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MANUEL AUGUSTO GRAÇA
Scientific Editors

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Global Importance of Local Experience

Coimbra • Imprensa da Universidade

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THE SUPRABENTHIC MYSID *Mesopodopsis slabberi* (VAN BENEDEN) IN THE MONDEGO ESTUARY

Abstract

The biology, production, biochemical composition and energy content of the mysid *Mesopodopsis slabberi* (van Beneden) are described. Significant positive correlations between total length (TL) and cephalic length (CL) (TL = 2.5 CL + 0.012) and between dry weight (DW) and total length (LnDW = 3.0298 LnTL - 6.0229) were found. The annual production was 13.17 mg.m^{-3}year^{-1}, and the P/B ratio was 9.32. This turnover rate strength the hypothesis that *M. slabberi* plays an important role in the Mondego estuary food web. Protein, carbohydrate, chitin, lipid, phospholipid, and cholesterol contents were determined from freshly caught juveniles, males, and females throughout the year. Energy equivalents were calculated using conversion factors. Statistical analysis revealed significant seasonal differences in biochemical composition, and also between juveniles, females, and males. The nutritional cycle (environmental conditions: trophic conditions) and reproductive cycles appeared both as the main processes influencing the biology of *M. slabberi*.

Key words: Mysids, secondary production, biochemical composition, energy content.

Introduction

Mysids play an important role in the functioning of soft-bottom benthic ecosystems (San Vicente and Sorbe 1995). The population of *M. slabberi* is an important component within the suprabenthic communities (Azeiteiro and Marques 1999) and nectobenthic communities or benthopelagic zooplankton. Due to the abundance of *M. slabberi* in the Mondego estuary we studied several aspects of the species biology. The knowledge of the species population dynamics and secondary

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production (Azeiteiro et al. 1999), biochemical composition (Azeiteiro et al. 2000, in press a) and energetics (Azeiteiro et al. in press b) allows the analysis of an important fraction of the suprabenthic and nectobenthic trophic stock and the comparison among various mysid populations in their respective distribution areas.

Material and methods

Five sampling stations were located along the south arm of the estuary in order to represent the whole subsystem (Fig. 1). Although we were aware from former studies (Gonçalves 1991, Azeiteiro 1999) that the *M. slabberi* population was particularly abundant in the mid-areas of the south arm, it was decided to survey the entire south arm. Suprabenthic and crepuscular-time plankton samples were collected monthly at the five stations, during spring tides, following always the same sequence, from June 96 and July 97. Mysids samples were taken from sub-surface waters using a WP2 modified net (60 cm diameter and 335 µm mesh) (sub-superficial tows) and a suprabenthic net (50 cm diameter and 500 µm mesh) (suprabenthic tows).

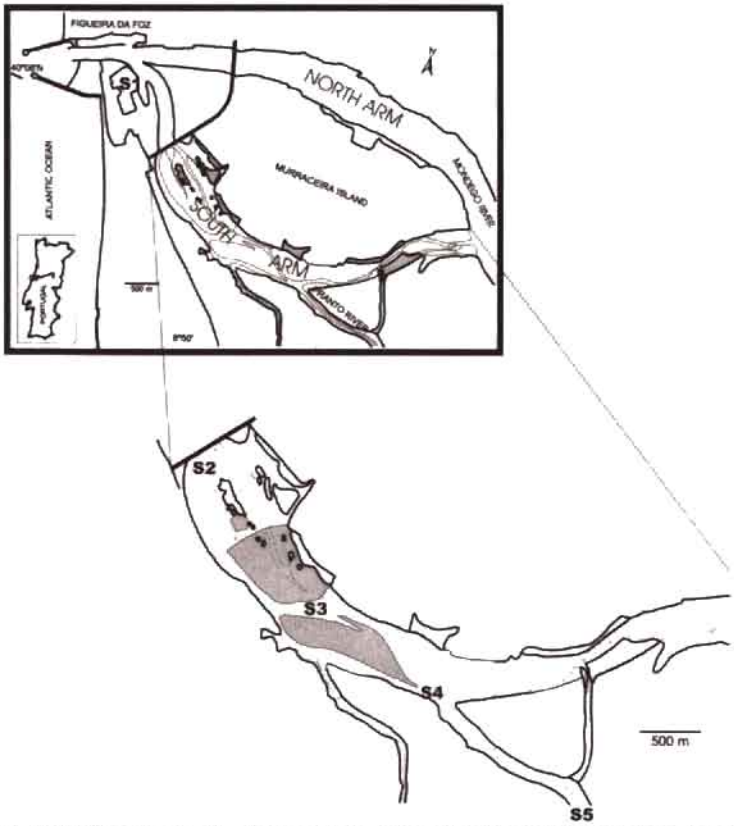

Fig. 1. Map of Mondego river estuary showing the locations of the five sampling stations in the southern arm.

Laboratory procedures

All samples were transported back to laboratory in good condition within 2h of collection. Those freshly caught animals were kept in ice at ±4 °C before they were classified and separated in juveniles, females, and males. Samples from each group were lyophilised, weighted, and kept at –30 °C; smaller portions of this material were later weighed and utilised for each analysis.

Production procedures

Specimens were measured (to the nearest 0.02 mm) from the anterior tip of carapace to the posterior tip of telson, as well as between the anterior and posterior tips of the carapace (Wooldridge 1986, Azeiteiro et al. 1999).

Individuals were classified into the following categories (Mauchline 1980, Sorbe 1984, Azeiteiro et al. 1999):

1. Juveniles: Secondary sexual characteristics absent;
2. Males;
3. Females (Immature females: secondary sexual characteristics in process of development; mature incubant females: marsupium fully developed and carrying eggs or embryos; and mature empty females: with empty expanded marsupium from where young have recently emerged).

To estimate mysid standing stock (mg of dry mass.m^{-3}) it was necessary to determine the relationships between cephalic length and dry weight and total length and dry weight. For this purpose, a set of specimens were measured and then dried for 24 h at 60 °C (Wooldridge 1986, Azeiteiro et al. 1999), after what they were individually weighted (to the nearest 0.01 mg) with a Mettler microbalance. According to Matthews (1973) and Jørgensen and Matthews (1975) we pooled the entire set of specimens, belonging to the different categories, in order to estimate morphometric relationships considered valid for the whole population (Azeiteiro et al. 1999).

Production was estimated using the Hynes (1961 *in* Sorbe 1984) average cohort method, modified by Benke (1979) with particular significance for multivoltine populations and called the size-frequency method by Waters and Hokenstrom (1980). The Hynes method for estimating aquatic invertebrates production involves first an estimation of the total number of individuals that developed into each size class and then the calculation of losses in numbers between size classes. Production is then estimated as the sum of biomass losses between successive size classes. The Hynes method does not require the recognition and tracking of individual cohorts. It is therefore suitable for populations with continuous reproduction and no synchronisation of larval release and egg extrusion (Sorbe 1984, Wooldridge 1986, Azeiteiro et al. 1999).

Biochemical analyses

Protein - Lyophilised material was homogenised in the proportion of 0,5 mg to 3 ml of pure water into different 10 ml test tubes. The water soluble protein content was analysed by the Lowry et al. (1951) method, modified by Fernandes et al. (1994) (Azeiteiro et al. 2000, in press a, b).

Carbohydrate - we prepared the samples for analysis following basically the same procedure as for proteins, but higher test tubes were used. The homogenates were analysed by the Raymont et al. method, described in Bamstedt (1976) and Omori and Ikeda (1984), using 1ml of 5 % phenol solution and 5 ml of concentrated sulphur acid (Azeiteiro et al. 2000, in press a, b).

Chitin – the analysis was performed using the Bamstedt (1976) method for dried homogenised material. However, instead of being incinerated, the chitin final product was analysed for its content in carbohydrate, using the method described above (Azeiteiro et al. 2000, in press a, b).

Total lipid – the analysis was performed following the method described by Lehtonen (1996), but we have done two washes instead of one. Approximately 15 mg of lyophilised material were weighed and homogenised in 0.5 ml of a chloroform/methanol (2:1) solution, and then centrifuged during 30 seconds. The precipitate was washed a second time with 0,5 ml chloroform:methanol (2:1) and centrifuged again for 30 seconds. We added 20 % volume of 0.9 % NaCl solution to the chloroform/methanol (2:1) solution from both washes and centrifuged again. The chloroform phase containing the lipids in solvent solution were placed into tared cups and the solvents were evaporated. Following the evaporation of the solvent solution, the cups were weighed and the weight of the lipids was calculated (Azeiteiro et al. 2000, in press a, b).

Lipid extracts were analysed for their phospholipid content through the quantification of phosphate. For this purpose we used the Bartlett (1958) phosphate determination with Fiske and Subbarow reducing agent, according to the method described in Sidney and Nathan (1969). All volumes were nevertheless reduced to one half of the indicated in the original description and spectrophotometer readings were done at 830 nm (Azeiteiro et al. 2000, in press a, b).

Lipid extracts were also analysed for their cholesterol content using the method described by Fernandes et al. (1994). The lipid chloroform extraction was evaporated to completely dryness. Lipids were dissolved with 20 ml of acetic acid and allowed to react with 1 ml of Liebermann-Burcherd reagent described by Huang et al. (1961), adapted to tissue by (Fernandes pers. comm.). We didn't find necessary to separate cholesterol from other lipids (Fernandes et al. 1994) because there wasn't any pigment interfering with spectrophotometer readings (Azeiteiro et al. 2000, in press a, b).

Energy equivalents calculation

From the biochemical analysis performed, energy equivalents were calculated using the conversion factors given by White et al. (1973): 4.1 cal/mg for protein, 4.3 cal/mg for carbohydrate, and 9.5 cal/mg for lipid (Azeiteiro et al. in press b).

Data analysis

The estimation of variation coefficients (CV) (CV = SD x 100 / X) (Bamstedt 1978) was use to provide an index of the relative variability for each biochemical component.

The first step in data analysis consisted of rejecting observations using a Q Test, defined as the ratio of the divergence of the discordant value from its nearest neighbour to the range of the values (Skoog and West 1972).

Secondly we performed an angular (arcsine) transformation of the data before analysing it. The arcsine transformation was chosen since it is recommended that data transformation is not warranted for analysis of variance with binomial data unless the largest sample size is more than five times greater than the smallest, and the smaller variances are associated with the smaller samples (Zar 1996). Now, it is known from statistical theory that percentages from 0 to 100 % or proportions from 0 to1 form a binomial, rather than a normal, distribution, the deviation from normality being great for small or large percentages (0 to 30 % and 70 to 100 %). So, if the square root of each proportion, p, in a binomial distribution is transformed into its arcsine (i.e., the angle whose sine is the square root of p), the resultant data will have an underlying distribution that is nearly normal (Zar 1996).

Finally, we performed an Analysis of Variance (ANOVA) to test differences between sexes and between months for all the components considered. An ANOVA Two Factor or factorial analysis of variance was carried out in first place to test for interaction among factors (Zar 1996). Since interaction was found the means of levels shouldn't be compared (Zar 1996). It was therefore necessary to perform a One-Way ANOVA for each factor, in order to reveal significant differences among the levels of a factor. Then we performed multiple comparison procedures (Zar 1996) following two methods: (1) the Tukey test (Tukey 1953 *in* Zar 1996), and (2), the Newman-Keuls test (Newman 1939 and Keuls 1952 *in* Zar 1996).

Results

The following body size/weight relationships were estimated for freshly caught specimens of *M. slabberi* (Figure 2): TL = 2,5 x CL + 0.012, LnDW = 3.0298 x LnTL - 6.0229.

Production estimates are summarised in Table 1. The annual net production was calculated at 13.17 $mg.m^{-3}.year^{-1}$, and the P/B ratio was estimated at 9.32.

Protein – It was the primary body component all over the year (Figure 3), constituting in average more then half of the dry weight. Protein contents varied between 58.2 and 74.8 %, for juveniles, between 61.7 and 83.8 %, for females, and between 58.1 and 78.7 % for males (Table 2). In general we could observe that, except for the winter season, the protein contents in juveniles was lower than in females and males. Juveniles showed a small decrease in protein contents in November, followed by a slow increase until the beginning of May. By the end of May a new and more

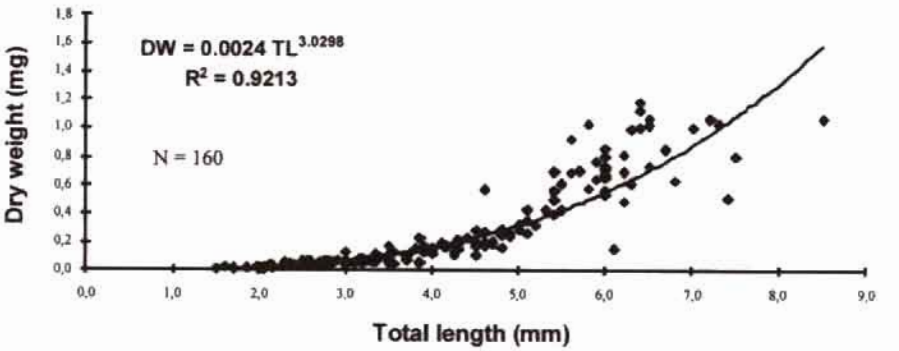

Fig. 2. Regression model for weight-length relationships. Correlation coefficients (R) and sample size (N) are indicated.

Table 1. Production estimates for *M. slabberi* in the Mondego estuary.

Total Length (mm)	Year Density	dm	dm_t-dm_{t-}	W (mg)	(mg/m³)	$(W_t \cdot W_{t-})^{-0.5}$	Biomass Lost Biomass	Biomass P (*18)
1,450	0,67	5,5E-02		7,390E-03	4,098E-04			
1,825	4,41	3,7E-01	-3,1E-01	1,484E-02	5,458E-03	1,047E-02	-0,0033	-5,888E-02
2,200	12,30	1,0E+00	-6,6E-01	2,614E-02	2,680E-02	1,970E-02	-0,0129	-2,330E-01
2,575	19,41	1,6E+00	-5,9E-01	4,212E-02	6,815E-02	3,319E-02	-0,0197	-3,541E-01
2,950	20,15	1,7E+00	-6,2E-02	6,360E-02	1,068E-01	5,176E-02	-0,0032	-5,750E-02
3,325	14,47	1,2E+00	4,7E-01	9,140E-02	1,102E-01	7,624E-02	0,0361	6,504E-01
3,700	13,13	1,1E+00	1,1E-01	1,263E-01	1,383E-01	1,075E-01	0,0119	2,150E-01
4,075	10,04	8,4E-01	2,6E-01	1,693E-01	1,416E-01	1,462E-01	0,0377	6,788E-01
4,450	7,54	6,3E-01	2,1E-01	2,210E-01	1,388E-01	1,934E-01	0,0404	7,266E-01
4,825	3,62	3,0E-01	3,3E-01	2,824E-01	8,513E-02	2,499E-01	0,0816	1,469E+00
5,200	4,27	3,6E-01	-5,5E-02	3,543E-01	1,261E-01	3,164E-01	-0,0173	-3,106E-01
5,575	4,00	3,3E-01	2,3E-02	4,376E-01	1,458E-01	3,938E-01	0,0090	1,615E-01
5,950	2,17	1,8E-01	1,5E-01	5,330E-01	9,621E-02	4,829E-01	0,0737	1,327E+00
6,325	1,30	1,1E-01	7,2E-02	6,414E-01	6,937E-02	5,847E-01	0,0423	7,615E-01
6,700	1,19	9,9E-02	9,2E-03	7,638E-01	7,555E-02	6,999E-01	0,0065	1,162E-01
7,075	0,49	4,0E-02	5,8E-02	9,008E-01	3,648E-02	8,294E-01	0,0485	8,723E-01
7,450	0,35	2,9E-02	1,1E-02	1,053E+00	3,073E-02	9,741E-01	0,0110	1,986E-01
7,825	0,10	8,6E-03	2,1E-02	1,222E+00	1,047E-02	1,135E+00	0,0234	4,209E-01
			8,6E-03			5,882E-06	0,0000	9,068E-07
				Sum(biom.) =	1,412E+00		Sum(p)=	6,583E+00
			P =	13,167	mg m⁻³ year⁻¹		P/B = 9,32	

accentuated decrease was observed, followed again by a slow increase. Female protein contents exhibited a permanent variation throughout the year, with the lowest and highest values being observed in May, respectively in the beginning and in the end of the month. A small decrease was also observed in November. Males never showed a great variation in protein contents, except for a clear decrease observed in December and a smaller one observed in June.

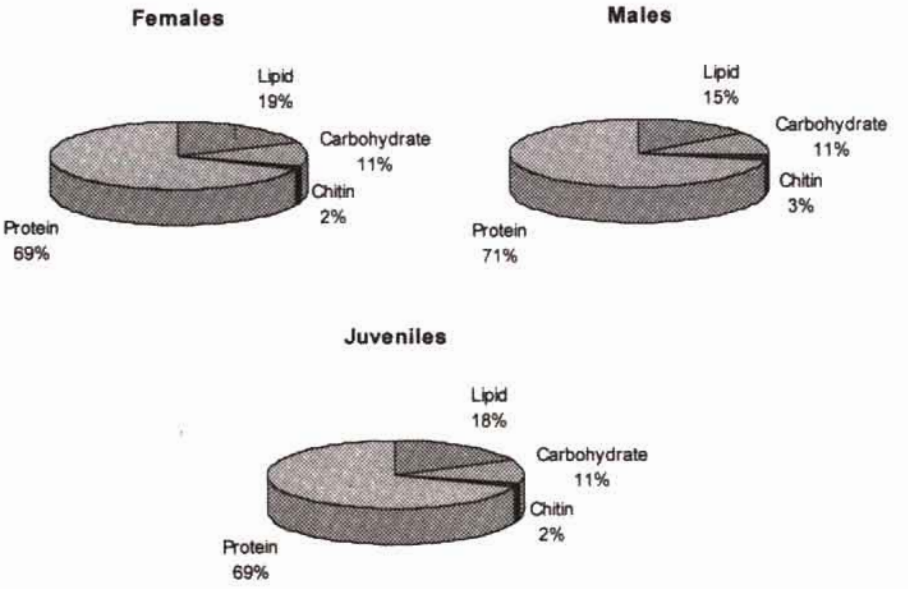

Fig. 3. Average annual composition of biochemical components (expressed as a % of tissue dry weight) in *Mesopodopsis slabberi* from the Mondego estuary.

Table 2. Seasonal variation in protein contents in *Mesopodopsis slabberi* from the Mondego estuary.

	Protein (% Dry Weight)					
	Juveniles		**Males**		**Females**	
	Average	Standard Deviation	Average	Standard Deviation	Average	Standard Deviation
October	74,8	7,9	70,0	5,2	74,6	7,6
November	64,3	2,4	73,8	6,6	61,7	3,0
December	67,7	4,9	58,1	1,9	70,3	5,1
March	69,7	2,9	74,0	2.5	67,6	2,9
May (9)	72,0	3,1	74,4	4,5	83,8	3,9
May (24)	58,2	4,7	75,2	3,7	61,8	2,7
June	61,0	3,3	70,8	3,1	69,4	6,5
July	70,3	1,7	78,7	1,5	72,0	2,1

Carbohydrate – Contrary to what we observed for proteins, juveniles consistently presented higher carbohydrate contents than females or males, which showed a similar variation (Table 3). Actually, carbohydrate contents varied between 6.24 and 16.12 %, for juveniles, between 4.86 and 28.99 % for females, and between 5.2 and 30.89 % for males. Juveniles showed the lowest value in November and the maximum by the end of May. With regard to males, we also observed the lowest values during winter, with

a minimum in November, and the highest ones during spring, with a maximum in October and the beginning of May.

Chitin - The variation of chitin contents was basically similar in juveniles, females, and males, the average varying between 0.48 and 7 % (Table 4). The highest values were observed in December and the lowest ones during spring.

Table 3. Seasonal variation in carbohydrate contents in *Mesopodopsis slabberi* from the Mondego estuary.

Carbohydrate (% Dry Weight)

	Juveniles		**Males**		**Females**	
	Average	Standard Deviation	Average	Standard Deviation	Average	Standard Deviation
October	10,32	1,11	30,89	39,18	28,99	31,47
November	6,24	2,16	5,20	0,66	12,35	4,14
December	11,94	1,64	8,39	1,24	6,02	0,55
March	11,81	2,80	6,79	1,75	7,24	2,69
May (9)	11,04	4,17	9,54	2,42	11,06	2,21
May (24)	16,12	3,40	8,73	1,06	9,40	1,60
June	10,93	1,76	8,57	2,56	4,86	1,53
July	8,64	2,35	8,64	1,42	9,27	1,78

Table 4. Seasonal variation in chitin contents in *Mesopodopsis slabberi* from the Mondego estuary.

Chitin (% Dry Weight)

	Juveniles		**Males**		**Females**	
	Average	Standard Deviation	Average	Standard Deviation	Average	Standard Deviation
November			2,25	0,52	3,66	1,04
December	4,06	0,96	7,00	2,58	5,44	2,72
March	3,14	1,67	3,64	1,83	2,11	0,55
May	0,98	0,34	0,91	0,23	0,81	0,21
June	0,75	0,15	0,48	0,16	0,66	0,2
July	0,61	0,19	0,71	0,23	0,66	0,24

Lipids – The variation in lipid contents was significantly different between juveniles and females, on one side, and males on the other side. In fact, lipid contents varied from 7 to 42 % in juveniles, between 10 and 43 % in females, and from 8 to 15 % in males (Table 5). Juveniles showed the highest values in November, then a clear decrease, with low values being kept during the winter and early spring, followed by a new increase in June. Female lipid contents exhibited a peak in March. As for males, there was almost no variation through the year, although slightly higher values could be found during the winter.

Table 5. Seasonal variation in total lipid contents in *Mesopodopsis slabberi* from the Mondego estuary.

	Lipid (% Dry Weight)		
	Juveniles	Males	Females
November	42	15	25
December	10	11	19
March	12	10	43
May (9)	11	8	14
May (24)	7	9	10
June	22	8	11
July	15	10	10

Phospholipids – There was little variation in phospholipids contents through the year in all population groups. Phospholipids contents ranged between 1.1 and 2.12 % in juveniles, from 1.12 to 2.17 % in females, and between 1,1 and 1,63 % in males (Table 6). Juveniles exhibited higher values in November and in June, while the lowest ones were recorded in May. Female phospholipids contents showed slightly higher values in November and again in March and July. Finally, in males, there is no conspicuous variation through the year.

Table 6. Seasonal variation in phopholipids contents in *Mesopodopsis slabberi* from the Mondego estuary.

	Phopholipids (% Dry Weight)					
	Juveniles		Males		Females	
	Average	Standard Deviation	Average	Standard Deviation	Average	Standard Deviation
November	2,12	0,55	1,63	0,32	2,17	0,29
December	1,75	0,08	1,10	0,15	1,30	0,08
March	1,54	0,42	1,19	0,14	1,59	0,11
May (9)	1,52	0,05	1,18	0,09	1,18	0,04
May (24)	1,10	0,35	1,24	0,08	1,24	0,05
June	1,82	0,08	1,51	0,12	1,12	0,12
July	1,43	0,05	1,57	0,13	1,48	0,25

Cholesterol – Yearly variation was clearly more evident in juveniles than in the adults. In fact, cholesterol contents ranged between 0.39 and 1.68 % in juveniles, while in females and males it ranged respectively between 0.41 and 0.61 % and from 0.57 to 0.73 % (Table 7). Therefore, while adults presented basically always the same cholesterol contents, juveniles exhibited a strong variation through the year, with the highest values in December, early May, and June, and the lowest ones in March, end of May, and July.

Table 7. Seasonal variation in cholesterol contents in *Mesopodopsis slabberi* from the Mondego estuary.

	Cholesterol (% Dry Weight)					
	Juveniles		**Males**		**Females**	
	Average	Standard Deviation	Average	Standard Deviation	Average	Standard Deviation
November	0,75	0,03	0,65	0,18	0,56	0,04
December	1,03	0,05	0,59	0,08	0,55	0,06
March	0,73	0,03	0,57	0,06	0,61	0,13
May (9)	1,68	0,15	0,59	0,02	0,58	0,07
May (24)	0,39	0,03	0,62	0,06	0,41	0,06
June	1,09	0,28	0,69	0,10	0,55	0,07
July	0,73	0,04	0,73	0,11	0,60	0,05

The largest variations occurred for carbohydrate and lipid contents, while protein contents were the most unchanging ones. The estimated CV values were as follows: in juveniles, protein 5.7 %; carbohydrates 23.4 %; phospholipids 16 % and cholesterol 20.8 %; in females, protein 6 %; carbohydrates 23.7 %; phospholipids 11.3 % and cholesterol 18.1 %, and, in males, protein 5 %; carbohydrates 19.6 %; phospholipids 8.2 % and cholesterol 18.7 %;

The protein caloric contents make the largest contribution to the total energy, remaining fairly uniform throughout the year (Table 8). The caloric content of the lipid fraction exceeded the values calculated for carbohydrates, suggesting that lipids are the major energy storage reserve (Table 8). The carbohydrate caloric energy makes a modest contribution to the total available caloric energy, remaining low throughout the year (Table 8).

Table 8. Seasonal changes in energy content in *Mesopodopsis slabberi* from the Mondego estuary.

	Energy content (cal/mg Dry Weight)								
	Proteins			**Carbo hydrates**			**Lipids**		
	Females	Males	Juveniles	Females	Males	Juveniles	Females	Males	Juveniles
October	3.133	2.940	3.142	1.218	1.298	0.433			
November	2.591	3.100	2.701	0.517	0.218	0.260	2.375	1.406	4.000
December	2.953	2.440	2.843	0.252	0.353	0500	1.843	1.026	0.912
March	2.839	3.108	2.927	0.302	0.286	0.496	4.123	0.969	1.102
May (9)	3.520	3.125	3.024	0.466	0.399	0.462	1.292	0.779	1.064
May (24)	2.596	3.158	2.444	0.395	0.305	0.676	0.950	0.865	0.637
June	2.915	2.974	2.562	0.193	0.445	0.601	1.017	0.741	2.109
July	3.024	3.305	2.953	0.361	0.479	0.424	0.931	0.960	1.397

The total caloric content (Table 9) was higher in females as compared with males in November, December, March and May (9). The total caloric content was higher in females as compared with juveniles in December, March, May (9), and May(24). The total caloric content was higher in males as compared with juveniles in May (24). In females the total caloric contents increased during June to July (summer), decreasing after March until May (24) (spring). In males the total caloric contents remain fairly uniform throughout the year except for a decrease in December (winter). In juveniles the total caloric contents after a decrease in May (24) increased notoriously in June (summer).

Table 9. Seasonal changes in total energy content in *Mesopodopsis slabberi* from the Mondego estuary.

Energy content (cal/mg Dry Weight)

	Females	Males	Juveniles
October			
November	5.483	4.724	6.961
December	5.048	3.819	4.255
March	7.265	4.363	4.525
May (9)	5.278	4.303	4.550
May (24)	3.940	4.388	3.757
June	4.125	4.160	5.272
July	4.316	4.744	4.773

The most pronounced differences in the total caloric contents between females and males were found in March, between females and juveniles were found also in March, and between males and juveniles were found in June (Table 9). The most pronounced differences in the total caloric contents between months were found in females between March and May (9) (Table 9).

ANOVA results are summarised in Tables 10 and 11. The factors tested were sex (considering juveniles, females, and males) and months (with 8 levels coincident with sampling dates: October, November, December, March, May - 09, May - 24, June and July). We performed an Analysis of Variance (ANOVA) to test differences between sexes and between months for all the components considered. An ANOVA Two Factor or factorial analysis of variance was carried out in first place to test for interaction among factors. Since interaction was found the means of levels shouldn't be compared. It was therefore necessary to perform a One-Way ANOVA for each factor, in order to reveal significant differences among the levels of a factor. Then we performed multiple comparison procedures following two methods: (1) the Tukey test and (2), the Newman-Keuls test.

Table 10. Analysis of variance: the variables under consideration are proteins, carbohydrates, chitin, phospholipids and cholesterol proportions (expressed as of total dry weight), in juveniles, females, and males of *Mesopodopsis slabberi* over a thirteen months period. The factors tested were sex (considering juveniles, females, and males) and month (with 8 levels coincident with sampling dates*: October, November, December, March, May - 09, May - 24, June and July).

ANOVA: Two-Factor with replication for testing interaction between factors: Sex groups X Months groups					ANOVA: Single Factor for testing interaction between all groups for each biochemical component				
Biochemical Component	*df*	*F calc*	*P-value*	*F crit*	Source of Variation	*df*	*MS*	*F calc*	*P-Value*	*F crity*
Proteins	14	5.5085	4.4655E-08	1.7750	Between Groups	23	0.0340	7.6636	1.391E-14	1.6197
					Within Groups	120	4.439E-3			
Carbohydrates	14	4.3935	2.7809E-06	1.7750	Between Groups	23	0.0235	4.1492	1.411E-07	1.6197
					Within Groups	120	5.675E-3			
Chitin	10	8.0821	3.5119E-09	1.9376	Between Groups	16	0.0242	7.8510	4.974E-11	1.7639
					Within Groups	85	3.088E-3			
Phospholipids	12	2.9989	1.2150E-03	1.8455	Between Groups	20	0.0019	4.0721	1.115E-06	1.6714
					Within Groups	105	4.712E-4			
Cholesterol	12	21.3605	1.1673E-20	1.8693	Between Groups	20	0.0010	34.2887	4.318E-32	1.6968
					Within Groups	84	3.001E-3			

* Specimens were collected only in these sampling dates. F calc = calculated F-value; F crit = critical F-value ($p \leq 0.05$).

Table 11. Multiple comparison of biochemical components average values: proteins, carbohydrates, chitin, phospholids, and cholesterol proportions (expressed as % of total dry weight) in juveniles, females, and males of *Mesopodopsis slabberi*, over a thirteen months period.

		Proteins		Carbohydrates		Chitin		Phospholipids		Cholesterol	
		P1	P2	P1	P2	P1	P2	P1	P2	P1	P2
October	Females	*	*	*	*						
	Males	*	*	**	**						
	Juveniles	*	*	**	**						
November	Females	**	**	*	**	*	*	*	*	***	***
	Males	*	*	**	***	*	**	*	*	***	***
	Juveniles	**	**	**	***			*	*	***	***
December	Females	*	*	**	***	*	*	*	*	****	****
	Males	**	***	**	**	*	*	*	*	***	***
	Juveniles	*	*	**	**	*	*	*	*	**	**
March	Females	**	**	**	**	*	*	*	*	***	***
	Males	*	*	**	**	*	*	*	*	****	****
	Juveniles	**	**	**	**	*	*	*	*	**	**
May (09)	Females	*	*	**	**	**	**	*	*	***	***
	Males	*	*	**	**	**	**	**	**	***	***
	Juveniles	*	*	**	**	**	**	*	*	*	*
May (24)	Females	**	***	**	**	**	**	*	*	*****	*****
	Males	*	*	**	**	**	**	*	*	***	***
	Juveniles	**	***	*	**	**	**	**	**	****	*****
June	Females	**	**	**	***	**	**	**	**	***	***
	Males	*	**	**	**	**	**	*	*	***	***
	Juveniles	**	**	*	**	**	**	*	*	**	**
July	Females	*	*	**	**	**	**	*	*	***	***
	Males	*	*	**	**	**	**	*	*	***	***
	Juveniles	*	**	**	**	**	**	*	*	***	***

Tests employed were: P - Tukey test and P' - Newman-Keuls test

Discussion

Body size/weight relationships were consistent with values previously reported for other mysid species (Ladurantaye and Lacroix 1980, Allen 1984, Sorbe 1984, San Vicente and Sorbe 1993, 1995, Chigbu and Sibley 1996).

The *Mesopodopsis slabberi* population has continuous reproduction in the Mondego estuary (Azeiteiro et al. 1999) like other mysids in other systems, namely, *Siriella armata* Milne Edwards, 1837, *Anchialina agilis* (G.O. Sars 1877), *Leptomysis gracilis* (G.O Sars 1864), *L. lingvura*, *Paramysis arenosa* (G. O. Sars 1877), *P. bacescoi* Labat, 1953, *P. nouveli* Labat, 1953, *Schistomysis kervillei*, *S. ornata*, *S. spiritus*, *Praunus flexuosus* (Muller 1776), *P. inermis* (Rathke 1843), *Neomysis integer* (Leach 1814) (Nouvel and Nouvel 1939, Labat 1957, Mauchline 1965, 1969, 1971 a, b, c, Parker and West 1979, Sorbe

1980) The *Mesopodopsis slabberi* population exhibited clear spatial and temporal (tidal and seasonal) migration patterns (Azeiteiro et al. 1999). This type of migration has been described in other estuaries (Greenwood et al. 1989, Webb and Wooldridge 1990) for *M. slabberi* and other mysid species (Ladurantaye and Lacroix 1980, Allen 1984). Marine populations of *M. slabberi* may undergo onshore/offshore migration (Mauchline 1980, Webb and Wooldridge 1990, Azeiteiro et al. 1999). Moreover, Collins and Williams (1982) considered *M. slabberi* to belong to a more estuarine-marine community in summer (April-August) and to a euryhaline-marine community in winter (January). Such seasonal onshore/offshore migrations may have underlying salinity-related reproductive significance (Greenwood et al. 1989). Although reproduction and recruitment were continuous throughout the year, main peaks were observed in late summer/autumn and late spring/early summer (Azeiteiro et al. 1999). A smaller peak was also recorded in early winter (Azeiteiro et al. 1999). Such a recruitment pattern suggests the occurrence of two (bivoltinism) or three (trivoltinism) generations per year (Azeiteiro et al. 1999). Spring females and males die after the late spring/early summer recruitment period (Azeiteiro et al. 1999). In fact, large mysids disappeared from the population in June as their progeny, the first summer generation, matured (Azeiteiro et al. 1999). A similar pattern was reported for *Mysidopsis bigelowi* (W.M. Tattersall) in a temperate estuary (Allen 1984), and for *Anchialina agilis* (G.O. Sars) in temperate neritic waters (Sorbe 1984). This common biological model among littoral and neritic mysids between 25° and 50° of latitude is also refered to *Schistomysis kervillei*, *S. spiritus* and *Neomysis integer* in the temperate West European Atlantic coasts (Mauchline 1967, 1971 a, Bremer and Vijverg 1982, San Vicente and Sorbe 1990). Other observations (Sorbe 1984, 1991) confirm that the mysid voltinism is directly influenced by temperature (Pezzack and Corey 1979). The yearly cycle, similarly to other estuarine/neritic temperate species, appears to cope with seasonal changes in each particular environment (Mauchline 1980, Sorbe 1984, Johnston and Northcote 1989). Temperature, salinity, oxygen and chlorophyll a biomass are determining factors affecting *M. slabberi* population dynamics and production in the Mondego estuary (Azeiteiro et al. 1999). Marques et al. (1994) claimed that the prevailing conditions in the Mondego estuary, namely eutrophication, should result in the development of opportunistic adaptive strategies among invertebrate species. This might be related to the fact that the production of *M. slabberi* was found to be relatively low as compared to other species in other systems but the P/B ratio is higher.

The P/B of the available measurements for zooplankton present a modal turnover rate about 10-20 times a year (Valiela 1995). The few available P to B rates of meiofauna indicates a turn over about 10 times per year, considerably larger than those for the larger macrofauna (modal macrobenthic turnover rate is one to two times a year) (Valiela 1995) (Table 12 provides a comparison between our results and data on the annual P/B ratios of different mysids). The high specific production –what we referred as the P/B- of *M. slabberi* population makes them important secondary producers. The faster turnover of smaller organisms means that although the biomass of small-sized species may be smaller than that of larger species, the P/B of smaller species makes them proportionately more important producers than larger species

Table 12. Annual P/B ratios for other mysid species

	Reference	annual P/B ratios
Neomysis americana	Richards and Riley 1963	3.66
Neomysis americana	Richards et al. 1967	3.66
Gastrosaccus spinifer	Arntz 1971	2.00
Mysis relicta	Hakala 1978	3.0-3.8
Mysis relicta	Sell 1982	2.2-3.3
Neomysis integer	Bremer and Vijverberg 1982	4.00
Rhopalophthalmus terranatalis	Wooldridge 1983	8.66
Mesopodopsis wooldridgei	Wooldridge 1983	8.00
Rhopalophthalmus terranatalis	Wooldridge 1986	7.85
Anchialina agilis	Sorbe 1984	4.29
Schistomysis ornata	Sorbe 1984, 1991	6.09
Schistomysis kervillei	San Vicente et al. 1990	9.38
Schistomysis parkeri	San Vicente and Sorbe 1993	9.73
Schistomysis spiritus	San Vicente and Sorbe 1995	6.77

(Vernberg and Cull 1974, Valiela 1995). *M. slabberi* production and turnover rate justify the hypothesis that this species plays a relevant role in the energy flow in the food web (Azeiteiro et al. 1999).

The marine invertebrates show a seasonal variation on biochemical composition. The protein, lipid and carbohydrate accumulation cycles show their maximums in spring (Ansell 1974, 1980, Newell and Bayne 1980, Lethonen 1996) appearing to be related with the nutritive disponibility, breeding cycle and temperature variations (Clarke 1977). Carbohydrates, lipids and proteins exhibited maximums in late autumn (November) and spring. The species appeared to accumulate lipids in the beginning of the phytoplankton maximum (February) (Azeiteiro 1999), females showed the lipid accumulation peak in March, and the juveniles in November, after a massive recruitment period occurring in late summer/autumn and spring/early summer (Azeiteiro et al. 1999), and the third phytoplankton minimum (September and October) (Azeiteiro 1999). Females appear to restore their body mass after the main recruitment periods when phospholipids peaks. Sex influence can be realised because a certain disinchrony in reaching spring maximums becomes evident (Azeiteiro et al. 1999).

Our results were basically consistent with information provided by literature on the biochemical composition of Crustaceans (Raymond et al. 1964, 1968, Bamstedt 1975, 1976, 1978, Omori and Ikeda 1984, Lethonen 1996), namely regarding other mysid species like *Boreomysis arctica* (Kroyer) and *Neomysis integer* (Leach). Although

there are not many studies on mysids to compare our results, these were nevertheless consistent with data obtained for a number of benthic and suprabenthic peracarid species (Raymond et al. 1964, Bamstedt 1975, 1976, 1978, Johnson and Hopkins 1978, Omori and Ikeda 1984, Lethonen 1996) and for the Louisiana red swamp crayfish (Fernandes et al. 1994, Mendonça 1995).

Proteins were the main body component all over the year, and also the least changeable one. In other groups (Moss and Lawrence 1972, Ortega et al. 1984) the slightly fluctuations in the protein content were related to the hydric condition, what may suggest that protein variation reflects seasonal fluctuations in the hydration level of the tissues (Ortega et al. 1984). The minimum values obtained in November, for juveniles and females, and in December, for males, months of adverse environmental conditions, may suggest that lost in weight during winter months (Azeiteiro et al. 1999) may be sustained also by proteins. On the contrary, carbohydrates and lipids, namely the lipids, suffered apparent seasonal variations. The carbohydrates showed a great temporal variability which indicates their rapid accumulation and also depletion (easy accessible reserve) (Stryer 1988). Although a great accumulation occurred in autumn (October), it decreases towards the winter (starvation period), namely the females. Juveniles showed the lowest value in November and the maximum by the end of May. With regard to adults, we also observed the lowest values during winter, with a minimum in November in the males and December in females, and the highest ones during spring, with a maximum in May which follows the higher chlorophyll a concentration months (Azeiteiro 1999). The variation of chitin contents were basically similar in juveniles, females, and males. The highest values were observed in December and the lowest ones during spring, which might not be an absolute variation in chitin but a changing relation between the area and volume of the individuals as they pass from a winter starvation period to a spring one well nutrished (Azeiteiro et al. 1999). Although we haven't those results we believe they would confirm the statement above because of protein variation results we achieved. Protein as the main body component is the most important component for weight variations, and has its lowest values in winter months. Lipid variation is a function of metabolism and reproductive strategy, depending therefore on the species yearly cycle (Ruizverdugo et al. 1997). In fact, many life history traits of aquatic invertebrates depend on investments in depot lipids (Lehtonen 1996, Ohman 1997). We could observe seasonal variations in cholesterol and phospholipids. Phospholipids showed a continuous raise from December to July, in males, June to July, in females, and May to June, in juveniles, which may indicate their structural role. Yearly variation in cholesterol was clearly more evident in juveniles than in the adults. Therefore, while adults presented basically always the same cholesterol contents, except for a small decrease in June in females, juveniles exhibited a strong variation through the year, with the highest values in November, December, March, and June, that are also peak recruitment months (Azeiteiro et al. 1999) which may indicate their role as a precursor of growth hormones. Seasonal changes in lipids, namely triglycerides, and carbohydrates, i.e., the major cellular components under which energy is stored (Stryer 1988), appear to be mainly a function of the nutritional cycle (since they peak after favourable environmental trophic conditions) (Azeiteiro 1999).

Changes in phospholipids and cholesterol appear to be directly related to the reproductive cycle. Actually, as structural components of cell membranes, phospholipids forcibly change depending on cells proliferation and degeneration (Cullis and Hope 1991). On the other hand, cholesterol plays a double role as a structural component of cell membranes (Bloch 1991) and as a precursor of sexual hormones involved in the reproductive control of crustaceans (Sastry 1983, Goddard 1988).

During early spring, *M. slabberi* females in the Mondego estuary stores energy. This accumulated energy is utilised in preparation for reproduction peaks, after that they recover. The results achieved indicate also that *M. slabberi* does not accumulate energetic reserves for use during winter. The storage of energy in *M. slabberi* females during March (early spring) may be primarily a function the synthesis of reproductive products. Actually, adult females requiring large amounts of energy for egg production store considerably during March (late winter to early spring) as compared with relatively low storage in adult males with no break in spring months.

In *M. slabberi*, like in other crustaceans, biochemical changes apparently resulted from metabolic purposes in relation with the nutritional cycle and/or synthesis of reproductive products (Chaisemartin 1979, Sastry 1983, Kabre 1983, Kabre and Chaisemartin 1987, Zekhnini et al. 1991). Therefore, both environmental and trophic conditions appear to play an important role in determining seasonal changes in biochemical composition and then the biology of the mysid species in the estuary.

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