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Composition of the Trophic Structure of Zooplankton in a Shallow Temperate Estuary (Mondego Estuary, Western Portugal)

Fernando Morgado[1,*], Carla Quintaneiro[1], Elisa Rodrigues[1], Manuel Ramiro Pastorinho[1], Paula Bacelar-Nicolau[2], Luis Vieira[1], and Ulisses Manuel Azeiteiro[2,3]

[1]*Department of Biology, University of Aveiro, 3810-193 Aveiro, Portugal*
[2]*Department of Exact Sciences and Technologies, Open University, 1269-001 Lisboa, Portugal*
[3]*IMAR-CIC, University of Coimbra, 3004-517 Coimbra, Portugal*

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Fernando Morgado, Carla Quintaneiro, Elisa Rodrigues, Manuel Ramiro Pastorinho, Paula Bacelar-Nicolau, Luis Vieira, and Ulisses Manuel Azeiteiro (2007) Composition of the trophic structure of zooplankton in a shallow temperate estuary (Mondego Estuary, western Portugal). *Zoological Studies* **46**(1): 57-68. The south arm of Mondego Estuary, western Portugal is characterized by shallow depths and marked longitudinal spatial gradients, namely the tidally induced salinity gradient and an eutrophication gradient. The aims of this work were to study the zooplankton composition and trophic structure of the 335 μm taxocenosis in 2 different locations of the salinity and eutrophication gradients in the south arm. The 2 sampling stations displayed significantly different patterns of temporal variations in environmental variables. The total zooplankton density at each station showed significant spatial and temporal variabilities. However, the number of *taxa* did not show significant differences among months or between sites. The densities of the most abundant *taxa* significantly differed between the sampling stations and throughout the study period. The zooplankton assemblages were dominated by omnivores, representing 43.9% of the total zooplankton (with herbivores and carnivores representing 4.4% and 0.5%, respectively). Omnivores were significantly more abundant during autumn, winter, and spring, particularly in Oct., Mar., and May, at station 2, and during Jan., Mar., and Apr., at station 1. Herbivores were significantly more abundant during autumn, late winter, and spring particularly at station 1. Carnivores showed low densities throughout the year, being more abundant in summer and autumn. Despite the detected similarities to other temperate estuaries, the results of this work may indicate environmental stresses in this ecosystem: the spatial structure dominates seasonal patterns; and there are low diversities and high numbers of resident populations. This kind of ecological pattern has been previously reported for other biological communities. The prevailing conditions in Mondego Estuary, namely eutrophication, should result in the development of opportunistic adaptive strategies among invertebrates.
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Key words: Zooplankton distribution, Zooplankton structure, Eutrophication, Mondego Estuary.

Estuarine ecosystems are very dynamic systems where water circulation and terrestrial influences (e.g. river and sewage inflows) induce high variabilities in the distributions and structures of planktonic populations. Increases in nutrients and organic matter enhance primary productivity in these coastal ecosystems, eventually developing into eutrophication processes (Lillebø et al. 1999, Nedwell and Rafaelli 1999, Pardal et al. 2000, Jonge et al. 2002) that are reflected in the distributions and structures of specific faunal compositions of the benthic communities (Marques et al. 1997, Martins et al. 1997, Lillebø et al. 1999, Pardal et al. 2000). It seems reasonable that such modifications have significant effects at other levels, and adverse effects on zooplankton structures may be expected through changes in the species composition, densities, diversity, and trophic struc-

*To whom correspondence and reprint requests should be addressed. Tel:351-234370786 Fax:351-234426408
E-mail:fmorgado@bio.ua.pt

tures. In general, pollutants reduce species diversity, increase population sizes, and cause episodic pulses in the zooplanktonic community (Siokou-Frangou and Papathanassiou 1991, Telesh et al. 1999). In shallow-water ecosystems, eutrophication creates a complex set of direct and indirect reactions that leads to major changes not only in producers but in the rest of the ecosystem; eutrophication operates mainly via bottom-up control, but interacts with top-down controls. Higher nutrient supplies make all producers more nutrient-sufficient, so that increased grazing pressure is expected as more nutrients become available, and therefore meaningful changes in the trophic dominance and community structure are also likely to occur.

The south arm of Mondego Estuary is characterized by shallow depths and marked longitudinal spatial gradients (Pardal et al. 2000), namely a tidally induced salinity gradient (Azeiteiro and Marques 2000, Azeiteiro et al. 2002, Vieira et al. 2002, Bacelar-Nicolau et al. 2003) and a eutrophication gradient (Flindt et al. 1997, Marques et al. 1997, Martins et al. 1997, Lillebø et al. 1999).

The aims of this work were to study the zooplankton distribution and structure of the 335 μm taxocenosis in 2 different locations of the salinity and eutrophication gradients in the south arm of Mondego Estuary.

MATERIALS AND METHODS

Study site

Mondego Estuary, located on the Portuguese west coast (North Atlantic Ocean) (40°08'N, 8°50'W), has an area of 3.3 km^2 and a volume of 0.0075 km^3. The hydrological basin of the Mondego River has an area of 6670 km^2 and provides an average discharge of 8.5 x 10^9 m^3 (Fig. 1). The circulation in the south arm of the estuary depends on tides and on a much smaller amount of freshwater discharge from a tributary - the Pranto River, which is controlled by a sluice located 3 km from its confluence with the Mondego River. The sampling stations were located along the south arm of the estuary (Fig. 1). Station 1 is closer to the mouth of the estuary (2.3 m deep at high tide), while station 2 is located in the inner

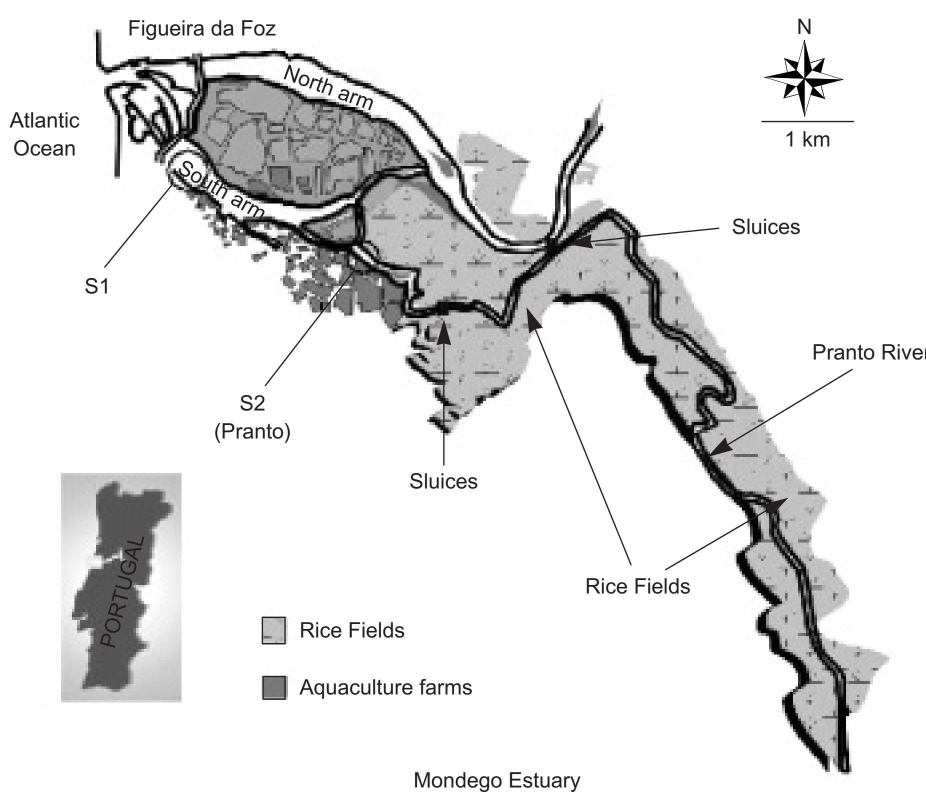

Fig. 1. Mondego River Estuary, showing locations of the sampling stations 1 (S1) and 2 (S2).

area of the south arm (1.7 m deep at high tide).

Sampling Program

Samples were taken monthly, from July 1999 to June 2000, during high spring tides for determination of environmental parameters, phytoplankton, and zooplankton. All samples were analyzed *in situ* for salinity, temperature, dissolved oxygen (DO), and pH. Samples were also analyzed in the laboratory (in triplicate) for their nutrient contents (NO_2^-, NO_3^-, NH_3, and PO_4^{3-}) and chlorophyll *a* (Bacelar-Nicolau et al. 2002, 2003, Vieira et al. 2002). Sub-surface (at 20 cm depth) phytoplanktonic samples (horizontal hauls) were collected with a 25 μm mesh net (Vieira et al. 2002). Sub-surface (at 20-40 cm depth) zooplanktonic samples (horizontal hauls) were collected using 335 μm mesh nets.

Laboratory procedures

Organisms were identified and counted, and densities were expressed as individuals per cubic meter (ind./m^3). In planktonic communities, the insertion of a certain organism in a trophic position (e.g. herbivores) is arguable, because even though some species have fixed food preferences, the great majority present great flexibility, being able to modify their feeding according to the availability and quality of food items in their environment. The species recorded were classified into 3 trophic groups - carnivores, herbivores, and omnivores - using the criteria of the morphology of the feeding apparatus, mode of feeding, and the nature and origin of the food. Species that could not be classed into one of these 3 groups were pooled under "undetermined". Bearing this in mind, the governing criterion of classification was to integrate each species in the corresponding predominant feeding regime as determined by the structure of its mouth parts (Rose 1933) and information in the literature (Russel 1953, Trégobouff and Rose 1957, Totton and Bargmann 1965, Fenaux 1967, Rice and Ingle 1975a, b, Fincham 1977, Mauchline in Blaxter et al. 1980, Fincham and Figueras 1986, Barnes 1994).

Community data analysis

Multiple regression models were developed in which species abundances and numbers of species were correlated with salinity, temperature, DO, chlorophyll *a*, pH, nitrites, nitrates, and phosphates (Zar 1984). Data were log-transformed prior to the analysis of variance (ANOVA) in all cases.

Cluster analysis of *taxa* was performed by the unweighted pair group method with arithmetic mean (UPGMA) method, using Pearson's correlation coefficient (Legendre and Legendre 1979). One-way ANOVA was used to test differences between the 2 stations and among months for all variables considered.

Two-way ANOVA was used to test differences in trophic level densities between sampling stations and seasons. Data were log-transformed prior to the ANOVA, in all cases.

RESULTS

Distribution of environmental variables and phytoplankton

A description and analyses of the environmental parameters (Table 1) were published by Bacelar-Nicolau et al. (2002, 2003) and Vieira et al. (2002).

At sampling station 1, the average temperature was 16.1°C, varying between 20.0°C in Aug. 2000 and 11.8°C in Dec. 1999. Salinity varied throughout the annual cycle between a minimum of 17.9‰ in Dec. 1999 and a maximum of 31.7‰ in Apr. pH fluctuated between 7.5 and 8.3. The percent saturation of DO varied between a minimum of 66.0% in June and a maximum of 99.4% in Feb., with an annual average value of 83.3%. Chlorophyll *a* had an average value of 0.544 mg/m^3, with a maximum in Oct. (1.080 mg/m^3) and a minimum in Jan. (0.190 mg/m^3) (Bacelar-Nicolau et al. 2002, 2003, Vieira et al. 2002).

At station 2, the annual average temperature was 18.0°C, varying between 25.0°C in Aug. 1999 and 11.0°C in Jan. 2000. Salinity varied between 9.5‰ in Apr.,and 31.0‰ in Sept. pH fluctuated slightly, with a minimum of 7.5 in Sept., an average value of 7.9, and a maximum of 8.4 in Dec. DO saturation presented a minimum value of 48.0% in Sept. and Nov., a maximum value of 91.0% in Jan., and an annual average of 69.4%. Chlorophyll *a* concentration presented an average annual value of 1.747 mg/m^3, greater than at station 1, with a maximum of 2.730 mg/m^3 in May, and a minimum of 0.810 mg/m^3 in Jan. (Bacelar-Nicolau et al. 2002, 2003, Vieira et al. 2002).

Temporal variations in environmental variables significantly differed ($p < 0.001$) for the 2 sampling stations. Station 1, under direct marine influence, was characterized by smaller annual variations in temperature, salinity, and pH, and DO values were usually high. In contrast, station 2 presented marked fluctuations in all variables and lower values of DO year round. Nitrites, nitrates, ammonia, and chlorophyll *a* values were consistently higher at station 2.

As to phytoplankton, the most abundant taxa were the Bacillariophyceae, Cyanoprokaryota, Dinophyta, Euglenophyta, and Chlorophyta. The composition of phytoplankton differed between the 2 sampling stations. The Bacillariophyceae dominated at station 1 throughout the year. At station 2, the Bacillariophyceae dominated from Sept. to Dec., and also in Feb. and May. Cyanophyta dominated in Aug. and Jun., and Chlorophyta was particularly abundant in Jan. and Mar. (Vieira et al. 2002).

The higher values of chlorophyll *a* and the presence of Cyanophyta at the upstream station during the summer months are an indication of a potential eutrophication situation that was not observed at the downstream station.

Zooplankton composition and distribution

The zooplankton composition and abundances of dominant species differed significantly among months (Table 2), as well as between the 2 sites (Table 3). Copepoda was mostly dominated by holoplanktonic *taxa*, but Chaetognata (4.8% in Sept. and 3.6% in Dec. 1999), Siphonophora (25.7% in Aug. and 2.1% in Oct.), and Isopoda (7.7% in Aug.) were also observed at station 1, and Mysidacea (13.9% in Oct. and 7.4% in Nov.) and Isopoda (48.9% in Aug.) were observed at station 2. In the meroplankton, Mollusca larvae and eggs (96.2% in Sept., 47.6% in Oct., 68.7% in Dec., 65.3% in Feb., and 70.6% in May), Decapoda larvae (42.2% in Aug. and 3% in Jan.), and Polychaeta larvae (0.4% in Feb.) were frequently observed, mainly at station 1, and larvae and eggs (1.1% in Feb. and 6.7% in May) were observed occasionally at station 2 (Fig. 2).

At station 1, the dominant species were *Acartia clausi*, *Clausocalanus arcuicornis*, *Acartia*

Table 1. Environmental data (temperature, salinity, pH, oxygen dissolved - saturation %, NO_2^-, NO_3^-, NH_3, PO_4^{3-} and chlorophyll *a* values) from monthly annual sampling cycle in the south arm of the Mondego Estuary, in both sampling stations, between July 1999 and June 2000

	July		Aug.		Sept.		Oct.		Nov.		Dec.	
	S_1	S_2	S_1	S_2	S_1	S_2	S_1	S_2	S_1	S_2	S_1	S_2
Temp (°C)	18.9	23.6	20.0	25.0	19.1	20.7	16.9	19.6	16.8	16.6	11.8	13.2
Salinity (‰)	24.5	18.1	23.0	26.0	25.0	31.0	27.0	22.0	31.1	19.5	17.9	29.3
pH	8.2	7.9	8.1	7.6	8.3	8.3	7.6	8.3	7.9	7.5	7.8	8.4
% DO	80.0	72.0	94.0	85.0	86.0	48.0	80.5	60.0	68.4	48.0	69.5	79.0
NO_2^- (mgL^{-1})	0.006	0.007	0.006	0.016	0.006	0.026	0.009	0.036	0.007	0.048	0.005	0.060
NO_3^- (mgL^{-1})	0.065	0.031	0.058	0.033	0.051	0.035	0.085	0.076	0.073	0.106	0.061	0.135
NH_3 (mgL^{-1})	0.002	0.113	0.008	0.173	0.015	0.233	0.003	0.181	0.007	0.172	0.010	0.163
PO_4^{3-} (mgL^{-1})	0.004	0.007	0.004	0.008	0.004	0.008	0.003	0.007	0.003	0.007	0.003	0.007
Chlorophyll *a*	0.605	1.445	0.415	2.275	0.250	2.270	1.080	1.620	0.670	1.390	0.260	1.160

	Jan.		Feb.		Apr.		May		June	
	S_1	S_2	S_1	S_2	S_1	S_2	S_1	S_2	S_1	S_2
Temp (°C)	11.9	11.0	14.1	14.1	14.2	14.0	15.8	18.3	18.0	22.3
Salinity (‰)	23.2	23.2	29.7	29.4	31.7	9.5	21.1	12.0	26.1	10.1
pH	7.8	7.9	7.9	7.6	7.5	7.6	7.7	7.6	8.2	8.3
% DO	89.5	91.0	99.4	72.4	85.0	74.0	97.4	75.2	66.0	59.0
NO_2^- (mgL^{-1})	0.005	0.006	0.008	0.055	0.008	0.042	0.007	0.028	0.012	0.071
NO_3^- (mgL^{-1})	0.129	0.193	0.164	0.163	0.171	0.274	0.178	0.384	0.091	0.177
NH_3 (mgL^{-1})	0.032	0.034	0.045	0.188	0.040	0.189	0.034	0.191	0.093	0.370
PO_4^{3-} (mgL^{-1})	0.003	0.009	0.004	0.007	0.003	0.008	0.003	0.008	0.003	0.005
Chlorophyll *a*	0.190	0.810	0.340	2.040	0.810	1.300	0.740	2.730	0.620	2.180

bifilosa var. *inermis*, *Temora longicornis*, *Littorina littorea* eggs, and post-veligers of *Hydrobia ulvae*. At station 2, which consistently showed a lower abundance of total zooplankton and species number, *Acartia tonsa* was by far the most abundant species followed by *Mesopodopsis slabberi*.

The overall monthly densities of total zooplankton ranged from 0.84 ind./m^3 in Sept. 1999 at station 2 to 2167 ind./m^3 in Mar. 2000 at station 1. The number of species ranged from 2 *taxa* in Sept. 1999 at station 2 to 27 *taxa* in Oct. at station 1 (Fig. 3). The total zooplankton density at each station showed significant spatial and temporal variabilities ($p < 0.001$); however, the number of *taxa* did not significantly differ among months or between sites (Tables 2, 3). Overall, higher zooplankton densities were found at station 1 in Oct. 1999 at 186.7 ind./m^3, in Jan. 2000 at 144.4 ind./m^3, in Mar. 2000 at 2167 ind./m^3, and in Apr. 2000 at 820.1 ind./m^3. The values for station 2 were generally lower. Nevertheless the patterns of variation throughout the year were similar.

The densities of the most abundant *taxa* significantly differed ($0.01 < p < 0.001$) over months and between stations in all cases (Tables 2, 3). The seasonal abundance patterns of *A. clausi* and *A. bifilosa* var. *inermis* almost paralleled that of the total zooplankton community at station 1, followed by *C. arcuicornis*, *T. longicornis*, and post-veligers of *H. ulvae*. The same was observed with the sea-

Table 2. Results of the one-way ANOVA of the effects of month on the total zooplankton concentration, number of species and on each of the most abundant *taxa*

	Month				
Source of variation	df	MS	*F*	*p*	
Total zooplankton	10	0.10747	8547.30	0.001	***
Number of species	10	557.01	0.99	0.507	n.s.
Clausocalanus arcuicornis	10	0.28148	3363.86	0.001	***
Temora longicornis	10	0.20242	4677.71	0.001	***
Acartia clausi	10	0.88302	1063.63	0.001	***
A. bifilosa var. *inermis*	10	0.29756	3163.86	0.001	***
A. tonsa	10	0.77043	1219.41	0.001	***
Mesopodopsis slabberi	10	0.10499	9044.49	0.001	***
Post-veliger *Hydrobia ulvae*	10	0.24589	3836.87	0.001	***
Littorina littorea eggs	10	0.12693	7511.06	0.001	***

n.s., not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 3. One-way ANOVA of the effects of sampling station on the total zooplankton concentration and number of species, and on each of the most abundant taxa

	Station				
Source of variation	df	MS	*F*	*p*	
Total zooplankton	2	0.58764	7807.29	0.001	***
Number of species	2	584.31	0.48	0.507	n.s.
Clausocalanus arcuicornis	2	0.23886	19816.70	0.01	**
Temora longicornis	2	0.11206	42245.90	0.01	**
Acartia clausi	2	0.66628	7045.70	0.001	***
A. bifilosa var. *inermis*	2	0.68991	6816.13	0.001	***
A. tonsa	2	0.40883	11490.34	0.001	***
Mesopodopsis slabberi	2	0.11358	41800.50	0.01	**
Post-veliger *Hydrobia ulvae*	2	0.31326	15053.68	0.001	***
Littorina littorea eggs	2	0.19565	24282.25	0.01	**

n.s., not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

sonal abundance of *A*. *tonsa* at station 2, followed by *A*. *bifilosa* var. *inermis* and *M*. *slabberi*. Although at station 1, besides the former species, *L*. *littorea* eggs in Oct. 1999 (88.6 ind./m^3), *C*. *arcuicornis* and *T*. *longicornis* in Oct. (24.6 and 6.7 ind./m^3) and Nov. 1999 (77.2 and 4.9 ind./m^3) showed higher densities. At station 2, *A*. *bifilosa* var. *inermis* also showed noticeable densities in Nov., Feb., Mar., and Apr., as did *M*. *slabberi* in Oct.

Zooplankton community structure

Despite the overall high resemblance of species distribution in the dataset, the communities structure of the 2 selected areas of the estuary differed. This is evidenced by the dominance of the spatial structure in the cluster analysis (Fig. 4): cluster A consisted of species which occurred at higher densities at the outer station (not impacted), including *A*. *clausi*, *T*. *longicornis*, *A*. *bifilosa* var. *inermis*, zoeae of *C*. *maenas* and post-veligers of *H*. *ulvae*, with all other species in cluster B, which occurred at both the inner and outer stations. Cluster A was divided into 2 sub-groups according to the seasonal occurrences: sub-group a1 was composed of species which occurred in autumn and spring, and sub-group a2 was composed of

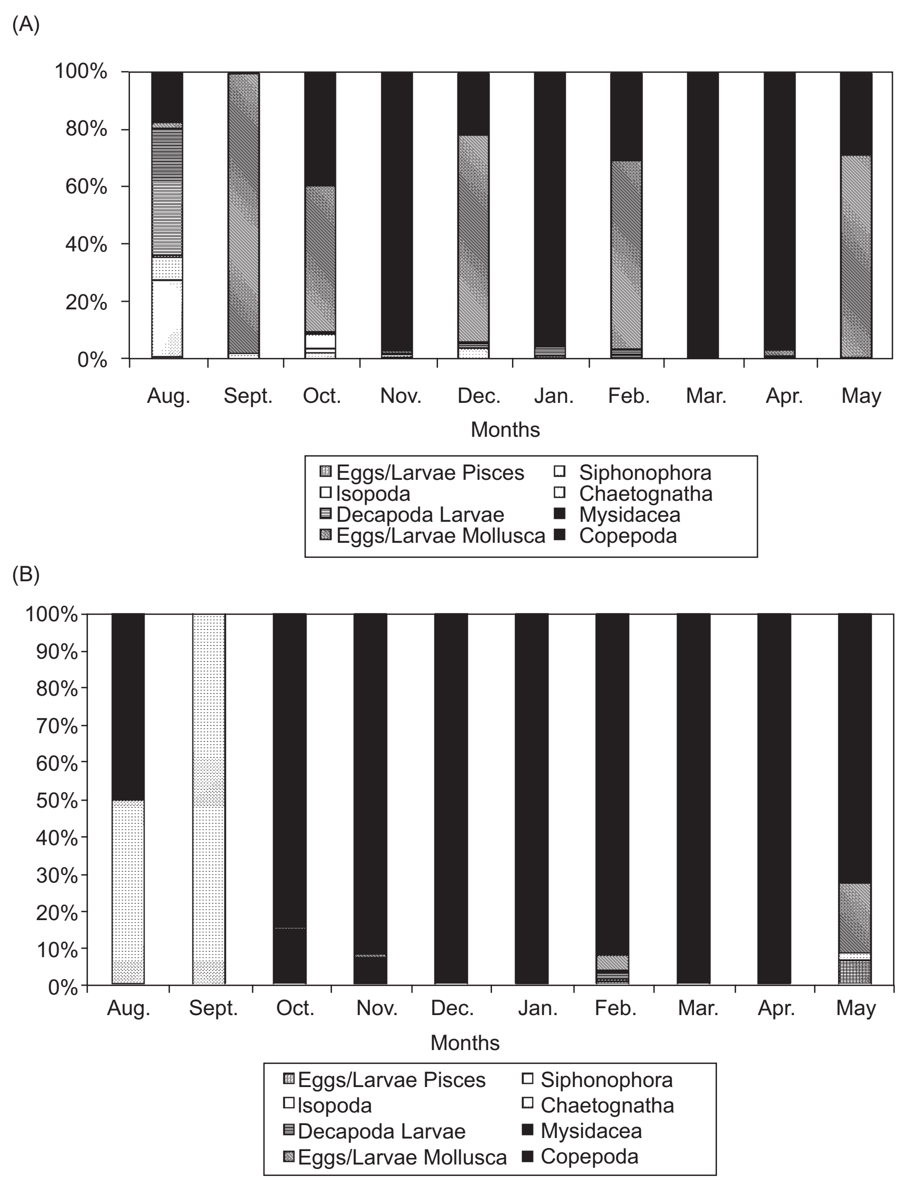

Fig. 2. Abundance percentage of the main zooplanktonic groups at the two sampling stations (A: S1) and (B: S2).

species occurring in winter and spring. Cluster a2 was further divided into 4 clusters: b1 containing species only found at station 1 in summer, autumn, and spring; b2 containing species found at station 1 during autumn and spring; b3 containing species with occurrences at both stations 1 and 2 during summer and spring; and b4 containing species only found at station 2.

Zooplankton trophic structure

Among the 50 zooplankton *taxa* identified at the 2 sampled sites, 18 were selected for analyses (Table 4). The omnivores that dominated the zooplankton assemblages represented 43.9% of the total zooplankton. Herbivores and carnivores represented 4.4% and 0.5%, respectively, of the entire community (Table 4). Omnivores were significantly more abundant ($p < 0.05$) during autumn, winter, and spring, particularly in Oct., Mar., and May at station 2, and Jan., Mar., and Apr. at station 1. Herbivores were significantly more abundant ($p < 0.01$) in autumn, late winter, and spring and also significantly more abundant ($p < 0.01$) at station 1. Carnivores were present in low densities throughout the annual cycle, with maximum abundance values in summer and autumn (Tables 5, 6).

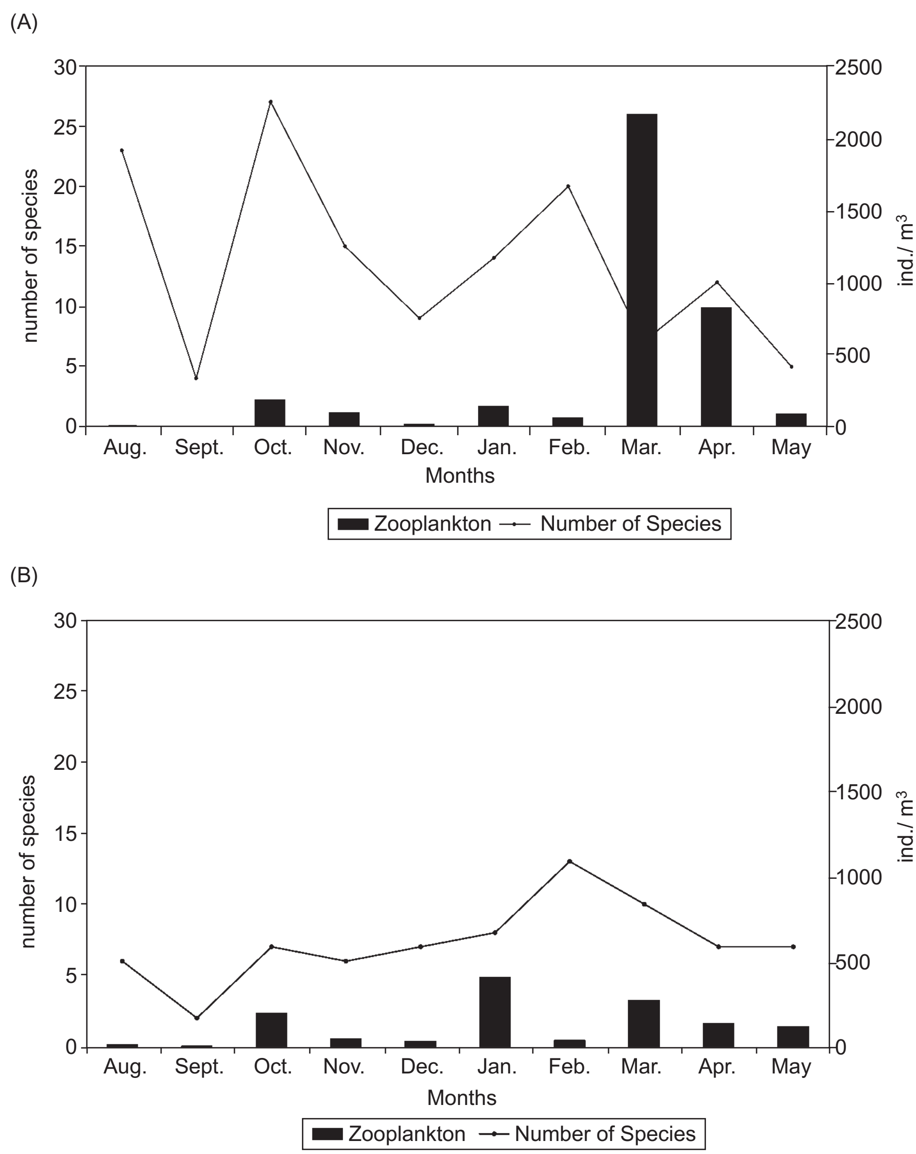

Fig. 3. Densities and number of species in the two sampling stations (A: S1) and (B: S2).

DISCUSSION

Environmental variables and phytoplankton

The observed distribution patterns of the environmental parameters mostly agreed with those observed earlier (Azeiteiro and Marques 2000, Azeiteiro et al. 2002, Bacelar-Nicolau et al. 2002 2003, Vieira et al. 2002) defining a clear spatial unidirectional salinity gradient and a secondary temperature-chlorophyll *a* temporal gradient in the south arm of Mondego Estuary (Azeiteiro and Marques 2000, Azeiteiro et al. 2002, Bacelar-Nicolau et al. 2002, 2003, Vieira et al. 2002). The estuarine and marine phytoplanktonic communities are frequently dominated by dinoflagelate and diatom species, as observed at both sampling sites of Mondego Estuary, where diatoms and dinoflagelates were the most abundant phytoplankton species. We also found Chlorophyta, Euglenophyta, and Cyanoprokaryota (Vieira et al. 2002). This flora conditions the primary consumers, due both to cell morphology and the associations that they establish with each other, and also because of the nutritional quality or "value" of the different species. The greater nutrient and chlorophyll *a* contents, and the presence of Cyanophyta in the upstream station are an indication of a potential eutrophication situation that was not found at the downstream station.

Zooplankton distribution

In estuaries, the seasonal patterns of zooplankton abundance and distribution are complex and extremely variable (Siokou-Frangou 1996, Gilabert 2001, Vieira et al. 2003). This variability results from interactions of various factors, such as the fact that zooplanktonic organisms are able to feed on other sources than phytoplankton (e.g., microzooplankton and detritus), and are consequently less dependent on phytoplankton dynamics. Tidal currents and river flows are also responsible for variabilities in zooplankton abundances by affecting the period of time that a given zooplanktonic population persists in the estuary.

Results show distinct zooplankton assemblages at both stations. The spatial differentiation

Table 4. Total density and dominance (%) of principal trophic groups and species in the south arm of Mondego Estuary at both sampling stations between July 1999 and June 2000

			Total Station 1	Total Station 2	Total Density	%
Carnivorous	*Muggiaie atlantica*		3.39	0.00	3.39	0.08
	Diphyes unid.		1.08	1.29	2.37	0.06
	Oithona nana		2.14	0.00	2.14	0.05
	Paragnathia formica		3.54	6.98	10.52	0.26
	praniza *P. formica*		2.32	4.34	6.66	0.16
	Sagitta friderici		13.83	0.00	13.83	0.34
		total	26.32	12.62	38.94	0.93
Herbivorous	*Paracalanus parvus*		14.08	0.00	14.08	0.34
	Clausocalanus arcuicornis		115.77	2.04	117.81	2.88
	Temora longicornis		43.85	2.53	46.39	1.13
	Acartia grani		15.24	0.00	15.24	0.37
	Post-vel. *Hydrobia ulvae*		140.33	25.63	165.96	4.05
		total	329.28	30.21	359.49	8.78
Omnivorous	*A. clausi*		1944.63	26.24	1970.88	48.15
	A. bifilosa var. *inermis*		984.53	56.83	1041.37	25.44
	A. tonsa		16.02	530.11	546.14	13.34
	Mesopodopsis slabberi		0.90	32.41	33.32	0.81
		total	2946.10	645.61	3591.72	87.75
Undetermined	zoeae *Carcinus maenas*		8.62	0.61	9.23	0.23
	zoeae *Pachygrapsus marmoratus*		3.74	0.00	3.74	0.09
	Litorina littorea eggs		88.75	1.29	90.04	2.20
		total	101.12	1.91	103.03	2.52

is revealed by the lower values observed, both in total zooplankton abundance and in the number of species, in the upstream area (which is less saline and more eutrophic). The *A. tonsa* dominance at station 2, the short trophic chain, and the low taxonomic richness of this area, as well as the absence of carnivorous species (medusae, siphonophores, and chaetognaths), reflect a situation that may be the result of eutrophication as directly indicated by chlorophyll *a* concentrations, nutrient enrichment, and bathymetry. Fulton (1984), and Kaartvedt and Svendensen (1995) showed that the increase in the abundance of *A. tonsa* is a population attribute of the species when it faces increased water temperatures and nutrients, and shallow depths; comparable results have been found in areas affected by pollution (Siokou and Papathanassiou 1991, Soetaert and Van Rijswijk 1993).

Trophic structure

Many omnivorous species select their prey on the basis of size rather than type, or change food types as individuals grow, e.g., most detritus feed-

Table 5. Variations in density and standard deviation of principal trophic groups in the south arm of the Mondego Estuary, in both sampling stations, between July 1999 and June 2000

	Aug.		Sept.		Oct.		Nov.		Dec.	
	St 1	St 2	St 1	St 2	St 1	St 2	St 1	St 2	St 1	St 2
Carnivorous										
Total	2.63	5.57	0.08	0.84	17.12	1.94	1.27	0.00	0.51	0.20
Std Dev.	0.48	1.68	0.03	0.29	2.98	0.54	0.42	0.00	0.21	0.08
Herbivorous										
Total	0.20	0.00	3.82	0.00	45.83	0.00	89.98	2.76	11.25	0.79
Std Dev.	0.08	0.00	1.71	0.00	9.94	0.00	33.24	0.79	4.23	0.35
Omnivorous										
Total	1.56	5.67	0.03	0.00	19.89	188.56	4.88	40.11	2.19	29.22
Std Dev.	0.74	2.84	0.01	0.00	5.68	73.53	0.97	15.48	0.32	9.32
Undetermined										
Total	3.75	0.00	0.00	0.00	89.02	1.30	0.00	0.00	0.22	0.00
Std Dev.	2.16	0.00	0.00	0.00	51.07	0.75	0.00	0.00	0.13	0.00

	Jan.		Feb.		Mar.		Apr.		May	
	St 1	St 2	St 1	St 2	St 1	St 2	St 1	St 2	St 1	St 2
Carnivorous										
Total	1.47	0.00	0.49	0.22	0.00	1.64	2.40	0.00	0.34	2.21
Std Dev.	0.41	0.00	0.20	0.09	0.00	0.67	0.98	0.00	0.14	0.90
Herbivorous										
Total	6.87	1.32	46.25	1.85	19.16	0.33	40.76	0.33	65.16	22.84
Std Dev.	1.53	0.59	17.31	0.64	7.30	0.15	7.31	0.15	28.48	9.61
Omnivorous										
Total	126.67	1.32	11.30	31.94	2111.89	260.35	642.61	5.93	25.08	82.52
Std Dev.	63.01	0.66	5.61	12.38	702.95	93.90	186.54	2.55	8.26	40.77
Undetermined										
Total	4.42	0.00	1.32	0.62	0.00	0.00	2.40	0.00	0.00	0.00
Std Dev.	2.55	0.00	0.67	0.36	0.00	0.00	1.38	0.00	0.00	0.00

ers are facultative predators, most predators can feed occasionally on dead organic matter, and certain herbivores can use animal prey at certain times (Valiela 1995). Many planktonic predators prey on each other, and usually have highly diversified diets. These features make it difficult to clearly define planktonic trophic levels.

Oligotrophic waters may have a greater range of zooplankton sizes than eutrophic waters. Predation is size-dependent, so the more size classes of plankton that occur there, the more kinds of predators that may be present. It is therefore possible to have a larger number of links in oligotrophic oceanic than in coastal or more eutrophicated food webs (Valiela 1995).

CONCLUSIONS

Nutrients and chlorophyll *a* values were higher in the upstream area of the estuary; this fact is related to the river discharge, the shallow depths, and the reduced water circulation, which increase residence times and induce a bentho-pelagic mixture, with both phenomena contributing to higher chlorophyll *a* concentrations in upper areas of the estuary. The results of this work may reflect the environmental stresses occurring in this ecosystem: lower diversities and high numbers of resident populations in the more eutrophicated areas with a short trophic chain.

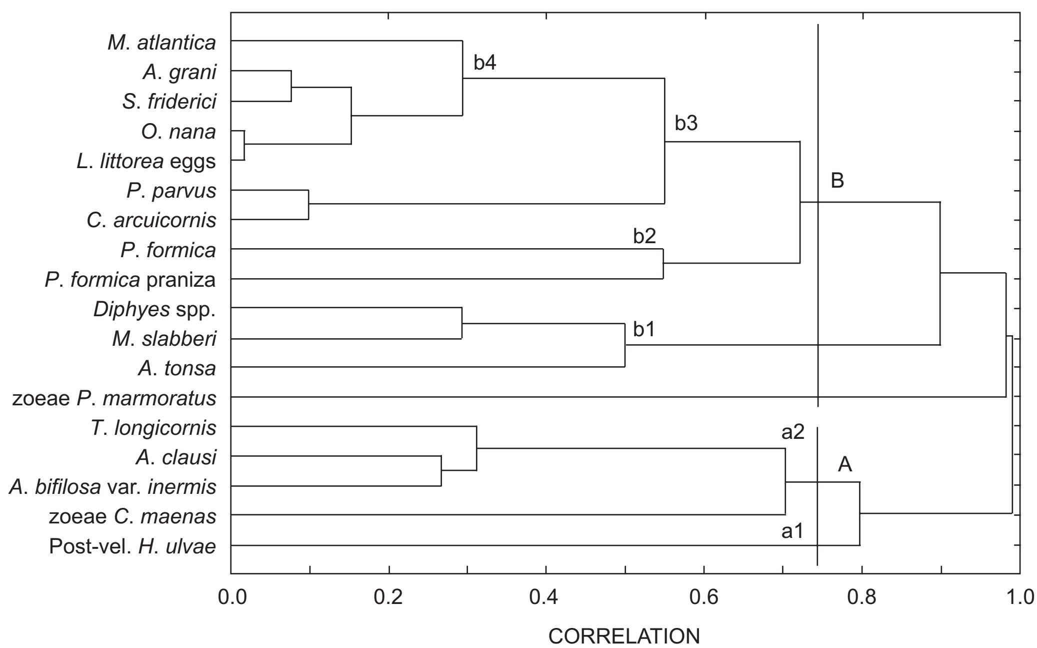

Fig. 4. Classification of the most abundant *taxa* obtained by the UPGMA method.

Table 6. Two-way ANOVA of the concentration of the principal trophic groups in the south arm of Mondego Estuary between July 1999 and June 2000. The null hypothesis was that when there are organisms in the water column, their average concentration between sampling stations and months do not differ across treatments

	Sampling station					Season					Sampling station x Season				
Source of variation	df	MS	*F*	*p*		df	MS	*F*	*p*		df	MS	*F*	*p*	
Carnivorous	1	0.123	0.174	0.684	n.s.	3	0.123	0.515	0.68	n.s.	3	0.123	0.756	0.540	n.s.
Herbivorous	1	0.159	24.780	0.0001	**	3	0.159	4.895	0.01	**	3	0.159	1.058	0.403	n.s.
Omnivorous	1	0.609	0.058	0.814	n.s.	3	0.609	3.389	0.05	*	3	0.609	1.463	0.274	n.s.
Undetermined	1	0.266	2.404	0.147	n.s.	3	0.266	0.278	0.84	n.s.	3	0.266	0.923	0.963	n.s.

df, degrees of freedom; MS, mean square; *F*, test value; *p*, probability value; n.s., $p > 0.05$; * $p < 0.05$; ** $0.01 > p > 0.001$; *** $p < 0.001$

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