

# Nekton Use of Salt Marsh Creeks in the Upper Tejo Estuary

JOÃO P. SALGADO<sup>1,\*</sup>, HENRIQUE N. CABRAL<sup>1</sup>, MARIA JOSÉ COSTA<sup>1</sup>, and LINDA DEEGAN<sup>2</sup>

<sup>1</sup> Instituto de Oceanografia, Faculdade de Ciências da Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal

<sup>2</sup> The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543-1015

**ABSTRACT:** The use of the Tejo estuary, Portugal, salt marsh creeks by nekton was examined based on sampling surveys with a fyke net from September 1998 until August 2001. From the 20 taxa (14 fish species, 5 decapod crustacean species, and 1 cephalopod species) identified in the studied creeks, 16 were regularly caught throughout the sampling period. The shrimp *Palaemonetes varians* was the most numerically abundant species in the creeks, while the biomass was dominated by the mullet *Liza ramada*. The nekton assemblage was mainly represented by marine-estuarine opportunist species, comprising 85% of the total number of species; when the number of individuals was considered, estuarine residents accounted for 96% of the total. A high seasonality was detected on the species abundance patterns: the most abundant species (*P. varians*, *Crangon crangon*, *L. ramada*, *Pomatoschistus microps*, *Syngnathus* sp., and *Anguilla anguilla*) occurred throughout the sampling period, *Sardina pilchardus*, *Dicentrarchus labrax*, and *Atherina boyeri* were particularly abundant in spring and summer, and *Engraulis encrasicolus*, *Liza aurata*, *Gambusia holbrooki*, *Palaemon longirostris*, and *Palaemon serratus* were most abundant in autumn and winter. *L. ramada* occurred in the tidal creeks in high numbers during neap tides, while the majority of the remaining taxa were most abundant during spring tides, suggesting a differential pattern of habitat use according to species.

## Introduction

Salt marshes are recognized as important nursery and feeding grounds for several nektonic species (Kneib 1997a). Shelter from predation and foraging profitability have been pointed out as the main reasons for the high abundance of nekton in these intertidal areas (Shenker and Dean 1979; Boesch and Turner 1984; McIvor and Odum 1988; Cattrijsse et al. 1994). Most of the literature associated with this subject is related to North American salt marshes, which are usually dominated by *Spartina alterniflora* (Rozas and Zimmerman 2000). In Europe mean tide level borders the low marsh (Beeftink 1977), in contrast to most of the North American salt marsh sites. Vegetated areas in European salt marshes are only flooded for short periods during relatively high spring tides. Nekton use of the intertidal salt marsh areas in Europe is generally limited to intertidal creeks (Cattrijsse et al. 1994).

Tidal period controls salt marsh use by nekton. Flood provides access to the highly productive intertidal areas, but ebbing tide carries the risk of stranding (Kneib and Wagner 1994). Different tidal amplitudes influence the time that a marsh is immersed and the duration of the availability of intertidal areas for nekton. The permanence of nektonic individuals in these systems should be a balance between maximizing shelter from preda-

tion and the opportunity to forage and minimizing the risks of stranding. According to Rozas (1995), longer periods of submergence should benefit individuals that forage and seek refuge in these areas. The active selection of nursery habitats is reflected by the responses of populations to environmental gradients (Baltz et al. 1998). Understanding temporal as well as spatial variations in the use of such habitats is essential for defining the processes involved in nekton dynamics in estuarine and coastal areas and their role in the movement of matter and energy within and from estuaries (Kneib and Wagner 1994).

A large number of studies were conducted in the Tejo estuary, Portugal, and have outlined its role as a nursery area for several fish and crustacean species (Costa 1982; Costa and Bruxelas 1989; Cabral 1998). These studies were conducted in subtidal or intertidal mudflat areas and no information exists for salt marsh habitats. The main goal of this work is to study the temporal and spatial variation in habitat use patterns of salt marsh creeks by the nekton assemblage in the upper part of the Tejo estuary.

## Materials and Methods

### STUDY AREA

The Tejo estuary (Portugal) has an area of 320 km<sup>2</sup> and is the largest estuary in western Europe (Fig. 1). It has a semi-diurnal mesotidal pattern with about 4 m of tidal range. The intertidal zone covers 113 km<sup>2</sup>, of which 100 km<sup>2</sup> are mud flats

\* Corresponding author; tele: 351-217500000; fax: 351-217500009; e-mail: jpsalgado@fc.ul.pt

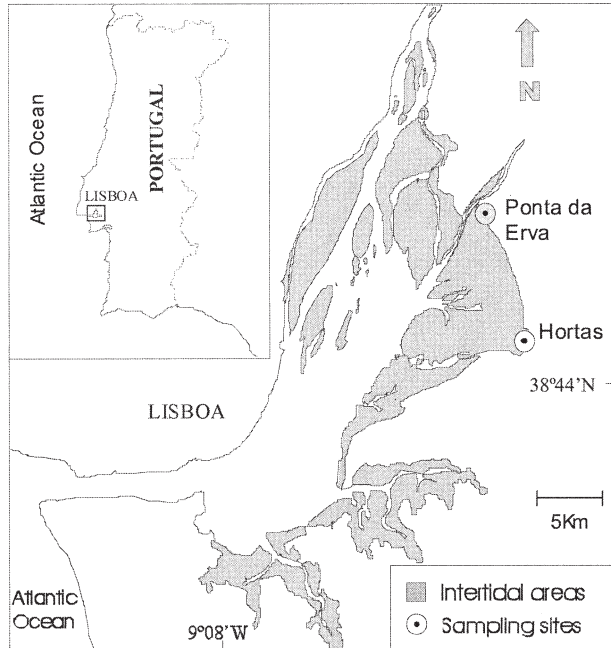


Fig. 1. Location of the sampling sites within the Tejo estuary.

and 13 km<sup>2</sup> are salt marshes (Catarino et al. 1985). Sampling was conducted in two 15-m wide tidal creeks approximately 150 m in length and with a maximum flood depth of 1.5 m between the mud bottom and the marsh surface. Tidal creek sampling sites were chosen for their size, accessibility, and because they drain almost completely at low tide. These creeks, located in the upper part of the estuary about 30 km away from the coastline, are flooded twice a day on average for 3.5 h per tide and are bordered by dense salt marsh vegetation, mainly composed of *Spartina maritima* L. in the pioneer and lower areas and *Halimione portulacoides* L. and *Arthrocnemum perenne* Miller in the middle marsh areas. Only 42% of the high tides flood the higher salt marsh vegetation areas (when the water level is 3.4 m above hydrographic zero).

#### SAMPLING PROCEDURES AND DATA ANALYSIS

Nekton was sampled using a fyke net (3-mm mesh size) that completely blocked the creek mouths. To avoid net clogging by large specimens and escape of large fish by jumping over the fyke net (especially mugilids), two gill nets (50-mm mesh size) were stretched in front of the fyke net. All samples were collected during ebb tide.

Samples were taken monthly from September 1998 until August 1999 and quarterly from September 1999 until August 2000, during daylight ebb tides of similar amplitude. Between June and August 2000 and 2001, samples were taken weekly in Hortas creek (Fig. 1) in order to study the ef-

fects of different tidal amplitudes on the abundance of nekton in the creek.

Fyke nets were set at high tide at the mouth of the creek. During each sampling session, nekton collections were made every 30 min (both for fyke and gill nets) from high tide until the creek was almost completely drained. For each collection, the fyke net bag (ca. 10 m length) was closed with a rope about 2 m from the end of the bag (where all the specimens caught were concentrated). The end of the bag was then emptied and the material collected. This procedure lasted for about 5 min, after which the middle portion of the fyke net bag was opened again by removing the rope. The net was in use during these procedures. At each collection, environmental variables (water temperature, salinity, dissolved oxygen, and turbidity) were measured using a Hydrolab multiprobe sonde.

All nekton specimens caught were counted, measured to the nearest 1-mm total length, and weighed wet with 0.001-g precision in the laboratory. For each species, the percentages of number (%N) and biomass (%W) in relation to the total number of individuals caught were determined. The frequency of occurrence (%FO) was also calculated. Species were assigned to six ecological guilds (adapted from Potter et al. 1986): freshwater, anadromous, catadromous, estuarine residents, marine estuarine-opportunistic, and marine straggler.

The spatial (two sites) and temporal (4 seasons in two consecutive years) variation in nekton assemblage was evaluated using correspondence analysis. This multivariate technique allowed us to directly relate the pattern of community variation with the pattern of environmental variation (Ter Braak and Prentice 1988). According to Ter Braak and Prentice (1988), this has several advantages when compared with other direct gradient analysis techniques, in particular when species have nonlinear and unimodal relationships to environmental gradients. In order to assess both spatial and temporal variation, species abundance data were averaged by sampling site, season, and year (winter, spring, summer, and autumn). The data collected at weekly intervals were not used in this analysis. Since results of the correspondence analysis are affected by the presence of rare species (Ter Braak 1995), species occurring less than 3 times through the entire sampling period were excluded from the analysis (i.e., *Sepioloa rondeletii*, *Pomatoschistus minutus*, *Solea senegalensis*, *Mugil cephalus*, and *Diplodus sargus*). This analysis was performed using log-transformed data as suggested by Field et al. (1982). Tide height, salinity, temperature, dissolved oxygen, and turbidity data were also included in the analysis as a covariable data matrix.

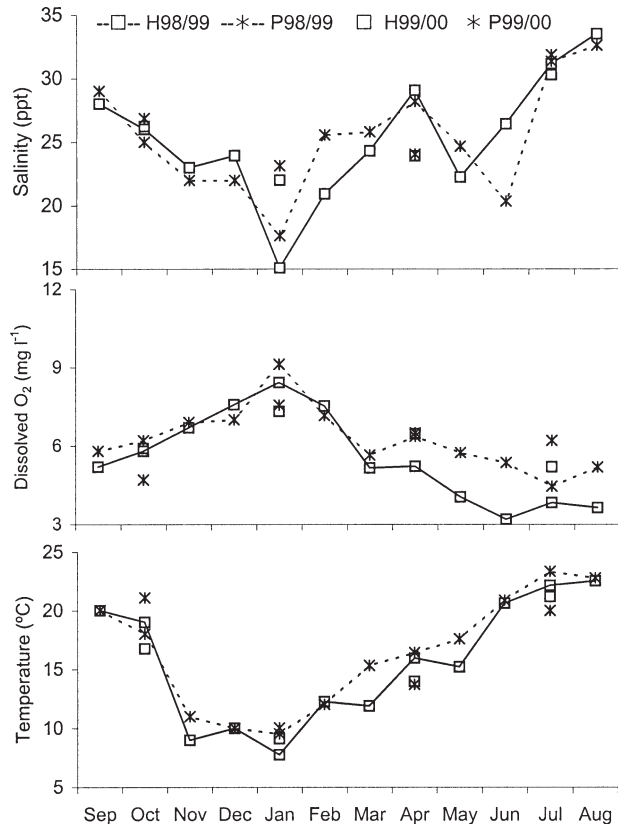


Fig. 2. Monthly mean values of salinity (‰), dissolved oxygen ( $\text{mg l}^{-1}$ ), and temperature ( $^{\circ}\text{C}$ ) in each sampling area, H (Hortas) and P (Ponta da Erva), and year 1998–1999 and 1999–2000.

Based on the data collected weekly at Hortas creek, the influence of tidal cycle phase (new moon, first quarter, full moon, last quarter) on the abundance of each of the 3 most common species was tested using a Kruskal-Wallis test (Zar 1996). The null hypothesis considered was that species abundance was similar for the four tidal cycle phases. When the null hypothesis was rejected, a posteriori test procedure (Dunn test) was performed (Zar 1996). Similar test procedures were used to evaluate the residence time of each species inside the creek within ebbing periods of full and new moon tides where species abundance were higher. The number of individuals caught for each of the 30 min periods was compared using a Kruskal-Wallis test as described above.

## Results

### ENVIRONMENTAL DATA

Variation of the environmental variables exhibited similar seasonal trends in both sampling sites (Fig. 2). Maximum temperature values occurred in July ( $23.3^{\circ}\text{C}$ ) at Ponta da Erva and in August

( $22.8^{\circ}\text{C}$ ) at Hortas, while minimum values were recorded in January ( $9.1^{\circ}\text{C}$  and  $7.8^{\circ}\text{C}$  for Ponta da Erva and Hortas, respectively). Salinity varied between  $15.0\text{‰}$  and  $33.5\text{‰}$  at Ponta da Erva and  $17.6\text{‰}$  and  $32.6\text{‰}$  at Hortas. In the second year of sampling, minimum salinity values were higher than those reported in the first year. Maximum values of dissolved oxygen were recorded in January ( $9.1 \text{ mg l}^{-1}$  at Hortas and  $8.4 \text{ mg l}^{-1}$  at Ponta da Erva) and minimums were recorded in July ( $4.5 \text{ mg l}^{-1}$ ) at Hortas and in June ( $3.2 \text{ mg l}^{-1}$ ) at Ponta da Erva.

### NEKTON ASSEMBLAGE

Twenty nektonic species were identified in the tidal creeks of the upper Tejo Estuary during the 2 yr of sampling, including 14 fishes, 5 decapods crustaceans, and 1 cephalopod species (Table 1). Estuarine and marine estuarine-opportunistic species were the most represented ecological guilds comprising 85% of the total number of species. Estuarine residents represented 96% of the total number of individuals. No marine straggler species were found.

Three species occurred in almost all samples: *Liza ramada* (FO = 100%), *Pomatoschistus microps* (FO = 90%), and *Palaemonetes varians* (FO = 97%). Although present in the tidal creeks, the crab *Carcinus maenas* was not included in the quantitative analysis because the sampling procedures used were not suitable for its capture. Two species represented more than 95% of the total number of the individuals caught. The shrimp *P. varians* was the dominant species with 76.8% (%N), followed by the fish species *P. microps* (%N = 18.9). *L. ramada* and *Sardina pilchardus* were also abundant in the tidal creeks. The biomass was dominated by the fish species *L. ramada* (%W = 87.7), which when combined with *P. varians* (%W = 11.3) represented almost 99% of the total biomass sampled.

Among the two sites, 3 species were only present in Hortas (Table 1): *M. cephalus*, *S. senegalensis* and *Diplodus sargus*. The higher number of individuals in Hortas was mostly due to the higher abundance of *P. varians*. *P. microps* was the most abundant taxa in Ponta da Erva, registering a higher number of individuals than in Hortas. The higher abundance of *L. ramada* individuals in Hortas, was the main responsible for the almost 15 times higher values of biomass, compared to Ponta da Erva.

The first two axes of the correspondence analysis on the species abundance in number and biomass accounted for about 50% of the total variance (50.4% for numeric abundance data and 47.0% for biomass data). The ordination diagram shows the main variation pattern in the nekton assemblage,

TABLE 1. Percentage values of occurrence (%FO), number of individuals (%N), biomass (%W), and ecological guild (EG; FW—freshwater, C—catadromous, E—estuarine residents, MEO—marine estuarine-opportunistic) for each species caught in the two salt marsh creeks (Hortas and Ponta da Erva) in the Tejo estuary. (\*)—species not quantified in this study (see text).

Species	EG	Hortas			Ponta da Erva		
		%FO	%N	%W	%FO	%N	%W
<b>Cephalopods</b>							
<i>Sepiola rondeleti</i>	MEO	6.25	<0.01	<0.01	7.14	<0.01	<0.01
<b>Decapods</b>							
<i>Crangon crangon</i>	MEO	93.75	0.74	0.08	64.29	0.07	0.03
<i>Palaemon serratus</i>	MEO	12.25	<0.01	<0.01	14.29	<0.01	<0.01
<i>Palaemon longirostris</i>	E	31.25	<0.01	0.02	21.43	0.01	0.08
<i>Palaemonetes varians</i>	E	68.75	92.49	10.61	85.71	20.29	20.24
<i>Carcinus maenas</i> (*)	E	—	—	—	—	—	—
<b>Fishes</b>							
<i>Anguilla anguilla</i>	C	68.75	0.01	0.01	35.71	0.02	0.05
<i>Liza ramada</i>	C	100.00	2.38	88.84	100.00	1.32	70.92
<i>Liza aurata</i>	MEO	31.25	<0.01	0.02	28.57	0.03	1.87
<i>Mugil cephalus</i>	MEO	12.25	<0.01	0.14	—	—	—
<i>Pomatoschistus minutus</i>	E	6.25	<0.01	<0.01	14.29	<0.01	0.01
<i>Pomatoschistus microps</i>	E	87.50	4.28	0.28	92.86	71.32	5.27
<i>Engraulis encrasicolus</i>	E	25.00	0.01	<0.01	42.86	0.12	0.03
<i>Sardina pilchardus</i>	MEO	31.25	0.04	0.01	64.29	6.72	1.42
<i>Atherina boyeri</i>	E	18.75	<0.01	<0.01	21.43	<0.01	0.05
<i>Dicentrarchus labrax</i>	MEO	31.25	0.01	<0.01	21.43	0.01	<0.01
<i>Solea senegalensis</i>	MEO	6.25	<0.01	<0.01	—	—	—
<i>Diplodus sargus</i>	MEO	6.25	<0.01	<0.01	—	—	—
<i>Syngnathus</i> sp.	E	31.25	0.02	<0.01	71.43	0.06	0.02
<i>Gambusia holbrooki</i>	FW	25.00	<0.01	<0.01	28.57	0.01	<0.01
		Total	1,093,060 ind	1,847,047.12 g		303,708 ind	131,023.52 g

representing the centers of the species' distributions in relation to sampling areas and seasons and their relationship to environmental variables. The ordination diagrams (Figs. 3 and 4) grouped the most common and abundant species in the tidal

creeks, i.e., *P. varians*, *Crangon crangon*, *L. ramada*, *P. microps*, *Syngnathus* sp., and *Anguilla anguilla*, near the origin. The projection along the first axis reflected a seasonal variation pattern. Spring and

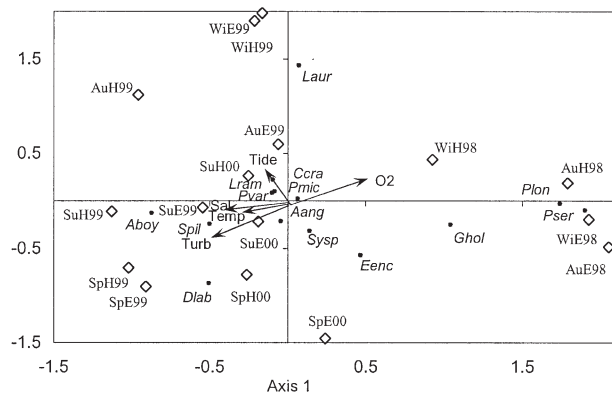


Fig. 3. Ordination diagram of the first two canonical axes of the correspondence analysis performed using species numeric abundance data. Au—Autumn; Wi—Winter; Sp—Spring; Su—Summer; H—Hortas area; E—Ponta da Erva area; 98, 99, and 00—sampling year; Aang—*A. anguilla*; Aboy—*A. boyeri*; Ccra—*C. crangon*; Dlab—*D. labrax*; Eenc—*E. encrasicolus*; Ghol—*G. holbrooki*; Laur—*L. aurata*; Lram—*L. ramada*; Plon—*P. longirostris*; Pmic—*P. microps*; Pser—*P. serratus*; Pvar—*P. varians*; Spil—*S. pilchardus*; Sysp—*Syngnathus* sp.; Sal—salinity; Temp—temperature; O<sub>2</sub>—dissolved oxygen; Turb—turbidity; Tide—tidal height.

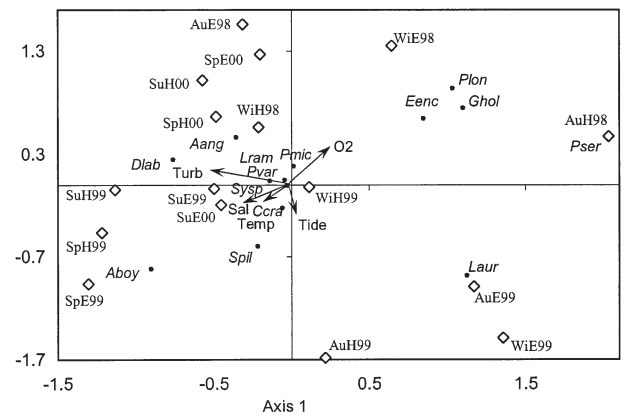


Fig. 4. Ordination diagram of the first two canonical axes of the correspondence analysis performed using species biomass data. Au—Autumn; Wi—Winter; Sp—Spring; Su—Summer; H—Hortas area; E—Ponta da Erva area; 98, 99, and 00—sampling year; Aang—*A. anguilla*; Aboy—*A. boyeri*; Ccra—*C. crangon*; Dlab—*D. labrax*; Eenc—*E. encrasicolus*; Ghol—*G. holbrooki*; Laur—*L. aurata*; Lram—*L. ramada*; Plon—*P. longirostris*; Pmic—*P. microps*; Pser—*P. serratus*; Pvar—*P. varians*; Spil—*S. pilchardus*; Sysp—*Syngnathus* sp.; Sal—salinity; Temp—temperature; O<sub>2</sub>—dissolved oxygen; Turb—turbidity; Tide—tidal height.

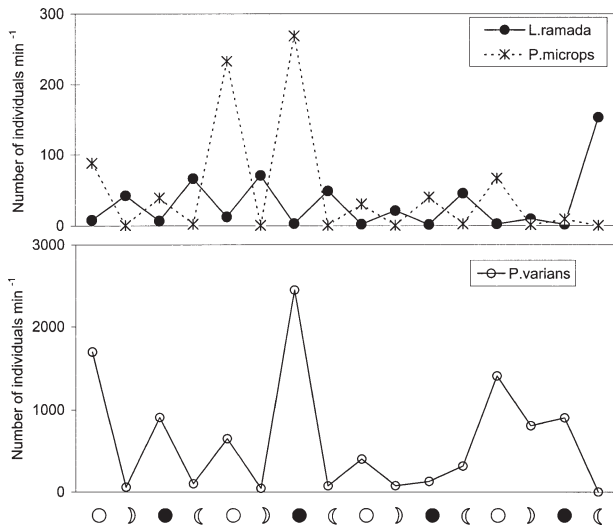


Fig. 5. Mean abundance values (number of individuals per minute) of *P. microps* (···\*···), *L. ramada* (—●—), and *P. varians* (—○—). New moon (○), 1st quarter moon (◐), full moon (●), and 3rd quarter (◑).

summer samples were located in the left side of the diagram and were associated with *S. pilchardus*, *Dicentrarchus labrax*, and *Atherina boyeri*, which were particularly abundant during those seasons. The environmental variables were mainly correlated with the first axis; water temperature, salinity, and turbidity were negatively correlated and dissolved oxygen was positively correlated. For the biomass data diagram a similar pattern was obtained (Fig. 4). Winter and autumn samples were mainly located on the right side of the diagram and were associated with *Engraulis encrasicolus*, *Liza aurata*, and *Gambusia holbrooki*. Within these sampling seasons, those performed in 1998 were particularly associated with *Palaemon longirostris* and *Palaemon serratus*. The relationship with environmental variables was similar to that described above for the numeric abundance data diagram.

#### VARIATION OF NEKTON ABUNDANCE WITH TIDAL CYCLE

Significant differences in the abundance of *L. ramada* ( $H = 12.20$ ,  $p < 0.05$ ), *P. microps* ( $H = 11.51$ ,  $p < 0.05$ ), and *P. varians* ( $H = 8.05$ ,  $p < 0.05$ ) in the tidal creeks were obtained between the tidal cycle phases studied (Fig. 5). *L. ramada* was more abundant in neap tides (both for first and third quarter moon phase; mean value  $56.94 \text{ ind min}^{-1}$  and maximum  $152.98 \text{ ind min}^{-1}$ ). The abundance values of this species during the tides of the first quarter of the moon were significantly different from those during spring tides (Dunn test,  $p < 0.05$ ). The abundances of *P. microps* (mean value  $96.81 \text{ ind min}^{-1}$  and maximum  $268.89 \text{ ind min}^{-1}$ )

TABLE 2. Mean ( $\pm$  SD) values of the percentage of individuals caught according to each 30 min periods after high tide (HT).

Periods after HT	<i>L. ramada</i>	<i>P. microps</i>	<i>P. varians</i>
1st	42.2 (22.2)	3.5 (1.5)	2.5 (1.7)
2nd	52.6 (21.6)	13.2 (4.3)	6.6 (5.8)
3rd	4.7 (2.8)	50.2 (19.1)	29.5 (15.5)
4th	1.0 (1.0)	33.1 (16.0)	61.5 (21.5)

and *P. varians* (mean value  $1,066.55 \text{ ind min}^{-1}$  and maximum  $2,447.17 \text{ ind min}^{-1}$ ) were higher during spring tides. Abundance of *P. microps* during tides of the first quarter moon were significantly different from those of spring tides (Dunn test,  $p < 0.05$ ). Species such as *D. labrax*, *A. anguilla*, and *Solea solea* only occurred in spring tide samples, although the reduced number of individuals captured did not allow statistical testing.

The most common species in the tidal creeks leave these areas during different phases of the ebb tide. Significant differences in the abundance of *L. ramada* ( $H = 12.20$ ,  $p < 0.05$ ), *P. microps* ( $H = 11.51$ ,  $p < 0.05$ ), and *P. varians* ( $H = 8.05$ ,  $p < 0.05$ ) were detected between the first four 30-min periods of ebbing. *L. ramada* specimens left the tidal creeks within the first hour of ebbing. On average, more than 90% of the individuals present in the tidal creeks abandoned them during this period of time (Table 2). The abundance in the first two periods of ebbing differed significantly from the fourth period (Dunn test,  $p < 0.05$ ). Different behavior was observed for *P. microps*, which left the creeks mostly in the last two periods of the ebb tide. Their abundance during these two periods was statistically different compared with the first half hour (Dunn test,  $p < 0.05$ ). The abundance of *P. varians* was higher in the last period of the sampled tides; 61% of their total captures occurred during that period, which differed statistically from the first two periods of sampling.

#### Discussion

##### NEKTON ASSEMBLAGE

The nekton assemblage of the upper Tejo salt marsh tidal creeks was characterized by the dominance of estuarine resident and marine estuarine-opportunistic species similar to several other European salt marshes (Frid 1988; Drake and Arias 1991; Cattrijsse et al. 1994; Laffaille et al. 2000; Mathieson et al. 2000). The dominance in number of individuals by estuarine resident species found in the Tejo salt marsh creeks has also been found in several studies conducted in Europe and North America (Shenker and Dean 1979; Cattrijsse et al. 1994; Kneib and Wagner 1994; Rozas 1995).

Few species usually dominate, both in number

and biomass, nekton assemblages of tidal creeks (Cain and Dean 1976; Bozeman and Dean 1980; Cattrijsse et al. 1994; Kneib 1997a; Laffaille et al. 2000). The decapod crustacean *P. varians* was numerically dominant in the Tejo salt marsh areas. Frid (1988) also found a high abundance of palaemonid shrimps in an eastern England salt marsh system, and Cattrijsse et al. (1994) reported the occurrence of *P. varians* in a Netherlands salt marsh area, although with low abundance values. According to Kneib (1997a), palaemonid shrimp are often the most abundant group of nekton in the intertidal marshes under all salinity conditions. Among the fishes, *P. microps* was the most abundant species observed in our study, which agrees with results obtained for the Bay of Cadiz (Drake and Arias 1991) and Westerschelde (Cattrijsse et al. 1994) marsh areas. Regarding biomass, *L. ramada* was the dominant species in the salt marsh nekton assemblage, corroborating the results obtained by Laffaille et al. (2000) for the salt marsh areas of the Mont Saint-Michel Bay.

The lack of salt marsh resident nektonic species found in the Tejo estuary agrees with the majority of studies performed in Europe (Cattrijsse et al. 1994; Laffaille et al. 2000) and clearly contrasts with those from North American tidal marshes (Kneib 1997a). In North America salt marshes, several authors (Kneib 1984; Kneib and Wagner 1994; Peterson and Turner 1994; Halpin 2000) described populations of nekton that may be found within intertidal pools and shallow flows of the creek channels during every stage of their life cycle; these species are among the dominant nektonic species of salt marshes. The most abundant residence species are typically members of the families Cyprinodontidae and Palaemonidae (Kneib 1997a). Several palaemonid species and some fish species were observed inside the tidal creeks but only rarely in pools or small rivulets during ebb tide (Salgado personal observations).

In a study conducted in the tidal channels of Bay of Cadiz, Drake and Arias (1991) reported the occurrence of *Fundulus heteroclitus*. This species, which spawns in the salt marsh ponds, was accidentally introduced into the Iberian Peninsula (Drake et al. 1987). Although present in southeastern Portugal (Gadiana River; Gomes personal communications), there are no records of its occurrence further north, where the Tejo estuary is located.

A marked seasonal pattern was noticed in the nekton assemblage of the Tejo salt marsh creeks. The individuals of the species that occurred in a particular season (e.g., *S. pilchardus*, *D. labrax*, and *A. boyeri*) were almost exclusively juveniles and the outlined seasonal trend reflected mainly successive

waves of colonization of salt marsh creeks by early life stages of several species (Salgado et al. in press). Laffaille et al. (2000) and Cattrijsse et al. (1994) identified three seasonal phases according to the structure of the fish assemblage, winter, spring and summer-autumn, when the highest densities of most of the fish species occurred. In this study these abundance peaks were mostly observed during spring and summer samples. This time lag, compared to the other studies, could not be dissociated from the distinct abiotic conditions that occur in more northern systems.

#### VARIATION OF NEKTON ABUNDANCE WITH TIDAL CYCLE

The abundance of different species using the salt marsh areas differed according to tidal cycle phase. The significantly higher abundances of *P. varians* and *P. microps* and the occurrence of *D. labrax*, *A. anguilla*, and *S. solea* juveniles during spring tides corroborates the results obtained by Kneib (1997b), i.e., maximum abundance of nekton occurs during tides with the highest range. These tides provide access for an extended period of time to areas exploited infrequently. Kneib (1993) found that growth rates of *F. heteroclitus* larvae were positively correlated with flooding duration of salt marsh, and Halpin (2000) reported higher growth rates for larvae occurring in intertidal creeks compared with those from subtidal channels.

According to Rozas (1995), if the risk of stranding can be minimized, exploiting the higher marsh areas may have advantages. High marsh environments may offer shallower waters with greater protection from predators and may contain more food than low marshes, because prey are exposed to fewer predators for shorter periods of time (Kneib 1984, 1993). Factors such as the reduced periods of marsh inundation and the highly dense vegetation covering the creek banks may reduce the advantages of exploiting higher marsh areas similar to those of the Tejo estuary.

*L. ramada* was the only species in the Tejo creeks that presented a different abundance pattern in relation to tidal cycle phase, with the highest abundance values being recorded during neap tides. During neap tides, low water occurs during the middle of the day, allowing for maximum daily photosynthetically active radiation at the sediment surface; also, tidal currents are the lowest along the spring-neap tidal cycle (Vale and Sundby 1987) and resuspension of benthic microalgal cells is expected to be minimal, resulting in favorable conditions for microalgal photosynthesis and for a net biomass accumulation (Serôdio and Catarino 1999). *L. ramada* presents a grazing behavior on

the superficial layer of the sediment (Almeida et al. 1993) ingesting benthic microalgae (Salgado et al. unpublished data). The abundance pattern that was obtained for *L. ramada* suggests that the use of tidal creeks is mainly related to feeding and that the most advantageous conditions occur during neap tides.

According to Cattrijsse et al. (1994), most of the species that occur in tidal creeks migrate towards the salt marsh areas during the first hour of the flood and return to the subtidal channels during the last hour of ebbing. Kneib (1984) described a migration pattern following the edge of the tide for *F. heteroclitus*. The time spent in tidal creeks by individuals of each species is strongly related to their feeding strategies and to foraging opportunities offered by these habitats. *P. microps* and *S. pilchardus* left the Tejo tidal creeks with significantly higher amounts of food in their gastrointestinal tracts (Salgado unpublished data). The use of salt marsh creeks as a feeding ground was also reported by other authors (Cattrijsse et al. 1994 and Laffaille et al. 1998, for *D. labrax*, *P. minutus*, and several species of shrimp).

Delaying the return to subtidal areas could be advantageous since decapod and fish predators are usually absent from these areas. The shallowness and turbid conditions offered by the creeks function as refuge to small fishes and crustaceans from fish and avian predators (Baltz et al. 1998). *L. ramada* individuals exhibited a different strategy from other species in their residence time inside the tidal creeks. Although arriving with the advancing edge of the flood tide, they left the salt marsh creeks mainly during the first hour of ebbing with significant higher amount of food in their stomachs (Salgado unpublished data). This strategy might be related to their larger body size, compared to other species present in this habitat type, which could lead to a higher risk of stranding inside the creeks.

The high abundance of nektonic individuals observed in the Tejo estuary salt marsh tidal creeks during the 2 yr of sampling confirms the importance of this habitat type in the processes governing estuarine nekton dynamics, as described for many other estuarine and coastal areas (e.g., Weinstein et al. 1980; Boesch and Turner 1984; Kneib 1997a). The functions of nursery and feeding grounds of the studied habitat is limited to a relatively reduced number of decapod crustaceans and fish species, compared to those that occur in the adjacent areas (Costa et al. 1994; Salgado et al. in press), most of them with reduced direct commercial value. They may be a crucial trophic connection linking intertidal production to juveniles

of species important for fisheries in adjacent subtidal nursery environments (Kneib 1993).

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#### LITERATURE CITED

- ALMEIDA, P. R., F. MOREIRA, J. L. COSTA, C. A. ASSIS, AND M. J. COSTA. 1993. The feeding strategies of *Liza ramada* (Risso, 1826) in the fresh and brackish water in the River Tejo, Portugal. *Journal of Fish Biology* 42:95–107.
- BALTZ, D. M., J. W. FLEEGER, C. F. RAKOCINSKI, AND J. N. MCCALL. 1998. Food, density, and microhabitat: Factors affecting growth and recruitment potential of juvenile saltmarsh fishes. *Environmental Biology of Fishes* 53:89–103.
- BEEFTINK, W. G. 1977. The coastal salt marshes of western and northern Europe: An ecological and phytosociological approach, p. 93–121. In V. J. Chapman (ed.), *Wet Coastal Ecosystems*. Elsevier, Amsterdam, The Netherlands.
- BOESCH, D. F. AND R. E. TURNER. 1984. Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries* 7:460–468.
- BOZEMAN, JR., E. L. AND J. M. DEAN. 1980. The abundance of estuarine larval and juvenile fish in a South Carolina intertidal creek. *Estuaries* 3:89–97.
- CABRAL, H. N. 1998. Utilização do estuário do Tejo como área de viveiro pelos linguados, *Solea solea* (Linnaeus, 1758) e *S. senegalensis* Kaup, 1858, e robalo, *Dicentrarchus labrax* (Linnaeus, 1758). Ph.D. Dissertation, Faculdade de Ciências de Lisboa, Lisboa.
- CAIN, R. L. AND J. M. DEAN. 1976. Annual occurrence, abundance and diversity of fish in a South Carolina intertidal creek. *Marine Biology* 36:369–379.
- CATARINO, F., J. D. TENHUNEN, V. BROTHAS, AND O. LLANGE. 1985. Application of CO<sub>2</sub>-porometer methods to assessment of components of photosynthetic production in estuarine ecosystems. *Marine Biology* 89:37–43.
- CATTRIJSSSE, A., E. S. MAKWALA, H. R. DANKWA, O. HAMERLYNCK, AND M. A. HEMMINGA. 1994. Nekton communities of an intertidal creek of a European estuarine brackish marsh. *Marine Ecology Progress Series* 109:195–208.
- COSTA, M. J. 1982. Contribution à l'étude de l'écologie des poissons de l'estuaire du Tage (Portugal). Ph.D. Dissertation, Université Paris VII, Paris.
- COSTA, M. J. AND A. BRUXELAS. 1989. The structure of fish communities in the Tejo estuary (Portugal) and its role as a nursery for commercial fish species. *Scientia Marina* 53:561–566.
- COSTA, M. J., J. L. COSTA, P. R. ALMEIDA, AND C. A. ASSIS. 1994. Do eel grass beds and salt marsh borders act as preferential nurseries and spawning grounds for fish?—An example of the Mira estuary in Portugal. *Ecological Engineering* 3:187–195.
- DRAKE, P. AND A. M. ARIAS. 1991. Composition and seasonal fluctuations of the ichthyoplankton community in a shallow tidal channel of Cadiz Bay (S. W. Spain). *Journal of Fish Biology* 39:245–263.
- DRAKE, P., A. M. ARIAS, AND M. C. SARASQUETE. 1987. Reproduction of *Fundulus heteroclitus* (Linnaeus, 1758) (Pisces, Ciprinodontidae) en medio hipersalino. *Investigacions Pesqueres* 51:183–197.
- FIELD, S. G., K. R. CLARKE, AND R. M. WARWICK. 1982. A practical strategy for analyzing multispecies distribution patterns. *Marine Ecology Progress Series* 8:37–52.

- FRID, C. L. J. 1988. The Marine invertebrate fauna of the North Norfolk salt marshes, and their ecology. *Transactions of the Norfolk and Norwich Naturalist's Society* 28:46–50.
- HALPIN, P. M. 2000. Habitat use by an intertidal salt-marsh fish: Trade-offs between predation and growth. *Marine Ecology Progress Series* 198:203–214.
- KNEIB, R. T. 1984. Patterns in the utilization of the intertidal salt marsh by larvae and juveniles of *Fundulus heteroclitus* (Linnaeus) and *Fundulus luciae* (Baird). *Journal of Experimental Marine Biology and Ecology* 83:41–51.
- KNEIB, R. T. 1993. Growth and mortality in successive cohorts of fish larvae within an estuarine nursery. *Marine Ecology Progress Series* 94:115–27.
- KNEIB, R. T. 1997a. The role of tidal marshes in the ecology of estuarine nekton. *Oceanography and Marine Biology: An Annual Review* 35:163–220.
- KNEIB, R. T. 1997b. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: Causes and questions. *Estuaries* 7:392–412.
- KNEIB, R. T. AND S. L. WAGNER. 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Marine Ecology Progress Series* 106:227–238.
- LAFFAILLE, P., S. BROSSE, E. FEUNTEUN, A. BAISEZ, AND J.-C. LEFEUVRE. 1998. Role of fish communities in particulate organic matter fluxes between salt marshes and coastal marine waters in the Mont Saint-Michel Bay. *Hydrobiologia* 373/374:121–133.
- LAFFAILLE, P., E. FEUNTEUN, AND J.-C. LEFEUVRE. 2000. Composition of fish communities in a European macrotidal salt marsh (the Mont Saint-Michel Bay, France). *Estuarine, Coastal and Shelf Science* 51:429–438.
- MATHIESON, S., A. CATTRIJSE, M. J. COSTA, P. DRAKE, M. ELLIOTT, J. GARDNER, AND J. MARCHAND. 2000. Fish assemblages of European tidal marshes: A comparison based on species, families and functional guilds. *Marine Ecology Progress Series* 204:225–242.
- MCIVOR, C. C. AND W. E. ODUM. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology* 69:1341–1351.
- PETERSON, G. W. AND R. E. TURNER. 1994. The value of salt marsh edge vs. interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. *Estuaries* 17:235–262.
- POTTER, I. C., P. N. CLARIDGE, AND R. M. WARWICK. 1986. Consistency of seasonal changes in an estuarine fish assemblage. *Marine Ecology Progress Series* 32:217–228.
- ROZAS, L. P. 1995. Hydroperiod and its influence on nekton use of the salt marsh: A pulsing ecosystem. *Estuaries* 18:579–590.
- ROZAS, L. P. AND R. J. ZIMMERMAN. 2000. Small-scale patterns of nekton use among marsh adjacent shallow nonvegetated areas of the Galveston Bay estuary, Texas (USA). *Marine Ecology Progress Series* 193:217–239.
- SERÓDIO, J. AND F. CATARINO. 1999. Fortnightly light and temperature variability in estuarine intertidal sediments and implications for microphytobenthos primary productivity. *Aquatic Ecology* 33:235–241.
- SHENKER, J. M. AND J. M. DEAN. 1979. The utilization of an intertidal salt marsh creek by larval and juvenile fishes: Abundance, diversity and temporal variation. *Estuaries* 2:154–163.
- TER BRAAK, C. J. F. 1995. CANOCO—A Fortran program for canonical community ordination by partial detrended canonical correspondence analysis, principal components and redundancy analysis. Agricultural and Mathematical Group, Ministry of Agriculture and Fisheries, ITI-TNO, Wageningen, Netherlands.
- TER BRAAK, C. J. F. AND I. C. PRENTICE. 1988. A theory of gradient analysis. *Advances in Ecological research* 18:271–317.
- VALE, C. AND B. SUNDBY. 1987. Suspended sediment fluctuations in the Tejo estuary on semi-diurnal and fortnightly time scales. *Estuarine, Coastal and Shelf Science* 25:495–508.
- WEINSTEIN, M. P., S. L. WEISS, AND M. F. WALTERS. 1980. Multiple determinants of community structure in shallow marsh habitats, Cape Fear River estuary, North Carolina, USA. *Marine Biology* 58:227–243.
- ZAR, J. H. 1996. *Biostatistical Analysis*, 3rd edition. Prentice Hall, Englewood Cliffs, New Jersey.

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