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Scientific Editors

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



Coimbra • Imprensa da Universidade

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## IMPACT OF EUTROPHICATION ON AMPHIPODS *Melita palmata* AND *Ampithoe valida* IN THE MONDEGO ESTUARY

### Abstract

The life cycle, population dynamics and production of *Ampithoe valida* and *Melita palmata* were studied in an intertidal mudflat in central Portugal. Sampling was carried out in eutrophicated areas, where macroalgae blooms of *Enteromorpha* spp. usually occur from January to early summer, and also in non-eutrophicated areas characterised as *Zostera noltii* meadows. Both amphipod species showed a contagious distribution, and the populations densities clearly changed during the study period along the eutrophication gradient. No migratory patterns were detected between the estuary and the sea, but dispersion inside the estuary might occur in these amphipods. Both species presented a two-generation life cycle involving a short-lived fast growing summer generation (7 months for *A. valida* and 4-5 months for *M. palmata*) and a longer-lived, slower growing generation that overwinters (9 months for *A. valida* and 6-7 months for *M. palmata*). Along the eutrophication gradient no differences were found regarding the biology of the species. Besides these features, differences were observed between eutrophicated and non eutrophicated areas in regard to productivity.

In a certain extent, the increase of macroalgae biomass may favour these herbivorous amphipods populations, but extensive blooms affecting the whole area of distribution of these species will determine its disappearance.

This Chapter includes new information and information already published in Marine Ecology Progress Series (2000, 196:207-219).

### Introduction

Eutrophication appears to be a common phenomenon in coastal waters around the world. The replacement of rooted macrophytes by opportunistic green macroalgae (*Chaetomorpha*, *Enteromorpha* and *Ulva*) seem to be also a major feature in these ecosystems when they suffer from organic pollution. (Hickel et al. 1993, Yeates 1993, Dijk et al. 1994, Hartog 1994, Flindt et al. 1997, Marques et al. 1997, Rafaelli et al. 1998).

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In the south arm of the Mondego estuary, seasonal intertidal macroalgae blooms (mainly of *Enteromorpha* spp.) have been reported for several years (Marques et al. 1993a, 1993b, 1997, Pardal et al. 1993, Pardal 1998, Flindt et al. 1997, Lillebø et al. 1999, Martins et al. 2001) due to nutrient enrichment of estuarine waters (Marques et al. 1997, Pardal 1998, Martins et al. 2001). As a consequence, *Zostera noltii* beds, which represent the richest habitat with regard to productivity and biodiversity, have been drastically reduced in the south arm of the estuary, presumably out competed by *Enteromorpha* (Rafaelli et al. 1991, Hodgkin and Hamilton 1993, Pardal 1998).

*Ampithoe valida* and *M. palmata* are grazers that can be found on rocky substrata and on muddy bottoms, often in the presence of green macroalgae or macrophytes (e.g. *Zostera noltii*). Both species present a wide distribution but they received little attention (Borowsky 1983, Pardal et al. 2000). Despite that there are just a few studies on the impact of macroalgae blooms on grazer amphipod species population dynamics (Drake and Arias 1995, Pardal et al. 2000). Such knowledge may definitely contribute for a better understanding of dynamic processes related with shift in primary producers a usual phenomenon in European and north America coastal waters.

## Materials and methods

In the south arm macroalgal blooms of *Enteromorpha* spp. have been regularly observed during the last 15 years (Flindt et al. 1997, Marques et al. 1997, Pardal 1998, Lillebø et al. 1999, Pardal et al. 2000, Martins et al. 2001). This is probably a result of excessive nutrient release into the estuary, coupled with longer persistence of nutrients (nitrogen and phosphorous) in the water column. Nevertheless, such macroalgae blooms may not occur in exceptionally rainy years (e.g. year 1994) due to low salinity for long periods, as a result of the Pranto river discharge (Pardal 1998, Martins et al. 2001).

The amphipods were monitored in the Mondego estuary during 18 months, from January 1993 to June 1994. Samples were taken fortnightly at three different sites along an estuarine gradient of eutrophication in the south arm of the estuary (Fig. 1). From a *Zostera noltii* meadow, up to a heavily eutrophicated zone, in the inner areas of the estuary, where *Enteromorpha* spp. blooms have been observed during the last two decades.

Each time at each site ten cores (with a 141 cm<sup>2</sup>) were taken to a depth of 15 cm and sieved through a 500 µm mesh sieve.

Amphipods were identified, counted, measured and sexed. Due to the difficulties in measuring Total body Length ( $T_L$ ) accurately in such a small organisms that are typically comma-shaped, an alternative and more accurate length was measured: The Cephalic Length ( $C_L$ ) (measured between the extremity of the rostrum and the base of the head). So for both species an equation for  $C_L$ - $T_L$  conversion was determined ( $T_L = -0.1355 + 9.4233 * C_L$ ,  $n = 262$ ,  $r = 0.965$  for *A. valida* and  $T_L = -0.62503 + 9.8771 * C_L$ ,  $n = 323$ ,  $r = 0.955$  for *M. palmata*). Length-weight relationships were determined for production estimates. A single regression equation was determined for each species ( $W = 0.00085 * C_L^{3.631}$ ,  $n = 95$ ,  $r = 0.983$  for *A. valida* and  $W = 0.00196 * C_L^{3.6535}$ ,  $n = 72$ ,  $r = 0.966$  for *M. palmata*).

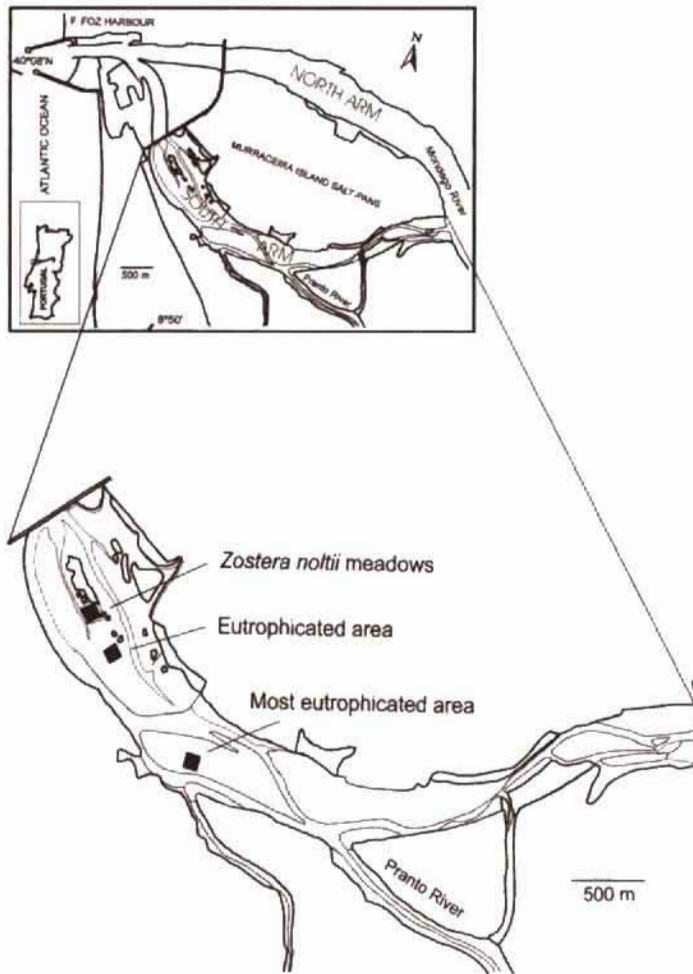


Fig. 1. Location of the sampling stations along a spatial gradient of eutrophication in the Mondego estuary.

For the determination of sex we used the same methodology described in Pardal et al. (2000, 2001). 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, Marques and Nogueira 1991, Marques et al. 1994, Pardal et al. 2000) five stages were considered: a) newly laid, eggs grouped and resembling a gelatinous mass; b) eggs well separated, internally homogeneous; c) embryo comma-shape, pereopods starting to be visible; d) constriction of the comma clearly visible, appendages segmented and looking slender, eyes visible, cephalothorax orange-red; e) hatched and free juveniles.

All the statistical analysis, concerning: a) population spatial dispersion; b) multiple regression models between the density and biomass of amphipods and biomass of green

macroalgae, salinity and water temperature; c) estimation of field growth rates; d) estimation of production (net production (P) and elimination production (E), were developed following the procedures and techniques explained in Pardal et al. (2000; 2001).

## Results

### Macrophytes and macroalgae biomass

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

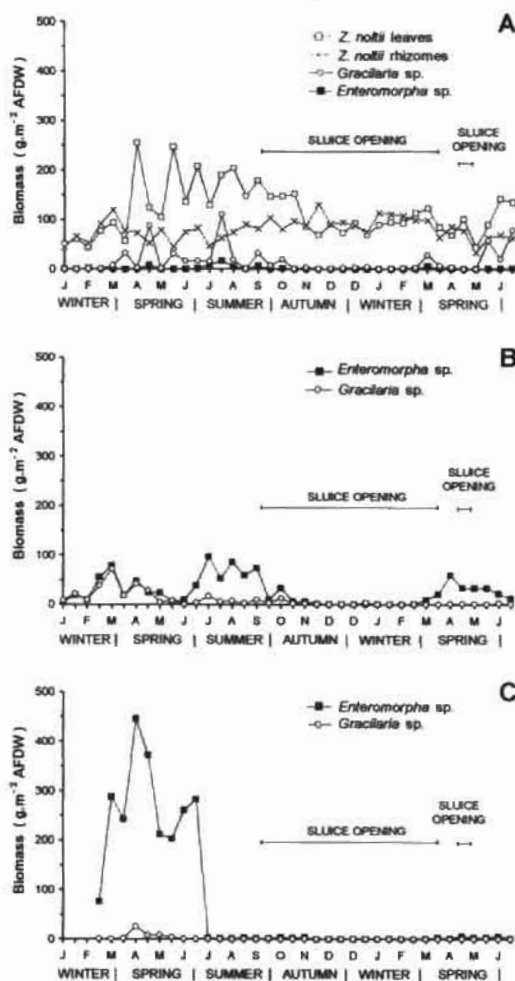


Fig. 2. Seasonal changes in plant biomass along the eutrophication gradient. (A) *Zostera noltii* meadows; (B) Intermediate eutrophicated area; (C) Most eutrophicated area.



In the inner areas of the estuary that corresponds to the most eutrophicated area *Enteromorpha* sp. exhibited a typical spring bloom in 1993. In the end of June an algal crash occurred causing a severe impact on the macrofauna (Figs. 2, 3). In 1994 no macroalgal bloom occurred because it was a very rainy year in central Portugal which increased freshwater discharges of the Pranto river that kept salinity low. Such conditions inhibit *Enteromorpha* growth, since salinity was below 10 ‰ for several months.

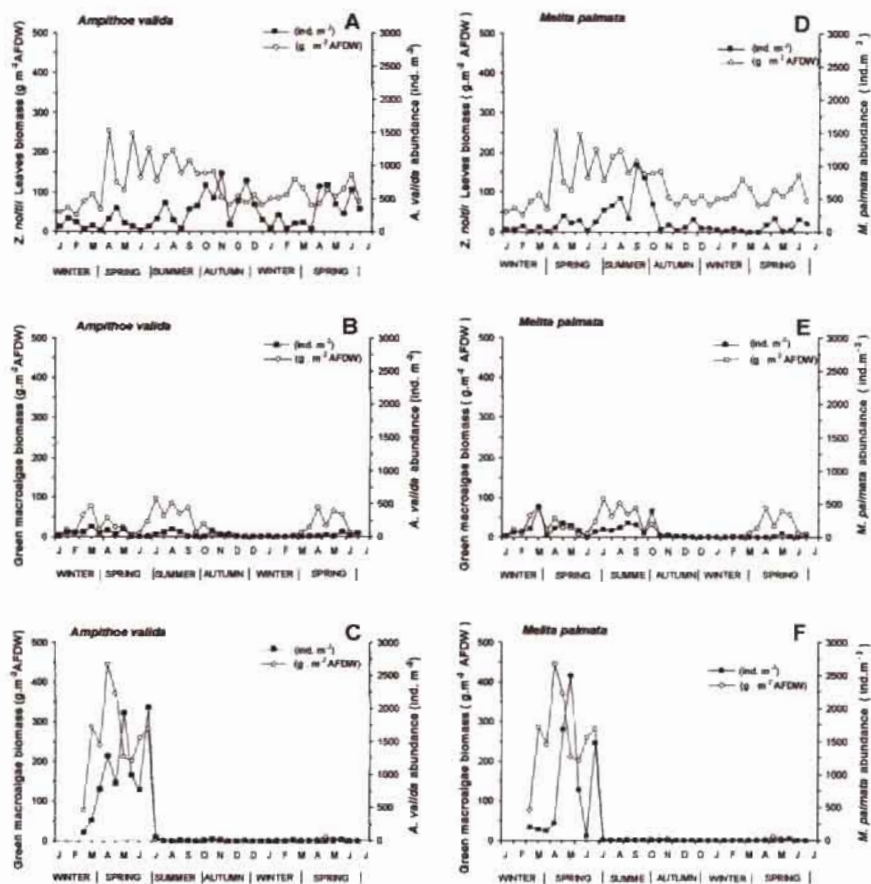


Fig. 3. Abundance of *A. valida* and *M. palmata* along the eutrophication gradient, *Zostera noltii* meadows (A and D); Eutrophicated area (B and E); Most eutrophicated area (C and F)

## Spatial distribution and abundance

Both amphipod species showed an aggregated spatial distribution in the three study areas along the eutrophication gradient (Elliot 1977). Population density of *A. valida* and *M. palmata* changed throughout the period of study but the variation pattern was not the same along the eutrophication gradient (Fig. 3). In the most eutrophicated area densities were consistently higher during the algal bloom. After the algae crash density of both species declined sharply and remained low, or organisms even disappear throughout the study (Fig. 3C and 3F). In the intermediate eutrophicated area the variation in density was correlate with the variation in macroalgal biomass ( $r = 0.87$ ,  $N = 26$  for *A. valida*), but densities never reached so high abundances as in the previous case (Fig. 3B). With such low abundances most of the statistical analysis that we performed in the present paper were not possible in this area. At the *Zostera noltii* meadows, as a pattern for both species, the population density increased during summer and fall (1993) and also during spring (1994) (Fig. 3A and 3D).

Stepwise multiple regression analysis indicated that abundance (A) and biomass (B) of both amphipods in the most eutrophicated area was positively correlated with *Enteromorpha* sp. biomass (ENT), *Gracilaria* sp. biomass (Grace) and temperature of the water (TEMP):

### *A. valida*

$$\ln (I + A) = 0,350 + 1,142 \ln (I + \text{ENT})$$

$$\ln (I + B) = - 0,030 + 0,030 \ln (I + \text{ENT}) + 0,096 \ln (I + \text{Grace})$$

### *M. palmata*

$$\ln (I + A) = - 4,633 + 0,660 \ln (I + \text{ENT}) + 0,248 (\text{TEMP})$$

$$\ln (I + B) = - 0,238 + 0,017 \ln (I + \text{ENT}) + 0,012 (\text{TEMP})$$

In the *Z. noltii* meadows only for *M. palmata* were found significant correlations between these population parameters and leaves biomass (LEA) and temperature of the water:

### *M. palmata*

$$\ln (I + A) = - 3,784 + 0,660 \ln (I + \text{LEA})$$

$$\ln (I + B) = - 0,88 + 0,007 (\text{TEMP})$$

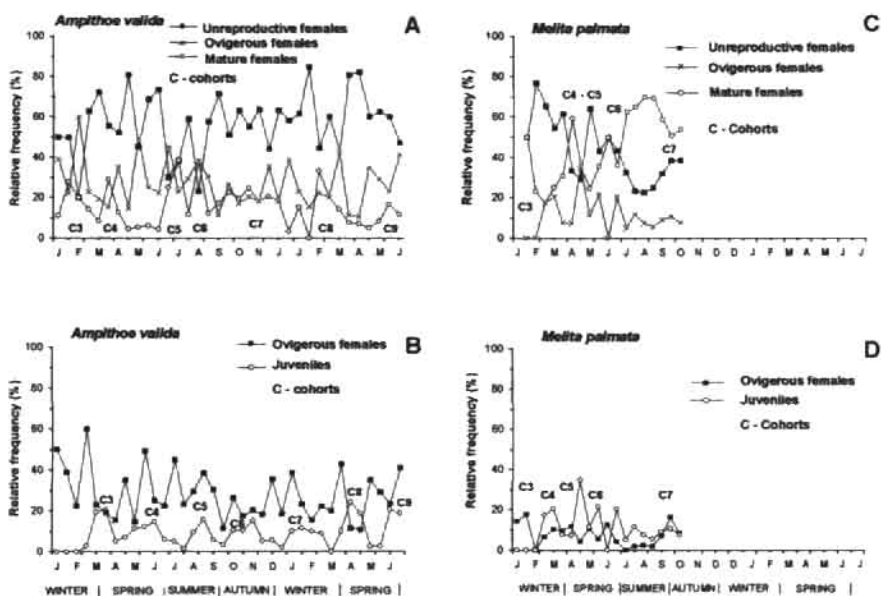


Fig. 4. Biological features of *A. valida* and *M. palmata* population. (A and C) Variation of females in different physiological stages in relation to the female population; (B and D) Variation of ovigerous females in the total female population and of juveniles in the population.

#### Reproduction, sex-ratio, and fecundity

The *A. valida* and *M. palmata* populations were sexually active throughout the year in the south arm of the Mondego estuary. However, taking into consideration the percentage of ovigerous females over the total female population (Fig. 4), sexual activity was higher from late spring to late summer. The variation of the percentage of juveniles in the population was clearly related to increases in recruitment of both species.

In *A. valida* and *M. palmata* females were usually more abundant than males overall, and no significant seasonal changes of this pattern were observed (Fig. 5). The fecundity of females of similar size was quite variable, and, no correlation between the number of developing embryos and female size was found in any of the studied species. Measurements of eggs in different developmental stages (Table 1) showed that, egg volume increase changes seasonally. For instance on *A. valida* an increase of 361% was estimated in summer, 452% in spring and 492% in autumn. It was also possible to recognise that for the same developing stage eggs' volume was greater in colder periods, while the average number of eggs per female was smaller (table 1 and 2).

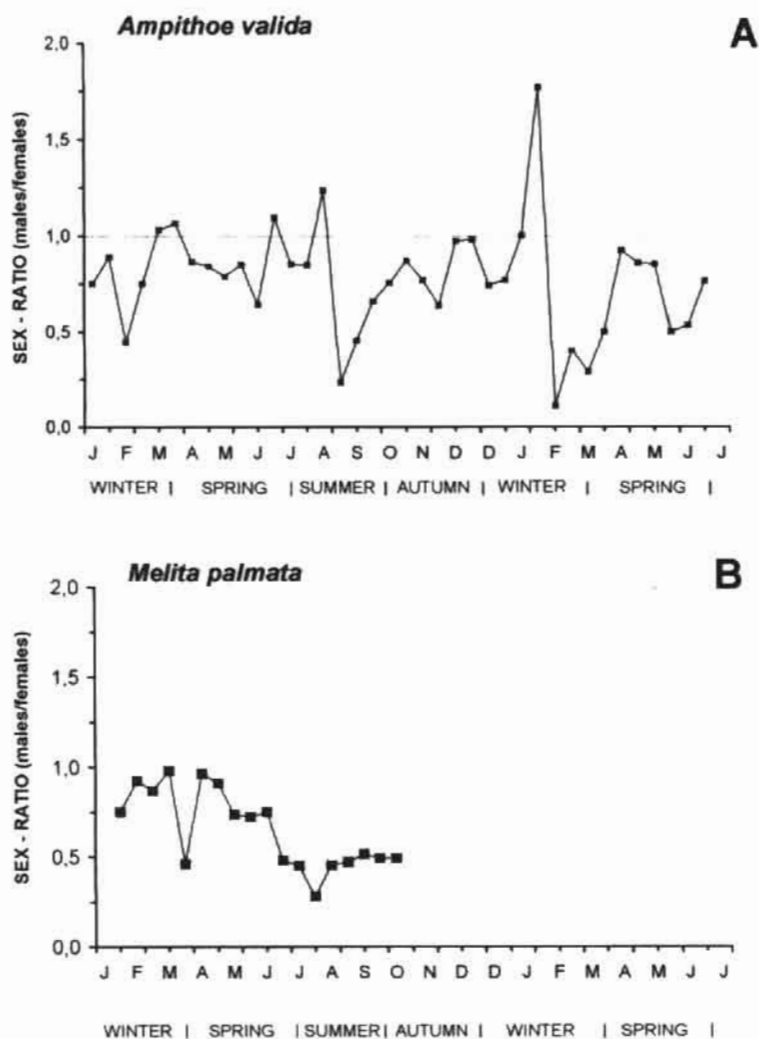


Fig. 5. Sex-ratio variation during the period of study. (A) *Ampithoe valida*; (B) *Melita palmata*.

Table I. Mean number (N) and volume (Vol) of eggs per female of *Ampithoe valida*, at development stages AB, C, D and E, in the Mondego estuary.

	AB		C		D		E	
	N	Vol (mm <sup>3</sup> )	N	Vol (mm <sup>3</sup> )	N	Vol (mm <sup>3</sup> )	N	Vol (mm <sup>3</sup> )
Winter	18	0,205	12	0,218	16	0,384	7	-
Spring	16	0,151	24	0,186	18	0,214	9	0,682
Summer	11	0,155	-	0,170	-	0,167	-	0,56
Autumn	6	0,218	11	0,232	-	0,233	-	1,073



Table 2. Mean number (N) and volume (Vol) of eggs per female of *Melita palmata*, at development stages A, B, C, D and E, in the Mondego estuary.

	A		B		C		D		E	
	N	V (mm <sup>3</sup> )	N	Vol (mm <sup>3</sup> )	N	Vol (mm <sup>3</sup> )	N	Vol (mm <sup>3</sup> )	N	Vol (mm <sup>3</sup> )
Winter	1,5	0,71	2,8	1,34	-	-	8	1,57	2,5	3,46
Spring	1	0,60	4,7	0,97	3,5	1,35	3,3	1,99	4,25	2,24
Summer	3	0,98	3,8	0,96	2	1,35	2,5	1,58	1,7	2,82
Autumn	-	-	-	-	2,5	1,26	4,5	1,89	1	3,63

The difference in time between peaks of eggs in the first stage of development (A) and the last one (E), provided us an estimation of the duration of the embryogenic development quite similar for both species (Fig.6). During spring and summer the embryogenic development was faster (30-45 days) than in autumn or winter (60 days).

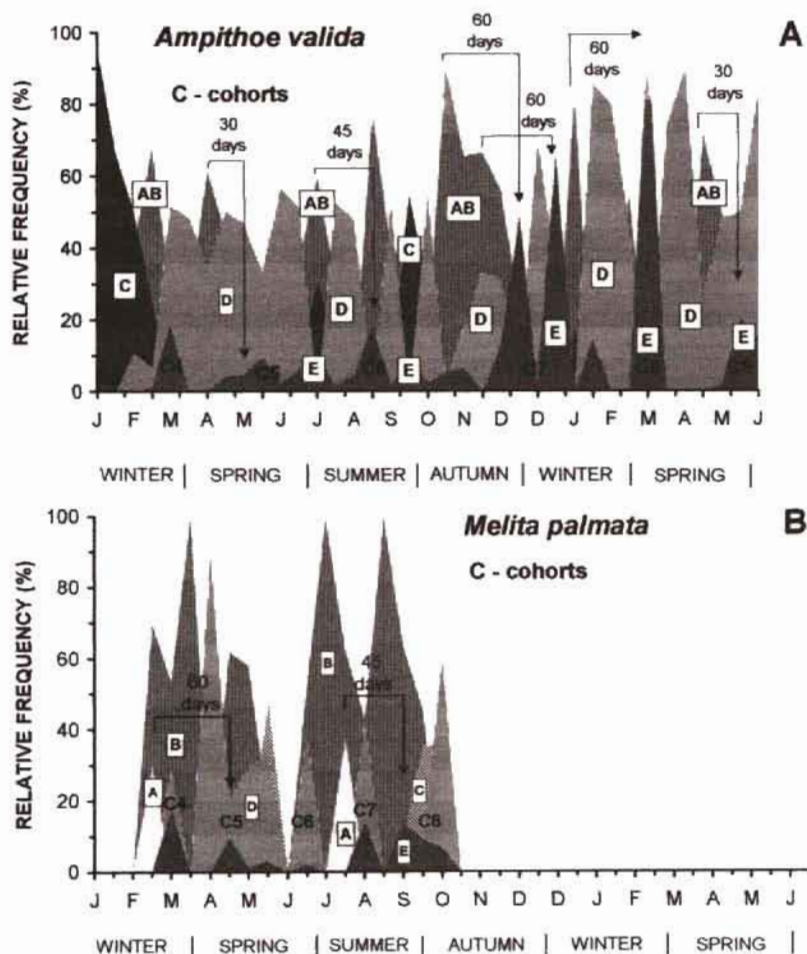


Fig. 6. Proportion of embryos in different developmental stages. Seasonal estimation of the duration of the embryogenic development. (A) *Amphithoe valida*; (B) *Melita palmata*.

## Growth and life span

Size frequency polymodal distributions were analysed for recognisable cohorts, allowing in first place to identify significant differences in the population structure on the *Zostera* beds and in the most eutrophicated area. As a pattern for these two species, Individuals reached larger dimensions at the most eutrophicated area in comparison with the other two areas (*Z. noltii* meadows and intermediate eutrophicated areas). Nevertheless, in the first months the recruitment pattern was the same all along the eutrophication gradient. Following the algae crash both populations disappeared from the most eutrophicated area and cohorts tracking became only possible at the *Z. noltii* meadows. For instance, for *A. valida* in January of 1993 three cohorts were identified, and six new ones were recognised during the study period ( $\chi^2$  and G not significant,  $P \leq 0.05$ ). Minimum average  $C_L$  of cohorts ranged from 0.327 (spring) to 0.397 mm (winter) corresponding to 2.946 and 3.606 mm of total length.

For both species growth was continuous through life (Fig. 7). Nevertheless, growth rates were higher during spring and summer and decreased during winter. Lower growth rates during winter were probably a function of lower temperatures and lower biomasses of macroalgae (food resources).

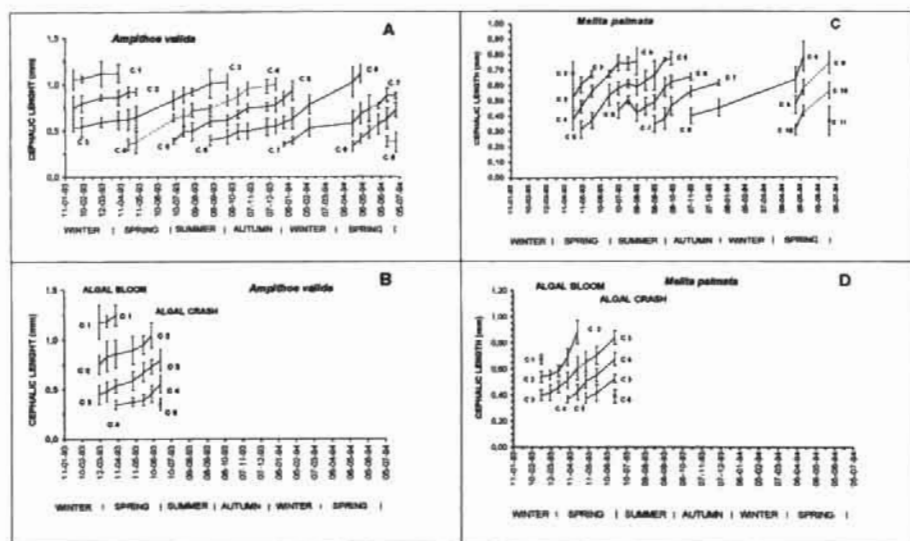


Fig. 7. Estimated growth (field growth data) of cohorts  $\pm$  standard deviation of *Amphithoe valida* and *Melita palmata*. (A and C) *Z. noltii* meadows; (B and D) Most eutrophicated area.

Life spans were estimated for *A. valida* at  $191 \pm 30$  to  $238 \pm 15$  days for summer and spring cohorts and at  $242 \pm 30$  days for the autumn cohort and for

*M. palmata* at  $120 \pm 30$  to  $148 \pm 15$  days for summer and spring cohorts and at  $182 \pm 30$  for the autumn cohort. Similarly, for both species the age at which females and males matured were lower in spring and summer cohorts than in the autumn-winter cohorts. Nevertheless, during the yearly cycle, males always reached maturity before females.

#### Production estimates

Length-weight relationships previously established (Pardal 1998, Pardal et al. 2000) were used in production estimates in the most eutrophicated area and in the *Z. noltii* meadows (Tables 3 and 4). Taking into account the whole period of study, results clearly showed that growth productivity ( $P$ ), elimination productivity ( $E$ ) and the relations  $P/\bar{B}$  and  $E/\bar{B}$  were much higher in the *Z. noltii* meadows. But in the most eutrophicated area during the algal bloom  $P$ ,  $E$  as well as population density, were clearly higher than in *Z. noltii* meadows (Tables 3 and 4).

Table 3. Production estimates for *Ampithoe valida* at *Z. noltii* meadows and at the most eutrophicated area taking into account different periods of time with different ecological conditions.

	$P$ ( $\text{g m}^{-2} \text{ time}^{-1}$ )	$\bar{B}$ ( $\text{g m}^{-2}$ )	$P/\bar{B}$	$E$ ( $\text{g m}^{-2} \text{ time}^{-1}$ )	$E/\bar{B}$
<i>Z. noltii</i> (18 months) (January 1993 to June 1994)	0.635	0.106	5.988	1.316	12.41
<i>Z. noltii</i> (13 months) (January 1993 to February 1994)	0.409	0.112	3.646	0.853	7.603
<i>Z. noltii</i> (13 months) (May 1993 to June 1994)	0.531	0.092	5.756	0.921	9.972
<i>Z. noltii</i> (3 months) (April 1993 to June 1993)	0.036	0.486	0.074	0.082	1.685
Eutrophicated area (3 months) (with a macroalgal bloom) (April 1993 to June 1993)	0.411	0.343	1.20	0.945	2.758
Eutrophicated area (4 months) (with a macroalgal bloom) (March 1993 to June 1993)	0.444	0.312	1.424	0.945	3.033

Table 4. Production estimates for *Melita palmata* at *Z. noltii* meadows and at the most eutrophicated area taking into account different periods of time with different ecological conditions.

	P (g.m <sup>-2</sup> time <sup>-1</sup> )	$\bar{B}$ (g.m <sup>-2</sup> )	P/ $\bar{B}$	E (g.m <sup>-2</sup> time <sup>-1</sup> )	E/ $\bar{B}$
<i>Z. noltii</i> (14,5 months) (April 1993 to June 1994)	0.473	0.063	7.561	0.767	12.26
<i>Z. noltii</i> (13 months) (June 1993 to June 1994)	0.456	0.064	7.144	0.734	11.49
<i>Z. noltii</i> (2 months) (April 1993 to June 1993)	0.059	0.029	2.030	0.062	2.131
Eutrophicated area (2 months) (with a macroalgal bloom) (April 1993 to June 1993)	0.496	0.397	1.248	0.683	1.720
Eutrophicated area (4 months) (with a macroalgal bloom) (March 1993 to June 1993)	0.728	0.236	3.088	0.702	2.977

## Discussion

### Abundance

For both species population density clearly changed along the eutrophication gradient as a result of the macroalgal annual dynamics, like observed before for *Microdeutopus gryllotalpa* (Drake and Arias 1995). In fact, in the most eutrophicated area, the occurrence of a macroalgal bloom in the first year prepared the conditions for the presence of large densities of *A. valida* and *M. palmata*. The algal crash, which acted as a catastrophic event (Marques et al. 1997) and the non occurrence of an algal bloom in the second year had a strong effect on the population's density in the inner parts of the estuary. Consequently, since in the second spring (1994) there were no macroalgae habitats available, *A. valida* and *M. palmata* individuals seemed to occur only in the *Z. noltii* meadows.

During the macroalgal bloom the population densities of both species were much higher than in the *Z. noltii* meadows in the same period. This may be related to habitat protection against potential predators (crabs, fishes and birds) and food resources (Greeze 1968, Duffy and Hay 1991), since they can feed directly on the algae. Next, during the algae crash, when anoxic conditions occurred, the amphipods



population suffered a sudden and drastic reduction. After the algae crash the amphipods population was never able to recover since no food resources were available. On the contrary, in the *Z. nolii* meadows both species increased in number after the algae crash. A possible movement of adult individuals inside the estuary moving to avoid the extreme conditions of anoxia, is the most probable explanation, together with new recruitments taking place in this area. It seems therefore that both species have a large potential for dispersion inside the estuary, avoiding as much as possible stressing situations caused by macroalgae blooms in early summer. It seems reasonable to conclude that in a certain extent the development of macroalgae biomass favours *A. valida* and *M. palmata* populations, but extensive blooms affecting the whole area of distribution of this species will determine its disappearance.

### Reproduction, growth and life cycle

Data showed that females of both species almost always outnumbered males, which is a common feature in amphipod populations (Hastings 1981, Dauvin 1988a, 1988b, Marques and Nogueira 1991, Morrit and Stevenson 1993, Covi and Kneib 1995, Sudo and Azeta 1996).

In our case embryonic development was fast but showed seasonal variations, from 30 days in spring up to 60 days in autumn and winter. In colder months the developing embryos (in fewer number) present larger volumes, which allow to optimise chances of survivorship since they contain higher nutritive reserves. Such volume increase was higher than the one observed by Moore and Wong (1996), although they were similar to the ones calculated by Marques and Nogueira (1991) for *Echinogammarus marinus*. Moreover, in spring and summer sexual maturity was reached at smaller sizes in comparison with autumn cohorts, which agrees with previous observations on other amphipods (Moore 1991, Powell and Moore 1991, Sudo and Azeta 1996).

Summer and spring growth rates were much higher than during colder months. This was also observed for other amphipod species in temperate areas (Hasting 1981, Dauvin 1988a, 1988b, Franz 1989, Marques and Nogueira 1991, Uitto and Sarvala 1991, Drake and Arias 1995, Wilson Jr. and Parker 1996), and growth rates estimated by us were similar to other species at the same latitude (Ali and Salman 1987, Marques and Nogueira, 1991, Drake and Arias, 1995).

Like other amphipod species, *A. valida* and *M. palmata* are semi-annual with short-lived spring and summer generations and long-lived autumn and winter generations (Moore 1981, Powell and Moore 1991, Beare and Moore 1994, Sudo and Azeta 1996).

Both species appeared as *r* strategists, with iteroparous females, multivoltine cycles, high individual fecundity and recruitment all over the year. This is the most common pattern in epifaunal species (van Dolah 1980) from physically controlled communities according to the stability-time theory (Sanders 1969). In environmental stressed systems like estuaries we should expect the evolution of opportunistic adaptive strategies to take place.

## Production estimates

Taking into account the whole period of study  $P$  (growth productivity) and  $E$  (elimination productivity) as well as  $\bar{B}$  (standing stock) showed significantly higher values in the *Z. noltii* beds than in the most eutrophicated area. Nevertheless, this difference does not reflect the entire reality. In fact we must look carefully to the dynamics of the two areas. In the most eutrophicated area for a short period (during the macroalgae bloom)  $P, E$  as well as  $\bar{B}$  were higher than in the *Z. noltii* meadows. This means that during the macroalgae bloom the most eutrophicated area was clearly the preferential habitat for the Amphipods probably due to resources availability.

The results clearly suggest that *A. valida* and *M. palmata* population dynamics and spatial distribution may change as a function of environmental changes through adaptative behavioural mechanisms. Nevertheless, it appears that macroalgae may represent mainly a good additional resource for population with a stable habitat like *Z. noltii* beds. But the macroalgae mats by it self can not sustain stable populations of amphipods due to its own dynamics. A conclusion would be that the total replacement of *Z. noltii* by macroalgae mats would negatively affect this kind of grazers.

The present results suggest that these species may play a more important role in the trophic dynamics than we might expected from their standing stock biomass. As pointed out by Fredette and Dias (1986), our data show that in warm shallow marine habitats relatively low biomass of benthic invertebrates can result in large production estimates (Kalejta and Hockey 1991).

As a whole, in the Mondego estuary, although macroalgae seem to be favourable to amphipods populations, if we look to the following effects of the algae crash it is reasonable to conclude that more extensive blooms, affecting the whole area of distribution of the species will on the contrary have a strong negative impact and could imply its disappearance.

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- Ali M.H. and Salman S.D. 1987. Growth and production of the amphipod *Parhyale basrensis* (Talitridae) in the Shatt al-Arab region. Mar. Ecol. Prog. Ser. 40: 231-238.
- Allen K.R. 1971. Relation between production and biomass. J. Fish. Res. Bd. Can. 28: 1573-1581.
- Beare D.J. and Moore P.G. 1994. Observations on the biology of a rare british marine amphipod: *Monoculodes gibbosus* (Crustacea: Oedicerotidae). J. Mar. Biol. Assoc. U.K. 74: 193-201.
- Birklund J. 1977. Biomass, growth and production of the amphipod *Corophium insidiosum* Crawford, and preliminary notes on *Corophium volutator* (Pallas). Ophelia 16: 187-203.
- Borowsky B. 1983. Reproductive behaviour of three tube-building peracarid crustaceans: the amphipods *Jassa falcata* and *Ampithoe valida* and the tanaid *Tanais cavolinii*. Mar. Biol. 77: 257-263.

- Bregazzi P.K. 1972. Life cycles and seasonal movements of *Cheinmedon femoratus* (Pfeffer) and *Tryphosella kergueleni* (Miers) (Crustacea: Amphipoda). Br. Antarct. Surv. Bull. 30: 1-34.
- Conlan K.E. and Bousfield E.L. 1982. The Amphipod superfamily Corophioidea in the North-Eastern Pacific region. Family Amphithoidae: Systematics and distributional Ecology. Nat. Mus. Canada Publ. Boil. Oceanog. 10: 41-75.
- Covi M.P. and Kneib R.T. 1995. Intertidal distribution, population dynamics and production of the amphipod *Uholchestia spartinophila* in a Georgia, USA, salt marsh. Mar. Biol. 121: 447-455.
- Dauvin J.C. 1986. Dynamique de la population d'*Abra prismatica* (Mollusque, Bivalve) de la baie de Mortaix (Manche occidentale). Anns. Inst. Océanogr. Paris 62: 1-12.
- Dauvin J.C. 1988a. Biologie, dynamique et production de populations de Crustacés Amphipodes de la Manche Occidentale. I. *Ampelisca tenuicornis* Liljeborg. J. Exp. Mar. Biol. Ecol. 118: 55-84.
- Dauvin J.C. 1988b. Life cycle dynamics and productivity of Crustacea-Amphipoda from the western English Channel. 4. *Ampelisca armaniana* Bellan-Santini et Dauvin. J. Exp. Mar. Biol. Ecol. 123: 235-252.
- 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. Tot. env. 145: 187-195.
- Drake P. and Anas A.M. 1995. Distribution and production of *Microdeutopus gryllotalpa* (Amphipoda: Aoridae) in a shallow coastal lagoon in the Bay of Cadiz, Spain. J. Crus. Biol. 15: 454-465.
- Duffy J.E. and Hay M.E. 1991. Food and shelter as determinants of food choice by an herbivorous marine amphipod. Ecology 72: 1286-1298.
- Elliot J.M. 1977. Statistical analysis of samples of benthic invertebrates. Freshwater Biological Association, Scientific Publications.
- Fish J.D. and Mills A. 1979. The reproductive biology of *Corophium volutator* and *C. arenarium* (Crustacea: Amphipoda). J. Mar. Biol. Assoc. U.K. 59: 355-368.
- 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.
- Franz D.R. 1989. Population density and demography of a fouling community amphipod. J. Exp. Mar. Biol. Ecol. 125: 117-135.
- 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.
- Gaschütz G., Pauly D. and David N. 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 gammand species (Crustacea, Amphipoda) in a French chalk stream. II: Standing crop. Bijdr. Dierk. (Contr. Zool) 51: 31-69.
- Greeze II. 1968. Feeding habits and food requirements of some amphipods in the Back Sea. Mar. Biol. 1: 316-321.
- 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) Helgolander wiss. Meeresunters 47: 243-263.
- Hodgkin E.P. and Hamilton B.H. 1993. Fertilizers and eutrophication in the southwestern Australia: Setting the scene. Fert. Res 36: 95-103.
- Kalejta B. and Hockey P.A.R. 1991. Distribution, abundance and productivity of benthic invertebrates at the Berg River estuary, South Africa. Estuar. Coast. Shelf Sci. 33: 175-191.
- 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.
- 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) 289-304.
- Lillebø A.I., Pardal M.A., Cardoso P. and Marques J.C. 2001. The effect of primary producers dynamics (macrophytes and macroalgae) on *Hydrobia ulvae* population dynamics, life cycle and production, in the south arm of the Mondego estuary. Aquatic ecology of the Mondego river basin. Global importance of local experience. (This volume)
- 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 Milleu* 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 caninata* (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., Jørgensen S.E. and Nielsen S.N. 1997. Modelling the effects of green macroalgae blooms on the population dynamics of *Cyathura caninata* (Crustacea: Isopoda) in an eutrophicated estuary. *Ecol. Model.* 102: 33-53.
- Martins I., Pardal M.A., Lillebø A.I., Flindt M.R. and Marques J.C. 2001. Hydrodynamics as a major factor controlling the occurrence of green macroalgae blooms in an eutrophic estuary: a case study. *Est. Coast. Shelf Sci.* 52: 165-177.
- 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.
- Moore P.G. and Wong Y.M., 1996. Observations on the life history of *Orchomene nanus* (Krøyer) (Amphipoda: Lysianassoidea) at Millport, Scotland as deduced from baited trapping. *J. Exp. Mar. Biol. Ecol.* 195: 53-70.
- Morritt D. and Stevenson T.D.I. 1993. Factors influencing breeding initiation in a beachflea *Orchestia gammarellus* (Pallas) (Crustacea: Amphipoda). *J. Exp. Mar. Biol. Ecol.* 165: 191-208.
- 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 do estuário do Mondego (Portugal). Ph.D. Thesis, University of Coimbra, Portugal.
- Pardal M.A., Marques J.C., Metelo I., Lillebø A.I. and Flindt M.R. 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.
- Pardal M.A., Marques J.C., Ferreira S., Martins I. and Lillebø A.I. 2001. Life Cycle, biology and production of na estuarine isopod (*Cyathura caninata*). Aquatic ecology of the Mondego river basin. Global importance of local experience. (This volume)
- 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., Limia J., Hull S. and Pont S. 1991. Interactions between amphipod *Corophium volutator* and macroalgal mats on estuarine mudflats. *J. Mar. Biol. Assoc. U.K.* 71: 899-908.
- Rafaelli D., Raven J. and Poole L. 1998. Ecological impact of green macroalgae blooms. *Oceanogr. Mar. Biol.* 36: 97-125.
- Sanders H.L. 1969. Marine benthic diversity: a comparative study. *Am. Nat.* 102: 243-282.
- Shearer M. 1978. Distribution and reproductive biology of *Corophium insidiosum* (Amphipoda) on the N.E coast of England. *J. Mar. Biol. Assoc. U.K.* 58: 585-596.
- Skadsheim A. 1982. The ecology of intertidal amphipods in the Oslo fjord. The life cycles of *Chaetogammarus marinus* and *C. stoerensis*. *Mar. Ecol.* 3: 213-224.
- Steele D.H. and Steele V.J. 1969. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. I: *Gammarus duebeni* Lillj. *Can. J. Zool.* 47: 235-244.
- Steele D. and Steele V.J. 1973. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. VIII. The duration of embryonic 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.
- Uitto A. and Sarvala J. 1991. Seasonal growth of the benthic amphipods *Pontoporeia affinis* and *P. femorata* in a baltic archipelago in relation to environmental factors. *Mar. Biol.* 11: 237-246.
- van Dolah R.F. 1980. A comparison of reproductive patterns in epifaunal and infaunal gammaridean Amphipoda. *Estuar. Coast. 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.





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