

Mudflat nekton assemblages in the Tagus estuary (Portugal): distribution and feeding patterns

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SUMMARY: Mudflats are an important component of estuaries, where they may occupy large areas and provide feeding and nursery grounds for many fish and bird species, as in the Tagus estuary. However, knowledge on their role and functioning is still expanding. Spatial and temporal dynamics of nekton assemblages in a mudflat of the Tagus estuary were evaluated to determine their role in the estuarine functioning. Feeding activity and daily rations of the most important nekton species are also analyzed. Two intertidal mudflat areas (upper and lower) were sampled, as well as the adjoining subtidal area. Sampling was conducted every two months, during a yearly cycle. A 24 h sampling cycle was conducted to investigate daily feeding patterns and determine daily rations. *Crangon crangon*, *Carcinus maenas*, *Palaemon longirostris*, *Palaemon serratus* and *Pomatoschistus microps* dominated the nekton community. A marked seasonal pattern was noticed with the highest densities recorded in spring and summer, corresponding to recruitment episodes of these species. Highest biomass values were recorded in the subtidal zone, while the highest densities were recorded in the intertidal zone. The mudflats seem to play an important role in the dynamics of the Tagus estuary, acting as a feeding and nursery areas for several nektonic species.

Keywords: nekton, community structure, daily rations, mudflat, intertidal areas, Tagus estuary.

RESUMEN: COMUNIDADES NECTÓNICAS EN SUBSTRATOS FANGOSOS DEL ESTUARIO DEL TAJO (PORTUGAL): DISTRIBUCIÓN Y PAUTAS ALIMENTICIAS. – Los substratos fangosos son componentes importantes de los estuarios, donde pueden ocupar amplias zonas y proporcionar alimento a las áreas de nursery de muchos peces y aves, como en el estuario de Tagus. Sin embargo, el conocimiento sobre su papel y funcionamiento es aún escaso. Se estudiaron la dinámica espacial y temporal de las comunidades bentónicas en una zona fangosa del estuario de Tagus, determinando su papel en el funcionamiento del estuario. Asimismo, se analizó la actividad alimenticia y las raciones diarias de las especies principales del nekton. Se muestrearon dos áreas fangosas intermareales (superior e inferior), así como las zonas submareales adyacentes. Los muestreos se realizaron cada dos meses durante un año. Se realizó un ciclo de 24 h para investigar las pautas alimenticias y determinar la ración diaria. *Crangon crangon*, *Carcinus maenas*, *Palaemon longirostris*, *Palaemon serratus* y *Pomatoschistus microps* dominan la comunidad nectónica. Se observa una pauta estacional clara, con las densidades más altas en primavera y verano, que corresponden a los episodios de reclutamiento de las especies mencionadas. Las biomásas más elevadas se obtuvieron en la zona submareal, mientras las densidades mayores se midieron en el intermareal. Los fondos fangosos del estuario de Tagus parecen jugar un papel importante en su dinámica, actuado como áreas de alimento y nursery de diversas especies nectónicas.

Palabras clave: nekton, estructura comunitaria, ración diaria, fondos fangosos, intermareal, estuario del Tajo.

INTRODUCTION

Estuarine systems are among the most productive and valuable ecosystems on Earth (Costanza *et al.*, 1997). Estuaries consist of a complex mixture of distinctive habitats and their importance, dynamics, functions and ecological connectivity are still poorly understood (Elliott and Hemingway, 2002).

Mudflats are a dominant habitat in many estuaries, often covering a considerable part of the total estuarine area. This particular type of habitat has been recognised to be of key importance for the estuarine food web due to its high productivity when compared to subtidal areas (Elliott and Dewailly, 1995). However, unlike estuarine salt marshes, which have long been considered highly productive habitats and thoroughly studied (Cattrijsse *et al.*, 1997; Rountree and Able, 1997; Halpin, 2000; Hampel *et al.*, 2003), mudflats have only recently become an object of study (Boer and Prins, 2002; Morrison *et al.*, 2002; Melville and Connolly, 2005; Dolbeth *et al.*, 2007).

Comparative studies between different estuarine habitats have focused mainly on the different role of vegetated and unvegetated habitats in estuarine biological communities. Seagrass habitats and macroalgal beds are extremely productive and important habitats for juveniles of many fish species (Weinstein and Brooks, 1983; Heck *et al.*, 1989; Sogard and Able, 1991). However, unvegetated estuarine habitats such as marsh creeks or mudflats have also been recently recognised as key habitats, acting as refuge and foraging areas for juveniles of many fish species (Paterson and Whitfield, 2000).

Several juvenile fish and crustacean species use estuarine mudflat areas as nursery grounds particularly when they can benefit from their great advantages, i.e. high productivity, abundance of food resources and refuge provided by shallow intertidal waters (Goldberg *et al.*, 2002; Amara and Paul, 2003; Kanou *et al.*, 2005; Vinagre *et al.*, 2006). The use of these habitats by nekton species can be analysed in terms of cost-benefit, particularly due to the high instability of abiotic conditions and the risk of stranding, which are selective factors for the occurrence of several species in these areas. However, species that tolerate such conditions can benefit from the advantages listed above (Morrison *et al.*, 2002; Kanou *et al.*, 2005; Salgado *et al.*, 2004; Vinagre *et al.*, 2006).

Mudflats are periodically immersed and emerged in each tidal cycle and are therefore only available to nekton during tidal inundation, which implies tidal

migrations to use this habitat. They are used by juveniles of several fish species which undertake tidal migrations mostly at night. (Morrison *et al.*, 2002; Kanou *et al.*, 2005; Vinagre *et al.*, 2006).

Mudflats represent a large part of the total intertidal area (between 20% and 40%) of the Tagus estuary (Portugal) and are intensively used as a feeding ground by large populations of resident and migratory birds (Moreira, 1999) and as a nursery area by many fish species (Cabral, 2000; Vinagre *et al.*, 2006). Additionally, Salgado *et al.* (2004) demonstrated the importance of this area for the Tagus estuary dynamics, showing that fish species richness was higher in the mudflat areas than in the tidal creeks, with different species occurring at each of these habitats. Although the importance of the Tagus estuary mudflat areas is well determined for some biological communities, namely benthic macroinvertebrates, little attempt has been made to assess the role of these habitats on the structure and dynamics of nekton assemblages. Furthermore, a quantitative assessment of the predation pressure of nekton on benthic prey has never been performed in these mudflat areas.

This study aims to characterise the nekton assemblage of the main mudflat area of the Tagus estuary and to assess its structure and spatial and seasonal distribution patterns in its upper and lower levels and in the adjoining subtidal area. Diel feeding patterns of nekton species and predation pressure on the main macrobenthic prey were assessed and the role that this mudflat plays in the overall dynamics and functioning of the Tagus estuary was also evaluated.

MATERIAL AND METHODS

Study Area

The Tagus estuary (38°40'N 9°15'W) is one of the largest estuaries on the Atlantic coast of Europe, with a length of 50 km and an area of 325 km². The tidal range is about 4 m and the intertidal and salt-marsh areas account for *ca.* 40% of the total estuarine area. The mean depth of the estuary is *ca.* 5 m and the maximum depth is 40 m near the mouth of the estuary. The river flow varies both seasonally and interannually, with a mean discharge of 400 m³ s⁻¹ (Bettencourt and Ramos, 2003).

The Tagus estuary includes several protected areas, one of the most important being the Tagus Estu-

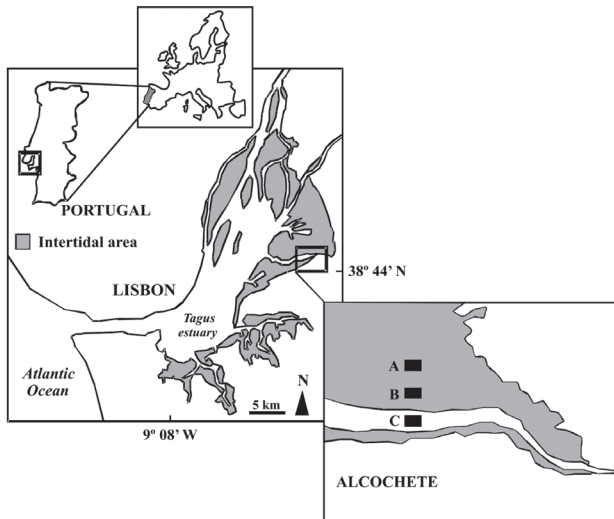


FIG. 1. – Location of sampling areas in the Tagus estuary: A- upper intertidal; B- lower intertidal; C- subtidal.

ary Nature Reserve, with an area of 145 km² (Farinha *et al.*, 2001). A large part of this area consists of mudflats that become emerged at low tide, playing an important role as feeding grounds for wintering birds that use the area as a stopover site during their winter migrations (Moreira, 1999). The study area was located in the upper estuary in a sheltered southern branch located near Alcochete (Fig. 1), in a large mudflat intertidal area with an adjacent channel representing the subtidal habitat.

According to the elevation of intertidal areas, two sampling sites were selected: one more elevated and the other near the subtidal channel zone. The mean emersion times for the two areas were calculated using the synoptic equations for the water level. The estimates obtained were 17 hours day⁻¹ for the upper part of the mudflat and 14 hours day⁻¹ for the lower part. The subtidal area (channel) was always submerged. Salinity in this area varies from 4 in winter to nearly 30 in summer, while water temperature ranges from 8 to 26°C (Cabral *et al.*, 2001).

The present study was carried out in 2005, which is considered to be a dry year with low overall precipitation values. River flow during this year showed a pronounced reduction. Hydrological data were obtained from INAG and the Portuguese Water Institute (<http://snirh.inag.pt>).

Sampling and laboratory procedures

Preliminary work was performed in this mudflat area in June and July 2004 in order to select the tidal phase and period of the day to be sampled during the

study period. In this survey, sampling was performed covering all possible combinations of diel (day, night and dawn/dusk) and semi-lunar cycles (full moon, new moon and quarter moon). Six replicates of each combination of these cycles were carried out (three in each month, whenever the combinations existed). Samples were taken on three consecutive days in each lunar phase. Since the tidal regime is semi-diurnal, two surveys per day could be conducted. Results from this preliminary work showed that the best period to perform the regular sampling in 2005 was during the night at neap tides (quarter moon), when the nekton abundances and biomasses showed the highest values.

According to Hemingway and Elliott (2002), in order to understand the functional role of nekton in open estuarine habitats, the use of appropriate sampling methods is especially important. In some cases, in order to effectively sample a variety of habitats within a given area, multi-method surveys may be employed as the capture of all components of a fish assemblage requires several methods to be used concurrently. In the present study, it was not possible to use the same method at the two different habitat types (intertidal and subtidal), so a brief description of each one is given.

In order to study estuarine nekton distribution throughout the intertidal area, two encircling nets were placed in the mudflats, one in the lower mudflat (closer to the channel), and one in the upper mudflat (closer to the salt marsh), approximately 200 m from each other. Sampling was conducted every two months, from January to November 2005. The nets were deployed simultaneously by boat at high tide peak. Both nets had a perimeter of 100 m and a mesh size of 5 mm, and were supported by 20 wooden sticks with a 3 m height. Metal weights were attached to the bottom of the nets so that they would be naturally buried in the mud when deployed. The operation took the shape of a closed circle trapping the nekton inside. In order to avoid scaring the fish, the boat was operated with sticks, the motor was turned off and silence was kept. At low tide the mudflat drains completely, leaving the organisms trapped in the nets. The organisms were hand collected, kept in plastics bags and preserved frozen. The net perimeter was used to calculate the area of the sampled circle in order to estimate densities of the organisms captured. The same procedure was repeated for three consecutive nights for each sampling month, so samples from one night constitute one replicate.

The encircling nets could not be used in the channel due to their dimensions, so this subtidal area was sampled using a beam trawl. The trawl opening (2.5 m) and the distance travelled (obtained using the coordinates recorded at the beginning and at the end of each trawl with a global positioning system, GPS) allowed us to determine the area sampled. The trawl net had a similar mesh size to the encircling nets: 5 mm. Three beam trawl replicates of 10 min duration were performed on one of the days when the encircling nets were deployed at the intertidal areas. The two methods used have similar selectivity, which means that both capture similar sizes and nektonic species. At the beginning of each trawl, and while the encircling nets were deployed, water salinity, dissolved oxygen (%) and conductivity (ms cm^{-1}) were measured with a multi-parameter probe (WTW). Temperature ($^{\circ}\text{C}$) was recorded every 15 min using three data loggers (HOBO H20-001) placed permanently at the three sampled areas. Data stored in the data loggers were downloaded after each sampling. At the end of each trawl, individuals were captured, placed in plastics bags and preserved frozen.

In order to estimate daily food consumption of the most abundant nektonic species, sampling was conducted at 2 h intervals over two 24 h periods in April 2005, at the channel which represents the subtidal habitat. Samples were taken using a beam trawl. Random samples of each species were taken from each haul and were immediately frozen. All individuals caught were identified, counted, measured (total length with 1 mm precision) and weighed (wet weight with 0.01 g precision) at the laboratory. Thirty individuals from each species were randomly selected from each haul of the 24 h cycles. These individuals were measured (total length with 1 mm precision), and weighed (wet weight with 0.01 g precision), and their stomach contents were weighed (wet weight with 0.001 g precision).

Data analysis

Nekton abundance data was expressed in number of individuals per m^{-2} and biomass data to g m^{-2} . Species richness (S) (total number of species), Pielou's evenness (J) and Shannon-Wiener's (H') diversity indices were calculated for each sampled habitat. Differences between species density and biomass in the three areas were evaluated by the Kruskal-Wallis test. A significance level of 0.05 was considered. Patterns of variation in community structure were

investigated by performing a canonical correspondence analysis (CCA), using nekton density and biomass values and the following environmental variables: temperature, salinity and the percentage of dissolved oxygen in water. Multivariate analyses were carried out using the CANOCO 4.5 package (Ter Braak and Šmilauer, 2002).

The consumption of prey by the most abundant nektonic species was assessed using the daily food ration. The model of Eggers (1977) was adopted to calculate the individual daily ration. The Eggers (1977) model is the most appropriate for computing daily rations based on stomach content data obtained from field studies, according to a literature review on this subject (Héroux and Magnan, 1996). The estimation of the daily ration C_{24} is given by:

$$C_{24} = W_{24} \times R \times 24$$

where W_{24} is the mean weight of the food content over 24 h (g) and R is the instantaneous evacuation rate (h^{-1}). Evacuation rates for the species studied were derived from the literature (Table 1). Since this parameter depends on the temperature, the values selected were obtained at temperatures similar to those obtained in the field during the study period.

Fullness index (FI, in %) was computed for each individual following the equation of Hureau (1969):

$$\text{FI} = \frac{S}{W} \times 100$$

where S is wet weight (g) of stomach contents and W is body wet weight (g), without stomach contents. The means of the fullness indices were plotted against actual time of haul to represent the diel feeding patterns.

RESULTS

Environmental variables

Mean values of the environmental variables considered were similar in the three study areas (Table 2). Mean temperature values were similar and the most marked differences were related to the maximum values, which were higher in the intertidal areas than in the subtidal area. The extreme values obtained for temperature in the intertidal areas correspond to periods when the water level at these sites

TABLE 1. – Instantaneous evacuation rates (R) estimates obtained for the studied nekton species, based on the literature.

Species	Temperature (°C)	R (g h ⁻¹)	Reference
<i>P. microps</i>	18.5	0.001	del Norte-Campos and Temming, 1994
<i>P. minutus</i>	18.5	0.006	del Norte-Campos and Temming, 1994
<i>S. senegalensis</i>	20.0	0.259	Vinagre <i>et al.</i> , 2007
<i>C. crangon</i>	18.5	0.003	del Norte-Campos and Temming, 1994

TABLE 2.-Maximum, minimum and mean values of the environmental variables recorded in the three sampling areas.

	Upper intertidal		Lower intertidal		Subtidal	
	Max - Min	Mean	Max - Min	Mean	Max - Min	Mean
Temperature (°C)	37.6-0.3	18.8	35.8-0.3	18.3	26.8-0.7	17.9
Salinity	29.1-17.3	22.8	29.3-17.6	22.8	32.6-12.5	23.6
Dissolved Oxygen (%)	96.0-41.1	71.1	92.0-42.1	71.1	95.5-29.6	66.9
Conductivity (mS cm ⁻¹)	47.6-23.3	32.8	46.8-23.5	32.5	49.9-17.5	36.7
Emersion time (hr day ⁻¹)	18.5-15.5	16.6	16.4-13.4	14.8	0.0-0.0	0.0

was extremely low. Salinity values were also similar for the three areas, with the largest amplitudes recorded in the subtidal area (Table 2).

The emersion period in the intertidal mudflat areas (number hours per day) was longer in the upper part of the intertidal mudflat. Nevertheless, the entire mudflat always remains completely drained for more than 12 hours each day.

Nektonic assemblages: species composition and abundances

A total of 13 fish and 6 decapod crustacean species were identified. Mean density (ind m⁻²) and biomass (g m⁻²) values of the species sampled in the three areas considered are presented in Table 3.

A small number of species dominated this nekton community: *Crangon crangon* (brown shrimp), *Carcinus maenas* (green crab), *Palaemon longirostris* (delta prawn), *Palaemon serratus* (common prawn), *Pomatoschistus microps* (common goby) and *Sardina pilchardus* (sardine). These species were also the ones that accounted for the highest biomass values. Nevertheless, *Liza ramada* (grey mullet) and *Solea senegalensis* (Senegal sole) also showed high values of biomass.

The lower part of the intertidal area showed the highest number of species (18), compared with 15 species in the other sampled areas. The Shannon-Wiener diversity index (H') was also highest in the lower intertidal zone, followed by the upper intertidal zone, with the lowest value being recorded in

TABLE 3 – Density (ind m⁻²) and biomass (g m⁻²) mean values of the nekton species in the three sampling areas. Standard deviation in brackets.

Species	Density			Biomass		
	Upper Intertidal	Lower Intertidal	Subtidal	Upper Intertidal	Lower Intertidal	Subtidal
<i>A. anguilla</i> (Linnaeus, 1758)	-	0.002 (<0.001)	-	-	0.021 (0.004)	-
<i>A. minuta</i> (Risso, 1810)	-	0.004 (<0.001)	-	-	0.001 (<0.001)	-
<i>A. presbyter</i> Cuvier, 1829	0.012 (0.004)	0.033 (0.027)	0.007 (0.004)	0.009 (0.006)	0.030 (0.027)	0.016 (0.011)
<i>C. crangon</i> (Linnaeus, 1758)	2.611 (5.124)	1.912 (2.62)	6.269 (10.5)	0.618 (0.937)	0.503 (0.612)	3.290 (5.92)
<i>C. maenas</i> (Linnaeus, 1758)	0.039 (0.07)	0.107 (0.33)	0.07 (0.06)	0.485 (0.935)	2.104 (7.145)	1.195 (1.171)
<i>D. labrax</i> (Linnaeus, 1758)	-	0.002 (<0.001)	0.005 (0.004)	-	0.033 (<0.001)	0.043 (0.04)
<i>E. encrasicolus</i> (Linnaeus, 1758)	0.003 (<0.001)	0.01 (<0.001)	-	0.003 (<0.001)	0.003 (<0.001)	-
<i>E. sinensis</i> H. Milne-Edwards	0.014 (0.018)	0.002 (<0.001)	0.008 (0.011)	0.713 (0.872)	0.062 (<0.001)	1.055 (1.89)
<i>L. aurata</i> (Risso, 1810)	0.002 (<0.001)	0.002 (<0.001)	0.001 (<0.001)	0.028 (<0.001)	0.044 (<0.001)	0.012 (0.001)
<i>L. ramada</i> (Risso, 1826)	0.019 (0.016)	0.037 (0.046)	0.018 (0.017)	0.744 (1.19)	0.237 (0.345)	0.319 (0.351)
<i>P. elegans</i> (Rathke, 1837)	-	-	0.003 (<0.001)	-	-	0.003 (0.001)
<i>P. longirostris</i> H. Milne-Edwards	0.329 (0.597)	1.332 (2.63)	0.049 (0.064)	0.170 (0.341)	0.397 (0.753)	0.028 (0.03)
<i>P. microps</i> (Krøyer, 1838)	0.600 (0.687)	1.171 (1.49)	0.899 (1.32)	0.145 (0.176)	0.300 (0.296)	0.354 (0.6)
<i>P. minutus</i> (Pallas, 1770)	0.011 (0.008)	0.018 (0.011)	0.118 (0.159)	0.021 (0.015)	0.017 (0.01)	0.222 (0.36)
<i>P. pagrus</i> (Linnaeus, 1758)	0.029 (0.003)	0.014 (0.004)	0.001 (<0.001)	0.023 (0.003)	0.014 (0.001)	0.001 (<0.001)
<i>P. serratus</i> Pennant	0.048 (0.042)	0.120 (0.098)	0.044 (0.047)	0.031 (0.021)	0.084 (0.068)	0.036 (0.04)
<i>S. acus</i> Linnaeus, 1758	0.002 (<0.001)	0.006 (0.005)	0.002 (<0.001)	-	0.004 (0.004)	0.002 (0.001)
<i>S. pilchardus</i> (Walbaum, 1792)	0.055 (0.074)	0.073 (0.099)	0.025 (0.024)	0.026 (0.043)	0.035 (0.049)	0.026 (0.02)
<i>S. senegalensis</i> Kaup, 1858	0.003 (0.002)	0.007 (0.008)	0.008 (0.006)	0.017 (0.027)	0.092 (0.112)	0.164 (0.23)

TABLE 4. – Values of species richness (S), Pielou's evenness (J) and Shannon-Wiener's (H') diversity indices for the three sampling areas.

	Upper intertidal	Lower intertidal	Subtidal
S	15	18	15
H'	0.897	1.3	0.604
J	0.331	0.453	0.223

the subtidal zone. The evenness index (J') showed a similar spatial variation pattern (Table 4).

Nektonic assemblages: spatial and temporal distribution patterns

The CCA performed based on nekton abundance data revealed that salinity, water temperature and dissolved oxygen were the most important environmental variables influencing the community structure (Fig. 2a). The first two CCA ordination axes accounted for 43.8% of total variance.

Temperature was responsible for the main gradient which seems to separate the different species. *Palaemon longirostris*, *Solea senegalensis* and *Pomatoschistus microps* appear on the right side

of the diagram, mainly related to higher values of temperature and salinity (Fig. 2a). Summer months are also placed on this side of the diagram. The points relative to May represent a well differentiated group, placed at the upper part of the diagram, related to a large number of species: *Pagrus pagrus*, *Eriocheir sinensis*, *Liza aurata*, *Pomatoschistus minutus* and *Carcinus maenas*. January, March and November are placed close to each other in the diagram and are mainly related to the highest abundance values of *Syngnathus acus*, *Atherina presbyter*, *Palaemon elegans*, *Engraulis encrasicolus* and *Crangon crangon*.

The CCA performed regarding species biomass showed a similar pattern to that obtained using densities, emphasising the role of temperature as a structuring factor of the nekton community (Fig. 2b). The first two CCA ordination axes explained 35% of total variance. The ordination plot shows a seasonal variation pattern: summer months are clearly separated from autumn and winter months, with the variables temperature and salinity closely associated with this pattern (Fig. 2b). The spatial variation pattern is not evident. The species associated with

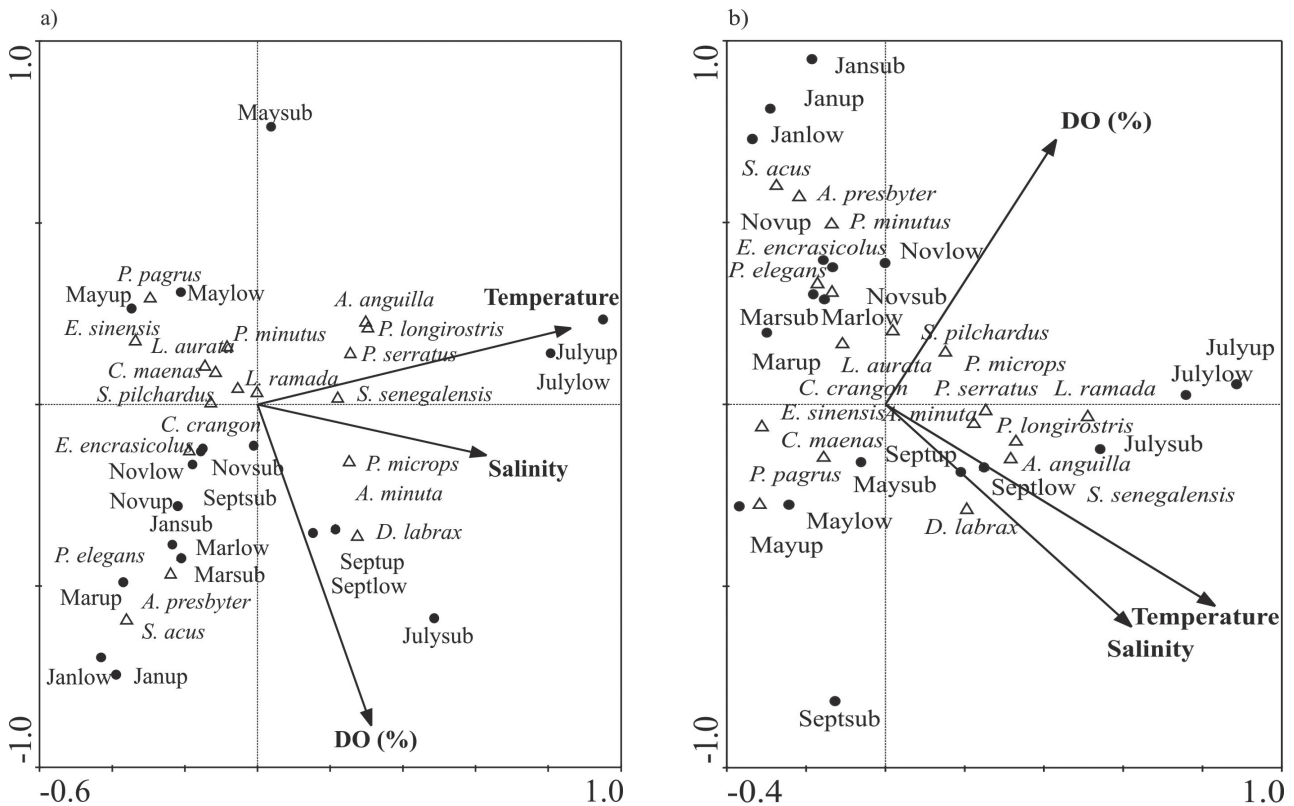


FIG. 2. – Canonical correspondence analysis (CCA) ordination diagrams based on densities (a) and biomass (b) of nekton species. (up, low and sub refer to upper intertidal, lower intertidal and subtidal zones, respectively; Jan- January; Mar- March; May- May; July- July; Sept- September; Nov- November).

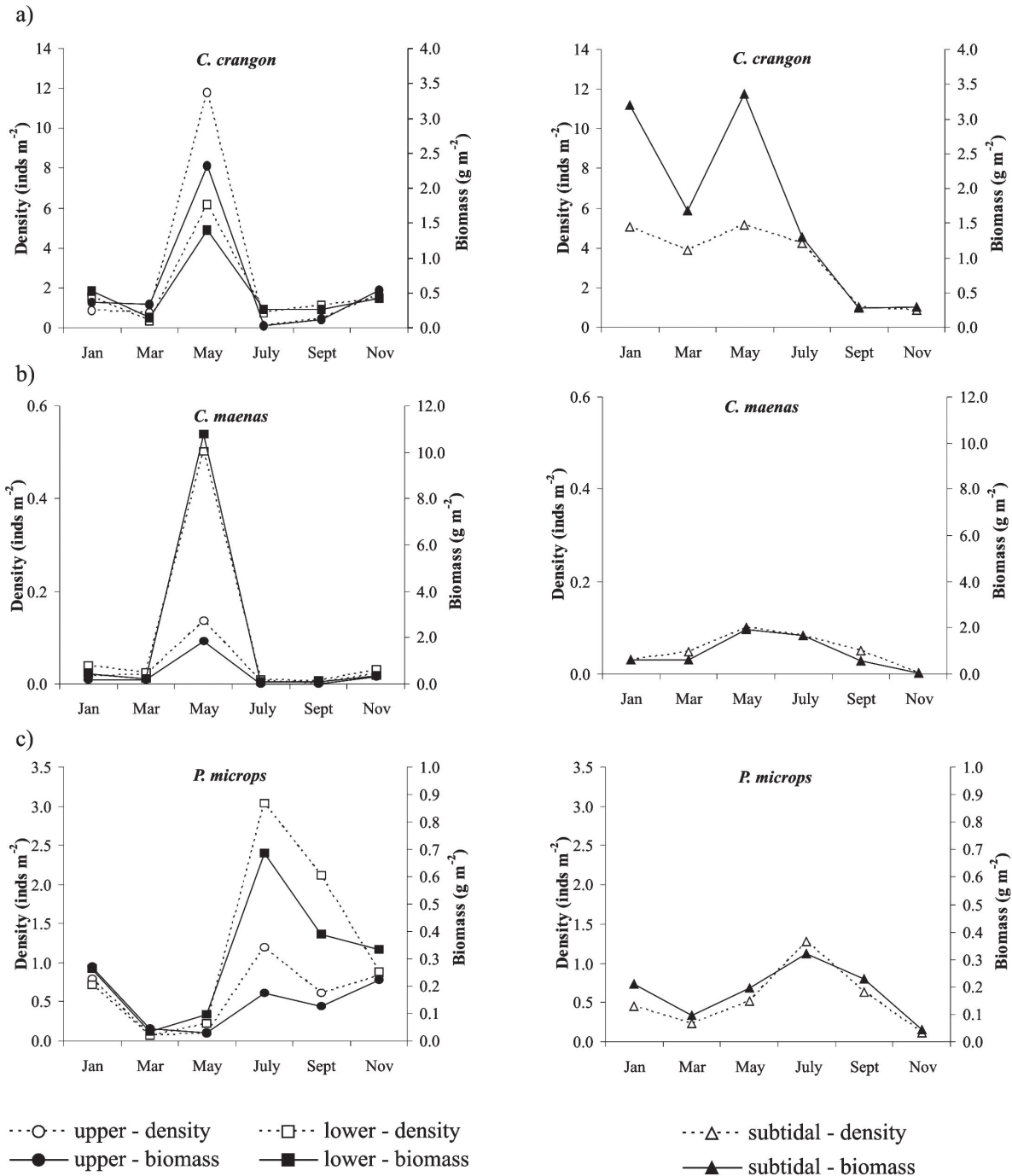


FIG. 3. – Seasonal and spatial patterns of the main nektonic species of the study area (a- *C. crangon*; b- *C. maenas*; c- *P. microps*)

the summer months are mainly *Palaemon longirostris*, *Dicentrarchus labrax*, *Anguilla anguilla*, *Liza ramada* and *Solea senegalensis*, while *Syngnathus acus*, *Atherina presbyter*, *Pomastochistus minutus* e *Engraulis encrasicolus* showed higher biomass values in winter.

The brown shrimp, *C. crangon*, was one of the most abundant species throughout the sampling pe-

riod in the three areas considered and its density and biomass values were higher in the subtidal zone during almost the whole year (Fig. 3a). In May a density peak was recorded for this species in all the sampled habitats, though its highest value occurred in the upper intertidal zone (11.8 ind m⁻²). In the same month the biomass of this species showed a strong increase, reaching a peak of 3.4 g m⁻² in the subtidal habitat.

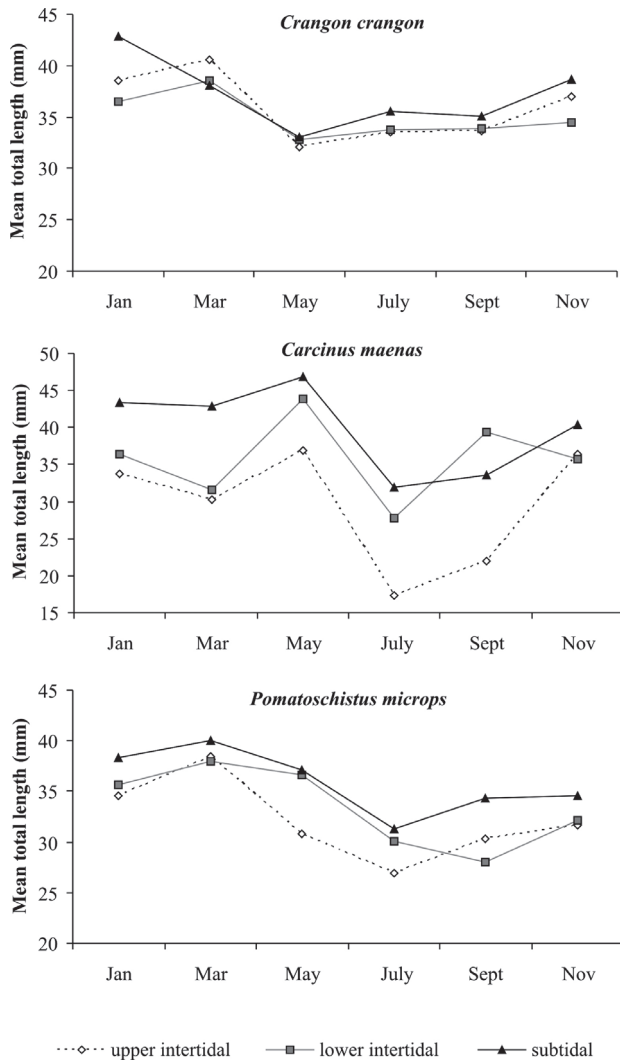


FIG. 4. – Spatial and seasonal variation pattern of mean total length (mm) of (a) *C. crangon*, (b) *C. maenas* and (c) *P. microps*.

Significant differences in the biomass values were found between the three areas considered ($H=7.37$; $P<0.05$). The smallest individuals were also captured in May (Fig. 4a). The largest individuals occurred during the winter months and seasonal variation in the individuals' total length was similar in the three sampled areas (Fig. 4a).

The green crab, *C. maenas*, showed a similar pattern, with the highest densities recorded in the subtidal zone during almost the whole year (Fig. 3b). May was also an exception for this species, with density and biomass peaks (0.5 ind. m^{-2} and 10.7 g m^{-2} , respectively) occurring in the lower intertidal zone (Fig. 3b). Significant differences between the three areas were found for this species' biomass ($H=7.38$; $P<0.05$). The smallest individuals were always captured in the upper intertidal zone, which showed

relatively low densities for this species, while the largest individuals occurred mainly in the subtidal zone. The smallest lengths were recorded in July (Fig. 4b).

The common goby, *P. microps*, showed similar patterns of abundance and biomass in the three study areas (Fig. 3c). Density and biomass values showed

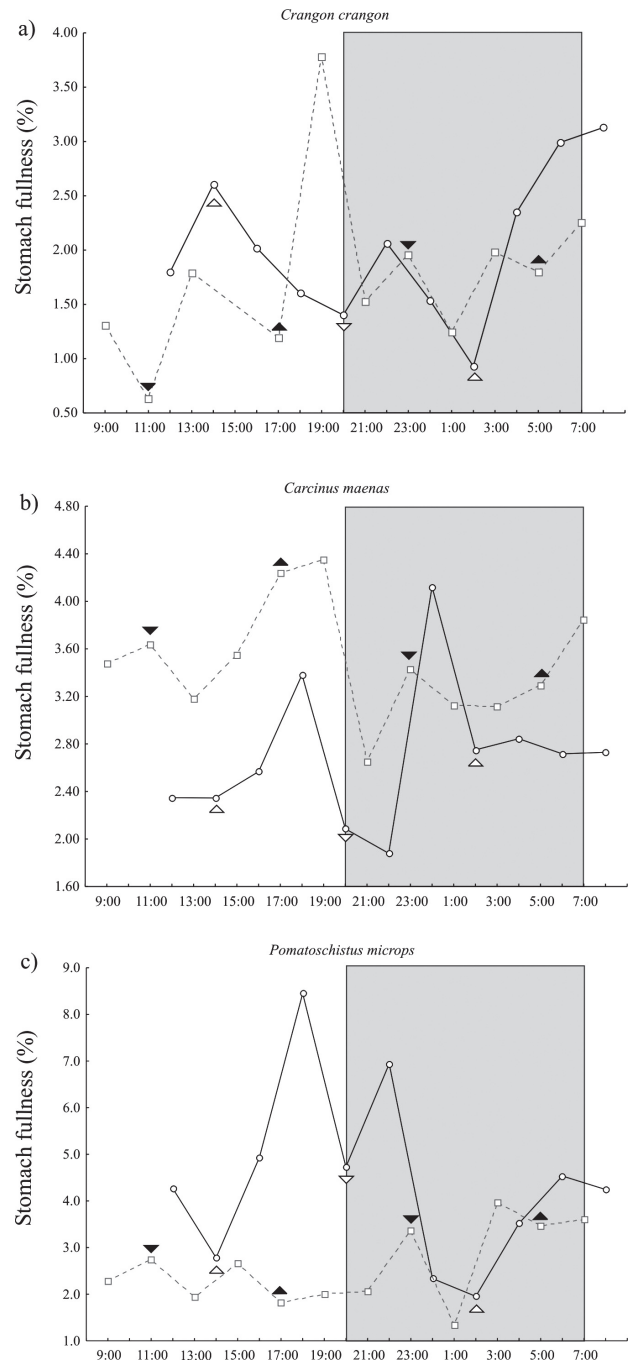


FIG. 5. – Diel feeding patterns of (a) *C. maenas*, (b) *P. microps*, (c) *C. crangon* and (d) *P. longirostris*. Arrows: low (∇) and high (\blacktriangle) tides in the first sampling day; low (∇) and high (\blacktriangle) in the second sampling day. Grey pattern representing night time. (\circ) first sampling day; (\square) second sampling day.

an increase in the spring and summer months, reaching their maximum values of 3.03 ind. m⁻² and 0.68 g m⁻², respectively in July, both in the lower intertidal zone (Fig. 3c). No significant differences in abundance and biomass values were found between the three study areas. The smallest individuals of *P. microps* were captured in July, which was also the month when the density and biomass peaks for this species were recorded (Fig. 4c). These small individuals were captured mainly in the upper intertidal zone, while the largest ones were found in the subtidal zone (Fig. 4c).

Diel feeding intensity and consumption

Figure 5a shows the 24 h feeding pattern of *C. crangon* for the two sampled days, based on fullness index. The feeding pattern of *C. crangon* showed a peak around 14:00 (Fig. 5a). On the second day of sampling, a clear peak was obtained at dusk, followed by a decrease in feeding at the beginning of the night. Both days showed an increase in stomach fullness towards dawn. This species also showed feeding peaks between low and high tide.

The feeding pattern of the green crab, *C. maenas*, was similar for both days, with increased feeding observed in the afternoon (Fig. 5b). Two clear peaks of feeding were recorded, one around dusk and the other during the night.

For the common goby, *P. microps*, a similar feeding pattern was noticed, with peaks of stomach fullness during the afternoon and night (Fig. 5c). An increased feeding until dawn was also observed for both days. The peaks of feeding observed for this species were recorded between low and high tide.

Consumption estimates varied considerably according to species (Table 5). *S. senegalensis* was the species for which the highest consumption estimate was obtained (1.77 g d⁻¹). Although the common goby *P. microps* was one of the most abundant species, its consumption estimate showed the lowest value (0.00047 g d⁻¹). The Senegal sole, *S. senega-*

lensis, contributed considerably to the overall consumption of the nekton assemblage in the studied mudflat.

DISCUSSION

Understanding the relationship between species distribution and environmental variables allows us to identify the ecological processes that regulate different populations and communities in ecology. However, besides all the changes in environmental conditions, many species change their habitats according to their ontogeny or seasonal rhythms, which means that relations between different species and their environment or habitat are dynamic spatial and seasonally (Morrison *et al.*, 2002; Kanou *et al.*, 2005).

Intertidal habitats are now receiving special attention in an attempt to establish their value for the species that use them at different stages of their life cycle. Little work has been done about the nekton communities that use mudflat habitats. The processes related to the use of these areas by highly mobile individuals like fish or crustaceans are still largely unknown.

The number of fish species recorded in the mudflat habitat of the Tagus estuary (13 species) was lower than that recorded in a previous study conducted in the same area, which reported 22 fish species (Salgado *et al.*, 2004). Nevertheless, the most abundant fish species were the same and showed similar densities to those obtained in the present study. Another study conducted in the same intertidal mudflat showed that the main predators of *S. senegalensis* juveniles were the same nekton species caught in the present work, with similar density values being obtained (Vinagre *et al.*, 2006). When compared to other geographical areas, the studied mudflat showed lower species richness: 17 fish species were recorded on an intertidal mudflat from an Australian estuary (Morrison *et al.*, 2002), 20 in the same habitat in an estuarine system in Japan (Kanou *et al.*, 2005) and 18 in France (Amara and Paul, 2003). Regarding the subtidal habitat sampled, the number of fish and crustacean species captured was also lower than that reported in previous works conducted in the Tagus estuary, near the study area (Cabral, 1998)

Comparative studies between vegetated and un-vegetated habitats are frequent and often show that vegetated habitats, namely salt marshes and sea grass meadows, support different and more abundant fish

TABLE 5. – Estimation of the daily ration of 4 nekton species from the study area. W_{24} , average stomach content over 24 h (g); R , instantaneous evacuation rate (g h⁻¹); C_{24} , daily ration (g d⁻¹).

Species	W_{24}	R	C_{24}
<i>P. microps</i>	0.019	0.001	0.00047
<i>P. minutus</i>	0.007	0.006	0.0010
<i>S. senegalensis</i>	0.285	0.259	1.77
<i>C. crangon</i>	0.014	0.003	0.001

assemblages and constitute important nursery areas for commercially important fish and crustacean species (Rozas and Reed, 1993; Szedlmayer and Able, 1996; Gray *et al.*, 1998; Hampel *et al.*, 2003). Salgado *et al.* (2004) reported the occurrence of 22 fish species in the same mudflat habitat as the present study and 14 in the marsh creeks, which demonstrates that only a limited number of the fish species occurring in the upper part of the Tagus estuary use the salt marsh habitats. For some tropical estuarine systems, a higher number of species has been reported in the mudflat habitat than in the adjacent mangrove area (Hindell and Jenkins, 2004).

The nekton community from the study area seems to be seasonally structured, reflecting the density peaks of the most abundant species. This pattern has been already described for the fish communities which use the salt marsh creeks from this area in the Tagus estuary (Salgado *et al.*, 2004), as well for other European estuarine systems (Beyst *et al.*, 2001; Amara and Paul, 2003).

In the present work, the subtidal channel recorded the highest values of biomass, with a similar seasonal variation pattern to that obtained for densities of nektonic species. However, the maximum density values were recorded in the intertidal areas. Therefore, a higher number of individuals per unit of area occur in the intertidal zone, but these individuals are smaller than the ones caught in the subtidal zone, which suggests that this habitat may play an important role for juvenile nekton species.

The most abundant species found in the present work were similar to those reported previously for this area (Salgado *et al.*, 2004) and for similar habitats in European estuaries: regarding decapoda crustaceans, the dominant species for this area were *P. longirostris*, *P. serratus*, *C. maenas* and *C. crangon*. The brown shrimp, *C. crangon* was the dominant species in the three sampled habitats. This species and the green crab, *C. maenas*, are common inhabitants of shallow-water habitats on European coasts (Cattrijsse *et al.*, 1997; Beyst *et al.*, 2001; Amara and Paul, 2003). *C. crangon* constitutes an important link in the estuarine trophic web: juvenile shrimp have been described as important predators of the meiobenthos and the microphytobenthos, while adults can exert a considerable predation pressure on macrobenthic communities, but the species itself is a major prey item for all dominant demersal fish species (Cattrijsse *et al.*, 1997). Furthermore, its high consumption and production rates underline its important role in

the functioning of the estuarine ecosystem (Redant, 1980; Cattrijsse *et al.*, 1997). In the present study this species was always more abundant in the subtidal habitat, with a peak density in May in the upper intertidal zone. This peak corresponds to the recruitment period of this species. During this period of the year, food availability throughout the intertidal mudflat is high and gobies, which are reported to be one of the major predators of this species (Norte-Campos and Temming, 1994), are mainly restricted to the subtidal habitats, suggesting that the increase in abundance of *C. crangon* in the intertidal zone may be related to these factors.

Regarding fish species, the highest abundance values were those of *P. microps*, *P. minutus*, *S. pilchardus* and *L. ramada*, with the common goby *P. microps* showing the highest density values throughout the sampling period. Similar abundance values for this species were recorded previously, for other shallow estuaries and coastal areas (Amara and Paul, 2003; Leitão *et al.*, 2006). The subtidal habitat seems to be important for the common goby, although the maximum density values were recorded at the lower part of the intertidal mudflat in July. Also, in this case the abundance peak seems to reflect the recruitment event for *P. microps*, as the individuals captured in this month were the smallest of the whole year. The juveniles of *P. microps* may benefit from the decrease in *C. crangon* abundance in the intertidal area during this time of the year.

Intertidal mudflats have already been recognised as key habitats for the estuarine food web because of their disproportionately high productivity in comparison with subtidal areas (Elliott and Dewailly, 1995). The macrobenthic community of this intertidal mudflat in the Tagus estuary was previously studied and results have shown that density and biomass values recorded in this area were high (França, 2006; Rodrigues *et al.*, 2006). When compared to the same type of community in the subtidal habitat, the differences were also pronounced, always with higher density and biomass values recorded in the intertidal mudflat (França, 2006; Vinagre *et al.*, 2006).

This fact, and the present results showing that larger individuals are found almost exclusively in the subtidal area, indicate that this Tagus estuary intertidal mudflat seem to play an essential role in the system dynamics as it is a prime candidate to be considered as a nursery area, e.g. high availability of food resources and refuge against predators. Mudflats have already been described as important nurs-

ery areas for some species in previous works (van der Veer *et al.*, 2001; Morrison *et al.*, 2002; Amara and Paul, 2003; Vinagre *et al.*, 2006).

This habitat separation between juveniles and adult individuals recorded in the present work was also analysed previously: Gibson (1973) studied the differences in abundance of several species with depth and concluded that there must be an active selection of depth by fish of a particular size. This spatial segregation may be related to feeding behaviour since smaller fish feed on organisms which have their maximum abundance intertidally and would also reduce intraspecific competition and prevent or reduce predation by other species (Gibson, 1973).

The present work did not record significant differences between the use of the upper and lower intertidal areas of the studied mudflat by the nekton species. Morrison *et al.* (2002) also showed, in a study conducted at a mudflat in New Zealand, that the whole tidal flat appeared to provide a habitat for most fish species, with no particular spatial segregation patterns. This indicates that fishes move between the deeper channels to the upper margin of the mudflat.

No clear pattern was detected regarding feeding activity of nekton species, although the most abundant species showed a tendency to increase feeding around dusk and dawn. Similar feeding patterns were found for gobies in the north Wadden sea (Norte-Campos and Temming, 1994). This pattern is usually associated with diurnal feeding species, as it is more advantageous not to forage during full daylight in order to achieve cover from predation and, at the same time, take advantage of the vulnerability of the prey (Pihl and Rosenberg, 1984; Norte-Campos and Temming, 1994).

Migrations to and out of the intertidal zone are fully synchronised with the tides, and this has been reported to influence the feeding behaviour of several species like *P. microps* to a larger extent than the diel cycle (Hampel and Cattrijsse, 2004). Norte-Campos and Temming (1994) found a peak of feeding activity for the common goby at high tide and a similar pattern was recorded for macrocrustaceans (Cattrijsse *et al.*, 1997). Generally, in intertidal areas, where species must adapt to constant changes in the environment, the tidal stimulus seems to be a prime factor governing the behaviour of nektonic species (Rozas and Reed, 1993).

The Senegal sole, *S. senegalensis* showed the highest values of consumption among the studied

nektonic species. The value of this mudflat habitat as a foraging area for this species has been reported previously (Vinagre *et al.*, 2006). The present work underlines this importance for this commercially important species that uses the Tagus estuary as a nursery area. The consumption values obtained for the other species were lower than the ones reported for other regions (Pihl and Rosenberg, 1984; Norte-Campos and Temming, 1994; Maes *et al.*, 2003; Hampel and Cattrijsse, 2004).

The results of the present study emphasise the importance of this mudflat habitat in the Tagus estuary for the nekton communities. Many of the species captured seem to benefit from the advantages of the intertidal habitat, particularly the high availability of food. Further studies about this intertidal mudflat and the communities that explore it are crucial in order to understand its structure, dynamics and relation to other estuarine habitats.

ACKNOWLEDGEMENTS

The authors would like to thank everyone involved in the field work. This study was supported by the Fundação para a Ciência e a Tecnologia (FCT).

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Scient. ed: E. Macpherson.

Received December 11, 2007. Accepted April 22, 2008.

Published online July 9, 2008.