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Vertical distribution and trophic structure of the macrozooplankton in a shallow temperate estuary (Ria de Aveiro, Portugal)

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SUMARY: The zooplankton of the lower part of Canal de Mira (Ria de Aveiro) was sampled during one lunar month. The sampling programme consisted of nine 25 hour fixed-cycles, separated weekly. In each cycle, samples were collected every two hours at three depths (surface, mid-water and above the bottom) with a 500 μm mesh net. The overall effect of the tidal phase was analyzed, taking into account the day and depth of the vertical position of the organisms through a 3-way analysis of variance (ANOVA). The zooplankton densities were, in general, higher at the surface during the night and near the bottom during the day, mainly at spring tide. The variation in the number of species followed a similar pattern to that observed for abundance. Significant differences ($p<0.01$) between diel and tidal phases were observed. Interaction between phase of the day and depth was also significant ($p<0.05$), with higher organism densities observed during night periods near the bottom. From a trophic point of view the zooplankton community of Canal de Mira was mainly composed of carnivorous and omnivorous species. Carnivores were significantly more abundant around the new and full moon ($p<0.001$), the omnivores at the new moon ($p<0.001$) and the herbivores and detritivores at the first quarter of the moon cycles ($p<0.001$). The density of carnivores was significantly higher at the surface at night and near the bottom during the day ($p<0.05$). Significant differences in the abundance of omnivores were observed between phases of the day and between depths, with higher values near the bottom during the day. The herbivores and detritivores had significantly higher densities during flood tides ($p<0.001$).

Keywords: macrozooplankton, vertical distribution, trophic structure, temperate estuary.

RESUMEN: DISTIBUICIÓN VERTICAL Y ESTRUCTURA TRÓFICA DEL MACROZOOPLANCTON EN UN ESTUARIO TEMPLADO (RIA DE AVEIRO). – El zooplancton de la parte inferior del Canal de Mira (Ria de Aveiro) fue muestreado durante un mes lunar. El programa de muestreo consistió en nueve ciclos de 25 horas, con periodicidad semanal. En cada ciclo, las muestras fueron recogidas cada dos horas, a tres profundidades (superficie, columna de agua y sobre el fondo) con una red de 500 μm. El efecto total de la fase de la marea fue analizado, teniendo en consideración el día y la profundidad en la posición vertical de los organismos con un análisis 3-Way ANOVA. Las densidades del zooplancton fueron en general más altas en la superficie durante la noche y cercanas al fondo durante el día, principalmente em la marea viva. La variación en el número de especies siguió un patrón similar al observado para la abundancia. Se observaron diferencias significativas ($p<0.01$) entre las fases del día y las fases de marea. La interacción entre la fase del día y la profundidad fue también significativa ($p<0.05$) con densidades de organismos más altas durante los periodos nocturnos en el fondo. De un punto de vista trófico, la comunidad zooplanctónica del Canal de Mira está principalmente compuesta por especies carnívoras y omnívoras. Los carnívoros fueram significativamente más abundantes cerca de la luna nueva y de la luna llena ($p<0.001$), los omnívoros en la luna nueva ($p<0.001$) y los herbívoros e detritívoros en el primero cuarto de los ciclos de la luna ($p<0.001$). La densidad de los carnívoros fue significativamente más alta en la superficie durante la noche y en el fondo durante el día ($p<0.05$). Para los omnívoros, fueron observadas diferencias significativas entre las fases del día y la profundidad, registando valores más elevados en el fondo durante el día. Los herbívoros y los detritívoros presentaron densidades significativamente superiores durante los ciclos de marea ($p<0.001$).

Palabras clave: macrozooplancton, distribución vertical, estructura trófica, estuario templado.

INTRODUCTION

Vertical distribution patterns of zooplankton are complex phenomena involving several categories of behaviours that change from species to species, and even from individual to individual, and depend on factors such as endogenous rhythms, age, sex and spawning (Wooldrige and Erasmus, 1980; Hammer, 1981; Orsi, 1986; Saint-Jean and Pagano, 1990; Stuart and Verheye, 1991; Hays, 2003). Vertical migrations of zooplankton are nearly ubiquitous in both freshwater and marine systems and thus are well documented in the literature (Enright, 1970; Schwassmann, 1971; Decoursey, 1983; Lampert, 1989; Neilson and Perry, 1990; Hays, 2003). External factors such as light intensity, season, lunar phase and tidal cycles, temperature and salinity may affect migratory behaviour (Hammer, 1981; Paffenhoper, 1983; Gajbhiye *et al.*, 1984; Magnesen, 1989; Magnesen *et al.*, 1989; Fragopoulu and Lykakis, 1990). Many evolutionary hypotheses have been developed to explain the mechanisms behind zooplankton vertical migrations. Predator evasion (Zaret and Suffern, 1976; Gliwicz, 1986; Harding *et al.*, 1986; Simard *et al.*, 1986; Dodson, 1988; Bollens and Frost, 1989a,b; Giske *et al.*, 1990; Neill, 1990; Stuart and Verheye, 1991; Yamaguchi *et al.*, 2004) and longitudinal transport control (Brookins and Epifanio, 1985; Epifanio, 1988; Hill, 1991a,b,c, 1995) are currently the most favoured hypotheses. Enright (1977) also suggested that vertical migration provides metabolic advantages.

Vertical migrations interact with horizontal currents and vary with depth, and so the extension and direction of horizontal transport may be modified by depth change of the organisms' distribution. The zooplankton community structure is mainly a result of physical constraints and trophic factors at both higher and lower levels. The zooplankton community is itself a main regulating factor for these trophic levels, making the pelagic system a dynamic system, where trophic interactions are seldom in equilibrium (Hansson *et al.*, 1990). Within the context of a broad trophic network that varies in time and space, the interactions of producers and consumers have profound consequences for aquatic ecosystems giving rise, for instance, to large regional and seasonal variations in the magnitudes of phytoplankton standing stocks (blooms), nutrient utilization and recycling efficiencies and export ratios (Marine Zooplankton Colloquium, 2001). Consequently, changes in zooplankton communities may lead to changes in the trophic structure and functioning of aquatic ecosystems. The extent to which zooplankton responds to different environmental cues is not well understood, in particular, it is not known how much of zooplankton behaviour is in response to the surrounding physical environment. There may also be an endogenous rhythm cuing the migration (Neumann, 1981; Forward, 1988), and other internal factors, such as nutritional status or accumulated energy, may play a role (Sekino and Yamamura, 1999). Day-night cycles are also reliable cues for their activities. Hence, estuarine organisms show activity patterns that are synchronized with both day-night and tidal cycles (Saigusa, 1985; Saigusa and Akiyama, 1995).

Analysis of feeding habits may provide essential information for understanding zooplankton dynamics and defining the type of aquatic structure. This would contribute to interpreting the mechanisms underlying adaptation of the species to estuarine circulation (Laprise and Dodson, 1993) and to a deeper knowledge of the functional aspects of the pelagic system as a whole (Magnesen, 1989; Magnesen *et al.*, 1989). A previous study analyzed species composition, function and patterns of emergence inside and in the coastal vicinity of the studied system (see Morgado *et al.*, 2003a,b). The objective of this paper is to describe the trophic structure dynamic interactions of the zooplanktonic compartment as a coherent assemblage.

In order to fulfil these objectives, field sampling was designed to reveal a set of variables, namely: i) the vertical distribution profiles in the water column for a complete lunar month; ii) the effects of the phases of the day, tide and moon on behaviour and species abundance; iii) the distribution patterns and the nictemeral, tidal and lunar trophic structures.

MATERIALS AND METHODS

Study site

Ria de Aveiro is a shallow bar-built estuary (Dias *et al.*, 2003) on the northwest Portuguese coast with a wet area of 47 km^2 at high tide and 42 km^2 at low tide, with a maximum length and width of 40 km and 10 km respectively. The lagoon has a rather complex topography, comprising an extensive reticulate of channels radiating from the contact with the

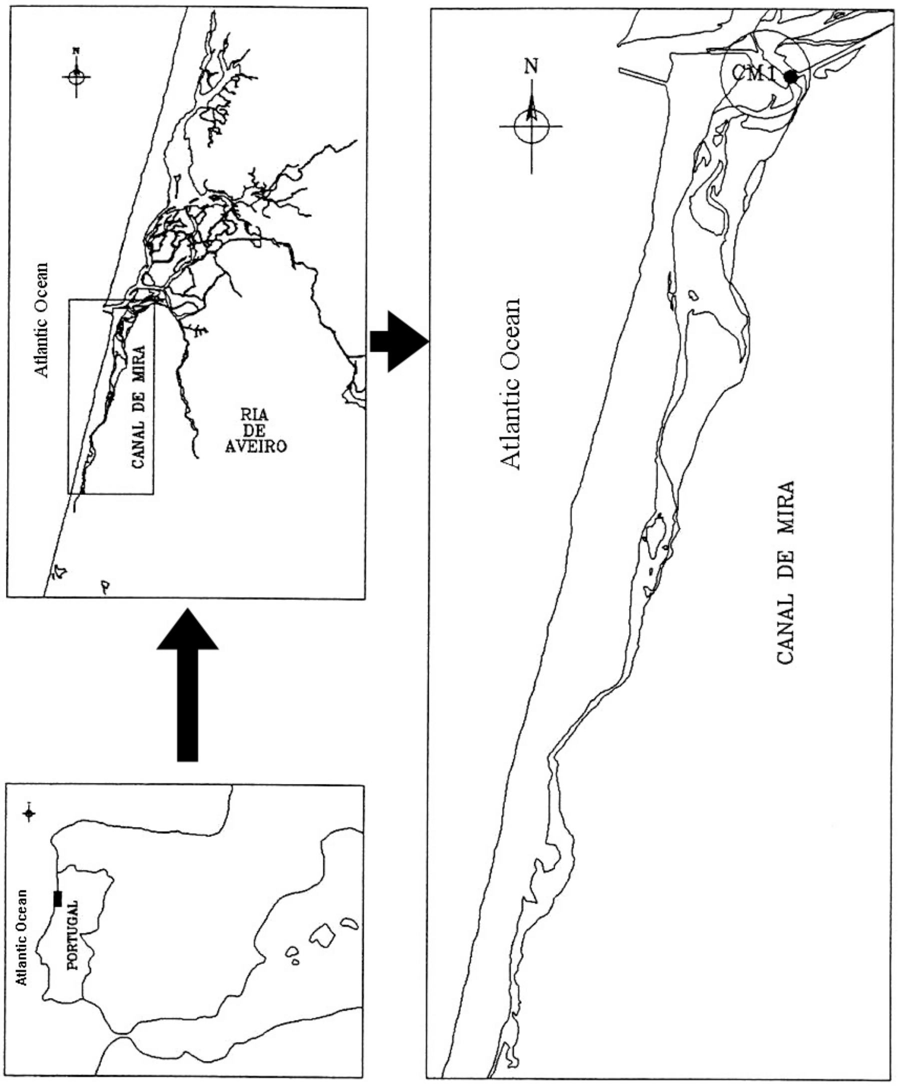

FIG. 1. – Canal de Mira, Ria de Aveiro, Portugal. Location of station used during the fixed station studies.

Atlantic (Fig. 1). Tidal influence is the main factor influencing circulation within the estuary. The volume of seawater entering the estuary on each flood is 25x10^6 m^3 (1 m tidal range), reaching up to 96x10^6 m^3 if the 3 m level is reached. The sum of all fresh water entering this water body (in the same period of time) only amounts to 2x10^6 m^3. The tidal regime is semi-diurnal with an average tidal range of 2.1 m at the inlet (Dias *et al*., 2003).

The study site was located in the Canal de Mira (which functions as a mesotidal estuary in itself) (Fig. 1) which evolves from the inlet towards the southeast, parallel to the coastline, with an approximate extension of 20 km and a maximum width of 1 km. It has a maximum depth of 9 m below mean sea level near the mouth and is seldom below 0.5 in its final 2/3. Freshwater flows in continuously from a system of creeks and lagoons. The average discharge is 7.8 m^{3}s^{-1}. This channel is characterized by a positive longitudinal salinity gradient influenced by tides and seasonal cycles. The residual circulation is a two-layer flow with vertical mixing.

Field sampling

In this study, nine 25 h plankton sampling cycles were performed at station #1, at weekly intervals. The mean depth of the sampling station was 6.5 m. The tidal range was 2.3 m throughout the study. Mean differences between bottom and surface flood current inversions did not exceed 4 minutes. However, the ebb slack had an average displacement of about 16 to 18 minutes between the surface and bottom.

The samples were taken along the deepest zone of the channel, every two hours, with a tow velocity of 1 to 2 ms^{-2}, against the water flow, for 5 minutes, using three 500 μm mesh size nets (neustonic, mid-water and epibenthic (Queiroga, 1995) deployed in quick succession, each of them equipped with a flowmeter. The neustonic net, with an opening of 0.60x0.30 m, was deployed so that the immersed part would be, on average, 20 cm deep. The mid-water net, of conic shape with a 0.40 m diameter opening, was towed through a frame hinged to the mouth of the net, with a 10 kg ballast. Tows were made taking the precaution that the towing cable never exceeded an angle >50º. Simultaneously this allowed extra precision in regulating towing depth. The epibenthic net, similar to the one used for mid-water hauls, was mounted on a sledge, which allowed a regular 0.30 m distance between the centre of the net opening and the bottom to be maintained. Despite the absence of a net opening-closing device the calculated overall interference was never bigger than 5% of the total filtered volume. Average filtered water volumes were 35.1, 30.7 and 25.3 m^{-3} for the neuston, mid-water and epibenthic nets respectively.

Samples were fixed and preserved in 5% buffered formaldehyde. Sub-sampling was made using a Folsom plankton splitter (McEwen *et al.*, 1954), counting a fraction of 100 individuals for the most abundant *taxa*, and at least 500 individuals per sample. The abundance of *taxa* was expressed as number of individuals per cubic meter.

Classifying planktonic species into herbivorous, carnivorous, detritivorous and omnivorous is a sensitive matter since, despite some species possessing relatively fixed feeding habits, the great majority are very flexible, and are capable of modifying their feeding behaviour according to the availability and/or the quality of food resources. Bearing this in mind, the presiding classification criterion was to place each species into the corresponding predominant feeding regime as determined by the structure of their mouthpieces; we considered herbivores+detritivorous, post-veligers *Hydrobia ulvae* and *Oikopleura dioica;* omnivorous *Acartia clausi*, *Gastrosaccus spinifer*, *Schistomysis spiritus*, *Gastrosaccus spinifer* juvenils and *Schistomysis spiritus* juvenils; carnivorous *Obelia* spp., *Dipurena ophiogaster, Muggiaea atlantica*, *Diphyes* spp., metatrocophores *Lanice conchilega*, *Calanus helgolandicus*, zoeae *Palaemon elegans*, zoeae *Crangon crangon*, post-larvae *Crangon crangon*, zoeae *Carcinus maenas* and zoeae *Pachygrapsus marmoratus* (Rose, 1933; Russell, 1953; Tregóbouff and Rose, 1957; Totton and Bargmann, 1965; Fenaux, 1967; Rice and Ingle, 1975a,b; Fincham, 1977; Maucline *in* Blaxter *et al*., 1980; Guerney, 1982; Fincham and Figueras, 1986; Ingle, 1987; Barnes, 1994).

Statistical analysis

The overall effect of the tide phase was analyzed, taking into account the time of day and depth through a 3-way analysis of variance (ANOVA). All samples collected during each sampling moment were considered replicates. They were classified as ebb or flood samples according to the phase of the tide, defined by high and low water slack times, during which the discrete time interval began. Similarly, the samples were classified as day or night, where the day was taken as the period between sunrise and sunset and the night as the balance of this period. The three sampling depths (surface, mid-water and bottom) constituted the levels for this factor. Prior to analysis, data were subjected to a $\log(x+1)$ transformation in order to achieve parametric analysis requirements (Zar, 1984).

RESULTS

Zooplankton density

The most abundant groups were the pelagic and the suprabenthic crustaceans, especially Decapoda larvae, Copepoda and Mysidacea, but also Mollusca larvae, Siphonophora, Hydromedusae, Polychaeta larvae and Appendicularia (Table 1). The dominant species were the zoeae of *Carcinus maenas*, eggs of *Littorina littorea*, *Acartia clausi*, *Gastrosaccus spinifer* and *Diphyes* spp., which represented 57% of the zooplankton community. However, species such as *Obelia* spp., *Dipurena ophiogaster*, *Muggiaea atlantica*, unidentified nectophores and gonophores, metatrocophores of *Lanice conchilega*, post-veligers of *Hydrobia ulvae*, *Calanus helgolandicus*, *Temora longicornis*, *Schistomysis spiritus*, zoeae of *Palaemon elegans*, zoeae of *Crangon crangon*, post-larvae of *Crangon crangon*, zoeae of *Pachygrapsus marmoratus* and *Oikopleura dioica* collectively represented 32% of the total zooplankton.

TABLE 1. – Taxonomical groups and most representative species, per group, identified in the samples. Average concentration (ind. m^{-3}) and percentage contribution to the mean total density.

Taxonomic Groups		Mean density (ind m^{-3})	Percentage (%)
Hydromedusae	*Obelia* spp.	1	1
	Dipurena ophiogaster	1	1
Siphonophora	*Muggiaea atlantica*	1	1.4
	Dyphies spp.	5	6
Polychaeta larvae	Metatrocophores *L. conchilega*	3	4.3
Mollusca larva /eggs	Post-veligers *Hydrobia ulvae*	1	0.7
	Littorina littorea eggs	11	13.6
Copepoda	*Calanus helgolandicus*	1	1.2
	Acartia clausi	*10*	*12.5*
Mysidacea	Juvenils *Gastrosaccus spinifer*	1	1.6
	Adults *Gastrosaccus spinifer*	8	9.6
	Juvenils *Schistomysis spiritus*	1	1.3
	Adults *Schistomysis spiritus*	2	2.4
Decapoda larvae	Zoeae *Palaemon elegans*	0.4	0.5
	Zoeae *Carcinus maenas*	12	15.6
	Zoeae *Crangon crangon*	3	4
	Post-larvae *Crangon crangon*	0.4	0.5
Appendicularia	*Oikopleura dioica*	3	4.3
Other			18.5

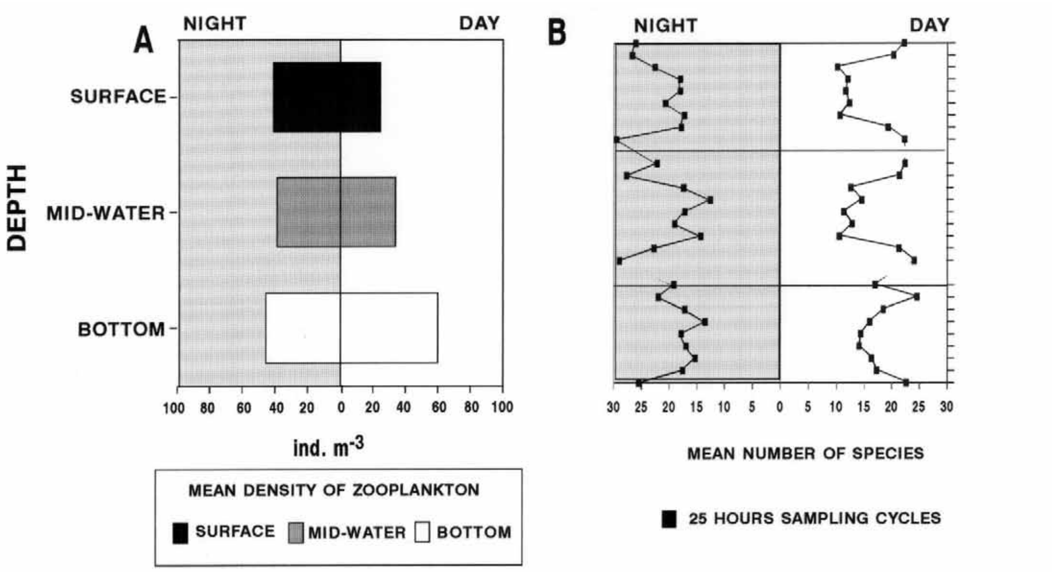

FIG. 2. – Mean density of zooplankton (A) and mean number of species (B), at the three depths, in the day and night periods. Concentrations (ind. m^{-3}) are represented by horizontal bars. Shaded area: night.

The analysis of variation of the zooplankton mean density as a function of depth and phase of the day, suggests that densities were higher near the bottom during both the day and night. Mean surface density during the night (41 ind. m^{-3}) was approximately half of that recorded during the day (25 ind. m^{-3}). Near the bottom, high densities were observed both during the day (60 ind. m^{-3}) and at night (46 ind. m^{-3}). The mean number of species was higher at the surface and mid-water, and during the day near the bottom (Fig. 2).

The analysis of the zooplankton mean density as a function of the phase of the tide and depth, suggests higher values during floods rather than during

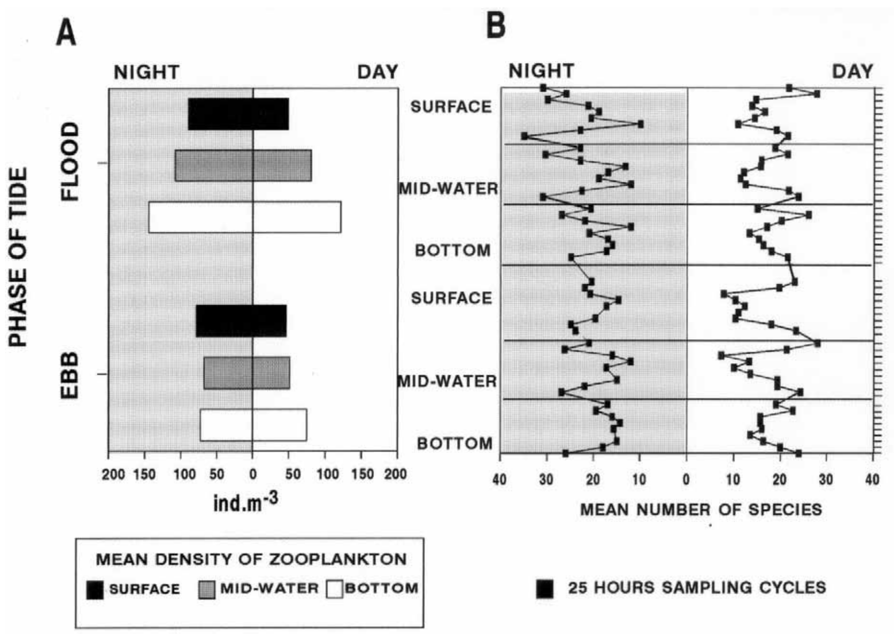

FIG. 3. – Mean density of zooplankton (A) and mean number of species (B), during flood and ebbs, in the day and night periods, at the three depths. Concentrations (ind. m^{-3}) are represented by horizontal bars. Shaded area: night.

ebbs. It also shows that during floods, both diurnal and nocturnal densities were higher in mid-water and near the bottom. For ebbs, the pattern was of higher densities at the surface during the night and near the bottom during the day. Generally, differences in concentrations were a lot higher during floods compared with ebbs (Fig. 3).

The analysis of the zooplankton mean density in the four moon phases as a function of the time of the day and depth, suggests that values were markedly higher during the new moon, both during the day and night, with a maximum value of 100 ind. m^{-3} near the bottom during the day. During the full moon and first quarter phases, striking differences with depth were observed only during the day. The highest mean densities were observed during full moon periods near the bottom during the day (68 ind. m^{-3}) and at the surface during the night (59 ind. m^{-3}), as well as during the first quarter in the daytime near the bottom (42 ind. m^{-3}) and at night at the surface (45 ind. m^{-3}). In the second quarter, densities were low, especially at the surface and in mid-water, both

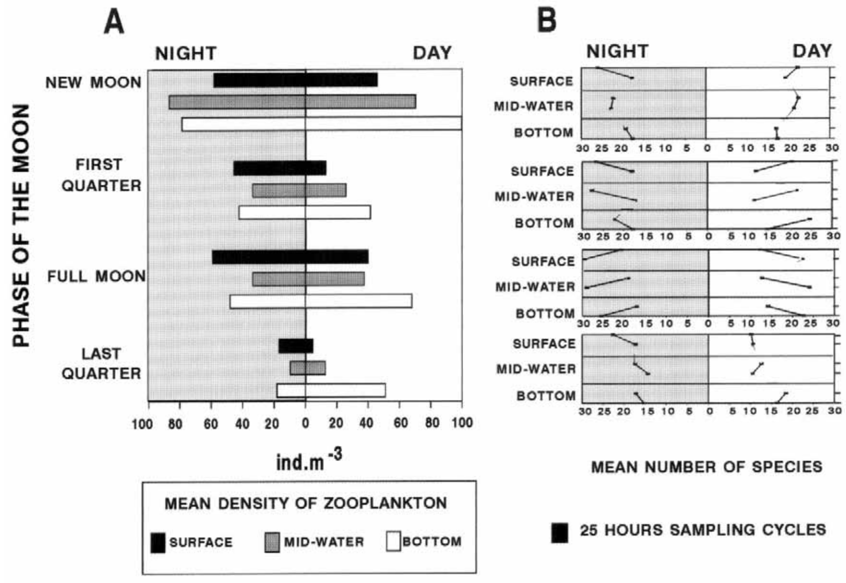

FIG. 4. – Mean density of zooplankton (A) and mean number of species (B), during the phases of the moon, in the day and night periods, at the three depths. Concentrations (ind. m^{-3}) are represented by horizontal bars. Shaded area: night.

TABLE 2. – Results of the 3-way ANOVAs of the effects of phase of tide, time of day, depth level and interactions, on the zooplankton concentration, the mean number of species and on the zooplankton trophic level concentrations; ns=not significant; *= p<0.05; **= p<0.01; ***= p<0.001.

	MS	Fs	P		
Zooplankton concentration					
Phase of the day		6.096	20.800	0.001	***
Depth		3.223	10.997	0.001	***
Mean number of species					
Phase of the day		0.895	18.972	0.001	***
Phase of the tide		0.183	3.884	0.050	*
Phase of the day by depth		0.289	6.114	0.002	**
Zooplankton trophic levels concentration					
Phase of the day	Omnivorous	16.151	53.006	0.001	***
Phase of the tide	Herbivorous + Detritivorous	1.164	6.179	0.013	*
Depth	Omnivorous	12.484	40.969	0.001	***
Phase of the moon	Herbivorous + Detritivorous	3.684	22.630	0.001	***
	Omnivorous	4.653	18.377	0.001	***
	Carnivorous	1.162	3.466	0.017	**
Phase of the day vs. Depth	Carnivorous	1.280	3.727	0.025	*
Phase of the moon vs. Phase of the day	Omnivorous	1.054	4.162	0.007	**

during the day and the night. Nevertheless, the density during this phase of the moon near the bottom and during the day (51 ind. m^{-3}) was of equivalent magnitude to the densities observed during the full moon and the first quarter phases (Fig. 4). The mean number of species was especially higher during the day in full moon phases. In the second quarter and new moon phases during the night an identical number of species was observed. Nevertheless during the day in the latter phase the number of species was markedly lower (Fig. 4).

In order to test the significance of the observed differences in zooplankton density and in the number of species as a function of day and tide phases, depth and the overall effect resulting from the interaction of all factors, an analysis of variance was performed (ANOVA). In terms of density, only differences between the phases of the day ($p<0.001$) and sampling depths were significant ($p<0.001$) (Table 2). The significant differences in terms of the number of species, were between the phases of the day ($p<0.001$) and phases of the tide ($p<0.05$), as well as for the interaction between the phases of the day and depths ($p<0.01$) (Table 2).

Distribution of *taxa* by trophic level

In the Mira channel, zooplankton communities were mainly composed of carnivores and omnivores, representing 42 and 30% of the total zooplankton respectively. Herbivores represented only 5% of the entire community. Carnivores were significantly more abundant at the surface during the night and at the bottom during the day in new moon and full moon cycles ($p<0.01$) (Figs. 5, 7). This interaction between depth and phase of the day was also observed for omnivores, which were more abundant during the night near the bottom in new moon cycles ($p<0.01$). Herbivores and detritivores exhibited significantly higher densities during floods, especially during the first quarter (Figs. 6, 7).

Analysis of the mean density of the different trophic levels as a function of the phases of the day and depths shows that both carnivores and omnivores were considerably more abundant than herbivores and detritivores. Carnivores always constituted more than 33% of the total zooplankton in both phases of the day at any depth; they exhibited the highest concentrations during the night at the surface and during the day near the bottom (Fig. 5). A significant interaction ($p<0.05$) was found between the phases of the day and depths (Table 2). Carnivores exhibited a mean density of 78 ind. m^{-3} at the surface during the night (representing, in this context, 80% of the total zooplankton) and 46 ind. m^{-3} near the bottom during the day (representing 52% of the total). Omnivores followed a similar pattern, with signif-

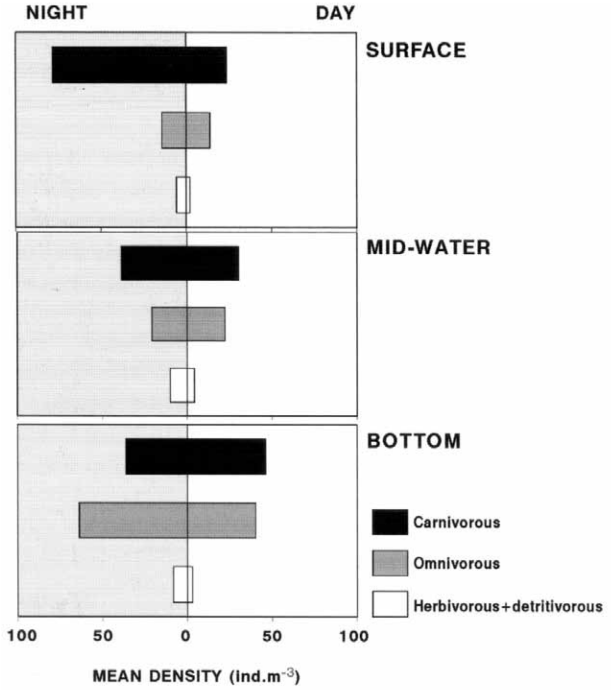

FIG. 5. – Mean density of the zooplankton trophic levels, at the three depths, in the day and night periods. Concentrations (ind. m^{-3}) are represented by horizontal bars. Shaded area: night.

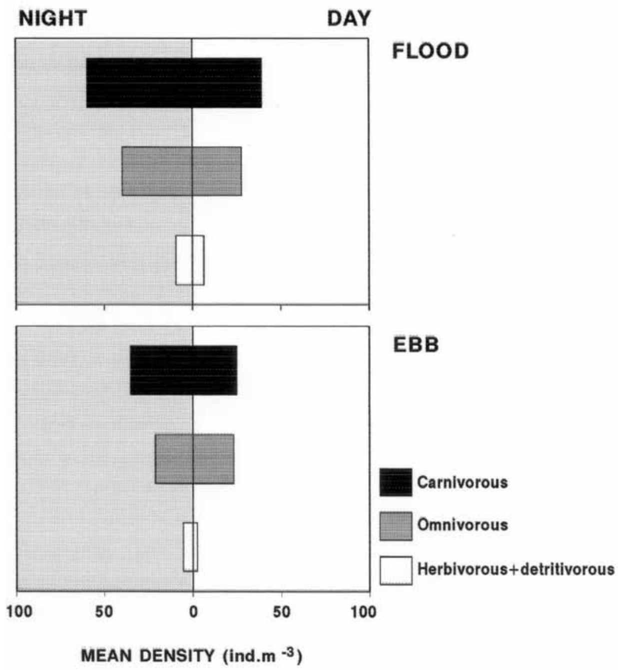

FIG. 6. – Mean density of zooplankton trophic levels, during flood and ebbs, in the day and night periods, at the three depths. Concentrations (ind. m^{-3}) are represented by horizontal bars. Shaded area: night.

icant concentration differences between the phases of the day ($p<0.001$) and between depths ($p<0.001$) (Table 2), with a maximum concentration of 64 ind. m^{-3} on the bottom at night (representing, in this context 59% of the total zooplankton). Herbivore and detritivore densities did not show any significant differences, either with the phases of the day or with depths.

When analyzing mean density variations under the influence of the tidal cycle and phases of the day, it is noticeable that all trophic levels were relatively more abundant during floods than during ebbs (Fig. 6). Nevertheless, significant differences were only found for herbivore+detritivore concentrations between tidal phases ($p<0.05$) and for omnivores between phases of the day ($p<0.001$) (Table 2).

The analysis of the influence of the moon and phase of the day on the mean densities of the different trophic levels showed significant differences ($p<0.01$) with the phase of the moon for all of them (Table 2). Higher densities were attained in new and full moon cycles for carnivores, new moon for the herbivores and first quarter for detritivores (Fig. 7). Omnivores exhibited significant differences ($p<0.001$) between the phase of the day, and furthermore, a significant interaction between the moon and the phases of the day ($p<0.01$) (Table 2).

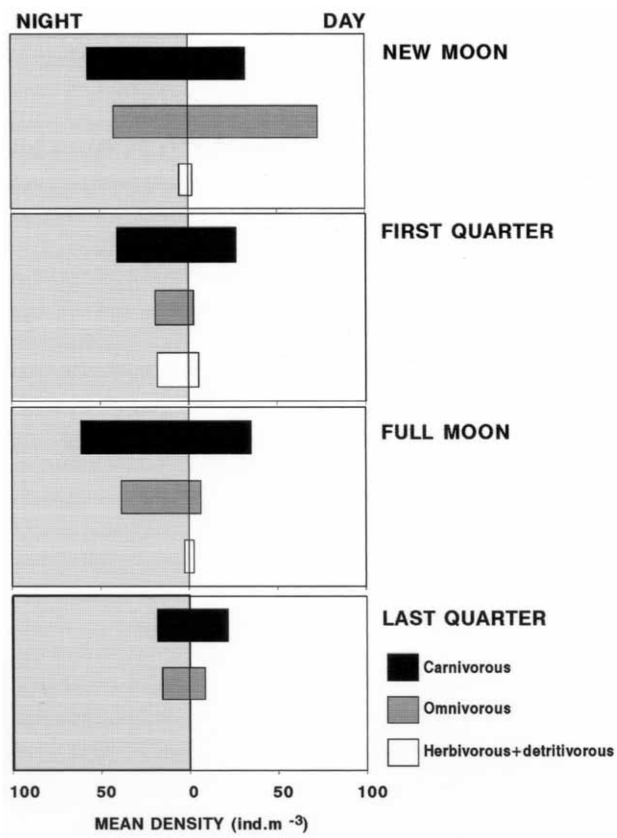

FIG. 7. – Mean density of zooplankton trophic levels, during the phases of the moon, in the day and night periods, at the three depths. Concentrations (ind. m^{-3}) are represented by horizontal bars. Shaded area: night.

DISCUSSION

The higher zooplankton densities at the surface during the night and at the bottom during the day, with the number of species following a similar pattern, can be highlighted as the conclusion of this study. Many marine and estuarine organisms within a wide range of taxonomic groups of zooplankton are known to display vertical migration in synchrony with the day-night cycle (Schwassmann, 1971; Gajbhiye *et al*., 1984; Patriti *et al*., 1984; Stubblefield *et al*., 1984; Forward, 1988; Bollens and Frost, 1989a,b, 1991; Okemwa, 1989; Hill, 1991a,b,c; De Stasio, 1993). They most commonly show either a nocturnal or twilight pattern. Nocturnal migration is characterized by a movement in which the animals rise to near the surface of the water at night, and attain their maximum depth during the day. Twilight migration is the movement in which the animals descend to their minimum depth near sunset (Forward, 1988). Organisms concentrating near the bottom during the day and migrating towards the surface during the night has been referred to as a way of avoiding predation from visually orientating predators (Zaret and Suffern, 1976; Stubblefield *et al*., 1984; Bollens and Frost, 1989a,b; Hill, 1995).

Significant differences were observed in the mean number of species between the phase of the day and depth. The higher number of species present at the bottom during floods indicates that a significant number of organisms possess rhythmic behaviour synchronized with tidal cycles. The tidal cycle can be translated into the fluctuations of a variety of environmental variables such as hydrostatic pressure, turbulence and stirring of water, temperature, salinity, and current speed. Among these factors the main inducer of these endogenous rhythms is water turbulence (Enright, 1965). According to Hays (2003) vertical migration may be a means of redistributing populations via vertically stratified horizontal currents. Nevertheless, the observed variation of species number was less dynamic near the bottom when compared with higher levels in the water, where wider variations took place. These observations highlight the migratory behaviour of the organisms within the water column, which can be related to the intensity of the currents, the direction of the tidal current, current velocity and tidal range (Enright, 1970; Decoursey, 1983; Hill, 1991a,b,c; Hill, 1995). Throughout a selective tidal stream transport organisms may experience retention or export mechanisms from the estuarine environment (Jagger, 1999; Pereira *et al*., 2000). Advection by currents constitutes one of the most significant sources of variability of zooplankton density (Gagnon and Lacroix, 1981; Norcross and Shaw, 1984), which affects all stages of development, eggs and adults, determining different patterns of behaviour in areas submitted to intensive dispersive fluxes (Norcross and Shaw, 1984).

In this work higher zooplankton densities were observed during the new and full moon phases. Some authors argue that differences in zooplankton density associated with the new and full phase of the moon are related to light intensity variations rather than variation in tidal amplitude (Gliwicz, 1986; Jerling and Wooldridge, 1992). Gliwicz (1986) suggests that the moon phase cycle in zooplankton is a global phenomenon induced by predation (demonstrated from an examination of gut contents), as predation on zooplankton occurs most efficiently on nights when the full or nearly full moon rises after sunset, i.e., when zooplankton approach the surface during darkness and become suddenly vulnerable in the first light of the rising moon. After the last quarter, zooplankton density is low, the moon gives little light, predators shift to alternate food sources, and the zooplankton populations grow exponentially again.

The distribution of the various *taxa* according to trophic level provided relevant information on the nictemeral, tidal and lunar dynamics of the Canal de Mira communities. From a matter transfer point of view we should consider an ascendant flux, which mainly influences the quantity and availability of food sources and conditions primary producer densities, and a descendant flux, which mainly makes an impact on predation and herbivory, with high relevance for the consumers (Hansson *et al*., 1990; Saint-Jean and Pagano, 1990).

The observed distributions of carnivore and omnivore zooplankters, which suggest nictemeral vertical migrations, can be considered as advantageous regarding competition for food and predatory avoidance. These behavioural patterns highlight important differences in feeding strategies, since carnivores that are dependent on light to identify and detect prey (Zaret and Suffern, 1976; Land, 1992; Lazzaro *et al*., 1992) come to the surface waters at night, whilst in the same period omnivores can be mainly found in the vicinity of the bottom, hence reducing predation and avoiding competition with carnivores. Herbivores and detritivores do not need to see their prey (Lazzaro *et al*., 1992), hence they are mainly active during the night, which reduces predation by carnivores and omnivores. According to the model developed by Enright (1977) the herbivores can take metabolic advantages with a daily decrease in foraging ability due to depletion of phytoplankton. In the proposed model, herbivorous zooplankton deplete the supply of phytoplankton so much during night time feeding that the metabolic advantage in migrating to lower depths outweighs that of remaining at the surface to feed on a scarce food source. Descent of herbivorous zooplankton may also be a mechanism for sustaining an equilibrium of food supply production (Hansson *et al*., 1990; Saint-Jean and Pagano, 1990).

The vertical patterns of abundance presented by the dominant species throughout the whole lunar month confirm that, for most species, there were significant interactions between the behaviour strategies and the cyclical variations of the environmental conditions. Species such as *Obelia* spp., *D. ophiogaster*, *M. atlantica*, *Diphyes* spp., metatrocophores *L. conchilega*, *G. spinifer*, *S. spiritus* and post-larvae *C. crangon* had significantly different densities within the phase of the day. *M. atlantica, Diphyes* spp., *C. helgolandicus*, *A. clausi*, *S. spiritus,* zoeae *C. crangon,* zoeae *C. maenas* and *O. dioica* registered significantly different densities according to the phase of the tide. Post-veligers *H. ulvae, L. Littorea* eggs, *G. spinifer, S. spiritus,* zoeae *P. elegans,* zoeae *C. crangon,* post-larvae *C. crangon* and zoeae *P. marmoratus* showed significant differences of densities with depth. Several interactions were also significant. The densities of *M. atlantica, Diphyes* spp, zoeae *C. crangon,* zoeae *C. maenas,* zoeae *P. marmoratus, A. clausi* and *S. spiritus* were significantly affected by the interaction between the phase of the day and the phase of the tide. The densities of *G. spinifer*, *S. spiritus*, zoeae de *P. elegans*, zoeae de *C. crangon*, post-larvae of *C. crangon* and zoeae of *C. maenas* were significantly affected by the interaction between the phase of the day with depth. The densities of *S. spiritus*, zoeae *P. elegans*, post-larvae de *C. crangon* e zoeae de *C. maenas* were significantly affected by the interaction between the phase of the tide and depth. Densities of *G. spinifer*, *S. spiritus* and post-larvae *C. crangon* were significantly affected by the simultaneous interaction of the three factors. The observed patterns for the most abundant species in Canal de Mira (Ria de Aveiro) were in accordance with previous reports from other temperate estuaries concerning gelatinous plankton (Alldredge and Hamner, 1980; Costello and Stancyk, 1983; Esnal *et al*., 1985), copepoda (Fragoupoulu and Lykakis, 1990; Saint-Jean and Pagano, 1990), demersal plankton (Williams and Collins, 1984; Orsi, 1986; Mees *et al*., 1993), as well as fish eggs and larvae of benthic species (Fish, 1979; Barnes, 1981; Christy, 1982; Ré, 1984a,b, 1987; Bachelet and Yacine-Kassab, 1987; Ré, 1990; Paula, 1993; Chase and Thomas, 1995; Queiroga *et al*., 1997).

For a detailed discussion on the individual species' behaviour inside and in the costal vicinity of the studied system see Morgado *et al*. (2003a,b).

A marked complexity emerged from the results of this study, concerning the diel and tidal vertical distribution of organisms in the water column, and several patterns may be superimposed in direct accordance with existing environmental factors. They also indicated that the organisms were able to modify their vertical distribution and their diel and tidal rhythms by vertical movements with the tide currents so as to avoid the surface during the daytime and adjust their position inside the water column in order to control the horizontal dislodgement.

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