

Life cycle, dynamics, and production of *Echinogammarus marinus* [Leach (Amphipoda)] in the Mondego estuary (Portugal)

Echinogammarus marinus
Mondego estuary
Life cycle
Population dynamics
Production

Echinogammarus marinus
Estuaire du Mondego
Biologie
Dynamique de populations
Production

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ABSTRACT

A benthic sampling programme was carried out in 1985/1986, in winter and summer, in order to characterize the intertidal community structure in the Mondego estuary (Portugal). *Echinogammarus marinus* (Amphipoda, Gammaridae) was considered a key species in the algal-covered areas, and was particularly associated with *Fucus* spp. A study of its life cycle, population dynamics and production was therefore carried out.

E. marinus showed a contagious distribution, and the population density changed seasonally, with maxima during spring and summer. No migratory patterns were detected between the estuary and the sea, but migrations inside the estuary might occur. Growth was continuous throughout life, although growth rates were higher during the early phases, and females were morphologically recognizable at smaller sizes than males. In addition, males became larger than females.

Females reached sexual maturity before males, producing a succession of broods throughout the remainder of their life. Fecundity increased with the size of females. Life span was estimated to be ten to twelve months, but females showed higher mortality rates than males. This was probably due to higher costs of reproduction, possibly responsible for a decrease in female survival.

Although sexual activity was continuous throughout the year, with an increase in spring and summer, recruitment was discontinuous. In the Mondego estuary *E. marinus* is semi-annual, with three or four generations per year. Reproduction through the year, iteroparous females, high fecundity, and a multivoltine life cycle revealed 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 8.808 g.m⁻² year⁻¹ of ash-free dry weight (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/B ratios ranged from 6.1 to 6.3 and E ratios from 6.28 to 7.89. These results reinforce the generalized notion that estuaries are highly productive systems, and reflect the important role of Amphipods in the productivity of habitats colonized by them.

Oceanologica Acta, 1991. Proceedings of the International Colloquium on the environment of epicontinental seas, Lille, 20-22 mars 1990, vol. sp. n° 11, 213-223.

RÉSUMÉ

Biologie, dynamique et production d'*Echinogammarus marinus* (Leach; Amphipoda) dans l'estuaire du Mondego (Portugal)

Pour caractériser la structure des communautés benthiques intertidales de l'estuaire du Mondego (Portugal), des prospections ont été réalisées en

1985/1986, en hiver et en été. *Echinogammarus marinus* (Amphipoda, Gammaridae), en fonction de sa distribution et de son abondance, a été considéré comme une espèce-clé dans les peuplements algaux, surtout en association avec *Fucus* spp. La biologie, la dynamique et la production de cette espèce ont fait l'objet de cette étude.

E. marinus présente une distribution de type contagieux et la densité varie tout le long de l'année, les valeurs maximales ayant été trouvées au printemps et en été. Il n'a pas été possible de montrer l'existence de migrations entre l'estuaire et la mer, mais il est possible que des migrations à l'intérieur de l'estuaire puissent se produire.

La croissance est continue tout le long de la vie ; elle est toutefois plus forte chez les juvéniles. La différenciation sexuelle est atteinte plus tôt chez les femelles ; cependant les mâles atteignent des tailles supérieures.

Les femelles atteignent la maturité sexuelle avant les mâles, et libèrent une succession de portées pendant le reste de leur vie. La fécondité augmente en fonction de la taille des femelles. La longévité ne dépasse pas dix à douze mois. Les taux de mortalité sont néanmoins plus forts chez les femelles, en relation probablement avec l'effort de reproduction, qui provoque une diminution de la longévité chez les femelles.

L'activité sexuelle est continue tout le long de l'année, avec un maximum au printemps et en été ; cependant le recrutement s'effectue en cohortes successives. Dans l'estuaire du Mondego, *E. marinus* est semi-annuelle, avec trois à quatre générations par an. La reproduction continue, les femelles itéropares, la haute fécondité et un cycle reproducteur de type multivoltin semblent correspondre à une stratégie adaptative de type r.

La production de *E. marinus* dans le peuplement de *Fucus* spp. a été calculée : production nette (P) de 6,36 à 8,808 g.m⁻².an⁻¹ de poids sec décalcifié (AFDW) (76,16 à 105,48 KJ.m⁻².an⁻¹) et production de transfert (E) de 6,33 à 11,44 g.m⁻².an⁻¹ (AFDW) (75,84 à 137,04 KJ.m⁻².an⁻¹). Les P/B estimés sont compris entre 6,1 et 6,3, et les entre 6,28 et 7,89. Ces résultats renforcent la notion générale que les estuaires sont des systèmes de haute productivité, et traduisent l'importance des amphipodes dans la production des habitats qu'ils habitent.

Oceanologica Acta, 1991. Actes du Colloque International sur l'environnement des mers épicontinentales, Lille, 20-22 March, 1990, vol. sp. n° 11, 213-223.

INTRODUCTION

A benthic sampling programme was carried out in 1985/1986, in the winter and summer periods, to characterize the intertidal community structure in the Mondego estuary (Marques, 1989). Amphipods appeared to have a very important role in the studied communities, in both hard and soft bottoms. Data analysis showed that only 18 of the 105 identified species had a relevant role in the observed structure (Marques *et al.*, 1988; Marques, 1989). Of these species, four (22 %) were Amphipods (*Echinogammarus marinus*, *Hyale stebbingi*, *Leptocheirus pilosus*, and *Melita palmata*), which therefore appeared as a group of primary importance. *E. marinus* (Gammaridae) with an extensive distribution and abundance in rocky habitats, was considered a key species in the algal covered habitat of *Fucus* spp.

E. marinus is in fact strongly euryhaline, able to support long emersion periods (Dorgelo, 1973; Pinkster and

Broodbakker, 1980), and consequently very well adapted to life in estuaries. Its known distribution extends from Norway to the coast of Portugal, and some studies have already been carried out on different aspects of its biology and ecology (Maren, 1974; 1975 a; 1975 b; Pinkster and Broodbakker, 1980; Skadsheim, 1982). Nevertheless, its biology and production have been poorly investigated. Therefore, a study of the life cycle, population dynamics and production of this species was carried out, from October 1985 to September 1987.

MATERIAL AND METHODS

Study site

The Mondego estuary, on the western coast of Portugal (Fig. 1) is a warm-temperate coastal system in a region with a basically Mediterranean temperate climate. It

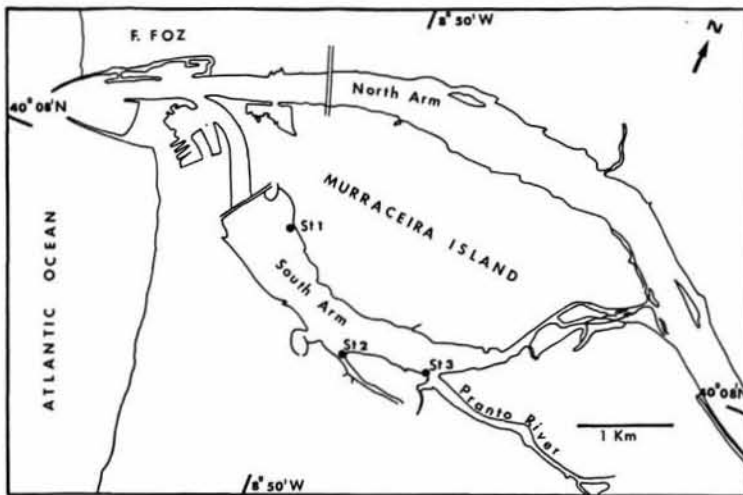


Figure 1

The Mondego estuary: location of the sampling stations in the southern arm.

L'estuaire du Mondego: localisation des stations d'échantillonnage dans le bras sud.

comprises two arms, northern and southern (Fig. 1), with very different hydrographic characteristics. The north arm is deeper, while the south arm is almost silted up in the upper zones, which causes the fresh water to flow essentially by the northern arm. Circulation in the southern arm is mostly assured by tides and the usually small freshwater input of the Pranto river. In addition, due to differences in depth, the penetration of the tide is faster in the northern arm. This causes daily changes in salinity to be much stronger, whereas daily temperature changes are greater in the southern arm (Marques, 1989).

Within both arms of the estuary hard substrates are covered primarily by *Fucus* spp., which constitutes an eulittoral macroalgae belt. These hard substrates are essentially the result of human occupation (*e. g.* harbour facilities, aquaculture farms, salt-works), and extend present to at least 60 % of the margins of the Mondego estuary, representing an important portion of the intertidal area.

From preliminary sampling, *E. marinus* abundances were expected to be high in this habitat, particularly in the south arm. Moreover, high densities of the species usually depend on the immediacy of mud bottoms. Examination of the population dynamics of *E. marinus* in this estuary, which is the southern limit of its known distribution (Marques, 1989), and the comparison with data from other locations should provide an opportunity to analyze the intraspecific life-history variation of a gammarid along a latitudinal gradient. In addition, it should permit estimation of production of an important warm-temperate estuarine species.

Field programme

To assess population dynamics and field growth rates a schedule of monthly field sampling in three stations (Fig. 1) in the southern arm was established, for a two-year period, from October 1985 to September 1987. The location of the sampling stations reflected the abundance of *E. marinus* in the southern arm, and the selection of points accessible all the year round. Although this sampling periodicity might be insufficient (Fredette and Diaz, 1986 *a*), due to logistic

constraints it was not possible to sample more frequently. Sampling was conducted at low tide, which facilitated 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 on to a sheet of polyethylene, which was later weighed (the biggest replicate was 0.2334 m², and the smallest one was 0.093 m²). Samples (algae plus sediment) were preserved in 4% buffered formalin, and later poured into a 0.5 mm mesh bag for sieving. Given the size of newly hatched juveniles, this mesh should retain all individuals. The specimens were then kept in 70 % ethanol. The values of salinity, temperature, dissolved oxygen, 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.

Laboratory procedures

Amphipods were counted, and the cephalic length (L) was measured to the nearest 0,02 mm. Since the bodies are comma-shaped, total length (L) is not a very convenient standard to judge age and growth. On the other hand, the cephalic length (L) (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: $L_T = -1.211995 + 10.668509 L_C$ ($r = 0.986$).

The determination of 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 similar criteria (Goedmakers, 1981; Skadsheim, 1982; Steele and Steele, 1969), five stages were considered: a) newly laid, eggs grouped and resembling 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 60°C for 72 h and weighed to the nearest 0.01 mg. Percentage of 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 microbomb 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). 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 values were then used to estimate amphipod abundance by multiplying A (number of amphipods per gram of algae in each sample) by B (mean grams of algae per square metre 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:

$$Y' = a + b_1X_1 + b_2X_2 + \dots + b_kX_k$$

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

X_1, X_2, \dots, X_k - are independent variables (*e. g.* salinity); the solutions are the estimate of the regression coefficients a, b_1, b_2, \dots, b_k . 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 least squares method and normal equations were solved by the matrix inversion method.

Growth rates were estimated by tracking recognizable

cohorts with size-frequency distributions (0.02 mm length classes) from successive sample dates. Size-frequency modal analysis was done by using the probability paper method (Harding, 1949) as performed by Cassie (1954; 1963). The reliability of the method was tested by using the G test [$P \leq 0.05$ (Fisher, 1950; Sokal and Rohlf, 1981)].

Growth rates are not constant throughout the year. Thus, to express field growth rates, we used a model that takes into consideration seasonal changes (Gaschtz *et al.*, 1980), expressed as:

$$L_t = L_{\infty} \{ 1 - e^{-[kD(t-t_0) + C(kD/2\pi) \sin 2\pi(t-t_s)]} \}^{1/D}$$

L_t : 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 one year;

k : intrinsic growth rate;

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

D : parameters that expresses metabolic deviations from the Von Bertalanffy 2/3 rule.

Production estimates were based upon cohort recognition. Growth increments or production increments (P) and elimination production (E) were calculated with a method derived from Allen (1971), as described in Dauvin (1986). Approximate values of P and E for each cohort during a time interval are expressed as:

$$P = [(N_t + N_{t+1})/2] * (\bar{W}_{t+1} - \bar{W}_t) \text{ for } \bar{W}_{t+1} > \bar{W}_t$$

$$E = [(\bar{W}_t + \bar{W}_{t+1})/2] * (N_t - N_{t+1}) \text{ for } N_t > N_{t+1}$$

N : density of the cohort in each sample date;

\bar{W} : mean individual biomass in each sample date;

t and $t + 1$: consecutive sample dates.

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

$$P = \sum_{t=0}^{t=n} [(N_t + N_{t+1})/2] \Delta \bar{W}$$

$$E = \sum_{t=0}^{t=n} [(\bar{W}_t + \bar{W}_{t+1})/2] \Delta N$$

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

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

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

P_{cn} and E_{cn} are the growth and elimination production of the cohort n .

\bar{P}/\bar{B} and \bar{E}/\bar{B} ratios were determined. \bar{B} (mean population biomass) is expressed as:

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

T : period of study;

N : number of successive cohorts in the period T ;

\bar{B}_n mean biomass of the cohort n ;

t : duration of the cohort n .

RESULTS

Population structure

Abundance, spatial dispersion

E. marinus showed a contagious distribution in the algal-covered habitats of *Fucus* spp. (the values of I, calculated for each group of nine replicate samples, 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 maxima during spring and summer (Fig. 2). Interannual differences of 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 are not consistent enough to demonstrate this. On the other hand, taking into consideration data from outside the estuary (Rosa Lopes and Marques, in press), it was not possible to detect any migratory patterns between the estuary and the sea.

Period of reproduction

The *E. marinus* population was sexually active throughout the year in the Mondego estuary. However, taking into consideration the percentage of ovigerous

females over the total female population (Fig. 3), sexual activity was higher from early spring (March/April) to the middle of summer (August), and then decreased until early winter (December). 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 ceased. The variation of the percentage of juveniles in the population (Fig. 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.

Sex-ratio

The sex-ratio almost always favoured females (Fig. 4). Nevertheless, maxima in the male proportion occurred in January/February and April/May, in 1986 and 1987, and in August 1987. These maxima were normally followed by increases in the percentage of females at sexual rest (oostegites present, with or without setae, but no broods) (Fig. 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 2

Abundance variation from October 1985 to September 1987: global values (mean of all samples) (GL) and values for each sampling station (station 1, station 2, station 3) are given.

Variation de l'abondance d'octobre 1985 à septembre 1987: Les valeurs globales (moyenne des prélèvements) (GL) et les valeurs concernant chaque station (station 1, station 2, station 3) sont données.

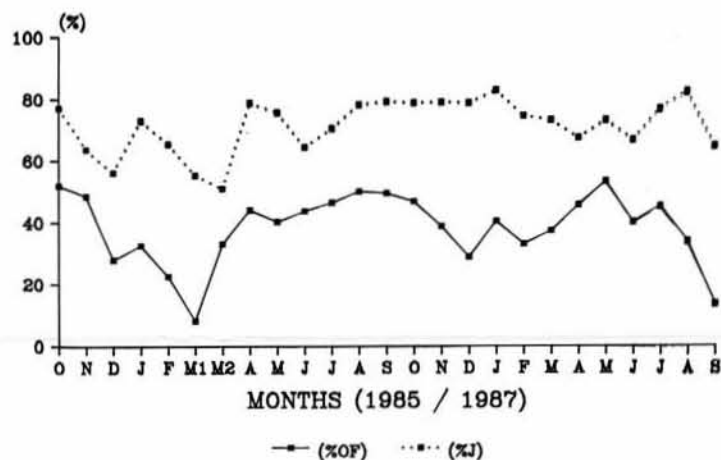
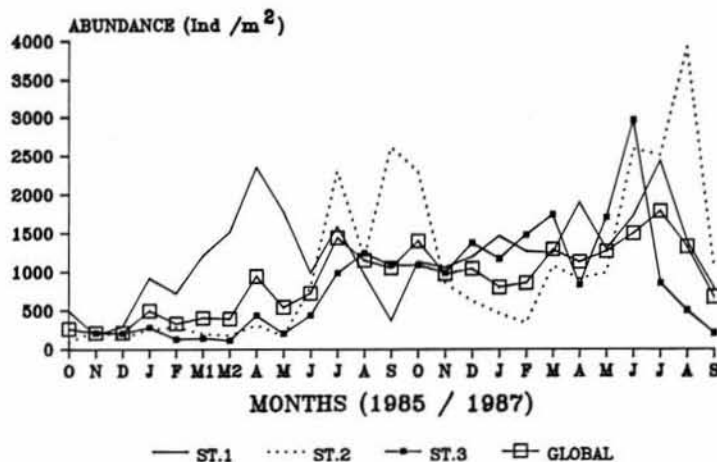


Figure 3

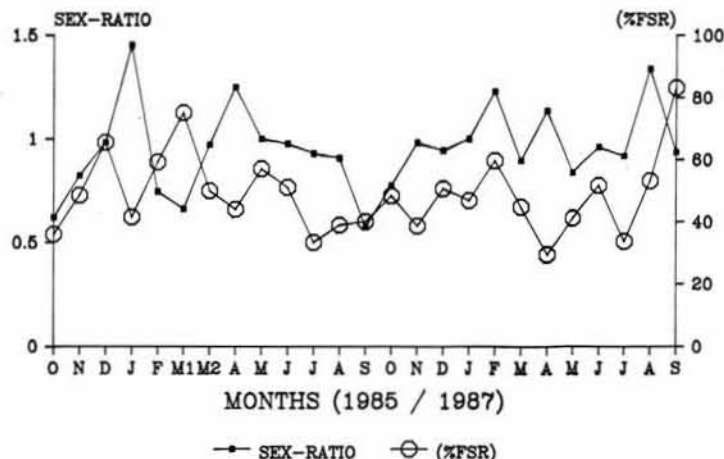
Variation of the percentage of ovigerous females in the total female population (% OF) and of the percentage of juveniles in the population (% J), from October 1985 to September 1987.

Variation du pourcentage de femelles ovigères par rapport au total de femelles (% OF) et du pourcentage de juvéniles dans la population (% J), d'octobre 1985 à septembre, 1987.

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.

Variation du sex-ratio et du pourcentage de femelles en repos sexuel [oostegites avec ou sans soies, pas d'oeufs (% FSR)], d'octobre 1985 à septembre 1987.



Fecundity

The fecundity of females of similar sizes was quite variable. 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 L_C
(80 females; r = 0.8220)

Stage B: - NE = - 33.570 + 44.662 L_C
(257 females; r = 0.5684)

Stage C: - NE = - 31.421 + 41.222 L_C
(82 females; r = 0.6239)

Stage D: - NE = - 33.673 + 39.153 L_C
(151 females; r = 0.5500)

For this purpose we did not take into consideration embryos in stage E, that can freely get in and out of brood

Table 1

Mean diameter and standard deviation of eggs at development stages A, B, C, and D, for *E. marinus* in the Mondego estuary.

Diamètre moyen et déviation standard des oeufs dans les états de développement A, B, C et D, pour *E. marinus* dans l'estuaire du Mondego.

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

Table 2

Multiple regression models for *E. marinus*: abundance (D), sex-ratio, 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), dissolved oxygen (OXYG), pH, nitrites (NTI), nitrates (NTA), and phosphates (PHOS). R: multiple regression coefficients. Values of significance tests (F and t) are given.

Modèles de regression multiple pour *E. marinus*: l'abondance (D), le sex-ratio, le pourcentage de femelles ovigères par rapport au total de femelles (% OF), le pourcentage de juvéniles dans la population (% J) et la fécondité (NE) sont rapportés avec la salinité (SAL), la température (T), l'oxygène dissous (OXYG), le pH, les nitrites (NTI), les nitrates (NTA) et les phosphates PHOS). R: coefficients de regression multiple. Les valeurs des tests significatifs (F et t) sont données.

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

		SAL	T	OXYG	pH	NTI	NTA	PHOS	R _{YY'}	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

pouches. Lost of eggs during development were therefore estimated as 28 %, which might be due to incomplete fertilization, disease, parasitism, or other accidental causes.

Since Amphipods have synchronized embryonic development, all the eggs in a given brood pouch are normally at the same stage. Measurements of eggs (Tab. 1) showed that, during development, they increase 36% in mean ovular diameter and 84 % in volume. Since losses of eggs were \approx 28 %, an increase of 32 % in the brood pouch volume might be enough to allow the observed 84 % augmentation in eggs volume.

The influence of salinity, temperature, dissolved oxygen, pH, nitrites, nitrates and phosphates in the water on abundance, sex-ratio (percentage of ovigerous females, percentage of juveniles in the population, and fecundity was analysed (Tab. 2).

Abundance was positively correlated with temperature and dissolved oxygen ($P \leq 0,05$). 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 increased abundance in spring and summer.

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 deoxygenation 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 recognizable cohorts (Fig. 5 and 6). In October 1985 we identified ten cohorts, and thirty new ones were recognized during the study period. Minimum mean L_C of cohorts ranged from 0.315 to 0.487 mm (2.15 to 3.98 mm L_T). This might have depended on the number of days from hatching to cohort

recognition, and therefore on sampling periodicity. Maximum mean L_C of cohorts ranged from 1.86 to 2 mm (18.62 to 20.13 mm total length). The biggest male had 2 mm L_C (20.16 mm L_T), and the biggest female 1.86 L_C (18.63 mm L_T ; Fig. 7).

Field growth rates were estimated from the mean size of recognizable cohorts. 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 ten to twelve months. However, as mentioned earlier, males live longer than females.

A growth model (Gaschütz *et al.*, 1980) was used on data from cohorts 10, 13, 17, and 21, firstly recognized in autumn, winter, spring, and summer sample dates (Fig. 8). In all cases a decrease in growth rate corresponding to the winter period become evident. This decrease was probably to lower metabolism caused by lower temperatures, and also to less available nutrients.

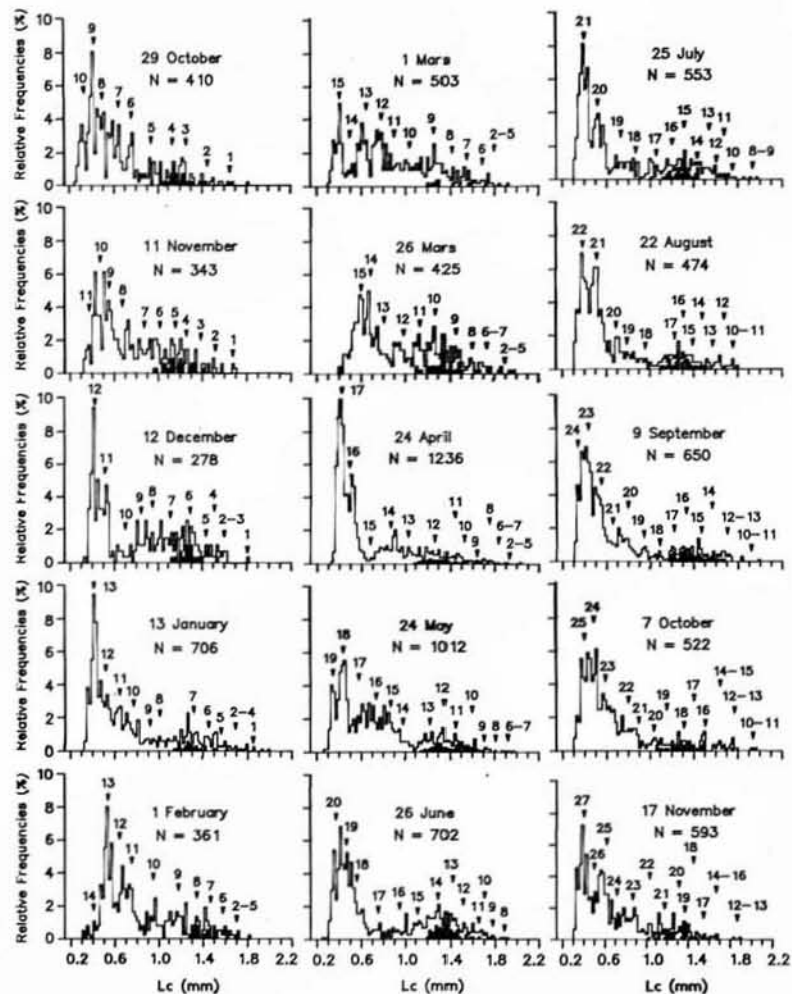


Figure 5

Size-frequency distribution of *Echinogammarus marinus* in the Mondego estuary, from October 1985 to November 1986. N: number of measured individuals; shadowed areas indicate ovigerous females; arrows indicate mean cephalic length of the numbered cohorts or groups of cohorts.

Histogrammes de fréquence des classes de longueur d'*Echinogammarus marinus* dans l'estuaire du Mondego, d'octobre 1985 à novembre 1986. N : nombre d'individus mesurés ; les parties pleines des histogrammes correspondent aux femelles ovigères.

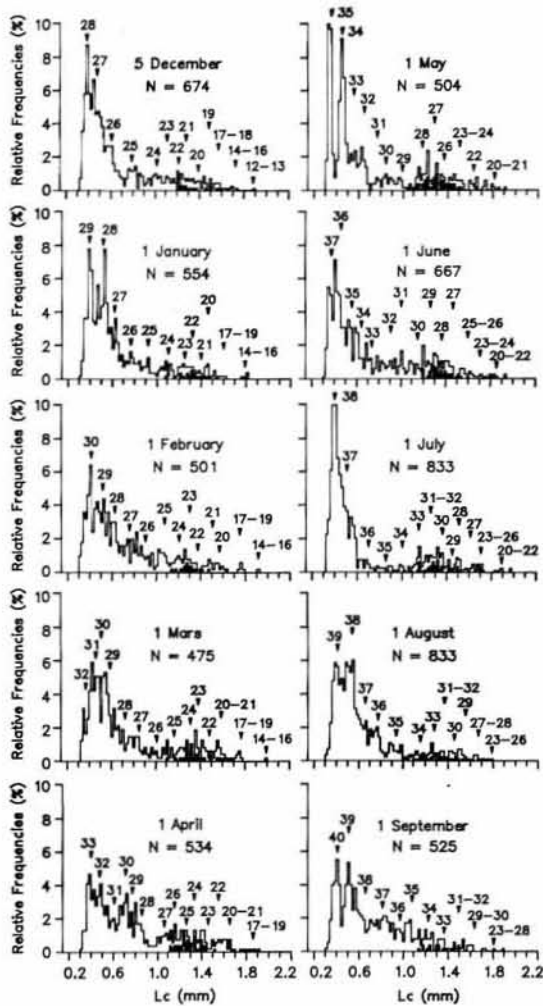


Figure 6
Size-frequency distribution of *Echinogammarus marinus* in the Mondego estuary, from December 1986 to September 1987. N; number of measured individuals; shadowed areas indicate ovigerous females; Arrows indicate mean cephalic length of the numbered cohorts or groups of cohorts.

Histogrames de fréquence des classes de longueur d'*Echinogammarus marinus* dans l'estuaire du Mondego, de décembre 1986 à septembre 1987. N : nombre d'individus mesurés ; les parties pleines des histogrames correspondent aux femelles ovigères.

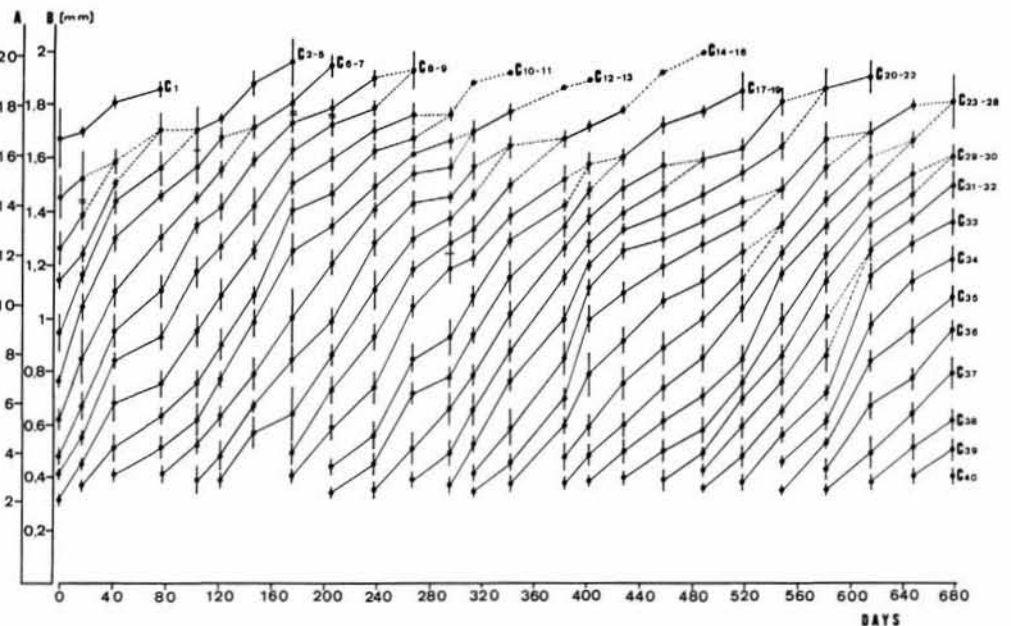


Figure 7
Growth of cohorts or groups of cohorts (mean cephalic length standard deviation), from October 1985 to September 1987. A: total length; B: cephalic length. Broken lines indicate probable evolutions.

Croissance des cohortes ou groupes de cohortes (longueur céphalique moyenne déviation standard) d'octobre 1985 à septembre 1987. A : longueur totale ; B : longueur céphalique. Les tirets indiquent des évolutions probables.

Males were recognizable with 0.86 0.06 mm L_C (standard 7 deviation) and females with 0.79 0.04 mm L_C (7.95 0.66 and 7.25 7% 0.42 mm L_T), i. e. 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 maxima in spring and summer, and therefore juveniles were always an important element of the population. The smallest seven ovigerous females had 1.12 0.074 mm L_C (10.68 0.8 mm L_T), which corresponded to an age of fourteen to nineteen weeks.

Percentage of ovigerous females in each cohort (Fig. 9) was determined from size frequency analysis (Fig. 5 and 6). We estimated that each female can 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 (multivoltin life cycle).

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:

$$W = 1,5929 * L_C^{3.9344} \text{ (W - ash-free dry weight)}$$

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^{-1} AFDW respectively). Growth production (P) ranged from 6.36 to 8.808 $g.m^{-2}.year^{-1}$ of ash free dry weight (AFDW) (76.16 to 105.48 KJ. $m^{-2}.year^{-1}$) and elimination production (E) from 6.33 to 7 11.44 $g.m^{-2}.year^{-1}$ DDW (75.84 to 137.04

Figure 8

Graphic adjustment of the growth curves of cohorts 10, 13, 17, and 21. Values of mean 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.

Ajustement graphique des courbes de croissance des cohortes 10, 13, 17 et 21. Les valeurs de la longueur céphalique moyenne calculée pour chaque instant sont aussi signalées. A : longueur totale ; B : longueur céphalique ; r : corrélation entre les courbes et les valeurs signalées.

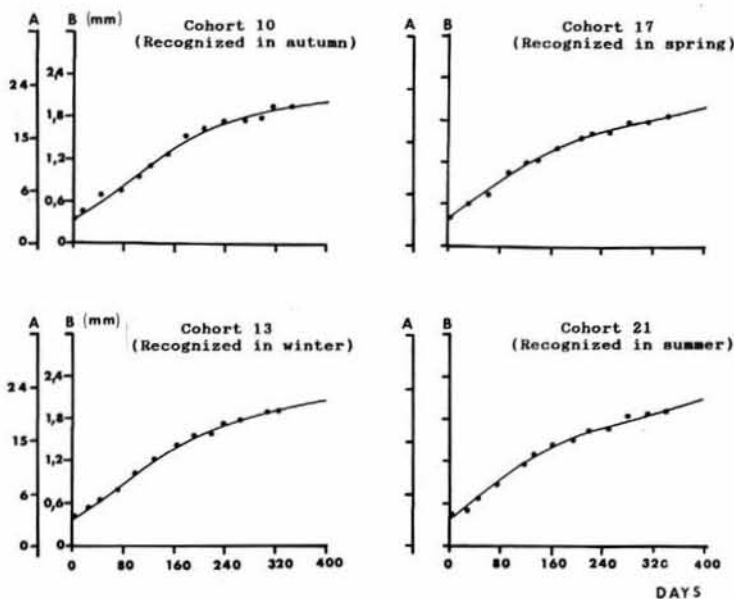
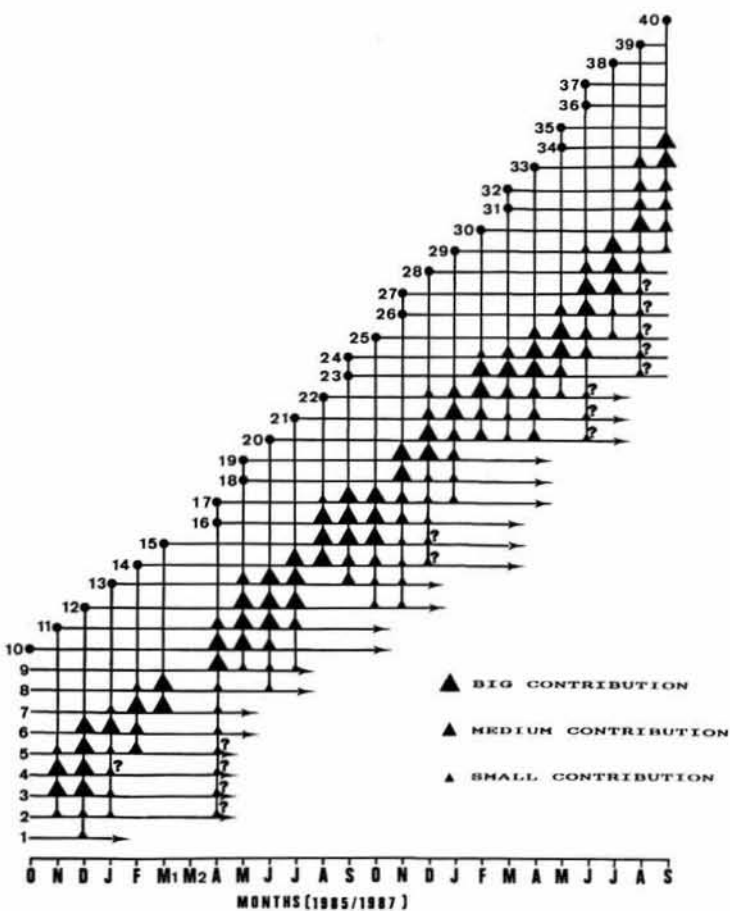


Figure 9

Analysis of sexual activity: The contributions of the females of each cohort or group of cohorts 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.

Analyse de l'activité sexuelle : les contributions des femelles de chaque cohorte ou groupe de cohortes sont indiquées. Big contribution : plus de 20 % du total de femelles ovigères ; contribution moyenne : de 10 à 20 % ; small contribution : moins de 10 % ; ? contribution possible.



$KJ.m^{-2}.year^{-1}$). P/\bar{B} ratios ranged from 6.1 to 6.3 and ratios from 6.28 to 7.89.

DISCUSSION

E. marinus showed a contagious distribution and the population abundance showed clear seasonal variations,

with maxima 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 are insufficient to confirm this. Thus, despite the significant correlation found between abundance and temperature, and salinity, 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 beriloni* (Goedmakers, 1981).

Growth is continuous throughout the life. Females are morphologically recognizable and reach sexual maturity before males, and then produce a succession of broods during the rest of their 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 a little 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 cohorts was dependent on sampling periodicity and on the retention of newly hatched juveniles within brood pouches. The release of juveniles might be related with spring tides, when survival conditions might be maximized.

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 his 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 univoltin in Denmark, in a cold-temperate to sub-polar climate (Skadsheim, 1982), and bivoltin 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.

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- Both growth production (P) and elimination production (E), when compared with values found in the 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; Müller and Rosenberg, 1982; Van Sensus and McLachlan, 1986) can be considered to be elevated. Data on *E. marinus* production from the Mondego reinforces the generalized notion of estuaries as highly productive systems. It also reflects the important role of amphipods concerning the production of habitats colonized by them.

Acknowledgements

The present work was supported by INIC and JNICT (Portuguese national institutions for scientific research).

The authors are indebted to D. Bellan-Santini (Station Marine d'Endoume, Marseille) and to Professor Luiz Saldanha (University of Lisbon, Portugal) for their scientific support.

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