JOURNAL OF PLANKTON RESEARCH | VOLUME 28 | NUMBER 3 | PAGES 297–312 | 2006

Zooplankton and ichthyoplankton communities in a temperate estuary: spatial and temporal patterns

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Received April 3, 2005; accepted in principle January 18, 2006; accepted for publication January 27, 2006; published online February 2, 2006

Communicating editor: R.P. Harris

Zooplankton and ichthyoplankton assemblages were studied from January 2003 to June 2004 in a temperate shallow estuary (Mondego estuary, Portugal). Monthly sampling was performed at five stations at high and low tides, with subsurface tows with 335 and 500 μm mesh Bongo nets. Analysis of variance (ANOVA) showed a significant effect ($P < 0.05$) of the mesh size of the net on the abundance of main zooplankton groups. On average, the abundance of the 500 μm taxocenosis was 67 and 102 times lower than the 335 μm taxocenosis at high and low tides respectively, especially in the south arm. More than 80 species were identified in the zooplankton samples. The upper reaches of northern arm are dominated by freshwater crustacean mesozooplankton like Acanthocyclops robustus *and* Diaptomus *spp. and the cladocerans* Daphnia, Ceriodaphnia *and* Bosmina, *often being codominant. In the southern arm, the resident estuarine copepod* Acartia tonsa *was dominant, eventually being the most abundant taxon. Marine reaches of estuary are usually dominated by the marine calanoid copepods* Acartia clausi *and* Temora longicornis *and the siphonophores* Muggiaea atlantica. *Concerning the ichthyoplankton, this was dominated by the larvae of estuarine resident species, mainly* Pomatoschistus *sp., and eggs of* Engraulis encrasicolus. *The abundance of* Pomatoschistus *sp. larvae was positively correlated with water temperature. Statistical analysis (canonical correspondence analysis) used to determine the spatiotemporal structure of the zooplankton assemblages and its correlation with environmental variables showed that salinity and temperature were the main factors influencing the distribution of zooplankton. The results obtained also showed that abundance was strongly influenced by the hydrological circulation pattern and direct or indirect human impacts that occur in each arm of the estuary.*

INTRODUCTION

Estuaries are transition areas between land and sea forming aquatic ecosystems that are characterized by a variety of inter-related biotic and abiotic structural components and intensive chemical, physical and biological processes (Flindt *et al.*, 1999; Kibirige and Perissinotto, 2003; Telesh, 2004). Estuarine variability is reflected in the dynamics of the biological populations, particularly planktonic ones. Spatiotemporal variation and habitat types are among the most important factors affecting patterns of species abundance, composition and size structure of estuarine plankton (Kennish, 1990; Hoffmeyer, 2004). Assemblages can also vary depending on the geographical location and on geological, hydrological and ecological factors (Gilabert, 2001; Beaugrand *et al.*, 2002; David *et al.*, 2005). The relationship between distribution of zooplankton or ichthyoplankton communities and physical and/or chemical variables has been studied in several estuaries, and frequently salinity and temperature have been shown to be the most important parameters affecting the distribution and abundance of plankton (Esteves *et al.*, 2000; Mouny and Dauvin, 2002; Tackx *et al.*, 2004).

This article was presented at Plankton Symposium III, held at Figuera da Foz, portugal, between 17 and 20 March 2005, under the auspices of the University of Coimbra and the University of Aveiro, and coordinated by Mário Jorge Pereira and Ulisses M. Azeiteiro.

doi:10.1093/plankt/fbi126, available online at www.plankt.oxfordjournals.org

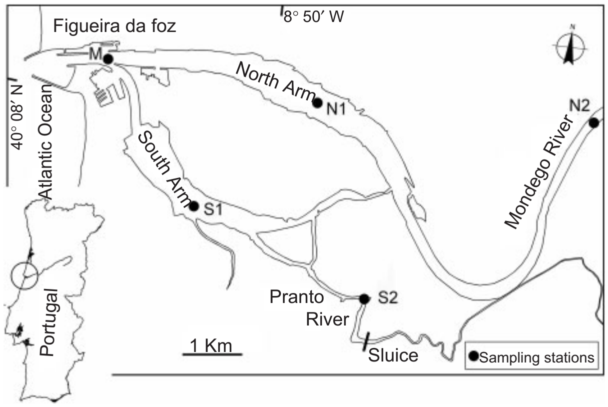

Fig. 1. Map of the Mondego estuary, located on the western coast of Portugal. Sampling stations surveyed in this study are indicated (M, mouth station; S1 and S2, southern arm stations; N1 and N2, northern arm stations).

The Mondego estuary is a temperate shallow estuary which is divided into two arms, north and south (Fig. 1), with different hydrographical conditions. As for many other regions, this system is subject to direct and indirect human effects related to intensive agriculture, harbour facilities and economical growth at the regional scale. This estuary shows symptoms of eutrophication (in the south arm) and suffers from regular dredging activity (in the north arm), which has resulted in reduced environmental quality (Pardal *et al.*, 2000; Cardoso *et al.*, 2004). Despite being a well-documented system and extensive literature concerning the effect of eutrophication on the benthic communities (Pardal *et al.*, 2000; Cardoso *et al.*, 2004; Verdelhos *et al.*, 2005; and references therein), knowledge of the planktonic assemblages is lacking, work to date focussing only on the influence of the saline gradient in the south arm of the estuary (Azeiteiro *et al.*, 1999; Gonçalves *et al.*, 2003; Vieira *et al.*, 2003). To date, no comparative analysis of the communities of both contrasting arms has been carried out. In this study, we aimed to analyse the temporal and spatial patterns of the zooplankton and ichthyoplankton communities between the two contrasting arms and to identify the major environmental parameters and stressors that may influence the distribution of these assemblages in this typical small temperate shallow estuary.

MATERIALS AND METHODS

Study site

The Mondego estuary (Fig. 1) is a mesotidal estuary situated on the western coast of Portugal. It consists of two arms, north and south, separated by an alluvium-formed island, with different hydrological characteristics. The northern arm with a lower residence times (<1 day) is deeper (4–8 m at high tide), constitutes the main navigation channel and is subjected to regular dredging activities (human direct disturbance). At neap tides, this arm is characterized by a salt-wedge during low tide, changing to partially mixed water column at high tide (Cunha and Dinis, 2002). Contrasting situations occur at spring tides, when it is partially mixed at low tide and well mixed at high tide (Cunha and Dinis, 2002). The southern arm is shallower (2–4 m deep, at high tide), with higher residence times (2–8 days), and shows clear symptoms of eutrophication (human indirect disturbance). This channel is largely silted up, especially in the upstream areas, forcing most of the freshwater discharge to flow out through the northern arm (Pardal *et al.*, 2000; Cardoso *et al.*, 2004). The water circulation in the south arm is predominantly due to the tidal cycle and to a relatively small freshwater input from a tributary, the Pranto River, which is artificially controlled by a sluice (Marques *et al.*, 2003). Usually completely mixed, it can be partially mixed during the rare fluvial floods (Cunha and Dinis, 2002). Owing to the eutrophication experienced by Mondego estuary since the 1980s, as a result of excessive nutrient release into coastal waters, several mitigation measures (nutrient-loading reduction, seagrass bed protection and freshwater circulation enhancement) have been implemented to promote the recovery of the entire surrounding environment (Marques *et al.*, 2003; Cardoso *et al.*, 2005).

Sampling procedure

Sampling was carried out monthly from January 2003 to June 2004 at five stations (Fig. 1): M, mouth station; S1 and S2, southern arm stations; N1 and N2, northern arm stations. Hydrological data were collected on each sampling occasion, only during high tide, due to logistical constraints. The following environmental factors were measured: temperature and salinity using a Cond 330i, dissolved oxygen concentration (WTW OXI 330i) and transparency (Secchi disc). Subsurface water samples were taken for determination of dissolved inorganic nitrogen and phosphorus. Samples were filtered (Whatman GF/F glass-fibre filter) and stored frozen at $-18°C$ until analysis following standard methods described in Limnologisk Metodik (Limnologisk Metodik, 1992) for ammonia (NH_3-N) and phosphate (PO_4-P) and in Strickland and Parsons (Strickland and Parsons, 1972) for nitrate (NO_3-N) and nitrite (NO_2-N). For determination of chlorophyll a (Chl a), 50–100 mL water samples was filtered onto Whatman GF/C glass-fibre filters followed by extraction following the protocol of Parsons *et al.* (Parsons *et al.*, 1985). Zooplankton and ichthyoplankton samples were collected by subsurface tows with 335 and 500 μm Bongo nets (diameter: 0.5 m) fitted with a Hydro-Bios flow meter fixed in the mouth (the volume filtered average 66 m^3). Net collections were fixed in 4% buffered formalin in seawater. In the laboratory, ichthyo- and zooplankton subsamples were obtained for numerical abundance using a Folsom plankton splitter. The organisms collected were counted and identified to the lowest possible taxon. Zooplankton densities were expressed as number of individuals per m^{-3} while ichthyoplankton densities as number of individuals per 100 m^{-3}.

Data analysis

The relationship between species distribution and environmental factors was investigated by canonical correspondence analysis (CCA), using the CANOCO version 4.0 package (ter Braak and Smilauer, 1998). Zooplankton abundance was ln +1 transformed, and environmental data were standardized. Downweighting of rare species was performed. A Monte Carlo test using 199 permutations ($P \leq 0.05$) was performed to test the significance of the correlations between the environmental factors and the species distribution. A one-way analysis of variance (ANOVA) (Zar, 1996) was applied to the abundance of the main zooplankton to test for differences between the two nets. Spearman rank correlations were also used to investigate the relationships between environmental parameters and ichthyoplankton abundance.

RESULTS

Environmental parameters

Hydrological data obtained during this study are given in Table I. The water temperature showed a seasonal cycle characterized by winter cooling and summer warming. Salinity was lower in winter/autumn, while higher salinity values were associated with summer/spring seasons. Along the estuary, low salinity values were recorded in the upper reaches, especially in the northern arm. Downstream stations showed reduced differences between them. Transparency increased from upstream to downstream stations in both arms. Concerning dissolved inorganic nitrogen, the sampling stations were also notably different, with higher values in the upper estuary. For nitrate, a clear decrease was observed during the warm season. Nevertheless, phosphate concentrations showed an irregular seasonal pattern, with higher values being associated with the upstream stations. During this study, Chl a ranged from 0.7 to 55.0 mg m^{-3}; peak concentration occurred during April–June. The lower Chl a concentrations were normally observed at the downstream stations.

Zooplankton taxonomic composition, distribution and abundance

Figure 2 shows the variation in abundance of the main zooplankton groups (ind m^{-3}) in the 335 and 500 μm taxocenosis, respectively. Total zooplankton abundance was highly variable in both tidal situations, with no distinct seasonal pattern. The general composition and abundance of the zooplankton community estimated by the two mesh nets was different. On average, the abundance estimated with the 335 μm net was 67 and 102 times higher than that with the 500 μm net at high and low tides respectively. Moreover, spatial differences in zooplankton abundance at the southern arm sampling stations were observed for the 335 μm taxocenosis (Fig. 2a), and no clear pattern was observed for the 500 μm taxocenosis (Fig. 2b). Not surprisingly, ANOVA (Table II) showed that abundance of the main zooplankton groups estimated by the two nets was significantly different, except for polychaete larvae, with higher values associated with the 335 μm taxocenosis. Despite the variation in zooplankton abundance observed between the two taxocenosis, a common pattern recurred with the holoplankton always being the most abundant. Concerning holoplankton in the 335 μm taxocenosis, copepods were the most abundant group (Fig. 3a), averaging 84.0 and 88.0% at high and low tides, respectively, followed by Cladocera and Siphonophora (Fig. 3b). Among meroplankton, the dominant groups were Hydromedusae and larvae of Cirripedia and Decapoda. The 500 μm taxocenosis exhibited a different pattern concerning the major zooplankton groups at high and low tides (Fig. 3). At high tide, Siphonophora were the most abundant taxon representing 30%, followed by Hydromedusae and Copepoda. At low tide, two major groups were noted: Cladocera representing 39% and Copepoda contributing with 26%.

Although data for the total zooplankton abundance for 500 μm taxocenosis were obtained in this study, we describe the dynamic patterns of the zooplankton community in the Mondego estuary based on the results obtained from the 335 μm net since these values provide a better estimate of the absolute abundance of zooplankton. A total of 85 zooplankton taxa were recorded in the study area. Figure 4 shows the temporal distribution at each sampling station of the main zooplankton species. Copepods were strongly dominant over the entire salinity range throughout the study period, with a slight abundance decrease observed in summer (Fig. 2). Dominant copepod species were the

Table I: Environmental conditions (mean ± SE) at the sampling sites in Mondego estuary, between January 2003 and June 2004

Station		Salinity	Temperature (°C)	DO_2 (%)	Transparency (m)	NO_3 (µM)	NH_4 (µM)	PO_4 (µM)	Chlorophyll a (mg m^{-3})
M	win03	7.2 ± 4.5	11.3 ± 0.9	98.5 ± 19.9	1.1 ± 0.1	6.6 ± 2.8	6.2 ± 2.4	0.4 ± 0.1	3.3 ± 1.4
	spr03	31.2 ± 2.1	15.2 ± 0.5	97.9 ± 7.7	1.9 ± 0.4	2.5 ± 1.5	7.5 ± 4.7	0.2 ± 0.1	5.0 ± 1.2
	sum03	31.1± 1.5	18.6 ± 0.8	99.0 ± 6.6	2.7 ± 0.3	0.9 ± 0.1	8.4 ± 6.5	0.1 ± 0.0	4.5 ± 0.8
	aut03	27.5 ± 1.2	16.7 ± 0.6	86.3 ± 0.9	2.0 ± 0.6	7.3 ± 3.2	3.6 ± 0.6	0.4 ± 0.1	2.9 ± 0.7
	win04	27.6 ± 1.0	12.7 ± 0.2	75.0 ± 15.0	1.4 ± 0.4	5.1 ± 1.4	4.3 ± 0.5	0.3 ± 0.1	1.6 ± 0.2
	spr04	34.7± 0.5	14.8 ± 0.3	106.2 ± 5.3	2.3 ± 0.6	1.3 ± 0.7	2.2 ± 0.4	0.1 ± 0.0	2.0 ± 0.7
	sum04	31.6	19.7	89.5	3.1	1.8	4.9	0.1	6.1
S1	win03	14.1 ± 2.8	11.9 ± 0.9	97.7 ± 14.0	1.2 ± 0.1	6.3 ± 2.4	5.9 ± 1.9	0.5 ± 0.1	1.2 ± 0.3
	spr03	26.2 ± 3.3	16.2 ± 0.9	92.2 ± 2.6	1.5 ± 0.2	3.1 ± 0.5	8.3 ± 4.6	0.3 ± 0.1	3.7 ± 0.7
	sum03	33.1 ± 0.5	17.8 ± 0.5	102.2 ± 3.9	2.0 ± 0.0	2.0 ± 1.2	1.7 ± 1.1	0.1 ± 0.0	4.6 ± 0.1
	aut03	28.6 ± 4.0	16.6 ± 0.5	89.5 ± 5.4	1.6 ± 0.4	4.5 ± 2.0	4.5 ± 2.1	0.3 ± 0.1	2.7 ± 0.8
	win04	30.0 ± 0.6	13.2 ± 0.3	85.5 ± 5.5	1.0 ± 0.2	4.3 ± 2.0	2.5 ± 1.4	0.3 ± 0.0	1.8 ± 0.7
	spr04	32.3 ± 0.9	15.7 ± 0.6	99.2 ± 1.9	1.2 ± 0.1	2.6 ± 0.5	3.9 ± 0.8	0.2 ± 0.0	3.5 ± 1.0
	sum04	31.2	18.0	110.7	2.3	1.3	2.3	0.2	6.3
S2	win03	7.7 ± 4.8	11.3 ± 1.4	77.8 ± 19.4	0.5 ± 0.1	9.0 ± 3.1	13.4 ± 3.3	0.5 ± 0.1	9.0 ± 2.7
	spr03	10.9 ± 5.3	19.0 ± 1.2	80.5 ± 7.6	0.5 ± 0.1	10.2 ± 0.7	22.7 ± 5.4	0.5 ± 0.1	9.4 ± 3.6
	sum03	16.7 ± 0.8	23.9 ± 0.0	77.5 ± 5.8	0.6 ± 0.0	1.7 ± 0.6	18.8 ± 4.0	0.4 ± 0.1	14.0 ± 4.8
	aut03	22.4 ± 2.3	17.1 ± 1.0	66.8 ± 8.5	0.4 ± 0.1	3.8 ± 1.2	17.0 ± 4.5	0.6 ± 0.1	4.2 ± 0.8
	win04	19.7 ± 0.2	11.7 ± 0.4	91.7 ± 2.6	0.6 ± 0.0	4.9 ± 0.7	13.0 ± 1.2	0.5 ± 0.0	6.4 ± 0.9
	spr04	22.4 ± 2.6	21.4 ± 1.8	84.3 ± 3.9	0.4 ± 0.1	3.7 ± 1.2	18.2 ± 4.8	0.5 ± 0.1	6.2 ± 2.8
	sum04	25.0	26.7	90.9	0.6	1.5	27.4	0.7	17.3
N1	win03	1.0 ± 0.8	11.3 ± 0.7	91.6 ± 14.4	0.8 ± 0.2	9.1 ± 2.8	7.0 ± 3.3	0.5 ± 0.1	2.4 ± 0.5
	spr03	25.5 ± 1.2	17.1 ± 1.7	97.3 ± 4.6	1.7 ± 0.4	2.7 ± 1.0	10.4 ± 4.6	0.3 ± 0.1	4.0 ± 1.3
	sum03	31.9 ± 0.8	18.0 ± 0.9	101.4 ± 5.3	2.1 ± 0.3	1.5 ± 0.3	0.9 ± 0.1	0.2 ± 0.0	4.1 ± 0.6
	aut03	25.7 ± 7.9	16.8 ± 0.6	93.7 ± 3.9	1.8 ± 0.6	5.5 ± 3.6	2.9 ± 1.7	0.3 ± 0.1	2.9 ± 0.9
	win04	31.1 ± 3.1	13.5 ± 0.4	89.5 ± 2.5	1.0 ± 0.5	3.5 ± 1.9	2.5 ± 0.4	0.3 ± 0.0	2.0 ± 0.4
	spr04	33.8 ± 0.2	15.1 ± 0.3	99.6 ± 4.2	1.6 ± 0.5	2.5 ± 0.6	2.3 ± 0.8	0.1 ± 0.0	2.6 ± 1.0
	sum04	33.3	18.2	81.6	2.5	1.2	2.8	0.2	3.6
N2	win03	0.0 ± 0.0	11.0 ± 0.5	92.3 ± 10.3	0.7 ± 0.2	10.0 ± 1.2	6.0 ± 3.7	0.5 ± 0.2	3.0 ± 1.0
	spr03	2.9 ± 2.7	17.0 ± 2.2	113.2 ± 18.7	1.1 ± 0.0	12.0 ± 2.9	6.2 ± 1.9	0.6 ± 0.2	20.0 ± 17.5
	sum03	8.0 ± 3.0	22.9 ± 0.4	83.7 ± 7.5	1.1 ± 0.2	10.9 ± 3.2	5.9 ± 2.0	0.5 ± 0.1	10.6 ± 3.4
	aut03	2.8 ± 2.7	17.3 ± 1.3	73.4 ± 2.5	0.6 ± 0.1	13.7 ± 2.8	8.5 ± 2.7	0.6 ± 0.1	4.6 ± 1.7
	win04	0.2 ± 0.1	10.8 ± 0.7	63.8 ± 8.8	0.9 ± 0.0	10.8 ± 4.7	15.8 ± 6.3	0.6 ± 0.1	5.9 ± 0.9
	spr04	9.1 ± 3.2	18.3 ± 1.1	94.1 ± 5.0	1.0 ± 0.2	12.2 ± 4.0	5.7 ± 2.3	0.4 ± 0.1	5.9 ± 2.7
	sum04	6.9	24.5	69.0	1.0	6.7	3.1	0.6	6.7

win, winter; spr, spring; sum, summer; aut, autumn.

calanoids, represented mainly by the estuarine species *Acartia tonsa*. This was more abundant in the brackish zone of the southern arm, with abundance peaks (>13 000 ind m^{-3}) in April and May 2004 at station S2 at low tide (Fig. 4). Other species that occurred regularly but in low numbers were the marine neritic species *Acartia clausi*, *Temora longicornis* and *Paracalanus parvus* and the freshwater copepods *Diaptomus* spp. and *Acanthocyclops robustus*. The former exhibited higher densities at downstream stations (M, S1 and N1) and the latter species appeared to be numerically more important at the upstream stations. *Acartia clausi* abundance was important at high tide (Fig. 4). Other copepod species occurred only sporadically. Among cladocerans, the freshwater genera *Daphnia*, *Ceriodaphnia* and *Bosmina* dominated, especially in the northern arm and at low tide. The marine genera, *Podon* and *Evadne*, appeared during spring and summer, but in much lower abundance compared to the freshwater forms. Gelatinous zooplankton were mainly represented by the

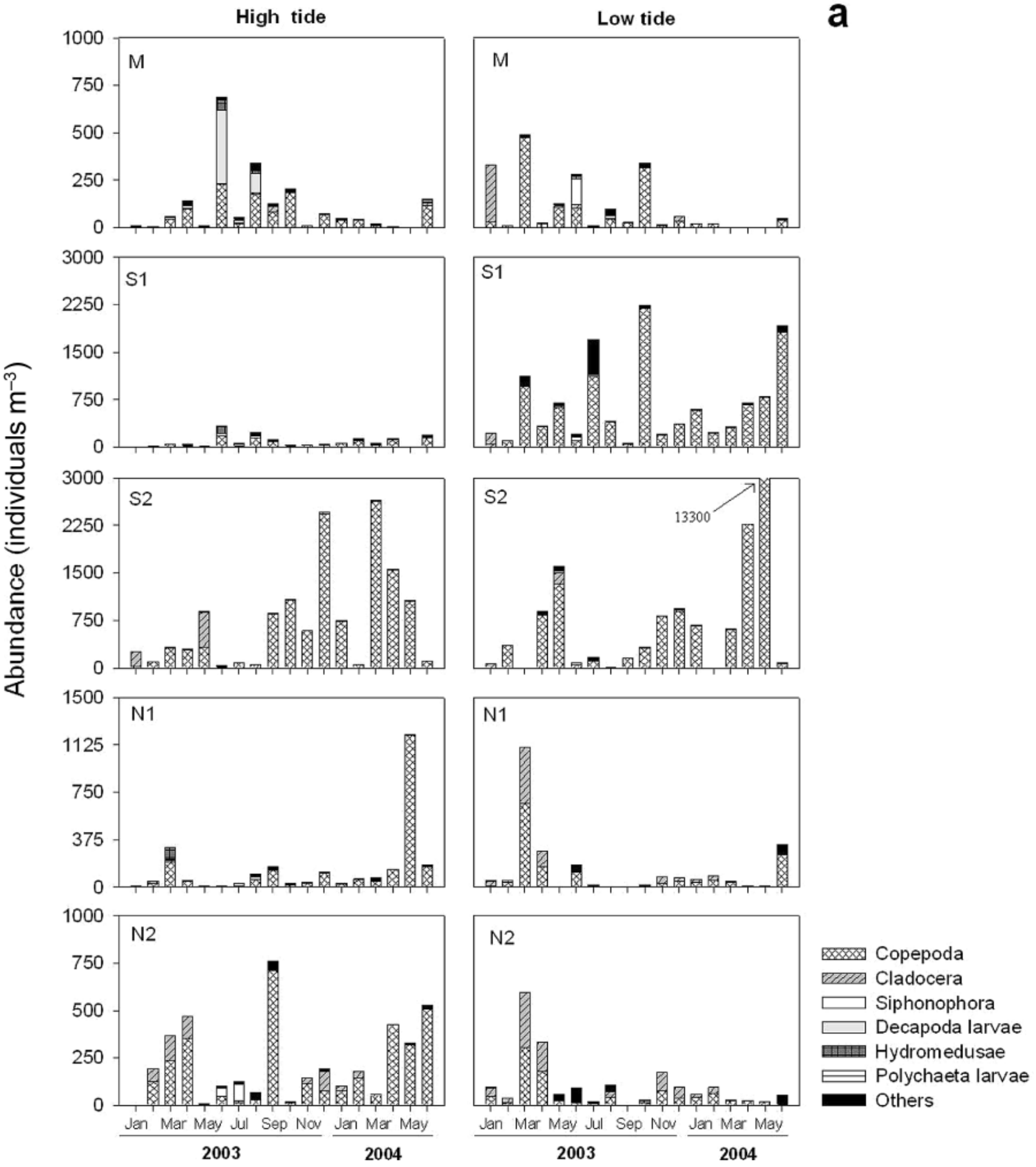

Fig. 2. Monthly pattern of the abundance of main zooplankton groups (ind m^{-3}) of (**a**) 335 and (**b**) 500 μm taxocenosis. Note to the different scales.

siphonophore *Muggiaea atlantica* and the jellyfish *Lizzia blondina* and *Obelia* sp. which showed a typical summer distribution exhibiting maximum densities in the lower reaches of the estuary and at high tide. Decapod larvae were only important in the summer months, and among them *Rhitropanopeus harrisii*, *Carcinus maenas* and *Palaemon* spp. zoeae were the dominant taxa. Appendicularians, dominated by *Oikopleura dioica*, were mainly distributed throughout the downstream stations. *Mesopodopsis slabberi* was the most abundant mysid, with higher densities at low tide in the inner areas of the south arm. Despite being present throughout the year, its abundance declined during winter.

Zooplankton community structure

Results of ordination using CCA analysis on the complete environmental and zooplankton data set are

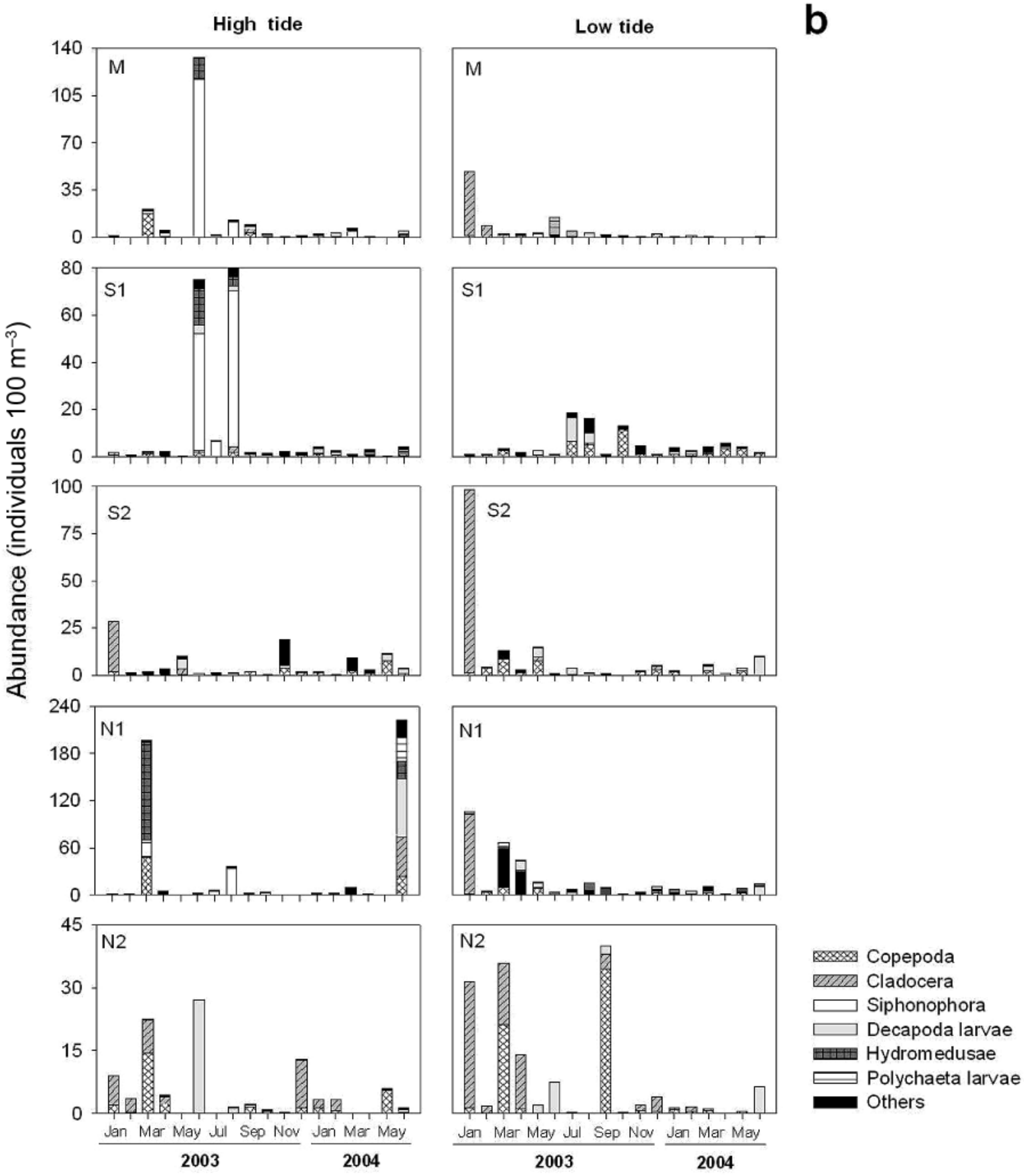

Fig. 2. continued

presented in Fig. 5. Among the environmental variables, Monte Carlo permutation showed that for the 335 µm taxocenosis, salinity, transparency, temperature and ammonia were significant in explaining the ordination (in decreasing order of importance). The environmental variables considered in the CCA explained 57.8% of the total variation of the zooplankton assemblages. The first two axes alone accounted for 73.7% of the variability explained in the 335 µm taxocenosis. As can be seen from the plot of stations (Fig. 5a) and environmental variables, the main spatial and seasonal gradients are associated respectively with axis 1 (salinity) and axis 2 (temperature). It is clear that the downstream stations (M, S1 and N1) situated at the left side of the plot are

Table II: One-way ANOVA results for the effect of the net mesh size on the abundance of the main zooplankton groups

Taxa	Degrees of freedom	Mean square	*F*	*P*
Copepoda	1	209.195	510.248	0.001
Cladocera	1	14.427	45.454	0.001
Siphonophora	1	2.350	37.150	0.001
Decapoda	1	0.737	5.104	0.05
Hydromedusae	1	0.569	7.140	0.01
Polychaeta larvae	1	0.000	0.003	Not significant
Mysidacea	1	0.773	8.585	0.001

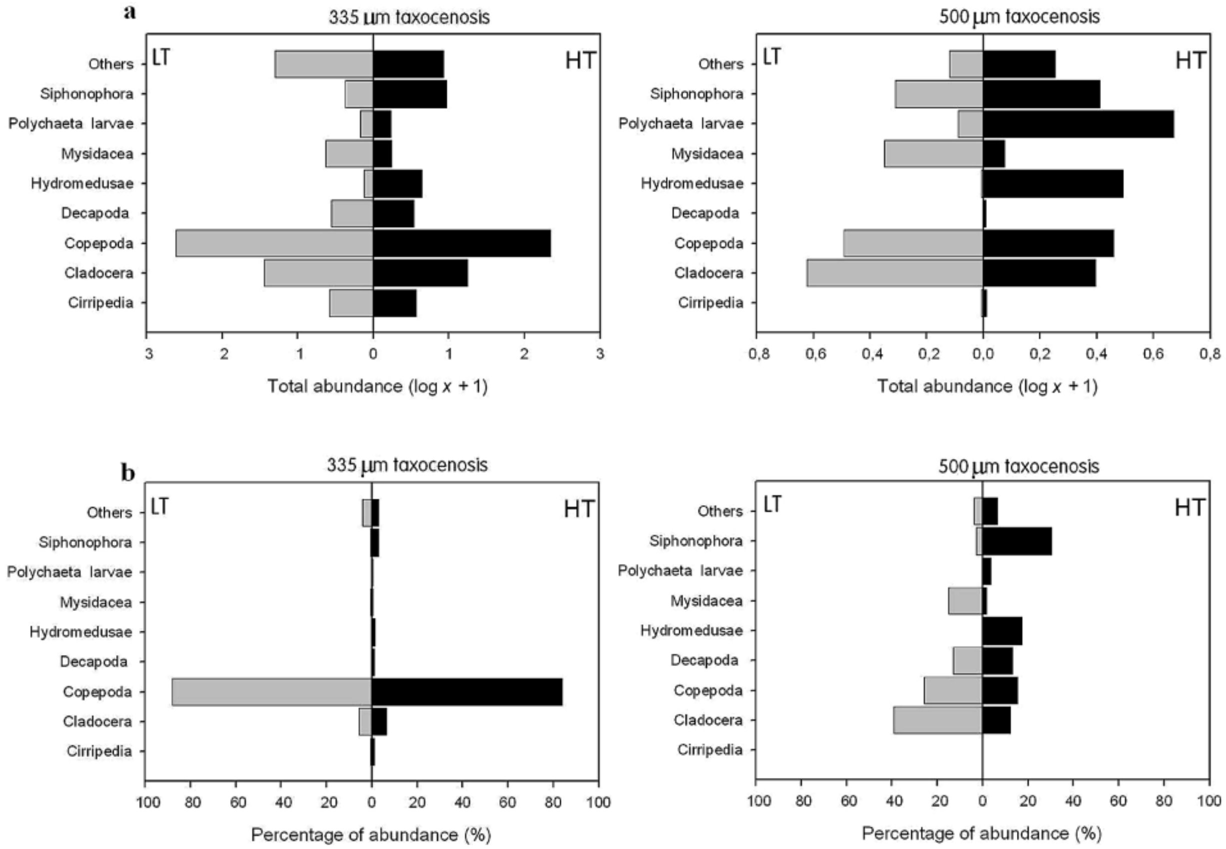

Fig. 3. Total abundance [log (x+1)] (**a**) and relative abundance (**b**) of the different zooplanktonic groups to total zooplankton abundance of 335 and 500 µm taxocenosis, in the Mondego estuary.

associated with high salinity, except for the winter observations (characterized by large freshwater flows) that are situated below axis 1, in opposition to the vector of temperature and salinity. In addition, these stations are also characterized by higher oxygen and transparency values, especially during summer. With few exceptions, upstream stations (S2 and N2) occupied the right side of the plot in opposition to salinity and water transparency and usually were characterized by higher nutrient concentrations and Chl a. The species plot is shown in Fig. 5b: the copepods *A. robustus* and *Diaptomus* spp. and the Cladocera (including *Daphnia*, *Ceriodaphnia* and *Bosmina*) typically inhabit the zone with lower salinity situated at the lower left side of the plot. *Eurytemora velox*, *A. tonsa*, *Calanipeda aquaedulcis* and *Mesopodopsis slabberi* situated in the upper right corner are associated with high

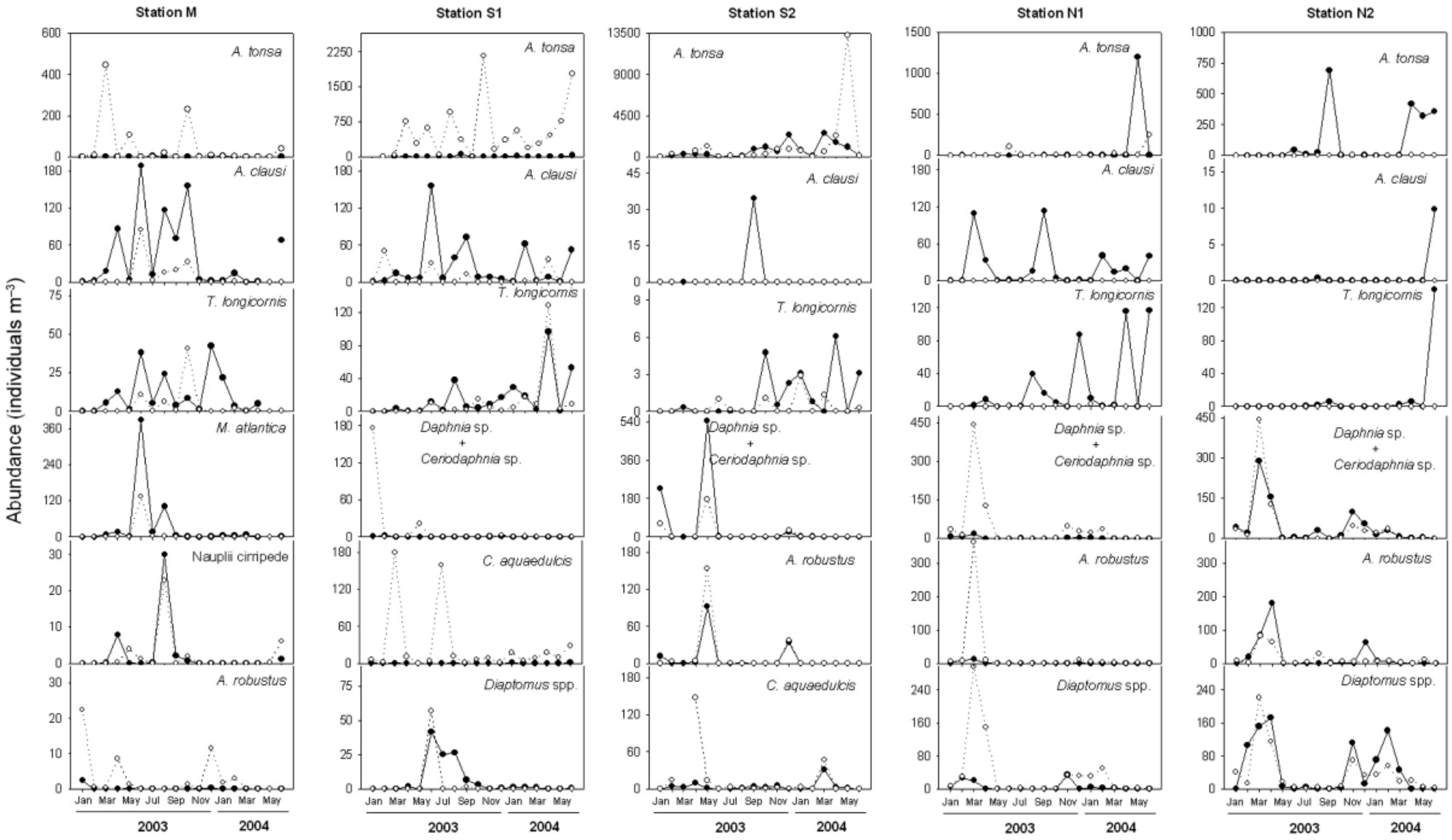

Fig. 4. Distribution of the most abundant species at each sampling station, from 335 μm net tows in Mondego estuary during sampling study. High tide: black circles and low tide: white circles. Note to the different scales.

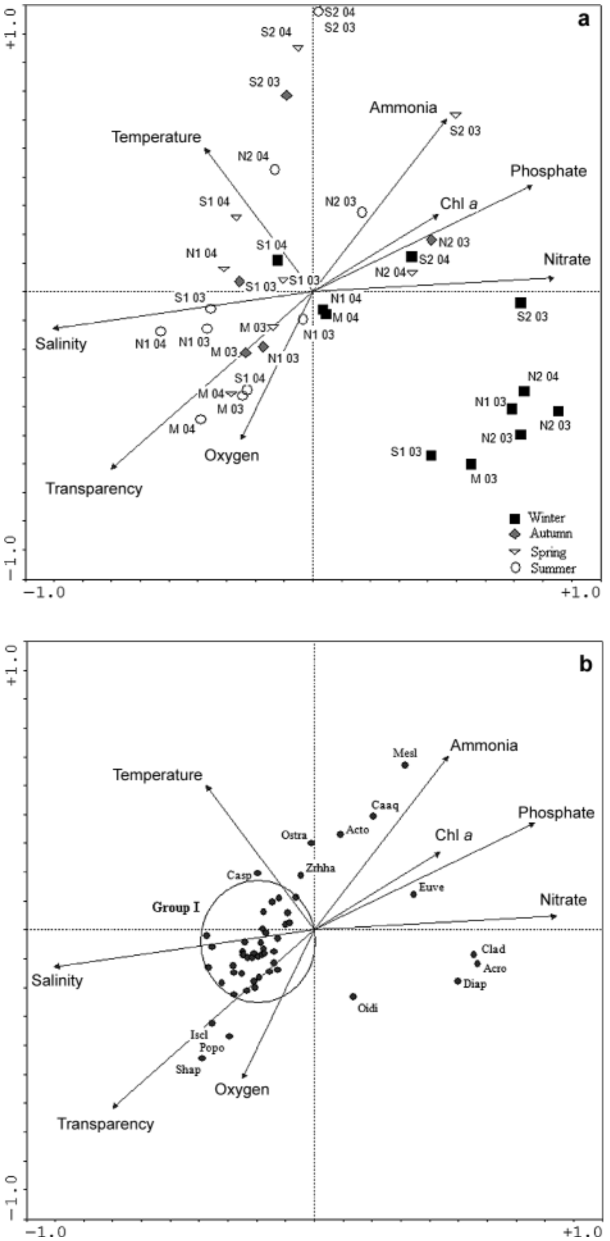

Fig. 5. Results of CCA analysis. (a) Principal component 1 and 2 for environmental variables vectors and stations and (b) Environmental variable vectors and species for the 335 μm taxocenosis.

temperature. *Acartia tonsa* that typically inhabits the brackish water zone of the estuary is also associated with higher salinity values. Ostracods, cumaceans, *R. harrisii* and *Caligus* sp. are observed in the upper part of the plot, associated with higher temperature. The marine copepod species, such as *A. clausi*, *T. longicornis*, *Calanus helgolandicus*, *Centropages* spp. *as* well as Cladocera (*Evadne* spp., *Podon* spp. and *Penilia*), Hydromedusae, Polychaeta and Echinodermata larvae, Decapoda zoeae and some gelatinous zooplankters constituted the group I (for a better description of group I see Table III) and are observed in the left side of the plot, related with the downstream stations and associated with high salinities and transparency values.

Ichthyoplankton assemblages

In this study, the following species of fish larvae were observed: *Pomatoschistus* spp., *Engraulis encrasicolus*, *Atherina presbyter*, *Sygnathus abaster*, *Sardina pilchardus* and *Solea senegalensis*. Only the eggs of *E. encrasicolus* were identified. Figure 6 shows the monthly variation of fish larvae and fish egg abundance (ind 100 m^{-3}) at each sampling station in both taxocenosis. The density of ichthyoplankton community changed over time, with abundance peaks in spring and summer. The larvae of *Pomatoschistus* spp. dominated and accounted for 65 and 58% (Table IV) of the total ichthyoplankton abundance in the 335 and 500 μm taxocenosis, respectively. Although the horizontal distribution of *Pomatoschistus* spp. extends to all stations, this group tended to dominate in the inner area of the south arm, with abundance peaks in April, particularly at low tide (Fig. 6). On average, higher abundances of *Pomatoschistus* spp. were associated with the 335 μm taxocenosis. *Pomatoschistus* abundance was significantly correlated ($P < 0.05$) with temperature ($r = 0.386$). Another important taxon that occurred mainly in the south arm was *E. encrasicolus*. Their abundance was numerically dominated by eggs that were slightly higher in the 500 μm than in the 335 μm taxocenosis. *Engraulis encrasicolus* larvae were numerically less important and present just in the lower reaches of the estuary at high tide. *Atherina presbyter* was found mostly in the northern arm at high tide. All the other species such as *S. senegalensis*, *S. pilchardus* and *S. abaster* were a small contribution to the ichthyoplankton community and had no clear seasonal pattern.

DISCUSSION

Previous research in the Mondego estuary has been motivated by the occurrence of eutrophication. Great efforts have been made since 1990s to improve environmental quality of the estuary as well to minimize the consequence of the eutrophication process (Marques *et al*., 2002). However, little information is still known about the zooplankton dynamics in this system. The purpose of the present study was therefore to examine temporal and spatial patterns in the ichthyo- and zooplankton community to increase our knowledge about this important component of the pelagic trophic web. A

Table III: Zooplankton taxa used in the CCA ordination during the full study period from January 2003 to June 2004

Taxon	Code (group)
Copepoda	
Acanthocyclops robustus	Acro
Acartia clausi	I
Acartia tonsa	Acto
Anomalocera sp.	
Calanipedia aquaedulcis	Caaq
Calanus helgolandicus	I
Caligus spp.	Casp
Centropages chierchiae	I
Centropages hamatus	I
Centropages typicus	I
Clausocalanus arcuicornis	I
Corycaeus clausi	I
Diaptomus spp.	Diap
Eurytemora velox	Euve
Euterpina acutifrons	Euac
Isias clavipes	Iscl
Microsetella spp.	I
Monstrilla grandis	I
Oithona helgolandica	I
Oithona nana	
Oithona plumifera	I
Oncae spp.	I
Paracalanus parvus	I
Pontellidae	I
Pseudocalanus elongatus	I
Shapphirina spp.	Shap
Temora longicornis	I
Ostracoda	Ostra
Echinodermata (larvae)	I
Cladocera	
Evadne nordmanni	I
Evadne spinifera	I
Penilia avirostris	I
Podon spp.	Popo
Podon intermedius	I
Podon leuckarti	I
Podon polyphemoides	
Freshwater cladocers	Clad
Decapoda zoeae	
Carcinus maenas	I
Pagurus spp.	I
Palaemon spp.	I
Pachigrapsus marmoratus	I
Pagurus spp.	I
Pisidia longicornis	I
Rhitropanopeus harrisii	Zrhha
Crangon crangon	I
Cumaceans	I
Bryozoa	I
Isopoda	
Idotea spp.	I
Paragnathia formica	I
Chaetognatha	
Sagitta friederici	I
Cirripedia	
Nauplii	I
cipris	I
Cnidaria	
Bougainvillia ramosa	I
Leuckartiara octona	I
Liriope tetraphylla	I
Lizzia blondina	I
Obelia spp.	I
Phialidium hemisphaerium	I
Podocoryne minima	I
Sarsia gemmifera	I
Sarsia prolifera	I
Sarsia tubolosa	I
Zanclea costata	I
Muggiaea atlantica	I
Polychaeta (larvae)	I
Phoronidae	
Phoronis spp.	
Mysidacea	
Gastrosaccus spinifer	I
Mesopodopsis slabberi	Mesl
Neomysis integer	I
Paramysis nouveli	I
Praunus flexuosus	I
Siriella clausi	I
Appendicularia	
Fritillaria borealis	I
Oikopleura dioica	Oidi
Tunicata	
Dolium spp.	I

I, group number in the CCA ordination.

lack of seasonality in abundance was observed, a feature that was also observed in other coastal marine areas (Calbet *et al.*, 2001; Fernández de Puelles *et al.*, 2003). The monthly fluctuations of zooplankton total abundance may result from the combination of specific and contrasting population patterns. In addition, the interaction between tidal currents and river flow can also potentially mask the seasonality of zooplankton by introducing a superimposed variability which is reflected by the complex response of zooplankton to the biological and environmental conditions (Ribera d'Alcalà *et al.*, 2004).

Table IV: Composition (mean ± SE) of ichthyoplankton taxa (ind 100 m^{-3}) and contribution to the total abundance (%) in the 335 and 500 μm taxocenosis for the Mondego estuary

	335 μm		500 μm	
	Mean	%	Mean	%
Fish larvae				
Pomatoschistus spp.	22.9 ± 15.8	65.2	25.1 ± 12.0	57.9
Atherina presbyter	0.7 ± 0.5	2.0	0.13 ± 0.7	0.3
Engraulis encrasicolus	0.2 ± 0.2	0.5	0.9 ± 0.6	2.0
Others	0.4 ± 0.2	1.5	1.7 ± 0.9	2.7
Fish eggs				
Engraulis encrasicolus eggs	4.6 ± 3.7	19.8	10.5 ± 5.8	24.3
Unidentified eggs	3.4 ± 1.3	9.8	5.0 ± 2.7	11.5

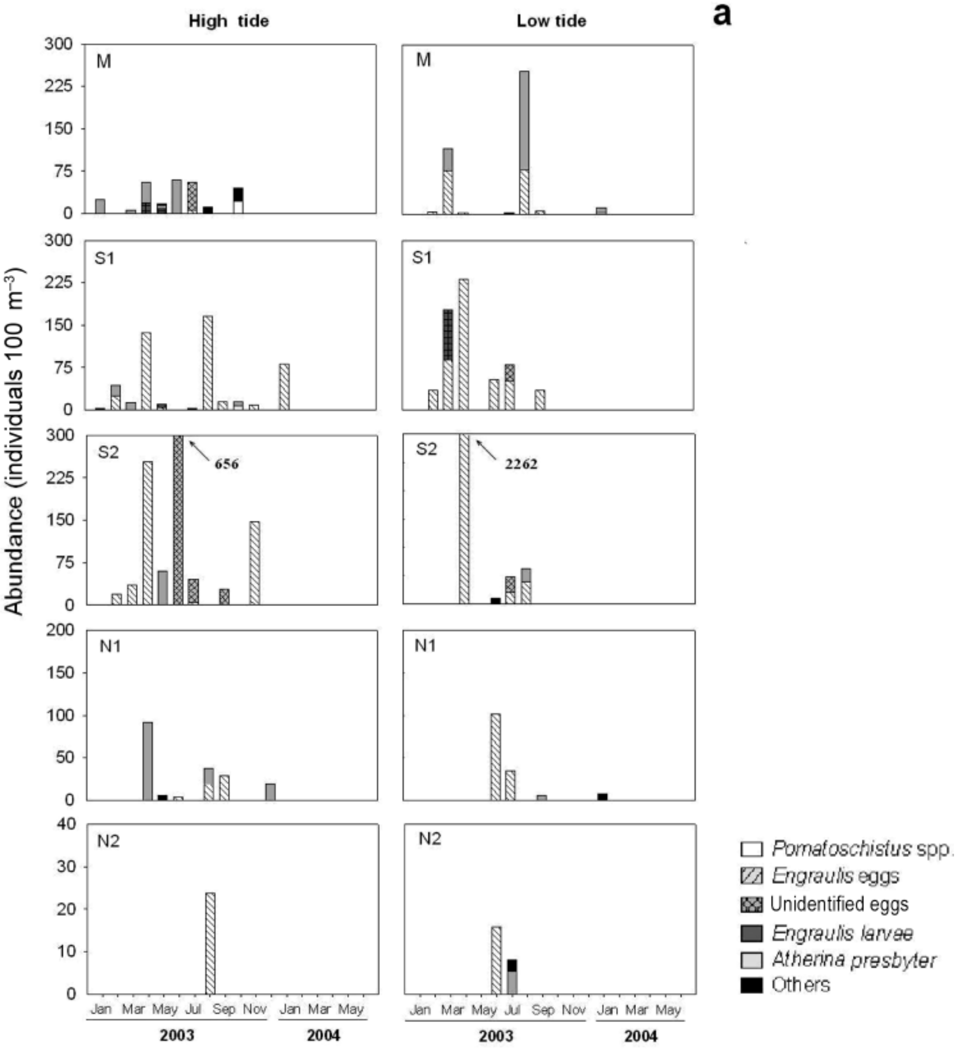

Fig. 6. Monthly pattern of abundance of main the ichthyoplankton groups (ind 100 m^{-3}) of (**a**) 335 and (**b**) 500 μm taxocenosis. Note different scales.

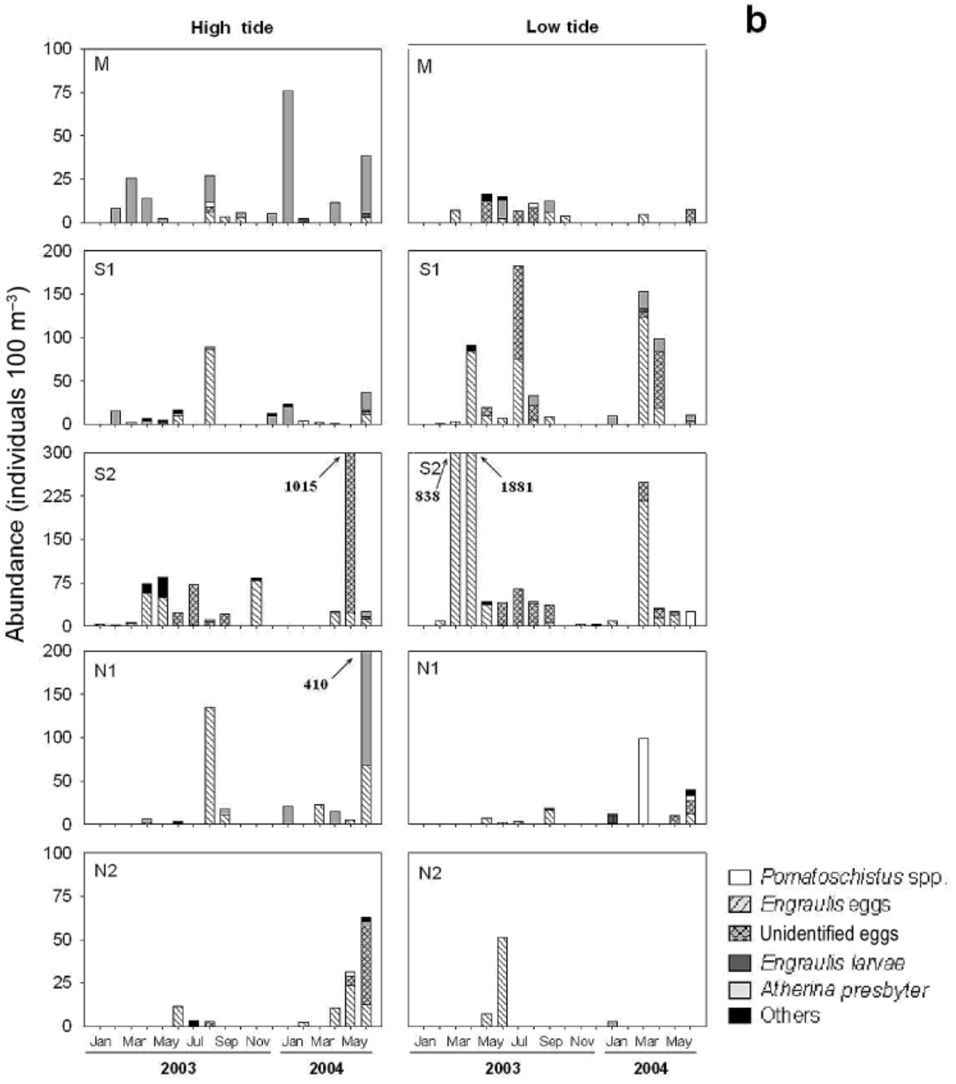

Fig. 6. continued

However, our results should be interpreted with some caution because the estuarine zooplankton populations are extremely dependent on the effect of tides. Since the sampling design in this study did not take into account the lunar cycle (spring tides or neap tides), this may have been a source of bias in the zooplankton abundance comparisons; the position of a zooplankton population along the estuary depends not only on the ebb-flood cycle but also on the neap-spring tidal cycle (Kennish, 1990). It should also be noted that the taxonomic groups were only sorted to the level of major groups, hydromedusae etc. There may be much species-specific seasonality going on that will be missed at this taxonomic level. The majority of the literature demonstrates seasonality in temperate estuaries; hence the apparently lack of seasonality may result from the taxonomic groupings used.

This study showed a difference between the zooplankton abundance obtained with the 335 and 500 μm mesh net sizes, and this may be helpful when defining plankton sampling strategies in estuaries. The use of a 500 μm mesh net may lead to a limited view of the ecology of planktonic systems, and the results should be considered with some caution. Even considering that the zooplankton assemblages were similar in both taxocenosis, the abundance of most zooplankton groups and their relative contribution was highly biased, depending on the mesh size used. Since copepods were the dominant group, the differences between nets were highest for this group. As expected, the bias resulting from the collection of the main zooplankton groups with large-size meshes masked some spatial patterns. For instance, the dominance of the *A. tonsa* in the zooplankton assemblages in the inner areas of the south arm was not evident when data from the 500 μm taxocenosis were used. Based on the data obtained, it is evident that zooplankton were adequately captured only with the 335 μm net. This indicates that, in general, the spatiotemporal pattern of the zooplankton assemblage is better represented by this mesh net size. In addition, the frequent undersampling of small copepod species may lead to a limited view of the ecology of planktonic systems and must be considered when comparing results (Calbet *et al.*, 2001; Turner, 2004). The small copepods are important links in marine food webs, serving as major grazers of phytoplankton and as prey for ichthyoplankton and other larger pelagic carnivores (Turner, 2004). A better spatial and temporal survey of zooplankton populations will probably confirm this and its biological implications in the Mondego estuary.

As in other marine coastal areas (Villate *et al.*, 1997; Fernández de Puelles *et al.*, 2003; Kibirige and Perissinotto, 2003; Auer *et al.*, 2004), copepods dominated the mesozooplankton in the Mondego estuary. Because they are preyed on by larger organisms including siphonophores, hydromedusae and fish larvae (Azeiteiro *et al.*, 1999) during summer conditions, the copepod populations tend to vary inversely with the siphonophore and hydromedusae populations. *Acartia* was the dominant genus, represented in this ecosystem by the species *A. clausi* and *A. tonsa* which were segregated in space and time. The absence of an *A. clausi* population in the middle zone of the estuary and upstream could result from predation by the dense resident *A. tonsa* population (White and Roman, 1992). *Acartia tonsa* fail to develop in more saline waters due to its sensitivity to salinity (Cervetto *et al.*, 1999; Gaudy *et al.*, 2000). From the quantitative point of view, *A. tonsa* was the dominant taxon, which is typical for estuarine environments located on the Atlantic European coast (Mouny and Dauvin, 2002; Hoffmeyer, 2004; Tackx *et al.*, 2004; David *et al.*, 2005). The particular effects of salinity on the distribution of *A. tonsa* were analysed by Cervetto and colleagues (Cervetto *et al.*, 1999) who showed that *A. tonsa* is well adapted to instantaneous variations in salinity if these do not exceed 10%. Owing to differences in depth, the penetration of the tide is greater in the north arm than in south arm, causing daily changes in salinity to be much pronounced in the north arm. Therefore, the lower densities in the north arm could be attributed to increases in salinity over a short time period. Concerning the population of *A. tonsa* found in the south arm, these are probably a well-established population whose physiological tolerances are adapted (Cervetto *et al.*, 1999). As has been observed in inshore waters (Schwamborn *et al.*, 2004), we can conclude that *A. tonsa* is tolerant to eutrophic waters where it can reproduce and recruit successfully allowing it to survive in ecosystems with severe eutrophic conditions such as the southern arm of the Mondego (Cardoso *et al.*, 2004; Pardal *et al.*, 2004).

Larval stages of benthic invertebrates represented the majority of the meroplankton in the Mondego estuary. The occurrence of decapod larvae was mainly restricted to the summer months. This well-defined pattern is related to the release of larvae into the water column during warmer months, when the environmental conditions are favourable (Gonçalves *et al.*, 2003).

Although the same mesh sizes were used in other Portuguese estuaries, differences among the main contributors to the zooplankton community are found. In the Mira estuary, mysids, decapods and copepods commonly represented about 5–40% of total zooplankton abundance. In the Guadiana estuary, copepods, cladocerans and decapods were the most abundant taxa (Esteves *et al.*, 2000). These differences are probably due to the particular characteristics of the study area and also maybe due to different zooplankton sampling techniques.

The CCA analysis revealed that, besides the seasonal temperature changes, the main environmental gradients were due to salinity. Salinity gradient is a common feature of temperate estuaries having a pronounced spatial effect on the zooplankton composition and distribution (Azeiteiro *et al.*, 1999; Mouny and Dauvin, 2002; Tackx *et al.*, 2004). Temperature is very important in determining the seasonality in zooplankton species composition (Calbet *et al.*, 2001; David *et al.*, 2005; Lionard *et al.*, 2005). It allowed the development of a freshwater community in the upper reaches of northern arm, especially during winter, which corresponds to periods of high river flow. Freshwater organisms were frequently found in the lower reaches of estuary, especially in the winter. We hypothesize that theses may have been advected from upstream to downstream by the freshwater flux of the Mondego River. Those species were also observed in the southern arm, but in much lower abundance. Instead, *A. tonsa* showed highest densities in this arm, suggesting that a favourable environment exists, enabling successful colonization. At the downstream stations, marine zooplankton species tend to become more important, particularly in spring/summer, where the intrusion of saline waters is more pronounced. The regular dredging in the northern arm favours the penetration of marine water into the upper reaches.

Coastal temperate ecosystems frequently exhibit spatial–temporal gradients, both in environmental variables and in plankton assemblages, as a result of their tight physical–biological coupling. In addition, this study revealed that major differences in zooplankton abundance were apparent between station groups, being generally higher within the southern arm stations. In all cases, such differences relate to the different hydrological characteristics of the two arms. The north arm where dredging takes place regularly exhibits lower residence time, and the environmental conditions are characterized by strong daily changes in salinity (Marques *et al.*, 2002). On the other hand, the stability of the water mass in the south arm due to the low hydrodynamics, shallow depth and low daily salinity changes and high nutrient enrichment (Marques *et al.*, 2002) result in higher zooplankton abundance, namely in the inner areas. For this reason, the particular characteristics of the two arms allow us to consider them as two different subsystems suffering from different human effects.

In comparison with other coastal ecosystems (Gordina *et al.*, 2001; Munk *et al.*, 2003), the Mondego estuary seems to support an impoverished larval fish community with low diversity. In the present study, the sampling was made during daylight, which may not be the correct strategy to sample the majority of fish larvae. Recent work indicates that a variety of taxa can rise to the surface during the night (Esteves *et al.*, 2000). These authors reported that fish larvae were relatively more abundant during the night, particularly the Gobiidae (the dominant taxa in the Mondego estuary), which was collected in higher numbers at dawn and dusk. Another explanation for the differences found could be based on the specific characteristics of a given coastal ecosystem. The specific conditions of each location (geographic location, currents, degree of enclosure, degree of anthropogenic influences, etc.) may strongly influence the ichthyoplankton abundance (Gordina *et al.*, 2001). The species composition and abundance of larval fish was similar for the 335 and 500 μm taxocenosis, which may suggest that a larger mesh size net would be more efficient for ichthyoplankton collection by excluding other groups. Some overlap in sample composition was also found on both arms. Clupeidae, Gobiidae and Atherinidae larvae are among the most common and representative families of fish in Portuguese estuaries (Ré, 1996; Esteves *et al.*, 2000), which is in accordance with our findings of dominance by these species. Clupeids are a basic component of an important pelagic fishery off the Atlantic coast of the Iberian Peninsula, and the other two families are described as resident species of many estuaries (Potter *et al.*, 1990; Gordina *et al.*, 2001; Satilmis *et al.*, 2003). The Gobiidae larvae, fish with benthic eggs, pre-dominated in inner areas of the south arm. In the Mondego estuary, two species of Gobiidae are frequently found, *Pomatoschistus microps* and *P. minutus* being the most abundant fishes in the estuarine assemblages (Leitão *et al.*, 2006). In the present study, the seasonal variation of *Pomatoschistus* sp. egg abundance is in agreement with the reproductive cycle (spawning) already defined for those two species, where temperature seems to be the main factor controlling this process and egg survival (Fonds and Van Buurt, 1974). Our findings also indicate that ichthyoplankters were consistently more abundant in spring and summer months. We argue that a combination of responses of fish communities to physical and biological factors is responsible for the pattern defined here, as reported by Kingsford and Suthers (Kingsford and Suthers, 1996). Estuarine spawning by species that produce planktonic eggs is not common since larvae can be rapidly flushed out of the estuary and dispersed by the net seaward transport of the surface layer (Ré, 1996). The majority of species that spawn in estuaries lay demersal eggs (Ré, 1996). However, anchovy seem to be an exception to this rule. *Engraulis encrasicolus* is the only European species of the Engraulidae family (Ribeiro *et al.*, 1996) and has a wide distribution in the north-eastern Atlantic (Ré, 1996; Esteves *et al.*, 2000; Satilmis *et al.*, 2003). In the Mondego estuary, anchovies spawn almost exclusively in the middle and upper part of the estuary during warmer months. Pelagic spawning inside estuaries by some Engraulidae became viable and apparently successful because of a rapid embryonic development and high food availability (Dando, 1984). Moreover, the fact that these fishes reproduce during warm months allows the minimization of the embryo-larval phase duration (Dando, 1984). Despite the occurrence of eggs and larvae of anchovy in the Mondego Estuary, it has been noted that in the last years, there has been a decrease in the abundance of adults. Such a tendency was also noted in other Portuguese estuarine ecosystems like the Tagus estuary, which is the opposite of what is found in adjacent coastal zones where the adults are abundant (Prista *et al.*, 2003). A possible explanation may rely on the impoverishment of water quality and/or changes in food quality and quantity in estuaries. Therefore, in future, it is important to study the life cycle of anchovy in estuaries and adjacent areas and also the factors that tend to control their population dynamics.

ACKNOWLEDGEMENTS

The present study was carried out in the scope of the research project Typology and Reference Conditions for Transitional and Coastal Portuguese Waters—TICOR, funded by INAG—Instituto da Água (Portugal). A special thanks to all colleagues who helped during field work.

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