) (76.16 to 105.48 $KJ.m^{-2}.y^{-1}$) and elimination production (E) from 6.33 to 11.44 $g.m^{-2}.y^{-1}$ (AFDW) (75.84 to 137.04 $KJ.m^{-2}.yr^{-1}$). $P/\overline{B}$ ratios ranged from 6,1 to 6,3 and $E/\overline{B}$ ratios from 6,28 to 7,89. The present contribution was mostly based on a previously published paper (Marques and Nogueira 1991).

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Introduction

A benthic sampling program was carried out in 1985/86, to characterise the intertidal community structure in the Mondego estuary (Marques et al. 1993a). Amphipods appeared to have a very important role in the studied communities, both in hard and soft bottoms. Data analysis showed that only 18 of the 105 identified species had a relevant role in the observed structure (Marques 1989, Marques et al. 1993a, 1993b). Of these species, 5 (28%) were Amphipods, (*Echinogammarus marinus* and *Hyale stebbingi* in rocky substrates, *Amphitoe valida*, *Leptocheirus pilosus*, and *Melita palmata* in soft bottoms), which appeared therefore as a group of primary importance. *Echinogammarus marinus* (Gammaridae), with an extensive distribution and abundance in rocky habitats, was considered a key species in the algal covered habitat of *Fucus spp.*

Actually, *E. marinus* is strongly euryhaline, able to support long emersion periods (Dorgelo 1973, Pinkster and Broodbakker 1980, Marques and Nogueira 1991), and therefore very well adapted to life in estuaries. Its known distribution extends from Norway to the coast of Portugal, and some studies were already carried out on different aspects of its biology and ecology (Maren 1974, 1975 a, 1975 b, Pinkster and Broodbakker 1980, Skadsheim 1982). A study of the life cycle, population dynamics, and production of this species was carried out, from October 1985 to September 1987 (Marques and Nogueira 1991). The present contribution is mostly based on this last work, although several modifications were inserted at the light of new discussions about the same subject that took place since then.

Material and methods

In both arms of the Mondego estuary hard substrates are covered primarily by *Fucus spp.*, which constitutes an eulittoral macroalgae belt. A preliminary survey showed that *E. marinus* abundances were high in this habitat, namely in the south arm (Marques et al. 1993 a) where there is a predominance of fine particles in the sediments. Actually, high densities of this species usually depend on the presence of muddy bottoms. The examination of the population dynamics of *E. marinus* in this estuary, which is the southern limit of its distribution (Marques 1989, Marques and Nogueira 1991), and the comparison with data from other locations, should provide an opportunity to analyse the intra-specific life-history variation of a gammarid along a latitudinal gradient. In addition, it should allow estimate the production of an important warm-temperate estuarine species and to evaluate its importance with regard to energy transfers in the trophic web.

Field program

The population dynamics and field growth rates were examined through a monthly field sampling programme at three stations (figure 1) in the southern arm, for

a two year period, from October 1985 to September 1987. It was recognised that such sampling periodicity could be insufficient (Fredette and Diaz 1986 a), but due to logistic constraints it was not possible to sample more frequently. Sampling was conducted during low tide, which facilitated the access to the sampling sites. Nine replicate samples were taken randomly each time. Each sample was obtained by scraping the rocky surface where the algae were attached. In addition, the superficial 1 cm sediment layer around the rocks, under the algae fronds, was also collected to reduce escape of organisms. The sampled surface was often irregular. Thus, the area was estimated by projecting its shape onto a sheet of polyethylene, which was later weighed (the biggest replicate was 0.2334 m^2, and the smallest one was 0.093 m^2). Samples (algae plus sediment) were preserved in 4% buffered formaldehyde, and later sieved into a 0.5 mm mesh bag. Based on the size of newly hatched juveniles this mesh should retain all individuals. The Amphipods were then kept in 70% ethanol. The values of salinity, temperature, oxygen dissolved, pH, nitrites, nitrates, and phosphates of the water were determined on each site. For this purpose, water samples were obtained from puddles near the algae. For the estimation of caloric contents fresh samples were obtained seasonally. In this case the organisms were kept alive up to the laboratory, and subsequently freeze-dried.
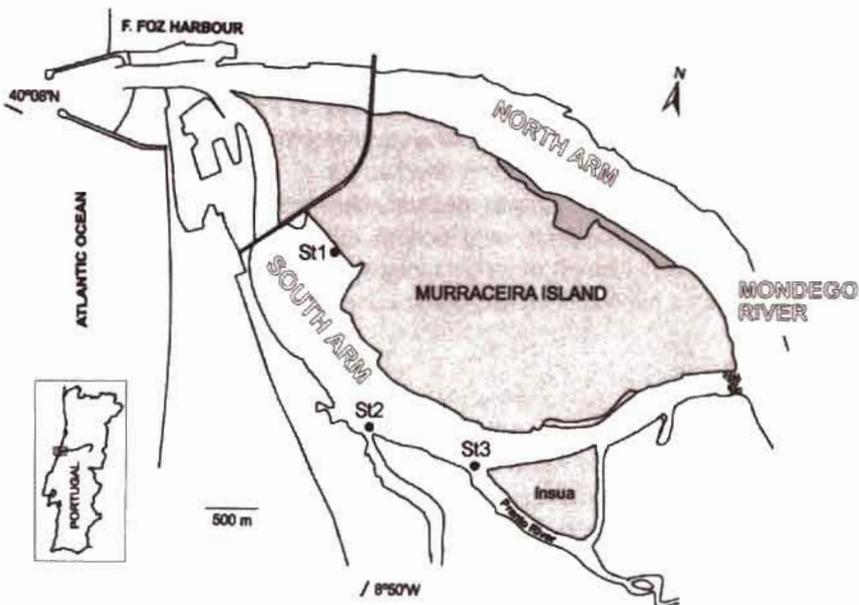

Figure 1. Location of the sampling station in the southern arm of the Mondego estuary.

Laboratory procedures

Amphipods collected were counted, and the cephalic length (Lc) was measured to the nearest 0,02 mm. Since the bodies of E. marinus, like most amphipods, are comma-shaped the total length (Lt) is not a very convenient standard to judge age and growth. On the contrary, the cephalic length (Lc) (measured between the extremity of the rostrum and the base of the head) is easier to determine. Thus, a sample of 90 individuals (22 males, 20 females, and 58 juveniles) were measured for both lengths, in order to provide a conversion equation: $L_T = -1.211995 + 10.668509 \, L_C$ ($r = 0.986$) (Marques and Nogueira 1991).

The determination of the sex was based on the presence or absence of oostegites and/or broods (females), and of genital papillae (males). Animals without these features were considered to be juveniles. Maturity of non-brooding females was determined by the presence of setae on the oostegites. When broods were present eggs were counted, to estimate the fecundity, measured, and examined to determine the development stage. Taking into consideration several resembling criterions (Goedmakers 1981, Skadsheim 1982, Steele and Steele 1969), five stages were considered: **A** – Newly laid, eggs grouped and looking like a gelatinous mass; **B** – Eggs well separated, internally homogenous; **C** – Embryo comma-shape and initiation of pereopods already visible; **D** – Constriction of the comma clearly visible, appendages segmented and looking slender, eyes visible, cephalotorax orange-red; **E** – Hatched and free juveniles. These may stay for some days in the brood pouch, particularly if conditions are unfavourable. Since eggs became oval in shape during development, an average of their length and width was taken as measurement of their size.

Measured amphipods were then dried at 60o C for 72 h and weighed to the nearest 0.01 mg. Percentage ash was assessed after heating samples for 3 h at 550° C. In both cases small amphipods were pooled to obtain measurable values. Caloric contents (expressed in Joules) of winter, spring, summer, and autumn populations were determined with a NEWHAM micro-bomb calorimeter.

Data analysis

Abundance of amphipods in the algal covers was related both to sampled area and algal density (Fredette and Diaz 1986 a, Marques 1989, Marques and Nogueira 1991). To adjust this potential bias the algae were separated from the samples, dried at 60 °C, and weighed to determine biomass. A moving average (using prior, present, and following dates) was applied to this value. This decreased the variability between intervals and gave better estimates of the algal standing stock. The amphipods abundance was then estimated by multiplying A (number of amphipods per gram of algae in each sample) by B (mean grams of algae per square meter on a sample date).

An index ($I = S^2/\bar{X}$; S^2 is the variance of abundances; $\bar{X}$ is the mean abundance) (Elliot 1977) was used to analyse the population spatial dispersion.

Multiple regression models for E. marinus were developed: abundance, sex ratio, percentage of ovigerous females, fecundity, and percentage of juveniles in the

population being correlated with the environmental parameters. The fitted regression models were expressed as:

$$Y' = a + b_1 X_1 + b_2 X_2 + ... + b_k X_k$$

Y' – are the values of a given dependent variable (e.g. abundance) predicted by the equation;

$X_1, X_2...X_k$ – are independent variables (e.g. salinity);

The solutions are the estimate of the regression coefficients a. b1. b2...bk. The significance of fitted regressions was tested by using analysis of variance technique (**F**), and the **t** test for the regression coefficients. as described in Edwards (1985). The models were fitted with data by the method of least squares and normal equations were solved by the matrix inversion method.

Although *E. marinus* sexual activity was continuous throughout the year, with just a short pause in late winter, it was assumed (Marques and Nogueira 1991) that it would be possible to recognise and track population groups from their origin up to their total disappearance. Despite the fact that this assumption could be controversial, this approach was considered suitable and growth rates were estimated by tracking recognisable population groups with size-frequency distributions (0.02 mm length classes) from successive sample dates (Marques and Nogueira 1991). The probability paper method (Harding 1949), as performed by Cassie (1954, 1963), was used to carry out size-frequency modal analysis. We used both the χ^2 and the **G** tests (P ≤ 0.05) (Fisher 1950, Sokal and Rohlf 1981) to test the reliability of the method. Computations were done using the ANAMOD software (Nogueira 1992), that was then under development.

Growth rates are usually not constant along the year. Thus, to express field growth rates we used a model that takes into consideration seasonal changes (Gaschütz et al. 1980 in Marques et al. 1994), expressed as:

$$Lt = L\infty \left[1 - e^{-kD\ (t-t0)\ +\ C\ (KD/2\pi(t-ts))} \right]^{1/D}$$

Lt – length of the organism at a given moment t;

L∞ – maximum possible length of the organism;

t – given instant;

t_0 – instant when the organism would have a length = 0;

t_s – time interval between growth start (when t=0) and the first growth oscillation; growth is expressed by a sine curve which the period is 1 year;

k – intrinsic growth rate;

C – constant, which the values can change from 0 to 1;

D – Parameter that expresses metabolic deviations from the Von Bertalanffy's 2/3 rule.

Production estimates were based upon population group's recognition. Growth increments or production increments (P) and elimination production (E) were

calculated with a method derived from Allen (1971), (Dauvin 1986, Marques et al. 1994). Approximate values of P and E for each population group during a time interval are expressed as:

$$P = \left[(N_t + N_{t+1})/2\right]\left(\overline{W}_{n+1} - \overline{W}_t\right) \quad for \;\; W_{t+1} > W_t$$

$$E = \left[(\overline{W}_t + \overline{W}_{t+1})/2\right]\left(N_t - N_{t+1}\right) \quad for \;\; N_t > N_{t+1}$$

N – density of the population group in each sample date;
$\overline{W}$ – mean individual biomass in each sample date;
t and t+1 – consecutive sample dates;

Total values of P and E for each population group are expressed as:

$$P = \sum_{t=0}^{t=n}\left[(N_t + N_{t+1})/2\right]d\overline{W}$$

$$P = \sum_{t=0}^{t=n}\left[(\overline{W}_t + \overline{W}_{t+1})/2\right]dN$$

Total values of P and E for the population are expressed as:

$$P = \sum_{n=1}^{N} P_{cn}$$

$$E = \sum_{n=1}^{N} E_{cn}$$

Pcn and Ecn are the growth and elimination production of the population group n. P/$\overline{B}$ and E/$\overline{B}$ ratios were determined. $\overline{B}$ (mean population biomass) is expressed as:

$$\overline{B} = \left(1/T\right)\sum_{n=1}^{N}\left(\overline{B}_n t\right)$$

T – period of study;
N – number of successive population groups in the period T;
$\overline{B}_n$ – mean biomass of the population group n;
t – duration of the population group n.

Results

Abundance and spatial dispersion

E. *marinus* showed an aggregated spatial distribution in the algal covered habitats of *Fucus spp* (the values of I, were always significantly higher than 1). Total abundance was lower from October 1985 to June 1986 than in the following period. In addition, it showed a clear seasonal variation, with peaks during spring and summer (figure 2). Inter-annual differences in abundance were important. In addition, abundance was quite variable between sampling sites, which might be due to the occurrence of migrations inside the estuary, although the available data is not sound enough to answer this.
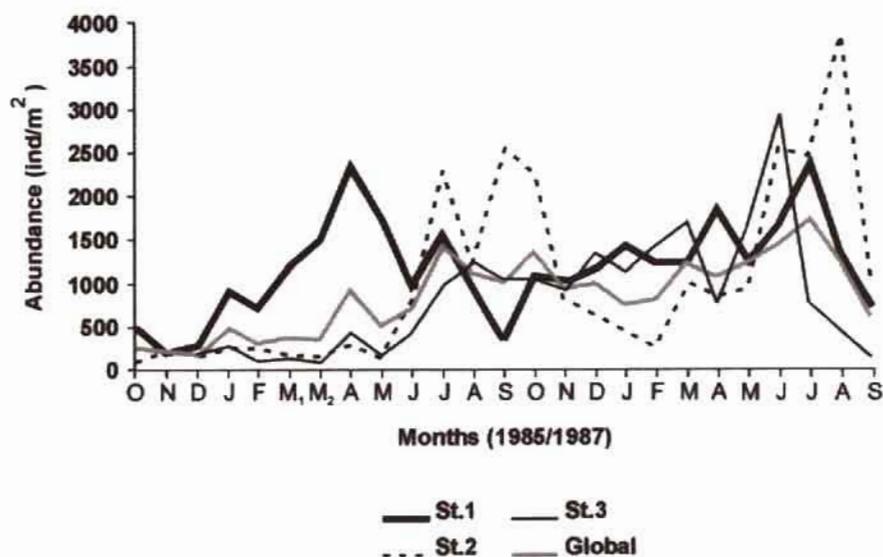

Figure 2. Variation of population abundance from October 1985 to September 1987: global values (average of all samples) (GL) and values for each sampling station (stations 1, 2, and 3) are given.

Period of reproduction

The E. *marinus* population was sexually active all over the year in the Mondego estuary. However, taking into consideration the percentage of ovigerous females over the total female population (figure 3), the sexual activity was higher from early spring (March/April) to the middle of summer (August), and then decreased until early winter (December), exhibiting therefore a clear seasonal pattern of variation. A slight increase

was observed in January 1986 and 1987, followed by a new decrease until the spring population bloom. In February/March 1986 sexual activity almost stopped. The variation of the percentage of juveniles in the population (figure 3) was parallel to the ovigerous females variation. Thus, the higher abundances in spring and summer were clearly related to an increase in recruitment. In addition, sexual activity was less intense in the winter 1985/1986 than in 1986/1987, which might explain lower abundances during winter and spring 1985/1986.
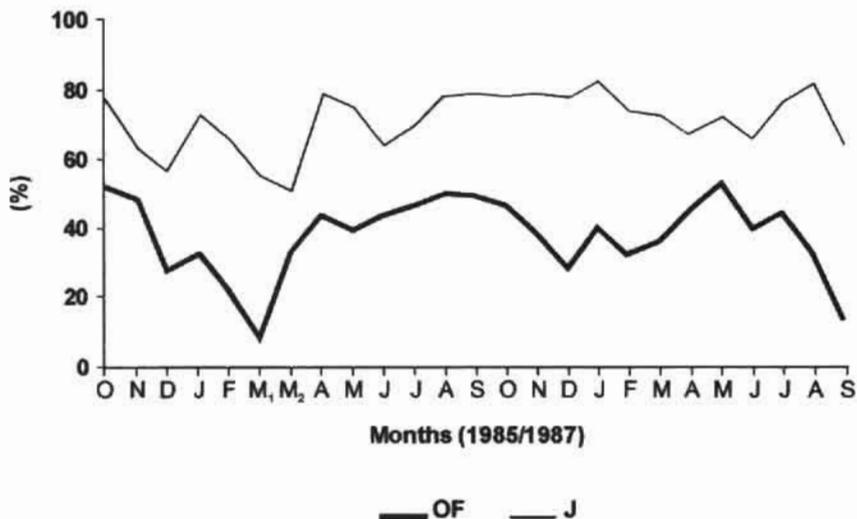

Figure 3. Variation of the percentage of ovigerous females in the total female population (% OF) and the percentage of juveniles in the population (% J), from October 1985 to September 1987.

Sex ratio

The sex ratio (males/females) was almost always favourable to females (figure 4). Still, peaks in the proportion males occurred in January/February and April/May, in 1986 and 1987, and in August 1987. These peaks were normally followed by increases in the percentage of females at sexual rest (oostegites present, with or without setae, but no broods) (figure 4). This was probably due to higher mortality rates of older females after laying eggs in winter, spring, and in summer (at least in 1987). Thus, males appeared to live longer than females.
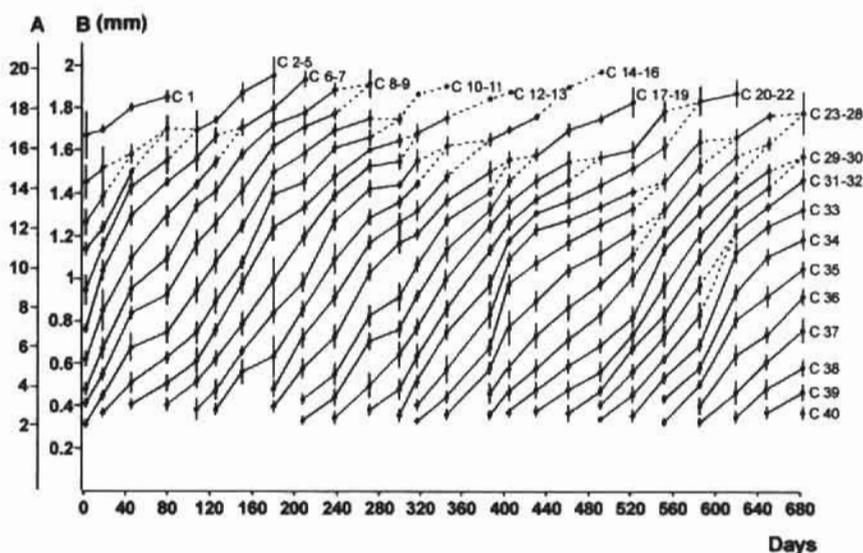
Figure 4 Variation of the sex-ratio and of the percentage of females in a state of sexual rest (oostegites present, with or without setae, but no broods) (% FSR), from October 1985 to September 1987.

Fecundity

The fecundity of females of similar sizes was quite variable. Although a significant correlation was found between number of eggs (NE) within the brood pouches and size of females. The fitted regressions were:

Stage A: – NE = -46.936 + 55.122 Lc (80 females; r = 0.8220)
Stage B: – NE = -33.570 + 44.662 Lc (257 females; r = 0.5684)
Stage C: – NE = -31.421 + 41.222 Lc (82 females; r = 0.6239)
Stage D: – NE = -33.673 + 39.153 Lc (151 females; r = 0.5500)

We did not take into consideration embryos in stage E, which can freely get in and out of brood pouches. Lost of eggs during development were therefore estimated as ≈ 28%, which might be due to incomplete fertilisation, disease, parasitism, or other accidental causes.

Since Amphipods have synchronised embryonic development, all the eggs in a given brood pouch are normally at the same stage. Measurements of eggs (table I) showed that, during development, they increase 36% in mean ovular diameter and 84% in volume. Since losses of eggs were ≈ 28%, an increase of 32% in the brood pouch volume might be enough to allow the observed 84% augmentation in eggs volume.

Table I. Average diameter and standard deviation of eggs at development stages A, B, C, and D, for *Echinogammarus marinus* in the Mondego estuary.

Stage	Diameter (mm) Average ± standard deviation
A	0.512 ± 0.049
B	0.537 ± 0.032
C	0.613 ± 0.025
D	0.695 ± 0.029

Influence of environmental parameters

The influence of salinity, temperature, dissolved oxygen, pH, nitrites, nitrates, and phosphates of water on abundance, sex ratio, percentage of ovigerous females, percentage of juveniles in the population, and fecundity was analysed (table II).

Abundance was positively correlated with temperature and dissolved oxygen (P ≤ 0,05). As organisms were sampled at low tide, higher concentrations of oxygen in the water might have favoured higher abundances of *E. marinus*. During emersion periods, however, organisms depend essentially on water retention. In addition, higher abundances in spring and summer are probably related to higher temperatures, and an increase in recruitment. Higher temperatures, effectively, determine shorter periods of embryonic development (Borowsky 1980).

The sexual activity, measured by the percentage of ovigerous females, which is obviously related with the percentage of juveniles in the population, was positively correlated with salinity and temperature. This explains the increase of abundance in spring and summer.

Table II. Multiple regression models for *Echinogammarus marinus*: abundance (D), sex ratio (males/females), percentage of ovigerous females in the total female population (% OF), percentage of juveniles in the population (%J), and fecundity (NE) are correlated with salinity (SAL), temperature (T), oxygen dissolved (OXYG), pH, nitrites (NTI), nitrates (NTA), and phosphates (PHOS). R – multiple regression coefficients. Values of significant tests (F and t) are given.

Multiple regression models (degrees of freedom: 66 in the numerator; 73 in the denominator)

	SAL	T	OXYG	pH	NTI	NTA	PHOS	Ryy'		F
D	0.003	0.250	0.365	0.411	-0.212	0.068	-0.092	-0.072	0.5104	4.673
Males/females	0.000	-0.207	0.365	0.307	0.002	-0.319	-0.004	-0.151	0.2953	1.996
% J	0.002	0.180	0.007	0.155	-0.037	0.008	-0.107	0.068	0.2282	1.573
NE	0.028	0.237	0.180	-0.124	0.122	0.145	-0.240	-0.336	0.4812	4.143

Values of t for the regression coefficients (66 degrees of freedom)

	SAL	T	OXYG	pH	NTI	NTA	PHOS
D	1.887	2.996	3.378	1.925	0.573	0.727	0.581
Males/females	1.411	0.050	2.268	0.014	2.407	0.032	1.096
% J	1.203	2.029	1.211	0.296	0.648	0.751	0.493
% OF	2.084	0.203	0.960	0.633	0.848	0.975	0.616
NE	1.758	1.456	0.997	1.085	1.196	1.880	2.665

The sex ratio was positively correlated with the percentage of dissolved oxygen, and negatively with the nitrite concentration. This might indicate that males are less tolerant than females to water oxygen depletion in the water column and to higher concentrations of nitrites.

The number of eggs per female was negatively correlated with the concentration of phosphates in the water. Although concentration values were always low (maximum was 0.086 mg/l), this might indicate a negative influence of this parameter over fecundity.

Growth and life span

Size-frequency distributions were analysed for recognisable population group. In October 1985 we identified 10 population groups, and 30 new ones were recognised during the study period. Minimum average Lc of new population groups ranged from 0.315 to 0.487 mm (2.15 to 3.98 mm Lт). This might have depended on the number of days from hatching to recognition of the new population group, and therefore on sampling periodicity. Maximum mean Lc of population groups ranged from 1.86 to 2 mm (18.62 to 20.13 mm total length). The biggest male had 2 mm Lc (20.16 mm Lт), and the biggest female 1.86 Lc (18.63 mm Lт) (figure 5).
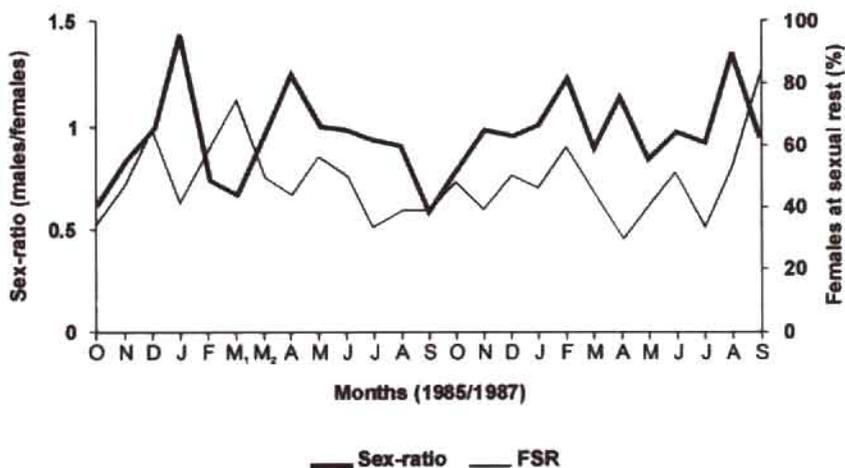

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Figure 5. Growth of population groups (average cephalic length ± standard deviation), from October 1985 to September 1987. A: total length; B. cephalic length. Broken lines indicate probable evolutions.

Field growth rates were estimated from the average size of recognisable population groups. Growth was found to be continuous through life, although growth rates were higher in early phases. Mean life span was estimated at 338 ± 29 days (confidence interval; $P \leq 0.001$), that is to say 10 to 12 months. However, as we said before, males seem to live longer than females.

A growth model (Gaschütz et al. 1980) was used on data from population groups 10, 13, 17, and 21, firstly recognised in autumn, winter, spring, and summer sample dates (figure 6). In all cases a decrease in growth rate corresponding to the winter period become evident. This decrease was probably due to lower metabolism caused by lower temperatures, and also less available nutrients.
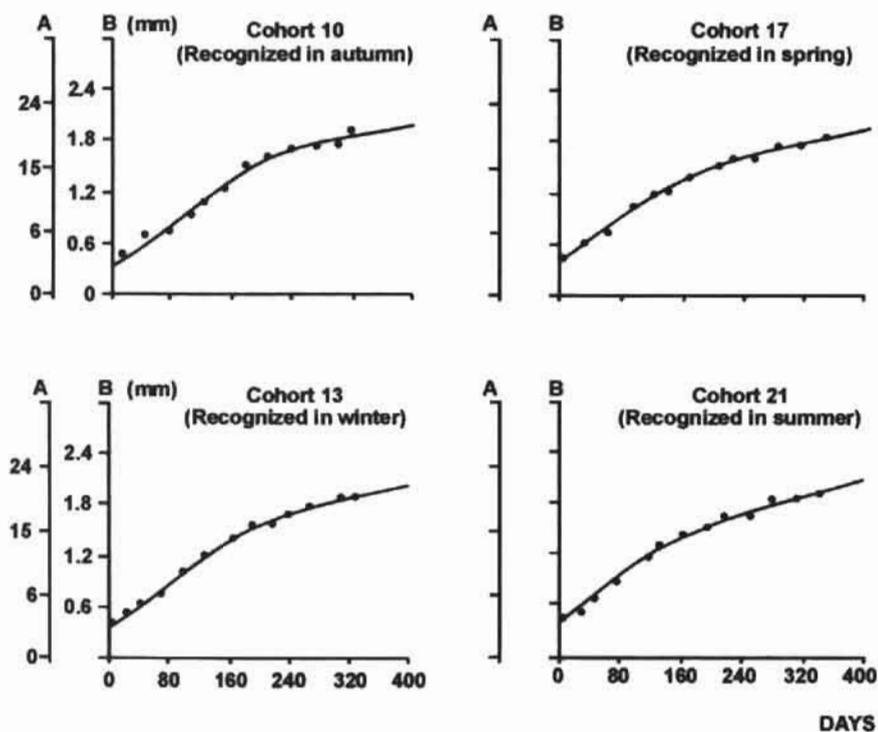

Figure 6. Graphic adjustment of the growth curves of population groups 10, 13, 17, and 21. Values of average cephalic length estimated for each given instant are also plotted. A: total length; B: cephalic length; r: correlation between the adjusted curves and the plotted values.

Males were recognisable with 0.86 ± 0.06 mm Lc (standard deviation) and females with 0.79 ± 0.04 mm Lc (7.95 ± 0.66 and 7.25 ± 0.42 mm Lt), that is to say with a minimum of 9 to 11 and 8 to 10 weeks respectively. Thus, sexual differentiation seems to occur earlier in females than in males, although this could also be due to higher growth rates in males.

Life cycle

Ovigerous females were present in the population throughout the year, with peaks in spring and summer, and therefore juveniles were always an important element of the population. The smallest ovigerous females had 1.12 ± 0.074 mm L_C (10.68 ± 0.8 mm L_T), which corresponded to an age of 14 to 19 weeks.

Percentage of ovigerous females in each population group (figure 7) was determined from size frequency analysis. We estimated that each female may have a minimum of three and a maximum of six or seven broods (iteroparous females; semi-annual species). Therefore, three or four generations per year occurred in the Mondego estuary (multivoltine life cycle).
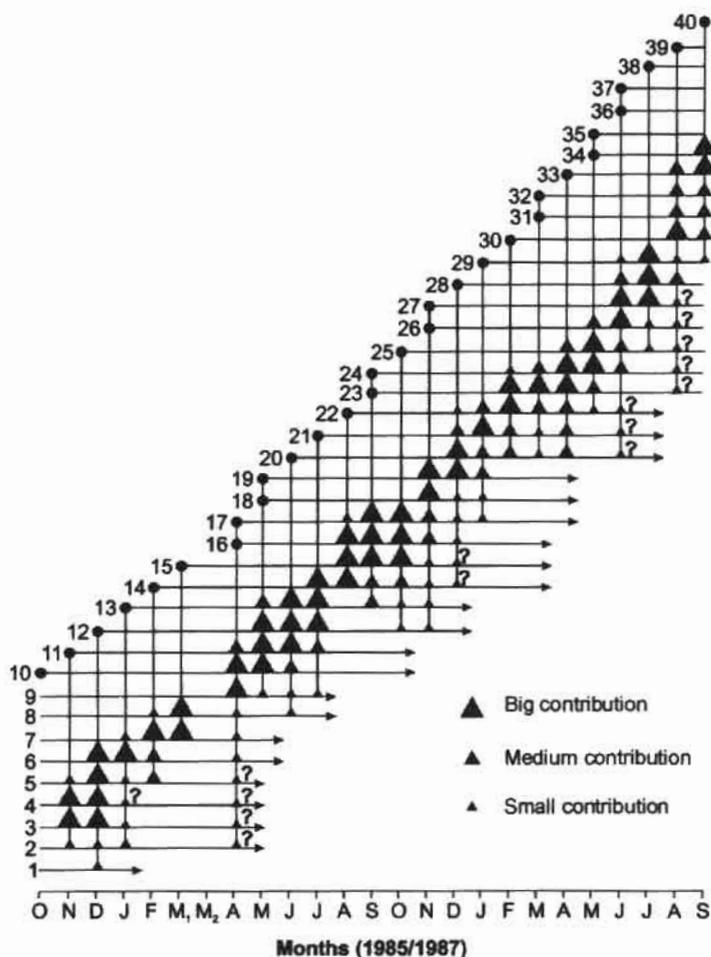

Big contribution

Medium contribution

Small contribution

O N D J F M₁ M₂ A M J J A S O N D J F M A M J J A S

Months (1985/1987)

Figure 7. Analysis of sexual activity. The contributions of the females of each population group are indicated. Big contribution: more than 20% of total ovigerous females; medium contribution: from 10 to 20%; small contribution: less than 10%; ? indicates a possible contribution.

Production estimates

Length-weight relations in each season were not different on the basis of an analysis of variance and a t test ($P \leq 0.05$). Thus, the entire data set was combined to provide a single regression expressed as:

$W = 1.5929 * Lc^{2.9344}$ (W – ash free dry weight)

Microbomb combustion of 941 individuals showed that juveniles had caloric contents slightly inferior to adults (11 KJ/g AFDW). In addition, females have caloric contents higher than males (12.3 and 11.5 KJ/g AFDW respectively). Growth production (P) ranged from 6.36 to 8.808 g.m^{-2}.year^{-1} (AFDW) (76.16 to 105.48 KJ.m^{-2}.year^{-1}) and elimination production (E) from 6.33 to 11.44 g.m-2.year^{-1} AFDW (75.84 to 137.04 KJ. m^{-2}. year^{-1}). P/$\overline{B}$ ratios ranged from 6.1 to 6.3 and E/$\overline{B}$ ratios from 6.28 to 7.89.

Discussion

E. marinus showed a contagious distribution and the population abundance showed clear seasonal variations, with peaks in spring and summer, due to an increase in recruitment. It was not possible to detect any migratory patterns between the Mondego estuary and the sea. This does not agree with the observations of other authors (Pinkster and Broodbakker 1980), and therefore this type of migration might depend on particular environmental conditions of each estuarine system. Nevertheless, migrations inside the estuary may occur, although the available data is insufficient to confirm this. Therefore, despite the significant correlation found between abundance and temperature, which is consistent with the observed seasonal variations, there is a probability that changes in abundance in each site might not depend only on population blooms, but also on any migratory patterns, as observed for *Echinogammarus berıloni* (Goedmakers 1981).

Growth is continuous throughout the life. Females are morphologically recognisable and reach sexual maturity before males, and then produce a succession of broods during the rest of the life. In addition, fecundity increases with the size of females. Although both males and females survived for at most a year, females showed higher mortality rates, and therefore males lived longer, as observed in several *Gammarus* species (Steele and Steele 1969, 1970). This was probably due to the intense sexual activity of females and the consequent phenotypic costs of reproduction. This might have caused a decrease in female parental survival, as observed for example in *Gammarus lawrencianus* (Steele and Steele 1986).

The sexual activity was continuous through the year, with a clear increase in spring and summer, but recruitment was found to be discontinuous. The recognition of new population groups was dependent on sampling periodicity and, probably, on the retention of newly hatched juveniles within brood pouches.

With regard to life cycles it is commonly accepted that the reproductive patterns of Gammarids evolved in relation to environmental constraints (Steele and Steele 1975, Wildish 1982). In the Mondego estuary, which is the southern limit of its known distribution, *E. marinus* is semi-annual, with three or four generations per year (multivoltine life cycle). Other populations of this species show very different life cycles, respectively univoltine in Denmark, in a cold temperate to sub-polar climate (Skadsheim 1982), and bivoltine in Normandy, in a maritime temperate climate (Pinkster and Broodbakker 1980).

Assuming that the observed life cycles are evolutionary stable (Maynard Smith 1974), we must conclude that Gammarids can have large intraspecific variations in reproductive patterns. This feature might have an important role in marine amphipod speciation. In addition to reproduction through out the year, iteroparous females, high individual fecundity, and a multivoltine life cycle revealed an r adaptive strategy of *E. marinus* in the Mondego estuary. This is to be expected in a warm-temperate estuary with physically controlled communities, and where opportunistic strategies normally occur.

Both growth production (P) and elimination production (E), when compared with values found in literature (e.g. Birklund 1977, Carrasco and Arcos 1984, Dauvin 1988 a, 1988 b, 1988 c, 1988 d, Fredette and Diaz 1986 b, Hastings 1981, Möller and Rosenberg 1982, Van Senus and McLachlan 1986) can be considered elevated. Data on *E. marinus* production from the Mondego reinforces the generalised notion of estuaries as highly productive systems. It also reflects the important role of amphipods concerning the production of habitats colonised by them.

References

Allen, K. R., 1971. Relation between production and biomass. J. Fish. Res. Bd. Canada 28: 1573-1581.

Birklund, J., 1977. Biomass, growth, and production of the Amphipod *Corophium insidiosum* Crawford, and preliminary notes on *Corophium volutator* (Pallas). Ophelia 16 (2): 187-203.

Borowsky, B., 1980. Reproductive patterns of three intertidal saltmarsh gammaridean amphipods. Mar. Biol. 55: 327-334.

Carrasco, F. D. and D. F. Arcos, 1984. Life history and production of a cold-temperate population of the sublittoral amphipod *Ampelisca araucana*. Mar. Ecol. Progr. Ser. 14: 245-252.

Cassie, R. M., 1954. Some uses of probability paper in the analysis of size-frequency distributions. Aust. J. Mar. Fresh. Res. 3: 513-522.

Cassie, R. M., 1963. Tests of significance for probability paper analysis. N. Z. Sci. Rev., 6: 474-482.

Dauvin, J. C., 1986. Dynamique de la population d'*Abra prismatica* (Mollusque, Bivalve) de la baie de Morlaix (Mancha Occidentale). Ann. Inst. Océanogr. (Paris). 62: 1-12.

Dauvin, J. C., 1988 a. Biologie, dynamique et production de populations de crustacés Amphipodes de la Manche Occidentale. 1. *Ampelisca tenuicornis* Liljeborg. J. Exp. Mar. Biol. Ecol. 118: 55-84.

Dauvin, J. C., 1988 b. Biologie, dynamique et production de populations de crustacés Amphipodes de la Manche Occidentale. 2. *Ampelisca brevicornis* (Costa). J. Exp. Mar. Biol. Ecol. 119: 213-223.

Dauvin, J. C., 1988 c. Biologie, dynamique et production de populations de crustacés Amphipodes de la Manche Occidentale. 3. *Ampelisca typica* (Bate). J. Exp. Mar. Biol. Ecol. 121: 1-22.

Dauvin, J. C., 1988 d. Life cycle, dynamics, and productivity of Crustacea – Amphipoda from the western English Channel. 4. *Ampelisca armoricana* Bellan-Santini and Dauvin. J. Exp. Mar. Biol. Ecol. 123: 235-252.

Dorgelo, J., 1973. Comparative ecophysiology of Gammarids (Crustacea: Amphipoda) from marine, brackish, and fresh-water habitats exposed to the influence of salinity-temperature combinations. III. Oxygen uptake. Neth. J. Sea Res. 7: 253-266.

Edwards, A. L., 1985. Multiple regression and the analysis of variance and covariance. 2nd Ed. W. H. Freeman and Co., New York, 221p.

Elliot, J. M., 1977. Statistical analysis of samples of benthic invertebrates. 2nd Ed., Freshwater Biological Association, Sci. Publ., 25, 160 p.

Fisher, R. A., 1950. The significance of deviation from expectation in a Poisson series. Biometrics 6: 17-24.

Fredette, T. J. and R. Diaz, 1986 a. Life history of *Gammarus mucronatus* Say (Amphipoda: Gammaridae) in warm temperate estuarine habitats, York River, Virginia. J. Crust. Biol. 6 (1): 57-78.

Fredette, T. J. and R. Diaz, 1986 b. Secondary production of *Gammarus mucronatus* Say (Amphipoda: Gammaridae) in warm temperate estuarine habitats, York River, Virginia. J. Crust. Biol. 6 (4): 729-741.

Gaschütz, G., D. Pauly and N. David, 1980. A versatile Basic program for fitting weight and seasonally oscillating length growth data. Pelagic, Demersal and Shellfish Cttes, 23 p.

Goedmakers, A., 1981. Population dynamics of three gammarid species (Crustacea, Amphipoda) in a french chalk steam. II. Standing crop. Bijdr. Dierkd 51 (1): 31-69.

Harding, J. P., 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc. U. K.28: 141-153.

Hastings, M. H., 1981. Life cycle and productivity of an intertidal population of the Amphipoda *Ampelisca brevicornis*. Estuar. Coast. Shelf Sci.12: 665-677.

Maren, M. J., 1974. Répartition et écologie d'Amphipodes (surtout gammarides) dans le bassin et l'estuaire de la rivière du Dorduff (Bretagne). Bull. zool. Mus. Univ. Amsterdam, 3 (22): 189-209.

Maren, M. J., 1975 a. Some notes on the intertidal gammarids (Crustacea, Amphipoda) from the Atlantic coast of the Iberian Peninsula. Beaufortia, 305 (23): 153-168.

Maren, M. J., 1975 b. The biology of Chaetogammarus marinus (Leach) and *Eulimnogammarus obtusatus* (Dahl), with some notes on other intertidal gammarid species (Crustacea, Amphipoda). Bijdr. Dierkd. 45 (2): 205-223.

Marques, J. C., 1989. Amphipoda (Crustacea) bentónicos da Costa Portuguesa: Estudo taxonómico, ecológico e biogeográfico. Dissertação apresentada à Faculdade de Ciências e Tecnologia da Universidade de Coimbra para prestação de provas de Doutoramento em Ecologia Animal.

Marques, J. C. and A. Nogueira, 1991. Life cycle, population dynamics, and production of Echinogammarus marinus (Leach) (Amphipoda) in the Mondego estuary (Portugal). Oceanol. Acta 11: 213-223.

Marques, J. C., L. B. Rodrigues and A. J. A. Nogueira, 1993 a. Intertidal benthic communities structure in the Mondego estuary (western Portugal): Reference situation. Vie Milieu, 43 (2-3): 177-187.

Marques, J. C., P. Maranhão and M. A. Pardal, 1993 b. Human impact assessment on the subtidal macrobenthic community structure in the Mondego estuary (Western Portugal). Estuar. Coast. Shelf Sci., 37: 403-419.

Marques, J. C., I. Martins, C. Teles-Ferreira, and S. Cruz, 1994. Population dynamics, life history, and production of *Cyathura carinata* (Krøyer) (Isopoda: Anthuridae) in the Mondego estuary (Portugal). J. Crust. Biol. 14 (2): 258-272.

Maynard Smith, J., 1974. The theory of games and evolution of animal conflict. J. Theor. Biol. 47: 209-221.

Möller, P. and R. Rosenberg, 1982. Production and abundance of the Amphipoda *Corophium volutator* on the West Coast of Sweden. Neth. J. Sea Res. 16: 127-140.

Nogueira, A. J. A., 1992. ANAMOD – Extracção dos componentes modais de distribuições de frequências de variáveis biométricas. Trabalho de Síntese. Provas de Aptidão Pedagógica e de Capacidade Científica, Universidade de Coimbra: 1-67.

Pinkster, S. and N.W. Broodbakker, 1980. The influence of environmental factors on distribution and reproductive success of *Eulimmnogammarus obtusatus* (Dahl, 1938) and other estuarine gammarids. Crustaceana (Suppl.), 6. 225-241.

Skadsheim, A., 1982. The ecology of intertidal amphipods in the Oslofjord. The life cycles of *Chaetogammarus marinus* and *C. stoerensis*. Mar. Ecol., 3 (3): 213-224.

Sokal, R. R. and F. J. Rohlf, 1981. Biometry. W. H. Freeman and Co., San Francisco. 859 p.

Steele, D. H. and V. J. Steele, 1969. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. I. *Gammarus duebeni* Lillj. Can. J. Zool. 47: 235-244.

Steele, D. H. and V. J. Steele, 1970. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. III. *Gammarus obtusatus* Dahl. Can. J. Zool. 48: 235-244.

Steele, D.H. and V.J. Steele, 1975. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. XI. Comparison and discussion. Can. J. Zool. 53: 1116-1126.

Steele, D. H. and V. J. Steele, 1986. The cost of reproduction in the Amphipoda *Gammarus lawrencianus* Bousfield, 1956. Crustaceana, 51 (2): 176-182.

Van Senus, P. and A. McLachlan, 1986. Growth, production and a partial energy budget for the Amphipod *Talorchestia capensis* (Crustacea: Talitridae) in the Eastern Cape, South Africa. P. S. Z. N. I: Mar. Ecol. 7 (2): 165-179.

Wildish, D.J., 1982. Evolutionary ecology and reproduction in gammaridean Amphipoda. International J Invertebr Reprod. 5:1-19.

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