

FEEDING ECOLOGY OF THE GREEN CRAB, *CARCINUS MAENAS*
(L., 1758) IN A TEMPERATE ESTUARY, PORTUGAL

BY

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ABSTRACT

The feeding ecology of *Carcinus maenas* was studied between June 2003 and June 2004 in three areas in the Mondego estuary, Portugal. Samples were collected monthly, during the night, at high water of spring tides using a 2 m beam trawl. Among 837 stomachs examined, 25 different food items were identified. *Crangon crangon*, *Hediste diversicolor*, and Teleostei were the most important food items by occurrence, numbers, and weight. As an opportunistic feeder, differences in diet found between areas and seasons reflected prey availability. No differences were found in prey selection according to sex and carapace width of individuals. The feeding intensity of moulting and ovigerous crabs was lower. The incidence of cannibalism was higher than reported in the literature. *C. maenas* seems to be a main top predator in the food web of the Mondego estuarine ecosystem.

RESUMO

A ecologia alimentar de *Carcinus maenas* foi estudada entre Junho de 2003 e Junho de 2004 em três locais no estuário do Mondego, Portugal. As amostras foram colhidas mensalmente, durante a noite, na vazante de marés vivas usando um arrasto de vara com 2 m. Entre os 837 estômagos examinados, 25 itens alimentares diferentes foram identificados. *Crangon crangon*, *Hediste diversicolor* e Teleostei foram os itens alimentares mais importantes por ocorrência, número e peso. Sendo um consumidor oportunista, as diferenças na dieta encontradas entre locais e estações do ano reflectem a disponibilidade das presas no meio. Não foram encontradas diferenças na selecção de presas de acordo com o sexo e a largura da carapaça dos indivíduos. A intensidade alimentar dos caranguejos em muda e fêmeas ovigeras foi baixa. A incidência de canibalismo foi mais elevada do que reportado na literatura. *C. maenas* parece ser um predador topo na teia alimentar do ecossistema estuarino do Mondego.

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INTRODUCTION

The green crab, *Carcinus maenas* (Linnaeus, 1758), is a foraging, omnivorous predator, feeding on a wide variety of prey items (Crothers, 1967), in particular molluscs (Ropes, 1968; Elner, 1981), crustaceans (Gaudêncio, 1991), and polychaetes (Le Calvez, 1987). The species is mainly active at night and at high tide, and its diet can markedly change as a result of lower diversity and seasonal changes in the availability of its prey species (e.g., Ropes, 1968).

A few laboratory experiments have demonstrated that the availability of potential food items is not the only factor determining the diet of this crab. The species shows preference not only for the type of prey, but also for a certain size group. This preference is thought to be related to higher prey value or profitability, expressed as the net energy intake per unit of handling time: the Optimal Foraging Theory (Elner & Hughes, 1978; Hughes & Seed, 1981; Kaiser et al., 1993; Mascará & Seed, 2001).

Several studies have confirmed that crab predation is an important factor structuring marine benthic communities (e.g., Raffaelli et al., 1989; Grosholz et al., 2000). Predation by green crabs can influence the abundance and distribution of commercially important bivalve species (e.g., Leber, 1985; Sanchez-Salazar et al., 1987; Raffaelli et al., 1989).

The aim of the present study was to examine the feeding ecology of *C. maenas* in the Mondego estuary, in order to evaluate its importance in the estuarine food web, since this species is locally abundant and of economic interest.

MATERIAL AND METHODS

Study site

The Mondego estuary, a small temperate estuarine system on the western coast of Portugal (fig. 1), consists of two arms, North and South, with very different hydrological characteristics. The North arm is deeper (5 to 10 m during high tide, tidal range about 2 to 3 m), and constitutes the principal navigation channel and the location of the Figueira da Foz harbour. The South arm is shallower (2 to 4 m deep during high tide) and is almost silted up in the upper zones, resulting in the freshwater outflow taking place mainly via the northern arm. Circulation in the southern arm is mostly dependent on the tides and on the freshwater input from the Pranto River, a small tributary of the Mondego. The discharge from this tributary is controlled by a sluice and is regulated according to the water needs of the rice fields in the Mondego Valley (Pardal et al., 2000, 2004; Marques et al., 2003; Cardoso et al., 2004).

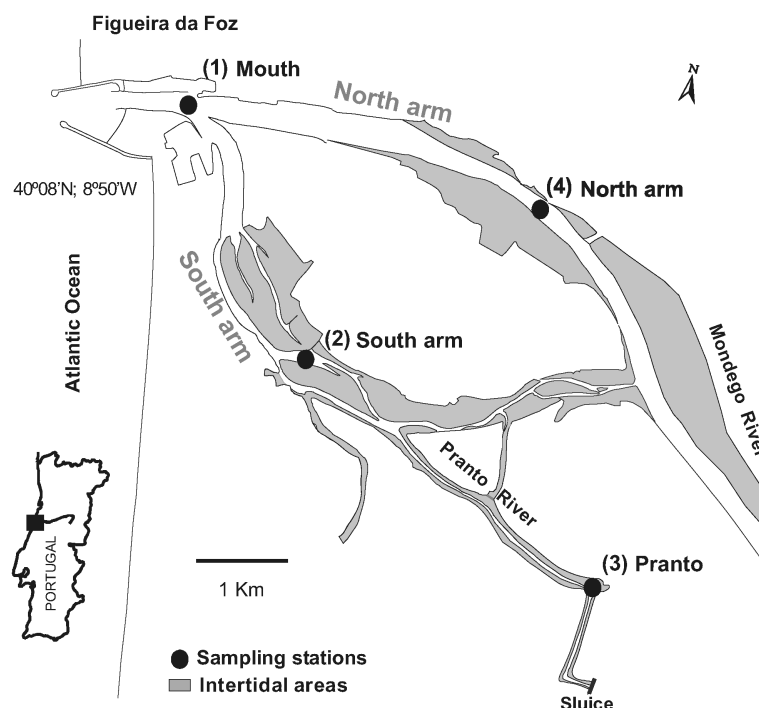


Fig. 1. The Mondego estuary, showing the location of the four sampling stations (Mouth, South arm, Pranto, and North arm).

As in many other estuaries, the south arm of the Mondego has undergone significant eutrophication due to organic enrichment (Pardal et al., 2000, 2004; Marques et al., 2003; Cardoso et al., 2004). The symptoms of such process include, among others, seasonal intertidal macroalgal blooms of *Enteromorpha* spp. (Pardal et al., 2000, 2004; Dolbeth et al., 2003; Marques et al., 2003; Cardoso et al., 2004; Verdelhos et al., 2005). A management programme is currently implemented, aiming at increasing the ecological quality of the system and at promoting the recovery of seagrass beds, which are currently restricted to the downstream areas of the estuary (Verdelhos et al., 2005).

Sampling programme

The population of *Carcinus maenas* was sampled monthly, from June 2003 to June 2004, at four stations (Mouth, South arm, Pranto, and North arm), using a 2 m beam trawl with a tickler chain and 5 mm mesh size in the cod end. All trawls were carried out during the night, at high water of spring tides. Since the population of *C. maenas* was very sparse in the north arm, the small number of individual collected there will not be taken in to account in the present work.

Sediment samples were collected in the summer and autumn of 2003, and in the winter and spring of 2004, using a Van Veen dredge, in order to determine prey availability at the sampling stations.

Laboratory procedures

Crabs were counted, measured (carapace width, CW), and examined for sex, reproductive condition (occurrence of ovigerous females), and moulting stage. Stomachs were removed and the contents preserved in 4% buffered formalin for later identification. Diet characterization was based on these stomach contents. The stomach contents of 837 crabs (442 males and 395 females) were examined. Each prey item was identified to the lowest taxonomic level possible, counted, and weighed (wet weight).

Data analysis

The relative importance of each prey item in the diet was expressed as a percentage of the occurrence of food items in stomachs (I_O), numerical abundance (I_N), and weight (I_W) (Hyslop, 1980).

A canonical correspondence analysis was used in order to evaluate the crabs' feeding patterns, and to relate age classes, sex, season, and sampling area with the food items. Computations were performed using CANOCO (Ter Braak & Smilauer, 1998).

Prey abundance in the sediment was expressed as the number of individuals per m². The numerical frequencies of prey according to the crab's age class, sex, season, and sampling station were compared using chi-square tests (χ^2).

Food selectivity was evaluated by comparing prey availability and diet composition in numerical terms, using Spearman rank correlations (Zar, 1996). Feeding activity was evaluated by the vacuity index (I_V), defined as the percentage of empty stomachs (Hyslop, 1980).

RESULTS

General feeding habitats

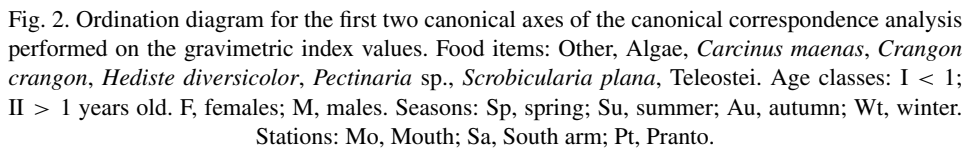
Carcinus maenas chiefly ate Crustacea, mainly *Crangon crangon* (Linnaeus, 1758), Polychaeta, particularly *Hediste diversicolor* (O.F. Müller, 1776) and Teleostei (table I). These food items were the most important by occurrence (I_O), number (I_N), and weight (I_W). *Scrobicularia plana* (Da Costa, 1778), *C. maenas*, and *Pectinaria* sp. were also common prey, but their index values were lower.

In the canonical correspondence analysis performed on the gravimetric index values, the first two axes accounted for 63% of the variance due to group-prey

TABLE I
Occurrence (I_O), numerical (I_N), and gravimetric (I_W) index values of prey found in stomachs of *Carcinus maenas* (L.) in the Mondego estuary

Prey taxon	Indices		
	I_O	I_N	I_W
Crustacea			
Amphipoda n.i.	2.27	2.08	0.31
Cumacea n.i.	1.14	1.79	0.25
Decapoda			
<i>Carcinus maenas</i> (Linnaeus, 1758)	6.96	4.92	9.40
<i>Crangon crangon</i> (Linnaeus, 1758)	21.82	18.93	22.70
<i>Palaemon</i> sp.	1.28	0.92	1.21
Decapoda n.i.	1.69	1.11	1.13
Mysidacea			
<i>Mesopodopsis slabberi</i> (Van Benden, 1861)	0.14	0.10	0.00
Mysidacea n.i.	1.95	3.66	0.98
Crustacea n.i.	3.39	2.42	1.27
Insecta			
Diptera	0.28	0.20	0.00
Insecta n.i.	0.28	0.20	0.00
Mollusca			
Bivalvia n.i.	0.14	0.10	0.05
<i>Cerastoderma edule</i> (Linnaeus, 1758)	1.42	1.32	0.79
<i>Cerastoderma glaucum</i> (Poiret, 1789)	0.43	0.40	0.39
<i>Mytilus galloprovincialis</i> (Lamarck, 1819)	0.14	0.10	0.00
<i>Scrobicularia plana</i> (Da Costa, 1778)	13.21	9.26	8.92
Cephalopoda			
<i>Sepiolo</i> sp.	0.28	0.20	1.06
Gastropoda			
Gastropoda n.i.	0.14	0.10	0.00
<i>Hydrobia ulvae</i> (Pennant, 1777)	0.43	0.40	0.00
Polychaeta			
<i>Hediste diversicolor</i> (O.F. Müller, 1776)	17.90	15.58	14.83
<i>Pectinaria</i> sp.	6.68	4.74	6.17
Polychaeta n.i.	2.69	1.89	2.67
Teleostei			
Gobiidae n.i.	0.71	0.63	1.82
Teleostei n.i.	25.53	19.36	25.51
Algae	10.09	7.14	0.50
No. of samples	704		
No. of prey items		1004	
Total weight of prey (g)			19.01

n.i. = not identified.



Crabs caught at the Mouth are found along the right edge of the diagram, associated with *Pectinaria* sp., mainly in summer and autumn, and with *Scrobicularia plana*, mainly in winter. The individuals from Pranto are found essentially in the upper left part of the diagram associated with Teleostei, mainly in spring and summer. Crabs from South arm are found mostly in the lower left corner of the diagram, associated with *Hediste diversicolor*, particularly in autumn and winter. In summer, the South arm crabs are associated with Teleostei. *Crangon crangon* is a very important prey item at all sampling stations and in all seasons, whilst the categories Algae and Others are the least important food items in the *C. maenas* diet. The incidence of cannibalism is high and occurs essentially at Pranto, mainly

in spring and autumn. No difference according to the crab's sex and age classes appears to occur. Canonical correspondence analyses performed using the values of occurrence and of numerical indices were also made, with similar results as that of the gravimetric index diagram. For this reason, just one of those diagrams is presented. In order to better understand these feeding patterns, the crab's diet was examined separately according to age class, sex, season, and sampling station (see below).

Diet variation with crabs age class and sex

The population size structure had already been studied and age classes (0+, 0++, 1+, 2+, 3+, 4+ years old) had been identified for both sexes (Baeta et al., 2005), assuming that *C. maenas* reaches sexual maturity within the 30 to 40 mm (carapace width) size interval (Broekhuysen, 1936; Klein Breteler, 1976).

No differences were found between juveniles (<1 year old) and adults (>1 year old) ($\chi^2_{0.05(7)} = 4.294$; $p > 0.05$ to I_N) (fig. 3A). However, juveniles showed lower levels of Teleostei in their diet and higher levels of small crustaceans, such as Amphipoda and Cumacea, in comparison to adult crabs. No differences were found between sexes ($\chi^2_{0.05(7)} = 2.166$; $p > 0.05$ to I_N) (fig. 3B).

Diet variation with season and sampling station

Carcinus maenas' diet differed according to season ($\chi^2_{0.05(7)} = 18.415$; $p < 0.05$) and sampling area ($\chi^2_{0.05(14)} = 74.682$; $p < 0.05$) (fig. 4A, B). In spring and summer it showed higher levels of Teleostei and lower of *S. plana*, in terms of occurrence, numbers, and weight. At the Mouth there was a higher consumption of Bivalvia, mainly *S. plana* (high I_O , I_N , and I_W comparative to the other areas), and the prey item *Pectinaria* sp. was only found at this station. At South arm, the prey *H. diversicolor* and Algae were more consumed than in the other sampling areas. At Pranto, the most important food item were Teleostei (high I_O , I_N , and I_W).

Food selectivity and feeding activity

The Spearman rank correlation showed that diet did not reflect prey availability at any of the three sampling stations (0.15, 0.52, and 0.44 for Mouth, South arm, and Pranto, respectively; $p > 0.05$) (table II). Vacuity was low at all times (mean values of 13, 15, and 19% for the Mouth, South arm and Pranto, respectively). Vacuity levels were higher in moulting crabs and ovigerous females (45% and 43%, respectively).

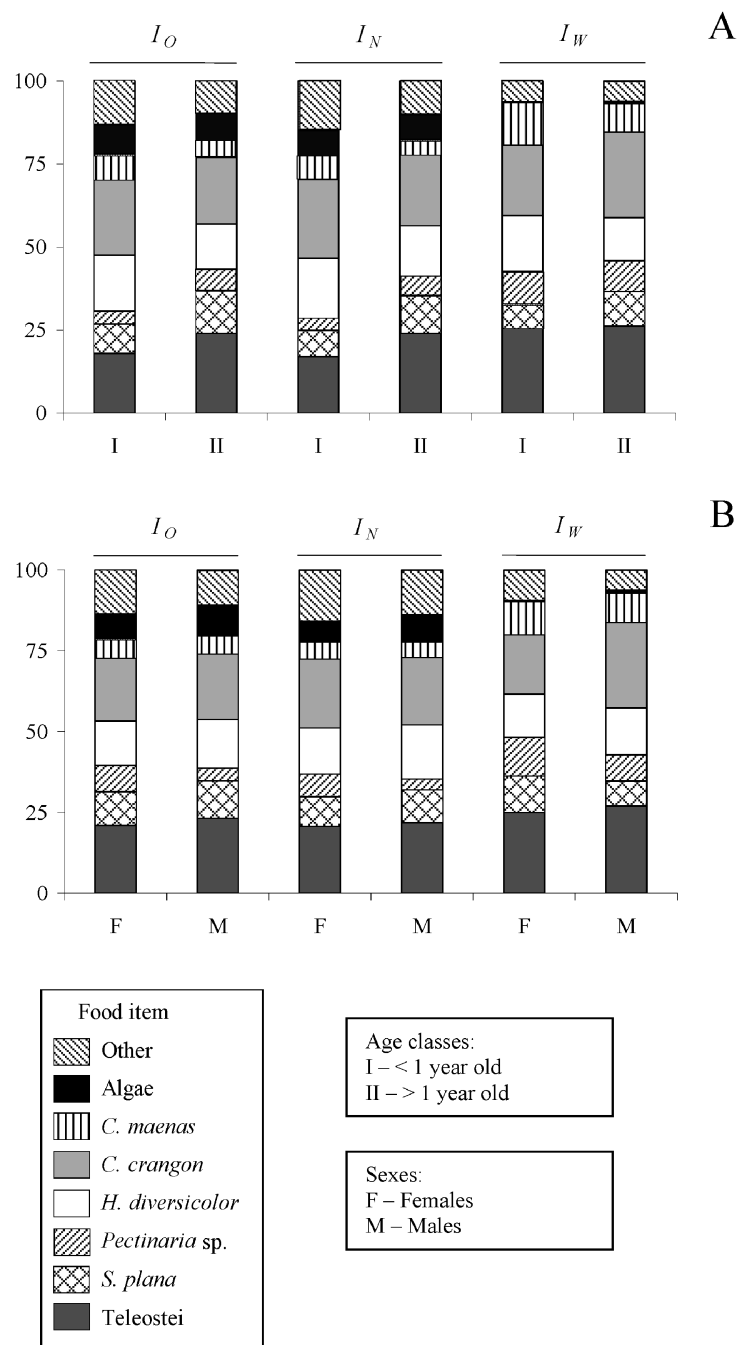


Fig. 3. Relative importance of food items in the diet of *Carcinus maenas* (L., 1758), according to: A, carapace width; B, sex; based on: I_O , occurrence index; I_N , numerical index; I_W , gravimetric index.

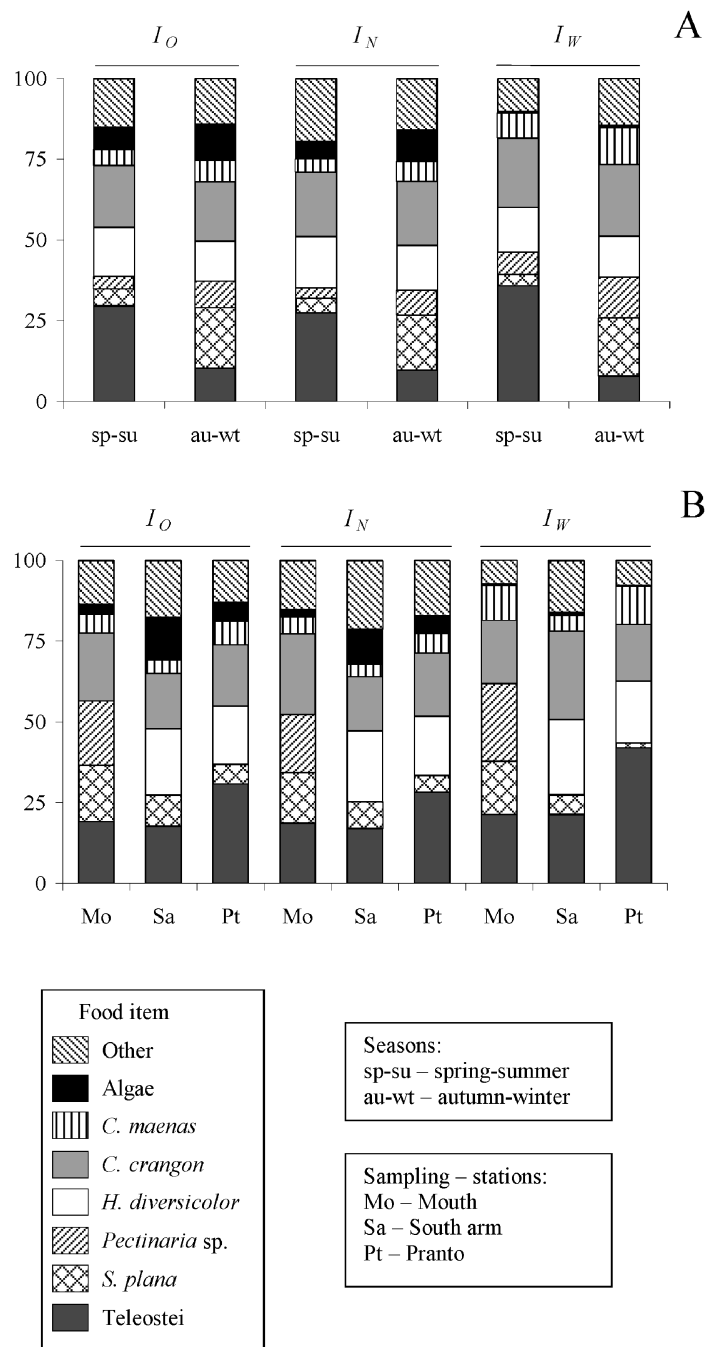


Fig. 4. Relative importance of food items in the diet of *Carcinus maenas* (L., 1758), according to: A, seasons; B, sampling stations; based on: I_O , occurrence index; I_N , numerical index; I_W , gravimetric index.

TABLE II

Ranks of abundance of benthic prey of *Carcinus maenas* (L.) at the sampling stations in the Mondego estuary (ranks are in decreasing order of importance)

	Mouth	South arm	Pranto
Amphipoda	1	7	8
<i>Carcinus maenas</i> (Linnaeus, 1758)	8	6	5
<i>Crangon crangon</i> (Linnaeus, 1758)	6	5	4
<i>Hediste diversicolor</i> (O.F. Müller, 1776)	7	3	2
Mollusca	3	4	6
Mysidacea	5	8	7
Polychaeta	4	2	3
<i>Scrobicularia plana</i> (Da Costa, 1778)	2	1	1

DISCUSSION

Previous studies on *Carcinus maenas* have reported that the most important prey items are Bivalvia (Ropes, 1969; Elner, 1981; Raffaelli et al., 1989; Le Roux et al., 1990), Crustacea (Albertini-Berhaut, 1973; Gaudêncio et al., 1991), and Polychaeta (Le Calvez, 1987). Our study revealed that *C. maenas* from the Mondego estuary has a less diversified diet, probably due to a different composition of the benthic fauna, but also here Crustacea, Polychaeta, and Teleostei are the most important food items in occurrence, numbers, and weight alike.

This species is thought to be a voracious, opportunistic predator. In the present study, this species showed preferences for a few slow-moving benthic invertebrates, probably due to their energetic value or their abundance in the intertidal areas (Cardoso et al., 2004; Pardal et al., 2004; Verdelhos et al., 2005). For instance, the average energy density (kJ.g^{-1} AFDW) of *Crangon crangon* and *Hediste diversicolor* is higher than that of *Scrobicularia plana* or *C. maenas* (22, 22.5, 21.8, and 21.5 kJ.g^{-1} AFDW, respectively) (Zwarts & Wanink, 1993). Moreover, these prey items, especially juvenile crustaceans, are more abundant in the intertidal areas and thus available for predation, since the green crab is thought to undertake intertidal migrations mainly at high tide (e.g., Hunter & Naylor, 1993; Warman et al., 1993).

Gaudêncio et al. (1991) reported that fish are a common food item in this species' diet, yet their results did not show a higher occurrence of that prey, as presented in this study. Although it is not easy, nor always possible, to identify the species of fish from the jaws and vertebrae they may well have been benthic species such as gobies (*Pomatoschistus* spp.). These are known to co-exist with *C. maenas* in their nursery areas, and are more abundant in spring and summer at the Pranto site (Leitão et al., 2006). Thus, the higher occurrence of fish in the diet of *C. maenas* during spring and summer coincides with their abundance.

Several authors consider that portunid crabs feed selectively on algae (Ropes, 1969; Le Calvez, 1987; Le Roux et al., 1990). In this study, the amount of algae found in the stomachs suggests that algae were ingested accidentally along with other food items. Nevertheless, the incidence of cannibalism was higher than what is found in literature (e.g., Ropes, 1969; Gaudêncio, 1991). This is believed to occur because this species is very abundant in this small estuary (Baeta et al., 2005), and hence frequently encounters its conspecifics when searching for prey.

No differences were found between the two age classes and sexes, probably due to the fact that they do-occur in the same areas. Of course, larger crabs ate larger prey, in order to maximize net energy intake when feeding. Phill (1985) reported that juveniles (crabs < 30 mm) are mainly detritivorous, results that are quite different from what is presented in this study, probably due to crab's opportunistic behaviour.

Seasonal and spatial variations in the diet reflected seasonal and spatial variations in the availability of food types in each particular season and habitat, and thus the crab's opportunistic foraging behaviour.

A higher proportion of empty stomachs was found in moulting crabs and in ovigerous females. These crabs are generally less active and feed less in order to avoid predation, as they are highly attractive to predators at that time (Reid et al., 1997). The Pranto was the sampling station with a higher I_V value, since the proportion of moulting crabs increased from downstream to upstream areas.

The results of this study strongly suggest that despite the diversity in its diet in the Mondego estuary, *Carcinus maenas* preferentially consumed several extremely abundant prey species such as *Scrobicularia plana* and Amphipoda, i.e., showing a preference for those types of prey that live in the surface of the sediment and are more easy subjects to predation. In conclusion, *C. maenas* seems to assume an important position in the food web of the Mondego estuary, not only because it is able to feed on a variety of surface or subsurface organisms that have themselves different feeding strategies, but also on organisms that live above the surface, such as fishes and decapods. In this estuary, *C. maenas* was not found to be an important prey for species of fish or birds (Múrias et al., 1996; Lopes et al., 2000). It can hence be considered a main top-predator in the food web of the Mondego estuarine ecosystem, playing an important role through influencing the structure of the marine benthic community in this area.

ACKNOWLEDGEMENTS

The present study was carried out within the framework of the research project "Dynamic model of stress induced changes on benthic communities" (POCTI/MGS/37431/2001) funded by the Portuguese FCT. A special thanks to all colleagues that helped during field work.

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First received 29 March 2006.

Final version accepted 2 May 2006.