MIGUEL ÂNGELO PARDAL
JOÃO CARLOS MARQUES
MANUEL AUGUSTO GRAÇA
Scientific Editors

Aquatic Ecology of the Mondego River Basin
Global Importance of Local Experience

Coimbra • Imprensa da Universidade

MIGUEL ÂNGELO PARDAL
JOÃO CARLOS MARQUES
MANUEL AUGUSTO GRAÇA
Scientific Editors

Aquatic Ecology of the Mondego River Basin

Global Importance of Local Experience

Coimbra • Imprensa da Universidade

Coordenação editorial
Imprensa da Universidade de Coimbra

Concepção gráfica
António Barros

Infografia
António Resende
Estímulus [design] • Coimbra

Execução gráfica
GRAFIASA

Ilustração da capa
P. P. Cunha e J. Dinis

ISBN
972-8704-04-6

Depósito legal
175038/02

OBRA PUBLICADA COM O PATROCÍNIO DE:
IMAR – INSTITUTO DO MAR
IPIMAR – INSTITUTO DE INVESTIGAÇÃO DAS PESCAS E DO MAR

Miguel Ângelo Pardal [1]
João Carlos Marques [1]
Susana Ferreira [1]
Irene Martins [1]
Ana Isabel Lillebø [1]

LIFE CYCLE, BIOLOGY AND PRODUCTION OF AN ESTUARINE ISOPOD *(Cyathura carinata)*

Abstract

The life cycle, population dynamics and production of *Cyathura carinata* (a keystone species in the Mondego estuary, Portugal) is described from an intertidal mudflat along a spatial gradient of eutrophication. New information is presented concerning the role of macroalgal blooms in the biology, dynamics and production of the estuarine isopod *C. carinata*. A previous hypothesis that large and extensive macroalgal blooms could bring about the disappearance of this species from the intertidal area was not supported. Moreover, it seemed that large biomasses of the macroalgal *Enteromorpha* sp. could favour the population in the Mondego estuary. Just one annual cohort was produced in June, in opposition to previous studies. Our results suggest that *C. carinata* is an annual species in the Mondego estuary, with univoltine life cycle.

Growth production (P) of *C. carinata* during the algal bloom was 10.543 $g.m^{-2}$ 4 $month^{-1}$, and 19.623 $g.m^{-2}$ $year^{-1}$, and without macroalgae 7.718 $g.m^{-2}$ 4 $month^{-1}$, and 11.795 $g.m^{-2}$ year-1. $P/\overline{B}$ and $E/\overline{B}$ ratios were always lower during the macroalgae blooms, which is consistent with the idea that the energy flow is smaller in these periods because the standing stock is much higher. Moreover, this paper reveals that conclusions based on just one annual cycle can be incorrect. Longer sampling programs are needed to have a better understanding of the real dynamics of macrobenthic species in very dynamic systems.

Introduction

Most European estuaries are affected by organic pollution, which often gives rise to eutrophication (Dijk et al. 1994, Flindt et al. 1997, Hickel and Mangelsdorf 1993, Marques et al. 1997, Martins et al. 2001, Pardal 1998, Pardal et al. 2000, Raffaelli et al. 1998, Yeates 1993). Eutrophication, as a response to nutrient enrichment, may commonly cause proliferation of opportunistic green macroalgae, such as

---

(1) IMAR – Instituto do Mar, Centro Interdisciplinar de Coimbra, a/c Departamento de Zoologia, Universidade de Coimbra, 3004-517 Coimbra, Portugal

Chaetomorpha, *Enteromorpha* and *Ulva*, which can cover extensive areas of the estuarine intertidal zones. For example, it has been observed that benthic eutrophication in coastal areas may drive a shift from rooted plants communities, dominated by slow growing species, (e.g. *Zostera*), towards faster growing macroalgae (Hartog 1994, Martins et al. 2001, Pardal 1998, Pardal et al. 2000), as well as changes in the biomass and species composition of macroalgae (Lavery et al. 1991, Pardal 1998). This shift in primary producers may of course determine changes in species composition at other trophic levels (e.g. macrofaunal composition) originating a new trophic structure (Pardal 1998).

Seasonal intertidal macroalgal blooms (mainly of *Enteromorpha* spp.) have been reported in the South Arm of the Mondego estuary for several years (Cabral et al. 1999, Flindt et al. 1997, Lillebø et al. 1999, Marques et al. 1993a, 1993b, 1997, Martins et al. 1997, 2001, Pardal et al. 1993, 2000, Pardal 1998). Nevertheless, such macroalgal blooms may not occur in exceptionally rainy years (e.g. year 1994) due to the occurrence of low salinity values and strong water currents for long periods, as a result of Pranto River discharge (Martins et al. 2001, Pardal 1998, Pardal et al. 2000).

The isopod *Cyathura carinata* is one of the most abundant macrofaunal species in the Mondego estuary and extensively distributed throughout intertidal mudflats especially in the South Arm (Marques and Nogueira 1991, Marques et al. 1993a, 1993b, 1994, Martins et al. 1997, Pardal 1998).

Cyathura carinata is very well adapted to life in estuaries and is widely distributed along the European coast, from the Baltic to the Mediterranean. Several studies on the biology and ecology of *C. carinata* were made (Bamber 1985, Burbanck and Burbanck 1975, Eslava 1994, Jadzewski 1969, Legrand and Juchault 1963, Marques et al. 1994 Martins et al. 1997, Ólafsson and Persson 1986), but the impact of the macroalgal blooms on the life cycle, population dynamics and production have received little attention. (Martins et al. 1997, Pardal 1998).

Materials and methods

Study site and sampling

The Mondego estuary is a warm-temperate coastal system (Fig. 1). It consists of two arms, north and south, with very different hydrologic characteristics. The northern arm is deeper, while the southern arm is largely silted up, especially in upstream areas, which causes most of the fresh-water discharge to flow through the northern arm. Consequently, the water circulation in the southern arm is mainly dependent upon tidal activity and on the, usually small, fresh-water input of the tributary, the Pranto River that is controlled by a sluice.

Although a large part of the intertidal area of the southern arm still remains more or less unchanged, macroalgae blooms of *Enteromorpha* spp. have been regularly observed during the last 15 years. This is probably a result of excessive nutrient release into the estuary, coupled with longer persistence of nutrients (nitrogen and

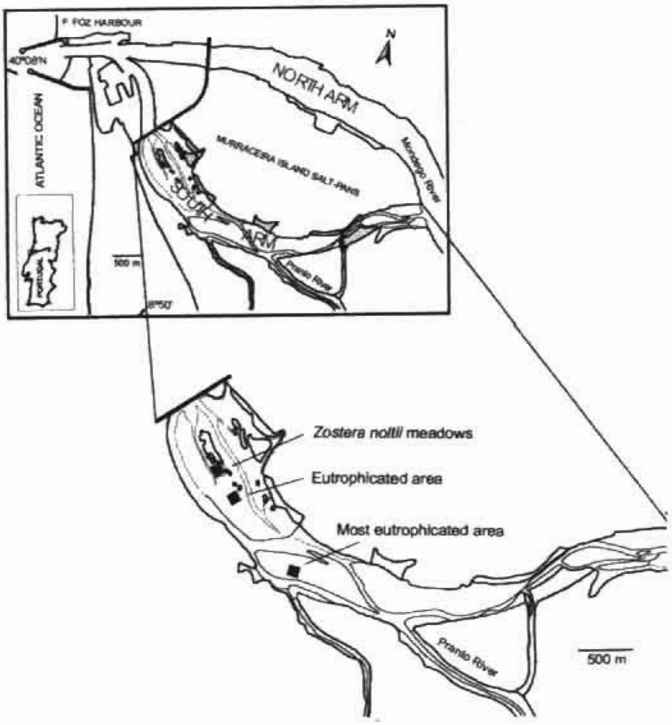

Fig. 1. Location of the sampling stations along a spatial gradient of eutrophication in the Mondego estuary, Portugal.

phosphorous) in the water column (Flindt et al. 1997, Marques et al. 1997, Martins et al. 2001, Pardal 1998, Pardal et al. 2000). Nevertheless, such macroalgae blooms may not occur in exceptionally rainy years (e.g. year 1994) due to the occurrence of low salinity values and strong water currents for long periods, as a result of the Pranto river discharge (Martins et al. 2001, Pardal 1998).

The population of *C. carinata* was monitored for 18 months, from January 1993 to June 1994. Samples of macrophytes, macroalgae, and associated isopods were taken fortnightly at three different sites, during low water, along an estuarine gradient of eutrophication in the south arm of the estuary (Fig. 1). From a non eutrophicated zone where a macrophyte community *(Zostera noltii)* was present, up to a heavily eutrophicated zone, in the inner areas of the estuary, from where the macrophytes have disappeared and *Enteromorpha* spp. blooms have been observed there over the last decade. In this area, as a pattern, *Enteromorpha* spp. biomass normally increases from early winter (January/February) up to July, when an algal crash usually occurs due to anoxia and most of the biomass is washed out into the Atlantic.

Each sampling date at each site, 10 cores (with 141 cm^2) were taken randomly to a depth of 15 cm. Each core was placed in a separate plastic bag and sieved within an hour of sampling by washing it in seawater through a 500 µm mesh sieve.

Laboratory procedures

Isopods were identified, counted, measured and sexed. Due to the difficulties inherent in measuring Total body Length (T_L) accurately in such a small species, an alternative and more accurate length was measured; the Cephalic Length (C_L). In the present paper we used the conversion equation C_L-T_L ($T_L = 0.745 + 9.01C_L$) and length-weight relationships ($W = 0.01906\ C_L^{2.7182}$) for production estimates determined in a previous study also made on the Mondego estuary (Marques et al. 1994). Individuals were dried at 60 °C for 72 h and weighed to the nearest 0.01 mg. AFDW was assessed after combustion of samples for 8 h at 450 °C. The same procedure was used to quantify the macroalgae and *Zostera noltii* biomasses.

The determination of sex was based on the presence or absence of oostegites in pereiopods and/or broods in females, or the presence of an appendix masculina on the second pair of pleopods in males. Animals without these features were considered to be juveniles. 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 (Bamber, 1985, Jadzewski, 1969, Marques et al, 1994) three stages were considered: a) newly laid eggs, which are slightly oblong, internally homogeneous, and have a double membrane; b) embryos which are clearly elongated, possess developing pereiopods and visible antennae; c) hatched juveniles contained in the brood pouch.

Data analysis

An index $I = S^2X / \bar{X}$; was used to analyse the population's spatial dispersion, where S^2 is the variance of abundance and $\bar{X}$ is the mean abundance (Elliot, 1977). Stepwise, least squares multiple regression models for *C. carinata* were developed, to examined the relationship between the density and biomass of *C. carinata* and the biomass of macroalgae, salinity and water temperature. All variables except temperature and salinity were subjected to a $ln\ (x + 1)$ transformation prior to analysis in order to minimise heteroscedasticity. Only variables with partial effects significant at $P < 0.01$ level were retained in the regression model. Regressions were performed using the Stepwise Forward Analysis method performed by the STATGRAPHICS 4.0 statistical package.

Growth rates were estimated as in previous papers (Lillebø et al. 1999, Marques and Nogueira 1991, Marques et al. 1994, Pardal 1998, Pardal et al. 2000) by tracking recognisable cohorts with size frequency distributions from successive sample dates.

Production was estimated as in previous papers (Lillebø et al. 1999, Marques and Nogueira 1991, Marques et al. 1994, Pardal et al. 2000, Pardal 1998) and was based upon cohort recognition. Growth increments or net production (P) and elimination production (E) were estimated with a method derived from Allen (Allen 1971), as described in Dauvin (1986).

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

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

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

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

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

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

where *T*: period of study; *N*: number of successive cohorts in the period *T*; B_n: mean biomass of the cohort *n*; *t*: duration of the cohort *n*.

Results

Macrophyte and macroalgae biomasses

As expected, *Zostera noltii* biomass exhibited a clear seasonal variation. During autumn and winter total biomass depended essentially on the rhizomes, and during spring and summer total biomass increased due to the growth of leaves (Fig. 2A).

The specific composition of macroalgal biomass changed very much along the eutrophication gradient. Red macroalgae, essentially *Gracilaria* sp., were relatively abundant at the *Zostera noltii* meadows, decreasing along the eutrophication gradient, while green macroalgae (*Enteromorpha* sp.) showed exactly the opposite pattern (Fig. 2).

In the eutrophicated area small amounts of green macroalgae were present in both spring seasons, but the biomasses estimated could not be considered a typical bloom.

In the most eutrophicated area *Enteromorpha* sp. presented a typical spring bloom in 1993, with biomass reaching 413 g.m^{-2} (AFDW) in April. In early summer an algal crash occurred which had a severe impact on the macrofauna in the area attained by the phenomenon (Figs. 2 and 3). In 1994 no macroalgal blooms were observed because it was a very rainy year and the sluice of the Pranto river discharged large amounts of freshwater direct in the estuary causing low salinities and strong water currents. Such conditions inhibited *Enteromorpha* growth, since salinity was below 10‰ for several months.

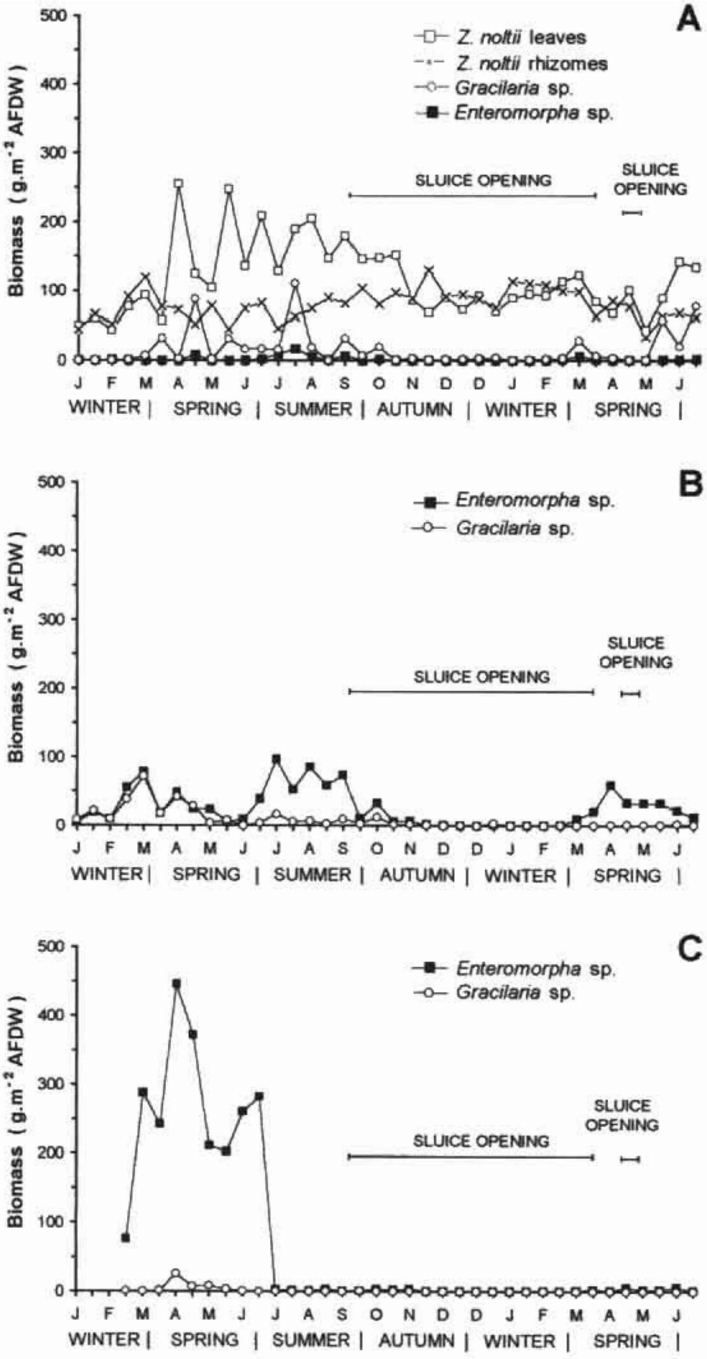

Fig. 2. Seasonal changes in plant biomass along the eutrophication gradient. (A) *Zostera noltii* meadows; (B) Eutrophicated area; (C) Most eutrophicated area.

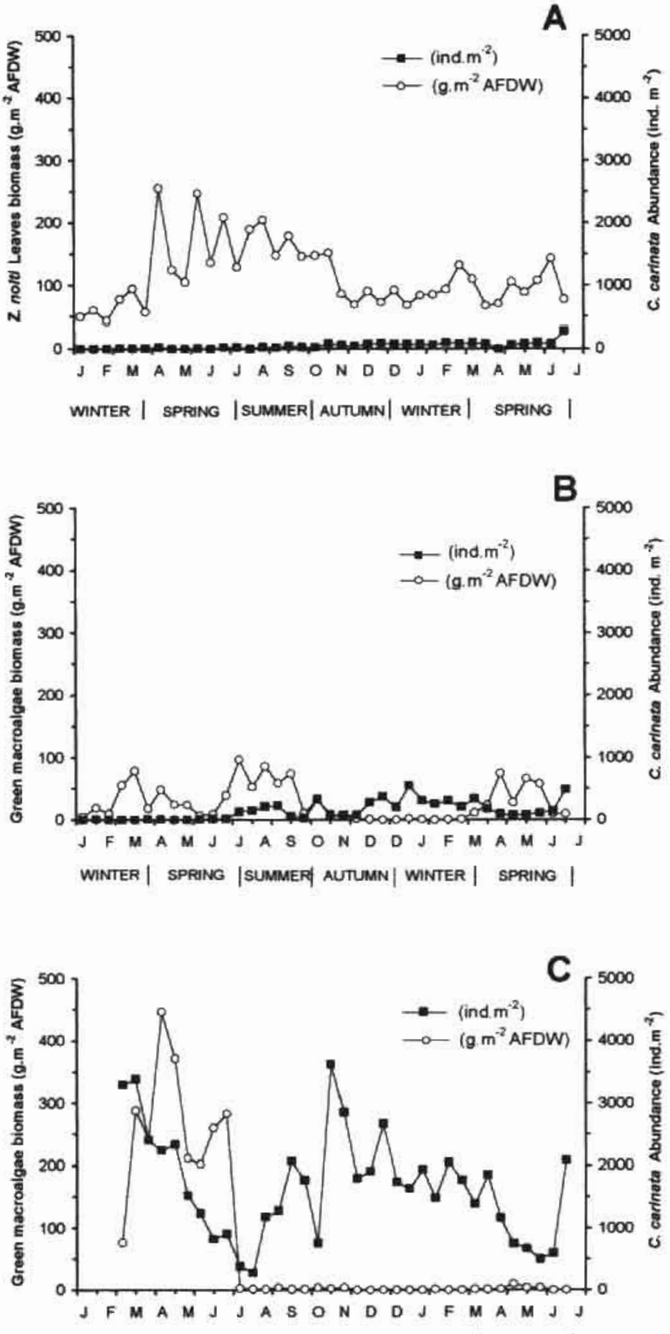

Fig. 3. Abundance of *C. carinata* along the eutrophication gradient. (A) *Zostera noltii* meadows; (B) Eutrophicated area; (C) Most eutrophicated area.

Spatial distribution and abundance

Cyathura carinata showed an aggregated spatial distribution in the three study areas along the eutrophication gradient. Estimated values of I were always higher than 1 (Elliot, 1977). Population density changed throughout the period of study but the pattern of variation was not the same at the three sampling stations (Fig. 3). At the most eutrophicated area densities decreased gradually from winter to late spring, increased from late spring through mid fall, and appeared to decline slightly from the end of fall. This means that during the algae bloom in 1993, isopod density was parallel to the surrounding macroalgal biomass. But the same pattern was observed in the following year where no macroalgae was found (Fig. 3C). At the other two areas the densities of *C. carinata* were always low (but always increasing through time) and did not allow the use of statistical tools.

Stepwise multiple regression analysis indicated that abundance (A) and biomass (B) of *C. carinata* in the most eutrophicated area were negatively correlated with temperature but biomass was also positively correlated with green macroalgae biomass (Ent):

$$ln\,(1 + B) = 2.625 + 0.227\, ln\,(1 + Ent) - 0.059\,(Temp)$$
$$ln\,(1 + A) = 8.304 - 0.0496\,(Temp)$$

Reproduction, sex-ratio, and fecundity

Females carrying developing embryos in brood pouches were first observed in early spring of both years (Fig. 4A). The percentage of juveniles in the population was clearly related to recruitment. Two peaks of free-living juveniles occurred from June to August (Fig 4B) which corresponded to two new cohorts.

European populations of *C. carinata* exhibited protogynous hermaphroditism, a metamorphosis from female to male form (Burbanck and Burbanck 1974, 1975, Legrand and Juchault 1963, Marques et al. 1994, Martins et al. 1997). In the Mondego estuary this is very clear because males only appear in the population by late winter, approximately 1.5 months before the first observations of females carrying eggs. The analysis of the sex-ratio variation (Fig. 5) indicates that all individuals are initially females, and in the reproduction period (spring season) 20 to 30% of the females will metamorphose to males. Recruitment then occurs continuously from June to August.

At the Mondego estuary the fecundity of females of similar size was quite variable, and no correlation between the number of developing embryos and female size was found. The difference in time between peaks of eggs in the first stage of development (A) and the last one (C) provided us with an estimation of the duration of the embryogenic development (Fig. 6). In both years (with and without macroalgae blooms) the estimation was 45 days.

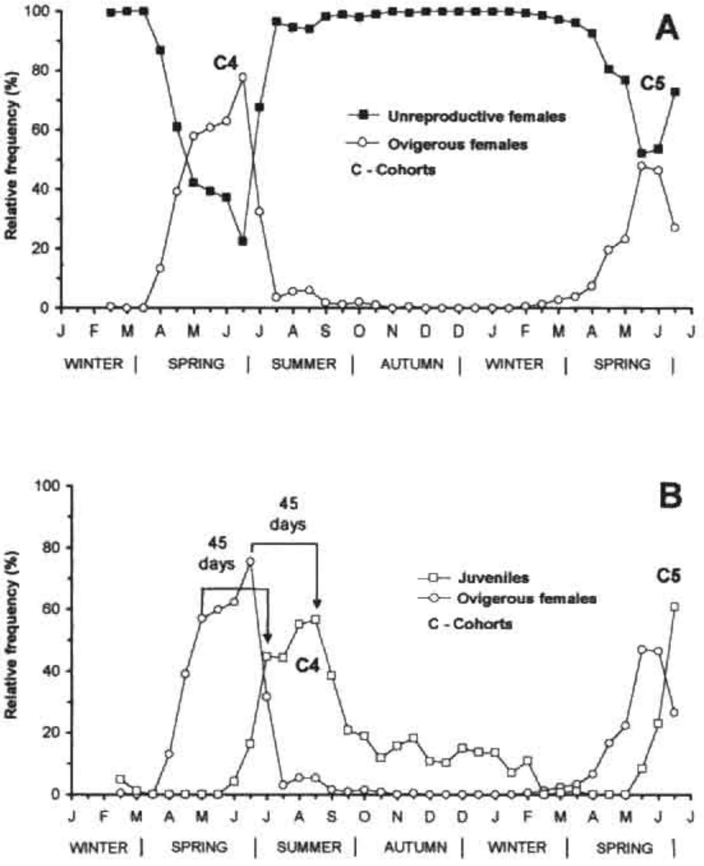

Fig. 4. Biological features of the population. (A) Variation of females in different physiological stages in relation to the female population; (B) Variation of ovigerous females in the total female population and of juveniles in the population.

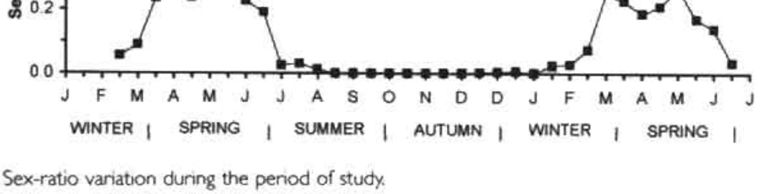

Fig. 5. Sex-ratio variation during the period of study.

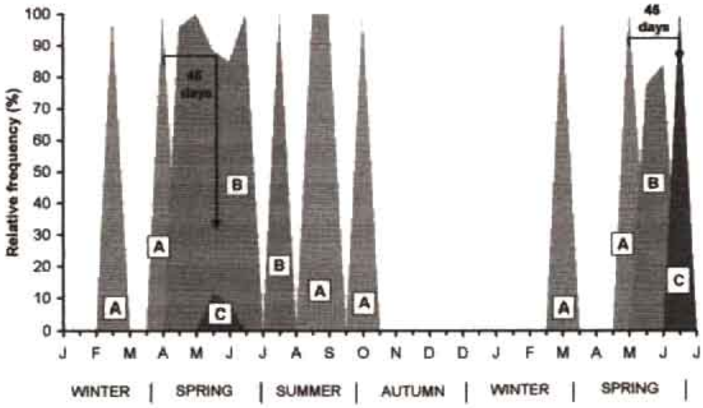

Fig. 6. Proportion of embryos in different developmental stages (definitions given in the text). Estimation of the duration of the embryogenic development in two consecutive years.

Growth and life span

Size frequency polymodal distributions were analysed for recognisable cohorts at the most eutrophicated areas (Fig. 7). Three cohorts (C1, C2 and C3) could be identified from data from the first sampling in February 1993. From modal analysis two new cohorts corresponding to small cohorts (C4 and C5) were clearly identified (χ^2 and G not significant, $P \leq 0{,}05$) on 6 June 1993 and 15 June 1994, respectively. Minimum average cephalic length (CL) of cohorts C4 and C5 was 0,152 mm (2,115 mm TL) and 0,2349 mm (2,862 mm TL) (Fig. 8). These values might have depended upon the number of days from hatching to cohort recognition, and therefore on sampling periodicity. The maximum average CL of cohorts ranged from 0,7714 mm (7,696 mm TL) to 0,976 mm (9,539 mm TL). Males were always bigger than females. The average CL of the 10 biggest males was 1,158 mm (11,179 mm TL) and of the 10 biggest females was 1,067 (10,359 mm TL).

Growth was found to be continuous through the life span of *Cyathura carinata*, although growth rates varied with size and temperature. Actually growth rates were clearly higher in early phases, from early summer to mid fall (see cohort C4) (Fig. 8), but by midfall growth rates decreased considerably, as the average size of individuals decreased, practically ceased in winter (see cohorts C3 and C4), and gradually increased again in spring. Lower growth rates during winter were probably a function of lower temperatures and lower organic matter content of sediments in the estuary. Life span was estimated by taking into consideration the recruitment period, growth rates and the disappearance of cohorts (table 1) and it was possible to see that different cohorts had quite different life spans (23-36 months). Based on present data it seems that when extensive macroalgal blooms occur the cohorts have longer duration (e.g. Cohorts C1 and C2).

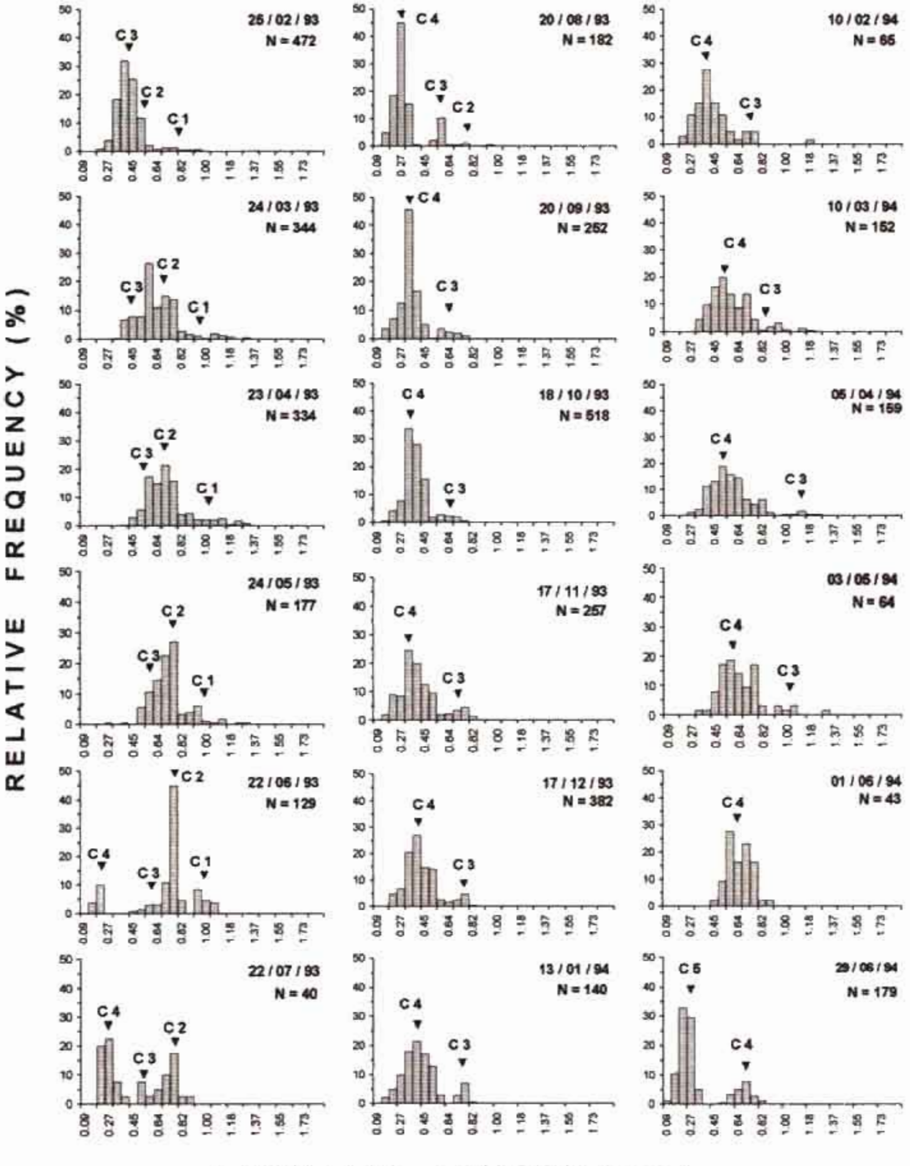

Fig. 7. Size-frequency polymodal distribution at the most eutrophicated area. Arrowheads indicate average cephalic length of numbered cohorts; (N) number of individuals.

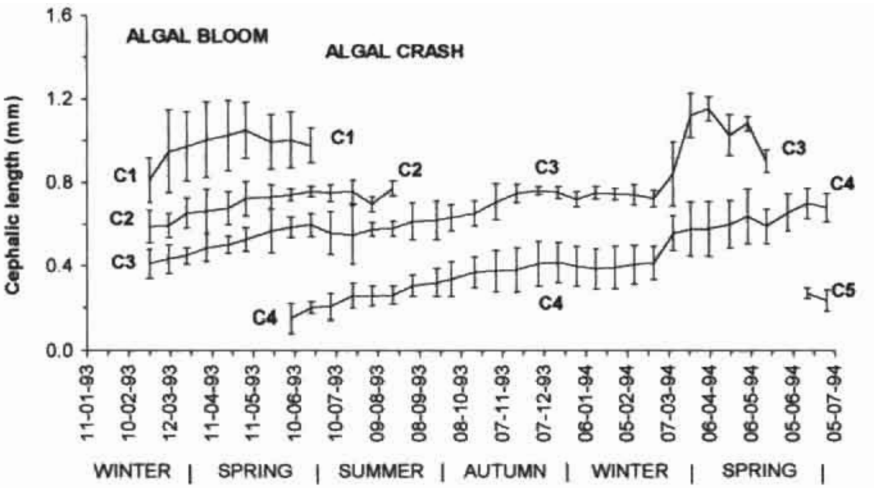

Fig. 8. Estimated growth (field growth data) of cohorts ± standard deviation at the most eutrophicated area.

Table 1. *Cyathura carinata*. Life span of cohorts 1, 2 and 3, in the most eutrophicated area

Cohorts	begining	end	Life span
C1	June 1990	June 1993	36 months
C2	June 1991	August 1993	27 months
C3	June 1992	May 1994	23 months
C4	June 1993	-	-
C5	June 1994	-	-

Production estimates

Previously established length-weight relationships were used in the production estimates on the most eutrophicated area (Table 2). The results clearly showed that growth productivity (P), elimination productivity (E) and the standing stock ($\overline{B}$) were much higher in the presence of extensive macroalgae blooms, but the relations $P/\overline{B}$ and $E/\overline{B}$ were much lower in the same conditions. It is also possible to see that the estimates of growth production and elimination production during the macroalgae bloom (4 months) correspond to nearly 60 % of the total yearly estimate taking the same period into account. Moreover the same values (of only 4 months) are very similar to the yearly estimations when the algae was not present (Table 2).

Based on the present results it is reasonable to assume that the large biomasses of macroalgae that usually grow in the south arm of the estuary are correlated in time with a great increase in the growth and elimination production of *Cyathura carinata* populations.

Table 2. Production estimates of the isopod *Cyathura carinata* at the most eutrophicated area taking into account different periods of time with different ecological conditions.

	P $(g.m^{-2}\ time^{-1})$	$\overline{B}$ $(g.m^{-2})$	$P/\overline{B}$	E $(g.m^{-2}\ time^{-1})$	$E/\overline{B}$
18 months (January 1993 to June 1994)	22.078	5,585	3,953	53,718	9,618
12 months **(with a macroalgal bloom)** (February 1993 to February 1994)	19,623	6,192	3,169	47,892	7,734
12 months **(without macroalgae)** (June 1993 to June 1994)	11,795	3,444	3,422	29,253	8,494
4 months **(with a macroalgal bloom)** (February 1993 to June 1993)	10,543	13,001	0,811	25,325	1,948
4 months **(without macroalgal bloom)** (February 1994 to June 1994)	7,718	3,690	2,092	11,649	3.157

Discussion

Abundance

From previous data (Marques et al. 1994, Martins et al. 1997), the abundance of *Cyathura carinata* was expected to be high in inner areas of the south arm of the Mondego, especially in sectors lacking vegetal cover. Examination of the population dynamics of this species in relation to different ecological conditions (with or without macroalgae blooms) provide an opportunity to analyse its intraspecific life history variation. In addition, production estimates will contribute to evaluating the role of this species in the trophic dynamics.

Population density clearly changed along the eutrophication gradient as a result of preferences for bare sediment (without plant coverage) and more sandy sediment. So large and stable populations were found in the inner areas of the estuary. In the eutrophicated area and in the *Zostera noltii* meadows, the densities observed were always very low but with a slight increase throughout the period of study. This was probably due to the increased eutrophication of the estuary that induced a decline in the macrophyte meadows. The areas occupied previously by *Z. noltii* are now starting to become more similar to the most eutrophicated one, in terms of disappearance of plant coverage and increased sand percentage in sediments. This is a natural feature because it is known that the leaves and rhizomes of macrophytes tend to stabilise the sediment and increase the organic matter content. So the general direction of change with increased eutrophication in the estuary would be the disappearance of the *Z. noltii* meadows and an increase in areas occupied by *Cyathura carinata* originated by movement of adult individuals inside the estuary together with new recruitments taking place in the area. It seems therefore that this species has a larger potential for dispersion inside the estuary then it was stated before (Marques et al. 1994, Martins et al. 1997).

In the most eutrophicated area the density of *Cyathura carinata* exhibited a seasonal pattern throughout the year. Density increased during summer as function of recruitment, and the decline from mid fall to late spring corresponded mainly to the death of older animals.

Our results (density variation along the eutrophication gradient and multiple regression analysis), based on 18 months of sampling, suggest that in the Mondego estuary, the abundance and biomass of *C. carinata* are not negatively affected by the large blooms of green macroalgae, as stated before (Martins et al. 1997). On the contrary, it seems reasonable to conclude that to a certain extent the development of macroalgae biomass favours *C. carinata* and that extensive blooms affecting the whole area will increase in time its areas of occupation.

Reproduction, growth and life cycle

Data showed that in spring females always outnumbered males and that all males disappeared by the end of summer, immediately after recruitment. Our results strongly suggest and confirm the occurrence of protogynous hermaphroditism stated by other authors (Cléret 1960, Jadzewski 1969, Legrand and Juchault 1963, Marques et al. 1994, Martins et al. 1997, Ólafsson and Persson 1986), with approximately 20-30% of adults changing from females to males.

The duration of the embryogenic development in peracarids is very long and can reach 6 months in extremely cold climates (Bregazii 1972). In contrast, in temperate coastal waters it is much faster, taking usually only a few weeks (Marques et al. 1994, Moore 1981, Pardal et al. 2000, Powell and Moore 1991, Steele and Steele 1973). In our case embryogenic development was fast, 45 days, in both years. This estimate is quite different from the one made before (32 days) for the same population (Marques et al. 1994). These authors simply counted the number of days between two peaks of embryos in stage C and accepted it as a rough estimation for the duration of the embryogenic development. In the present study we used a more accurate but simple method which consisted of counting the number of days between peaks in embryos from stage A to stage C.

Summer and spring growth rates were much higher than during colder months, which was also observed frequently in other peracarid species (Hastings 1981, Marques et al. 1994, Ólafsson and Persson 1986, Pardal et al. 2000, Wilson and Parker 1996). The previous life span estimate for *C. carinata* in the Mondego estuary was 18-22 months (Marques et al. 1994). Our new estimates are much bigger and range from

23 to 36 months (table1). These new estimates are in agreement with more northern populations (Amanieu 1969, Bamber 1985, Jadzewski 1969, Ólafsson and Persson 1986). Nevertheless, all populations studied (Baltic Sea, English Channel, French west coast and Mondego estuary) present univoltine life cycles (a single generation per year). Therefore, as stated before, (Marques et al. 1994), intraspecific variations of the reproductive patterns as a function of latitude do not seem to be very significant in *C. carinata* in opposition to other peracarid species (eg. Amphipods) (Marques and Nogueira 1991, Pardal et al. 2000, Sudo and Azeta 1996) that tend to increase voltinism in ecosystems with warmer temperature regimes.

According to the stability-time theory (Sanders 1969) in environmentally stressed systems, such as eutrophic estuaries, we should expect the evolution of opportunistic adaptative strategies to take place. An example includes *Ampithoe valida* (Amphipoda) in the same system (Pardal et al. 2000) which appeared as an r strategist, with iteroparous females (except summer generation), a multivoltine cycle, high individual fecundity and recruitment throughout the year. This is the most common pattern in epifaunal species (van Dolah 1980) from physically controlled communities. In contrast, females of *C. carinata* may be able to reproduce two times during life and the population produces a single generation per year, which is not a typical r adaptive strategy. Since populations of *C. carinata* are capable of maintaining the same localities for long periods (Burbanck and Burbanck 1975, Marques et al. 1994) or even disperse to new others (present study), results suggest that for a given estuarine environment large stable populations might be more k-selected.

Production estimates

Taking into account the whole period of study, P (growth productivity) and E (elimination productivity) as well as $\overline{B}$ (standing stock) showed significantly higher values than the ones estimated before for the same species in this estuary (two times more). Moreover, these values are far higher than the ones estimated for other peracarid species in other estuarine systems (Birklund 1977, Fredette and Diaz 1986, Marques and Nogueira 1991, Moller and Rosenberg 1982, Ólafsson and Persson 1986, Pardal et al. 2000). Nevertheless, this difference does not reflect the entire reality. In fact, we must look carefully at the dynamics of the estuarine system in the two different years. For a short period (during the macroalgal bloom) P, E and were much higher than in the same period of the following year, and represent more than 50% of the yearly production estimation in 1993. Moreover they present similar values as for the total yearly estimation without macroalgae (year 1994). This means that during the macroalgae bloom, the population was not stressed as stated before (Martins et al. 1997) but clearly was favoured, probably due to resource availability.

As in other intertidal areas of Europe, *C. carinata* is quite accessible to aquatic predators. High values of P and E found in the most eutrophicated areas during the algal bloom, suggest that this species may play a very important role in the trophic dynamics.

As a whole, the present work reinforces the generalised notion that estuaries are highly productive systems, and reflect the important role of epifaunal macrobenthic species in the productivity of habitats colonised by them. Moreover this paper reveals that the conclusions based on just one annual cycle data can be incorrect. So longer sampling programs are needed to have a better understanding of the real dynamics of macrobenthic species in very dynamic systems.

Acknowledgements

This paper was supported by the programme MAST II (MAS 2 CT 92 0036 and by FCT - Portuguese Foundation for Science and Technology. The authors are indebted to all colleagues from the Coimbra University who assisted in field and laboratory work.

References

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

Amanieu M. 1969. Variations saisonières de la tailleet cycle reproducteur à Arcachon de *Cyathura carinata* (Krøyer). J. Exp. Mar. Biol. Ecol. 4: 79-89.

Bamber R.N. 1985. The autecology of *Cyathura carinata* (Crustacea: Isopoda) in a cooling water discharge lagoon. J Mar Biol Ass U.K. 65: 181-194.

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

Bregazzi P.K. 1972. Life cycles and seasonal movements of *Cheirimedon femoratus* (Pfeffer) and *Tryphosella kergueleni* (Miers) (Crustacea: Amphipoda). Br. Antarct. Surv. Bull. 30: 1-34.

Burbanck M.P. and Burbanck W.D. 1974. Sex reversal of female *Cyathura polita* (Stimpson, 1855) (Isopoda, Anthuridae). Crustaceana 26: 110-112.

Burbanck W.D. and Burbanck M.P. 1975. Growth of a transplanted population of the estuarine *Cyathura polita* (Crustacea: Isopoda), Cape Cod, Massachusetts. Verhandlungen der Internationalen vereinigung für theoritische und angwandte Limnologie 19: 3001-3006

Cabral J.A., M.A. Pardal, R.J. Lopes, T. Múrias and J.C. Marques 1999. Impact of macroalgae blooms on the benthic upper trophic levels in the Mondego estuary (West Portugal). Acta Oecol. 20 (4): 417 – 428.

Cléret J.J. 1960. Étude de *Cyathura carinata* (Krøyer) (Isopode Anthuridae) 1. Redescription de l'espèce et discussion systématique. Cah. Biol. Mar. 1: 433-452.

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

Dijk G.M., Liere L., Admiraal W., Bannink B.A. and Cappon J.J. 1994. Present state of the water quality of European rivers and implications for management. Sci. Total Environ. 145: 187-195.

Elliot J.M. 1977. Statistical analysis of samples of benthic invertebrates. Freshwater Biological Association, Scientific Publications.

Eslava J.C.S. 1994. Etudio de la comunidad reducida de Macoma en el estuario del Bidasoa. Ph.D. Thesis, University of Navarra, Spain.

Flindt M.R., Kamp-Nielsen L., Marques J.C., Pardal M.A.; Bocci M.; Bendoricho G.; Nielsen S.N. and Jørgensen S.E. 1997. Description of the three shallow estuaries: Mondego River (Portugal), Roskilde Fjord (Denmark) and the Lagoon of Venice (Italy). Ecol. Model. 102: 17-31.

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

Hartog C. 1994. Suffocation of a littoral *Zostera* bed by *Enteromorpha* radiata. Aquat. Bot. 47: 21-28.

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

Hickel W., Mangelsdorf P. and Berg J. 1993. The human impact in the German Bight: Eutrophication during three decades (1962-1991) Helgol. Meeresunters. 47: 243-263.

Jadzewski K. 1969. Biology of two hermaphroditic Crustacea, *Cyathura carinata* (Krøyer) (Isopoda) and *Heterotanais oerstedi* (Krøyer) (Tanaidacea) in waters of the polish Baltic Sea. Zoologica Poloniae, 19: 5-25.

Lavery P.S., Lukatelich R.J. and McComb A.J. 1991. Changes in the biomass and species composition of macroalgae in a eutrophic estuary. Estuar. Coast. Shelf Sci., 33: 1-22.

Legrand J.J. and Juchault P. 1963. Mise en evidence d'un hermaphroditisme protogynique fonctionnel chez l'isopode Anthuride *Cyathura carinata* (Krøyer) et étude de mecanisme de l'inversion sexuelle. C.R. Acad. Sci. II Paris 256: 2931-2933.

Lillebø A.I., Flindt M.R., Pardal M.A. and Marques J.C. 1999. The effect of macrofauna, meiofauna and microfauna on the degradation of *Spartina maritima* detritus from a salt marsh area. Acta Oecol. 20 (4): 249-258)

Lopes, R.J., M.A. Pardal. and J.C. Marques 2000. Impact of macroalgae cover and wader predation on intertidal macroinvertebrates. Experimental evidence in the Mondego estuary. J. Exp. Mar. Biol. Ecol. 249: 165-179.

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

Marques J.C., Maranhão P. and Pardal M.A. 1993b. 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., Martins I., Teles-Ferreira C. and Cruz S. 1994. Population dynamics, life history and production of *Cyathura carinata* (Krøyer) (Isopoda: Anthuridae) in the Mondego estuary, Portugal. J. Crust. Biol. 14: 258-272.

Marques J.C., Pardal M.A., Nielsen S.N. and Jørgensen S.E., 1997. Analysis of the properties of exergy and biodiversity along an estuarine gradient of eutrophication. Ecol. Model. 102: 155-167.

Martins I., Marques J.C., Jorgensen S.E. and Nielsen S.N., 1997. Modelling the effects of green macroalgae blooms on the population dynamics of *Cyathura carinata* (Crustacea: Isopoda) in an eutrophicated estuary. Ecol. Model. 102: 33-53.

Martins, I., M.A. Pardal, A.I. Lillebø, M.R. Flindt and J.C. Marques 2001. Hydrodynamics as a major factor controlling the occurrence of green macroalgae blooms in an eutrophic estuary: a case study. Estuar. Coast. Shelf Sci., 52: 165-177.

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

Moore P.G. 1981. The life histories of the amphipods *Lembos websteri* Bate and *Corophium bonnellii* Milne Edwards in Kelp holdfasts. J. Exp. Mar. Biol. Ecol. 49: 1-50.

Ólafsson E.B. and Persson L.E. 1986. Distribution, life cycle and demography in a brackish water population of the isopod *Cyathura carinata* (Krøyer) (Crustacea). Estuar. Coast. Shelf Sci. 23: 673-687.

Pardal M.A., Marques J.C. and Bellan G. 1993. Spatial distribution and seasonal variation of subtidal polychaete populations in the Mondego estuary (western Portugal). Cah. Biol. Mar. 34: 497-512.

Pardal M.A. 1998. Impacto da eutrofização nas comunidades macrobentónicas do Braço Sul dp estuário do Mondego (Portugal). Ph.D. Thesis, University of Coimbra, Portugal.

Pardal, M.A., J.C. Marques, I. Metelo, A.I. Lillebø and M.R. Flindt, 2000. Impact of eutrophication on the life cycle, population dynamics and production of *Ampithoe valida* (Amphipoda) along an estuarine spatial gradient (Mondego estuary, Portugal). Mar. Ecol. Prog. Ser. 196: 207-219.

Powell R. and Moore P.G. 1991. The breeding cycles of females of seven species of amphipod (Crustacea) from the Clyde sea. J. Nat. Hist. 25: 435-479.

Rafaelli D., Raven J. and Poole L. 1998. Ecological impact of green macroalgae blooms. Oceanography Marine Biology Annual Review 36: 97-125.

Sanders H.L. 1969. Marine benthic diversity: a comparative study. Am. Nat. 102: 243-282.

Steele D. and Steele V.J. 1973. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. VIII. The duration of embrionic development in five species at various temperatures. Can. J. Zool. 51: 995-999.

Sudo H. and Azeta M. 1996. Life history and production of the amphipod *Byblis japonicus* Dahl (Gammaridea: Ampeliscidae) in a warm temperate zone habitat, Shijiki bay, Japan. J. Exp. Mar. Biol. Ecol. 198: 203-222.

van Dolah R.F. 1980. A comparison of reproductive patterns in epifaunal and infaunal gammaridean Amphipoda. Estuarine Coastal Shelf Sci 2: 593-604.

Yeates J.S. 1993. Soils and fertilizer use in southwestern Australia. Fert. Res. 36: 123-125.

Wilson Jr W.H. and Parker K. 1996. The life history of the amphipod, *Corophium volutator*: the effects of temperature and shorebird predation. J. Exp. Mar. Biol. Ecol. 196: 239-250.

Série

Investigação

•

Coimbra
Imprensa da Universidade

2002