TROPHIC GROUP PATTERNS OF MACROBENTHOS IN BRACKISH COASTAL SYSTEMS

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With 11 figures and 2 tables

ABSTRACT. The trophic group structure of subtidal soft bottom macrofaunal communities of three estuarine/lagoonal systems (SW Portugal) suggests, in spite of the hydrological and sedimentological differences, some general trends. Two of these water bodies - Odeceixe and Aljezur - have estuarine characteristics but the third - Carrapateira - is usually closed to the sea. While in the first two the fauna is predominantly estuarine, lagoonal species are dominant in the latter. Each *taxon* was assigned to, at least, one of the following trophic groups: suspension-feeders, deposit-feeders, carnivores and herbivores. In Odeceixe and Aljezur the spatial site distribution of the trophic groups showed a gradient in their relative importance. Carnivores reached their maximal proportion in well calibrated sands occurring at river mouths, whilst, suspension-feeders were mainly related to upstream more stable sandy sediments. The deposit-feeders, the dominant group, reached their maximal proportion in sediments with higher levels of organic matter. No clear pattern was observed concerning the herbivores. The faunal composition of Carrapateira was more homogeneous, and the sediment more uniform, thus similar results were only apparent after the opening to the sea caused by strong rainfall. The dynamics associated with tidal currents and fluvial discharge seemed to play a major role in the control of the structural pattern of the trophic groups. This can be supported by the response of the Carrapateira macrobenthic communities which quickly changed to the predictable pattern described for the other systems after the inlet opening.

KEY WORDS: Macrobenthos, trophic functional groups, estuaries, SW Portugal.

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RESUMO. A estrutura dos grupos tróficos das comunidades subtidais da macrofauna bentónica de três sistemas estuarino-lagunares (SO de Portugal), sugere a existência de tendências gerais, apesar das diferenças sedimentológicas e hidrológicas. Dois destes sistemas – Odeceixe e Aljezur – apresentaram características estuarinas, mas o terceiro – Carrapateira – esteve normalmente encerrado e sem contacto com o mar. Enquanto nos dois primeiros a fauna foi predominantemente estuarina, as espécies lagunares foram dominantes no último. Cada *taxon* foi associado a pelo menos uma das funções tróficas seguintes: suspensívoros, detritívoros, carnívoros e herbívoros. Em Odeceixe e Aljezur a distribuição espacial dos grupos tróficos evidenciou a existência de um gradiente de acordo com a respectiva importância relativa. A função 'carnívoros' atingiu a proporção máxima nas areias bem calibradas das embocaduras, enquanto que a 'suspensívoros' foi predominantemente associada às areias mais estáveis situadas um pouco a montante. A função 'depositívoros' que constituiu o grupo dominante, registou a proporção máxima nos sedimentos com maior teor de matéria orgânica. Ao grupo 'herbívoros', não pode ser associado nenhum padrão de distribuição definido. A composição faunística da Carrapateira foi mais homogénea, tal como o sedimento, pelo que resultados similares aos dos sistemas anteriores só foram referenciados após o estabelecimento da comunicação com o mar na sequência de fortes precipitações. A dinâmica associada às correntes de maré e à escorrência fluvial pareceu ser o principal controlador do padrão estrutural dos grupos tróficos, tanto mais que as comunidades do macrobentos da Carrapateira responderam rapidamente após o estabelecimento da comunicação com o mar e à dinâmica que se lhe seguiu, ajustando-se ao padrão previsível e já descrito para os outros sistemas.

PALAVRAS-CHAVE: Macrobentos, grupos tróficos funcionais, estuários, SO de Portugal.

INTRODUCTION

In spite of the controversial about Lindeman's concept (LINDEMAN, 1942) of discrete trophic levels (COUSINS, 1985), it is generally agreed that ecosystems are occupied by a major group of "multitrophic level" species (COMMITO & AMBROSE Jr., 1985) that interconnect with each other building a complex trophic network, and structuring the ecological communities. Different authors explained the varying importance of distinct trophic groups along different estuarine or lagoonal gradients, stressing the importance of the physical environment (i.e. turbulence and its effect on the sedimentary environment (PEARSON, 1971), biological interactions or both (RHOADS & YOUNG, 1970; PEARSON & ROSENBERG, 1987).

The relative importance of any trophic group along a given gradient is a function of a complex set of physico-chemical and biological factors, whose understanding is far beyond the state of our present knowledge. Despite this, the analysis of the changing importance of a trophic group along a gradient may provide an interpretable guide to the changing ecological structure and its relationship with the variation of some environmental factors (PEARSON, 1971; PEARSON & ROSENBERG, 1978; CHARDY & CLAVIER, 1988; GAMBI *et al*., 1992).

The purpose of this study was to analyse the trophic-group structure of three estuarine/lagoonal systems, Odeceixe, Aljezur and Carrapateira, at the end of little rivers, which drain to the West coast of Algarve. We attempted to reveal and discuss the patterns observed, based on the spatial distribution and relative importance of these functional groups.

The most widely accepted classification of the marine and estuarine benthic species, according to their feeding behaviours, recognises four major trophic groups: suspension-feeders, deposit-feeders, carnivores and herbivores (PEARSON & ROSENBERG, 1978, 1987; CHARDY & CLAVIER, 1988). We used this classification for the present study due to its relative simplicity and precision in contrast with more detailed ones (*e. g.* GAMBI *et al*., 1992).

MATERIAL AND METHODS

Study area

The Portuguese SW coast remains one of the least disturbed coastlines of southern Europe. The high species richness is related to its estuaries that play a major role in the life cycle of several species (SILVA e COSTA *et al*., 1983). Odeceixe, Aljezur and Carrapateira estuarine systems are at the end of small torrential rivers draining part of the SW of Portugal with catchment areas of 250 Km^2, 200 Km^2 and 111 Km^2, respectively. The average rainfall is higher from October to March (PULLAN, 1988) and the driest months are July and August. Their discharge to the sea is frequently prevented by the development of sand barriers, reason why they can be considered estuarine/lagoonal systems.

A two year study concerning water, sediment and macrobenthos was undertaken in 1984-85. During this period, Odeceixe and Aljezur were permanently opened to the sea, whilst Carrapateira was usually closed, except in winter after heavy rainfall (MAGALHÃES *et al*., 1987).

Sampling design

Several sampling stations were chosen in the terminal sections of the three estuarine/lagoonal systems, (Fig. 1). From March 1984 to December 1985 quarterly lowtide sediment samples were collected at each station. In addition, surface and bottom

data on salinity, dissolved oxygen, temperature and pH were obtained by *in situ* with sensors. Subtidal sediment samples were collected with a hand corer for grain-size, total organic matter and sediment phytopigment analysis. Samples (0.1 m^2 of total area) were collected and sieved through a 1 mm square mesh sieve (JOSEFSON, 1986) for the study of the macrobenthos. Details on the physical characterisation and macrobenthic communities of the three systems described can be found on earlier studies (MAGALHÃES *et al.*, 1987; DUARTE, 1988; MAGALHÃES, 1988; CANCELA DA FONSECA & MAGALHÃES, 1989; MAGALHÃES & CANCELA DA FONSECA, 1989; COSTA *et al.*, 1988; COSTA *et al.*, 1989; COSTA *et al.*, 1990).

Trophic groups

The identified *taxa* were assigned to at least one of the following trophic groups: suspension-feeders, deposit-feeders, carnivores and herbivores. The assignment of a *taxon* to a group was done by first dividing the number of individuals of that *taxon* by the number of functional groups in which it could be included. The obtained results were then added to the totals of each group. Data were converted to percentages as a measure of the relative importance of each group. These calculations were done for each sampling point and sampling season. The use of carnivores, herbivores, suspension- and deposit-feeders throughout this paper refers not to an organism as individual, but to its simple or multitrophic function within the system described *i. e.*, a "functional individual" (DUARTE *et al.*, 1990).

The assignment of each taxon to the appropriate trophic group was based on: HUNT (1925), MUUS (1967), MASSÉ (1972), NAYLOR (1972), FENCHEL *et al.* (1975), KOFOED (1975 a, b), FAUCHALD & JUMARS (1979), TACHET *et al.* (1980), LEVINTON & BIANCHI (1981), MARCHAND (1981), BRINKHURST (1982), JOSEFSON (1986), CERETTI & POLUZZI (1988), R. ROSENBERG (pers. com.) and J. C. MARQUES (pers. com.).

Statistics

For the purposes of this work two data sets were used for each ecosystem: The abundance and the numerical percentage of the trophic groups at each sampling station and sampling time. The abundance values were analysed by Pearson correlation coefficients between all pairs of trophic groups and by Principal Components Analysis (PCA), with values for all sites and sampling campaigns. The PCA analysis was carried out on log transformed data. In this case, the largest principal component obtained is an overall abundance component, related to the original variables by coefficients of the same sign, whereas the other components represent proportional variation in abundance if they have coefficients of opposite sign (GREEN, 1979). This allows analysing not only total abundance, but also relative abundance patterns. The direct usage of percentage data in PCA is not recommended due to the poor statistical behaviour of percentage data.

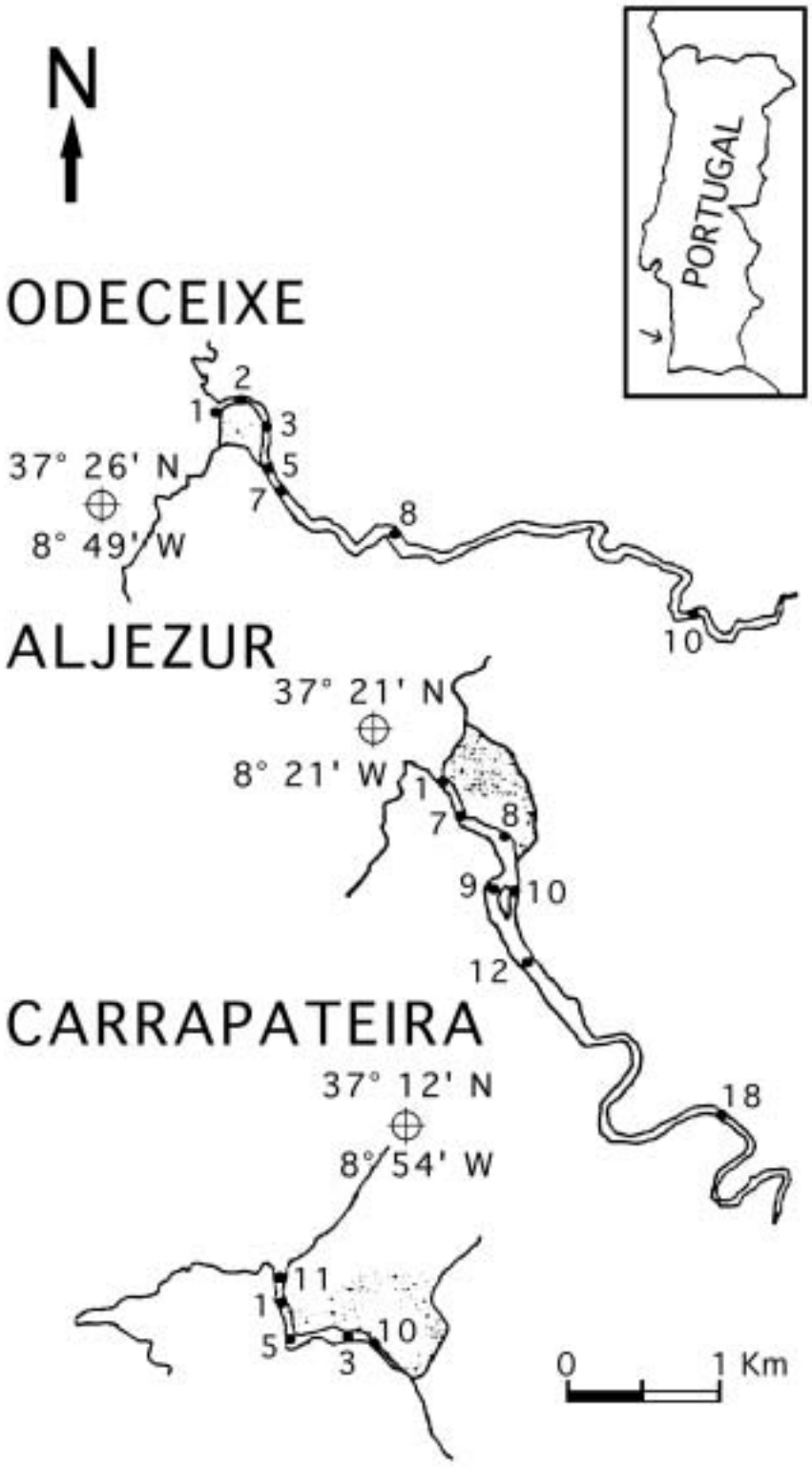

Fig. 1 - Location of the three study sites and sampling points (SW Portugal).

RESULTS

Environmental draft

According to previous studies (MAGALHÃES *et al*., 1987), no critical values of dissolved oxygen were recorded. Salinity ranged between 0 and 37‰. Odeceixe had a maximum of 37‰ (St.1, September 1985) and a minimum of 0‰ (St.10, December 1984, June 1985 and St.1, 2, 3, 7, 8 and 10 at March 1985, after heavy rainfall). In Aljezur, salinity values of a similar range (37‰ at St.1 - December 1985 and 0‰ at St.18 - June 1985) were also observed. In Carrapateira, a maximum of 20.5‰ (St.1 - December 1985) and a minimum of 0‰ (St. 3 and 10 - March and June 1985) were observed. In general, the salinity variations were very strong, especially at Odeceixe and Aljezur and did not follow a predictable pattern.

The study of grain size distribution showed four sedimentary areas: i) sands in all the sampling points of Carrapateira, and near the mouth of Odeceixe and Aljezur rivers, followed by ii) sandy-muds and iii) muds at Aljezur (St. 18) or iv) sandy-gravely muds at Odeceixe (St. 10). The organic matter content of the sediments was higher in the upstream muddy stations of Odeceixe and Aljezur, and minimal in the sandy ones. All the Carrapateira stations were poor in organic matter, with values comparable to those obtained from the sandy sediments of the other two systems (MAGALHÃES *et al*., 1987).

The highest average values of Chlorophyll *a* found in the upper layer of the silty-sandy sediments emphasise the importance of those intermediate sedimentary situations for the production of the microphytobenthos. In contrast, the lowest values were always found in clean sands near the river inlets. The highest recorded water mass values of Chlorophyll *a* where also coincident with the brackish situations, corresponding to intermediate values of salinity (COSTA *et al*., 1988).

Macrobenthic fauna

The number of macrozoobenthos species that have been identified in each of the three systems studied were 78, 107 and 141, in Odeceixe, Aljezur and Carrapateira, respectively (Table 1). At Odeceixe and Aljezur, the benthic fauna was mainly estuarine, while Carrapateira presented a faunal composition predominantly lagoonal. The most abundant *taxa* in Odeceixe and Aljezur were polychaete and oligochaete worms (*Scoloplos armiger, Streblospio shrubsolii, Capitella capitata, Hediste diversicolor, Alkmaria rominji, Tubifex* sp. - both systems - and *Stylaria lacustris* in Odeceixe), gastropod snails (*Hydrobia ulvae* at both systems, and *Potamopyrgus jenkinsi* in Aljezur), bivalve molluscs (*Cardium edule* and *Scrobicularia plana* - both systems - and *Cardium glaucum* - Aljezur), crustacean isopods and amphipods (*Cyathura carinata, Eurydice pulchra, Sphaeroma hookeri, Haustorius arenarius, Pontocrates arenarius, Gammarus* sp., *Corophium orientale*) and insects: Tanipodinae indet. in

Odeceixe, and Chironomidae indet. in Odeceixe and Aljezur (DUARTE, 1988; COSTA *et al*., 1990).

Odeceixe and Aljezur systems showed a shift from dominance by *taxa* of marine origin like *Eurydice pulchra*, at the mouth of the rivers, to typically estuarine ones as *H. diversicolor, S. shrubsolii, H. ulvae, C. edule, S. plana, C. carinata*. Finally, at the upstream stations, the influence of land drainage was reflected by the presence of insects, both larvae and adults (COSTA *et al*., 1990).

This marine estuarine shift, could also be seen at Carrapateira, but with a greater mixing of *taxa* of marine or riverine affinities. Colonisation by, and/or recruitment of marine *taxa* was observed after the lagoon opening in March 1985 and several times during spring tides when the sea water entered into the lagoon. The polychaetes were only represented by *H. diversicolor*, and one of the most abundant oligochaetes was *Nais communis*. The gastropods *P. jenkinsi* and *Physa* spp., the isopods (*E. pulchra, S. hookeri*), amphipods (*Gammarus chevreuxi, C. orientale*) and the larvae of chironomids were some of the most abundant *taxa*. Oligochaetes and Insects were the major groups as deduced from the respective number of *taxa* present in the lagoon (MAGALHÃES, 1988; CANCELA DA FONSECA & MAGALHÃES, 1989; MAGALHÃES & CANCELA DA FONSECA, 1989). Globally, the riverine macrozoobenthic *taxa* were more abundant in Carrapateira than in Odeceixe or Aljezur.

Trophic groups

All significant correlations between the numerical abundance of the trophic groups (Table 2) were positive. In Odeceixe and Aljezur all correlations were positive although in the latter there was only one significant value – between the herbivores and the deposit-feeders.

The results on the abundance of the trophic groups along the estuarine/lagoonal gradients, expressed by its distance from the inlets, are shown in Figs. 2, 3 and 4. It can be seen that the abundance of the groups exhibited peaks at different locations along the mentioned gradient. In Odeceixe, Aljezur and Carrapateira the most abundant group are the deposit-feeders. In Carrapateira the less abundant group are the suspension-feeders, whereas in the other two systems the suspension-feeders are comparable in abundance with the herbivores and the carnivores.

The PCA scores obtained for the abundance of the trophic groups are shown in Figs. 5, 6 and 7. All the coefficients of the first component (Factor 1) are positive for the three systems. This is an abundance component and it suggests a positive relation between the abundance of the trophic groups. This is roughly in accordance with the predominantly positive correlation coefficients referred before. The second and the third components (Factors 2 and 3) have both positive and negative coefficients. In all three systems the carnivores and the herbivores have coefficients of the same sign in opposition to the suspension and the deposit-feeders, in relation to Factor 2. Regarding

the third component the opposing groups are the suspension and the deposit-feeders, on one side and the herbivores and the carnivores, on the other side. The obtained results suggests that there were opposing patterns on the relative abundance of the different trophic groups but not on their total abundance.

TABLE 1 - Number of species of macrozoobenthos per major taxa collected from the three estuaries during the sampling period (1984/86).

	Odeceixe	Aljezur	Carrapateira
Hydrozoa	1	1	–
Turbelaria	–	2	4
Nemertina	3	2	–
Nematoda	–	1	10
Polychaeta	10	30	1
Oligochaeta	4	2	38
Hirudinea	–	–	1
Sipunculida	–	2	–
Polyplacophora	1	–	–
Gastropoda	2	9	15
Bivalvia	6	13	6
Acari	1	–	1
Ostracoda	1	–	2
Cirripedia	–	1	–
Tanaidacea	1	–	–
Isopoda	5	9	5
Amphipoda	9	20	3
Decapoda	4	10	2
Ephemeroptera	5	–	3
Plecoptera	1	–	1
Odonata	3	–	11
Heteroptera	–	–	4
Homoptera	–	–	1
Coleoptera	11	–	16
Trichoptera	–	–	1
Diptera	9	1	10
Bryozoa	1	1	6
Echinodermata	–	3	–
Total	**78**	**107**	**141**

TABLE 2 - Symmetric correlation matrixes between the abundance of the trophic groups (Marked (bold) correlations are significant at $p < 0.05$).

Odeceixe (n = 54)	Herbivores	Carnivores	Suspension-feeders
Carnivores	**0.60**		
Suspension-feeders	0.20	**0.44**	
Deposit-feeders	**0.43**	**0.48**	**0.71**

Aljezur (n = 53)	Herbivores	Carnivores	Suspension-feeders
Carnivores	0.02		
Suspension-feeders	-0.06	0.22	
Deposit-feeders	**0.62**	0.09	0.26

Carrapateira (n = 37)	Herbivores	Carnivores	Suspension-feeders
Carnivores	0.20		
Suspension-feeders	-0.02	-0.08	
Deposit-feeders	**0.90**	**0.34**	-0.03

The results on the numerical percentage of the trophic groups along the estuarine/lagoonal gradients, expressed by its distance from the inlets, are shown in Figs. 8, 9 and 10. It can be seen that the numerical importance of the groups exhibited peaks at different locations along that gradient. At river mouth the carnivores had their maximal percentage values. Upstream, the suspension-feeders reached their maximal values in relation to more stable sandy sediments. The deposit-feeders, the dominant group, had maximal values in muddy sediments with higher organic matter contents.

This pattern was clearly observed at Odeceixe and Aljezur in 5 out of 8 sampling campaigns, and partially in the other 3 (Figs. 8 and 9). The results obtained for Carrapateira were similar only after the opening of the inlet channel by strong rainfall (March 1985 - Fig. 10). In this case, however, the observed gradient of numerical importance was not related to different types of sediments, since all stations were located on well calibrated sands, poor in organic matter. The maximum value for the numerical importance of the carnivores appeared at the mouth of the river (St.11, Fig. 1).

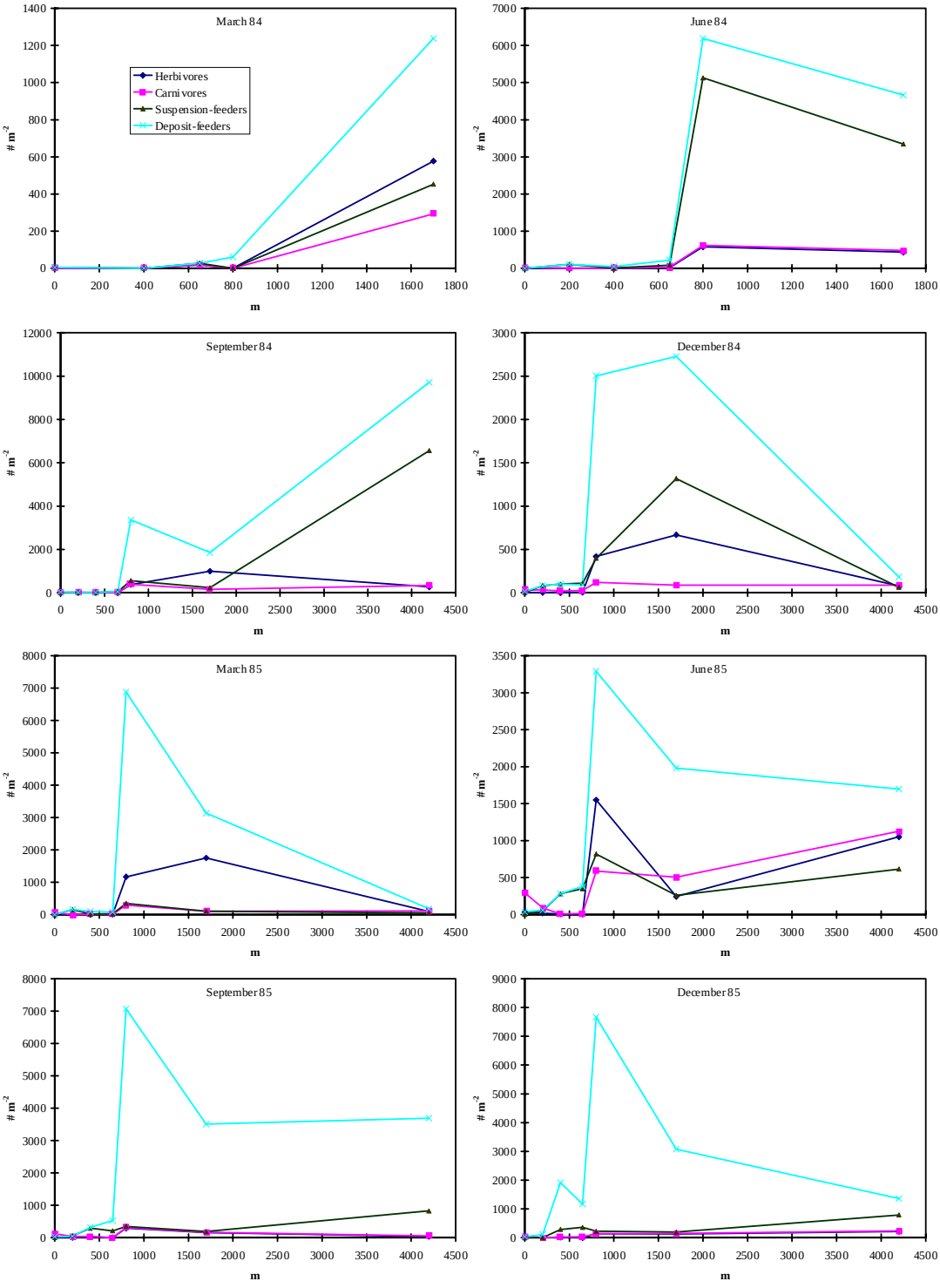

Fig. 2 - Abundances (individuals per m^2) of the herbivores, carnivores, suspension and deposit-feeders as a function of distance from the sea in Odeceixe.

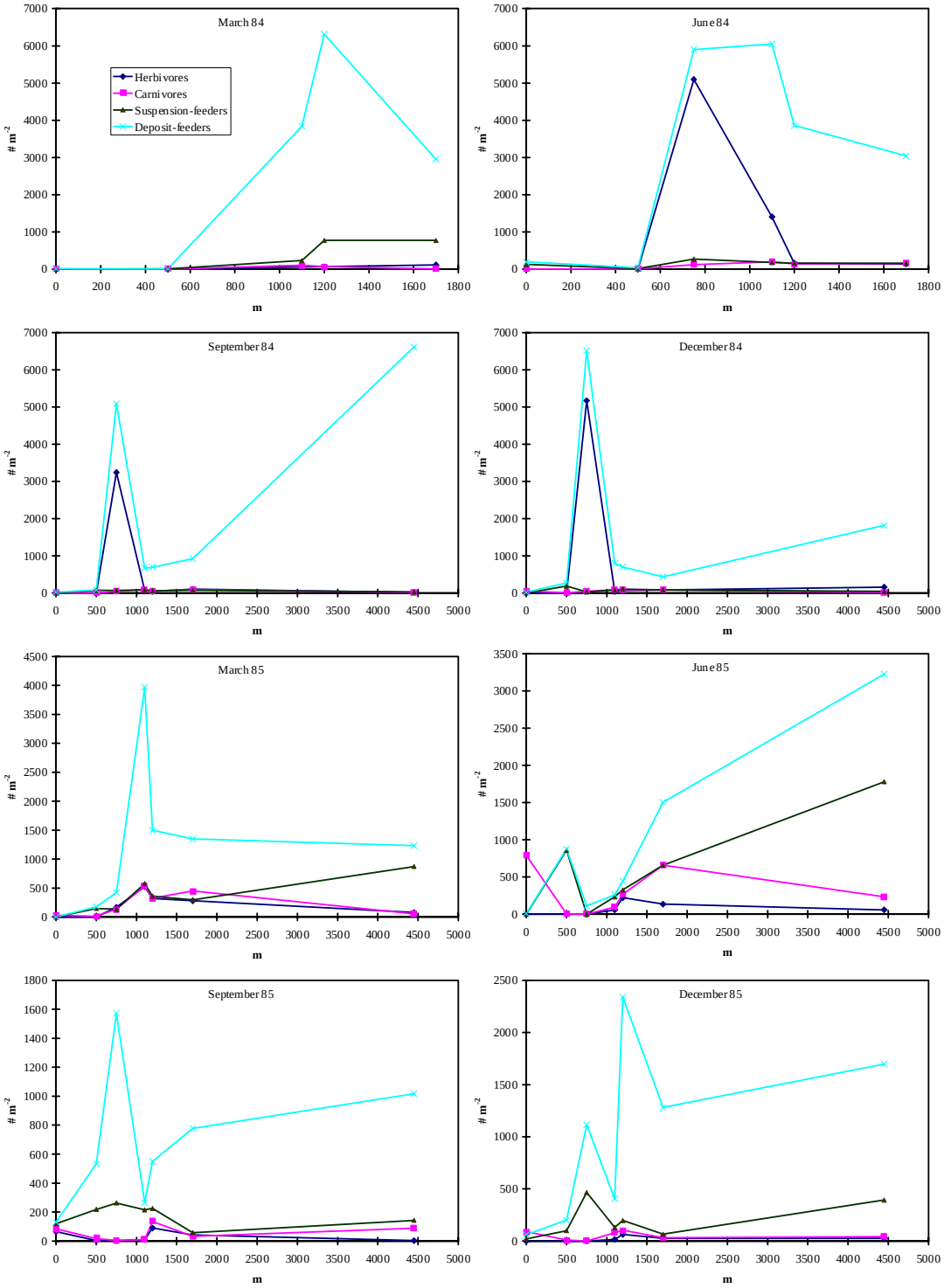

Fig. 3 - Abundances (individuals per m^2) of the herbivores, carnivores, suspension and deposit-feeders as a function of distance from the sea in Aljezur.

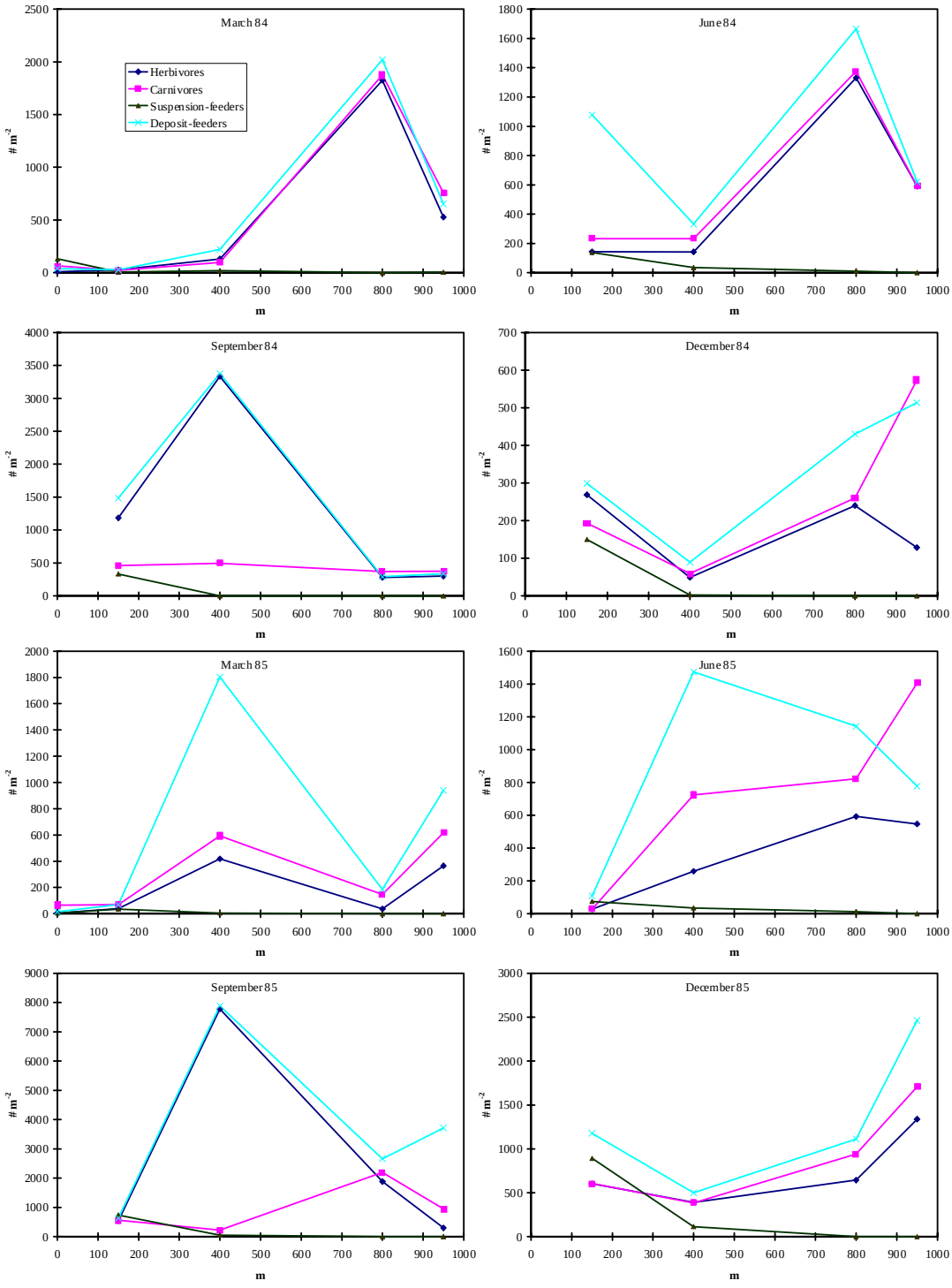

Fig. 4 - Abundances (individuals per m^2) of the herbivores, carnivores, suspension and deposit-feeders as a function of distance from the sea in Carrapateira.

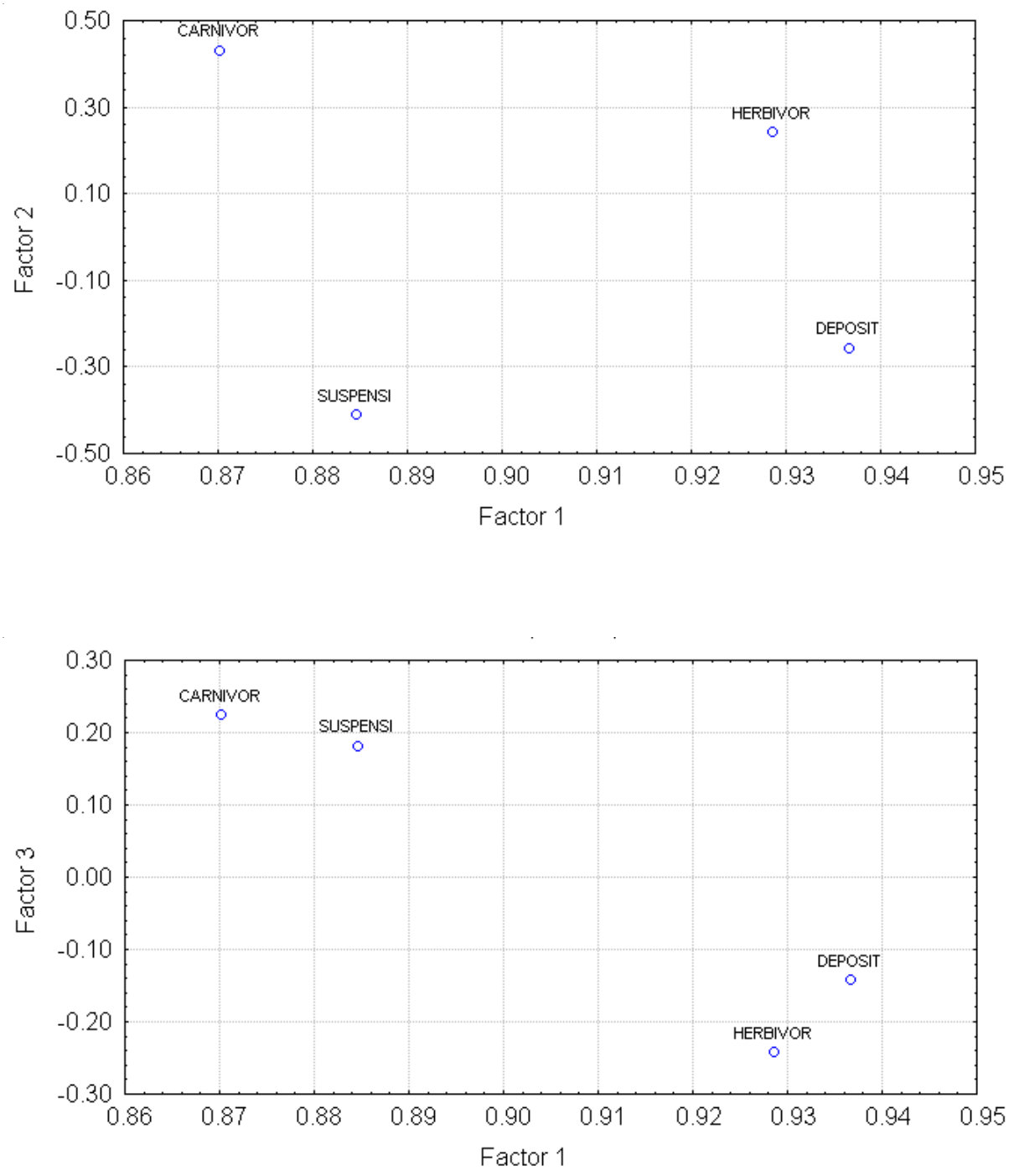

Fig. 5 - PCA results (first, second and third axis loadings) for Odeceixe trophic group abundances.

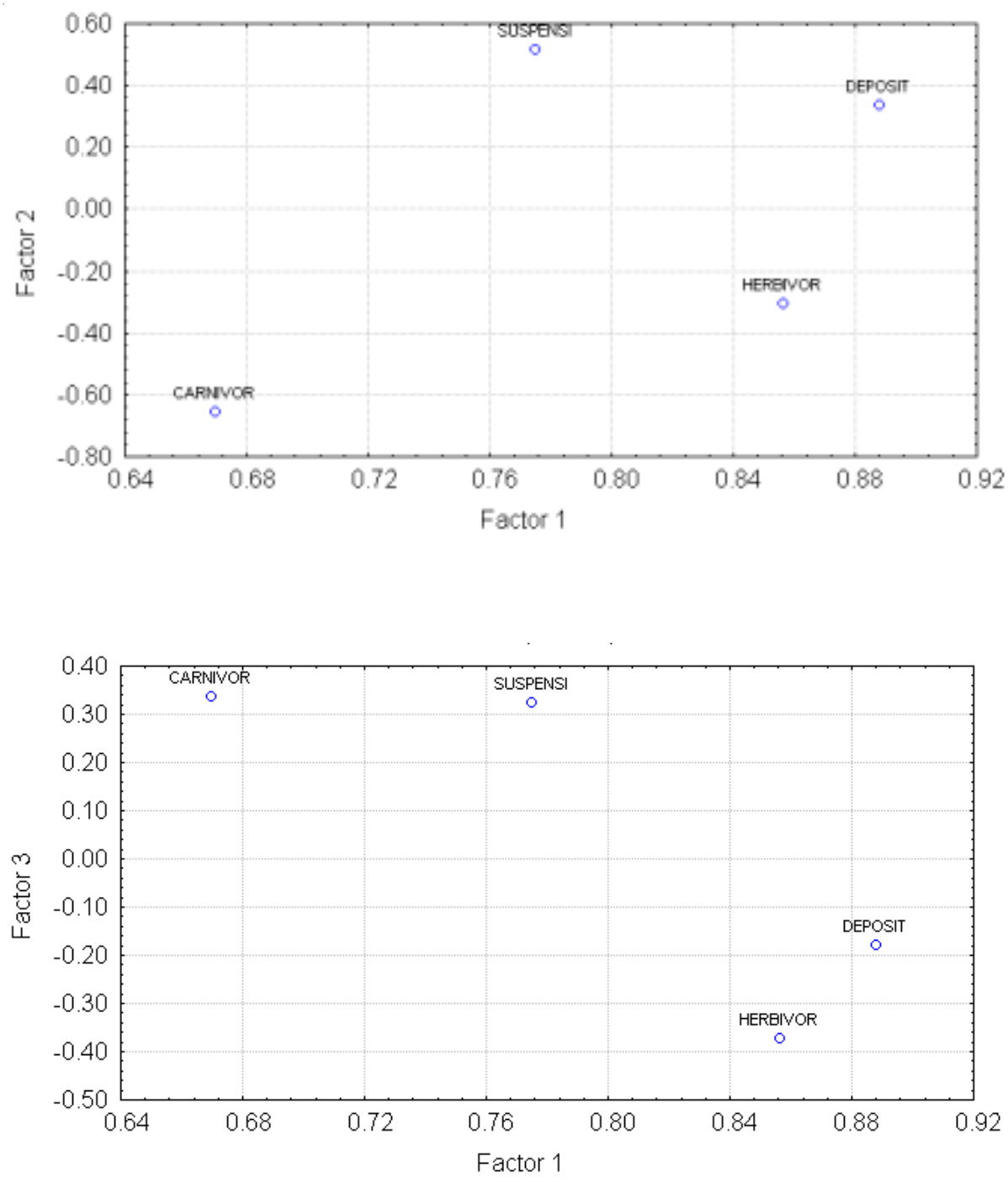

Fig. 6 - PCA results (first, second and third axis loadings) for Aljezur trophic group abundances.

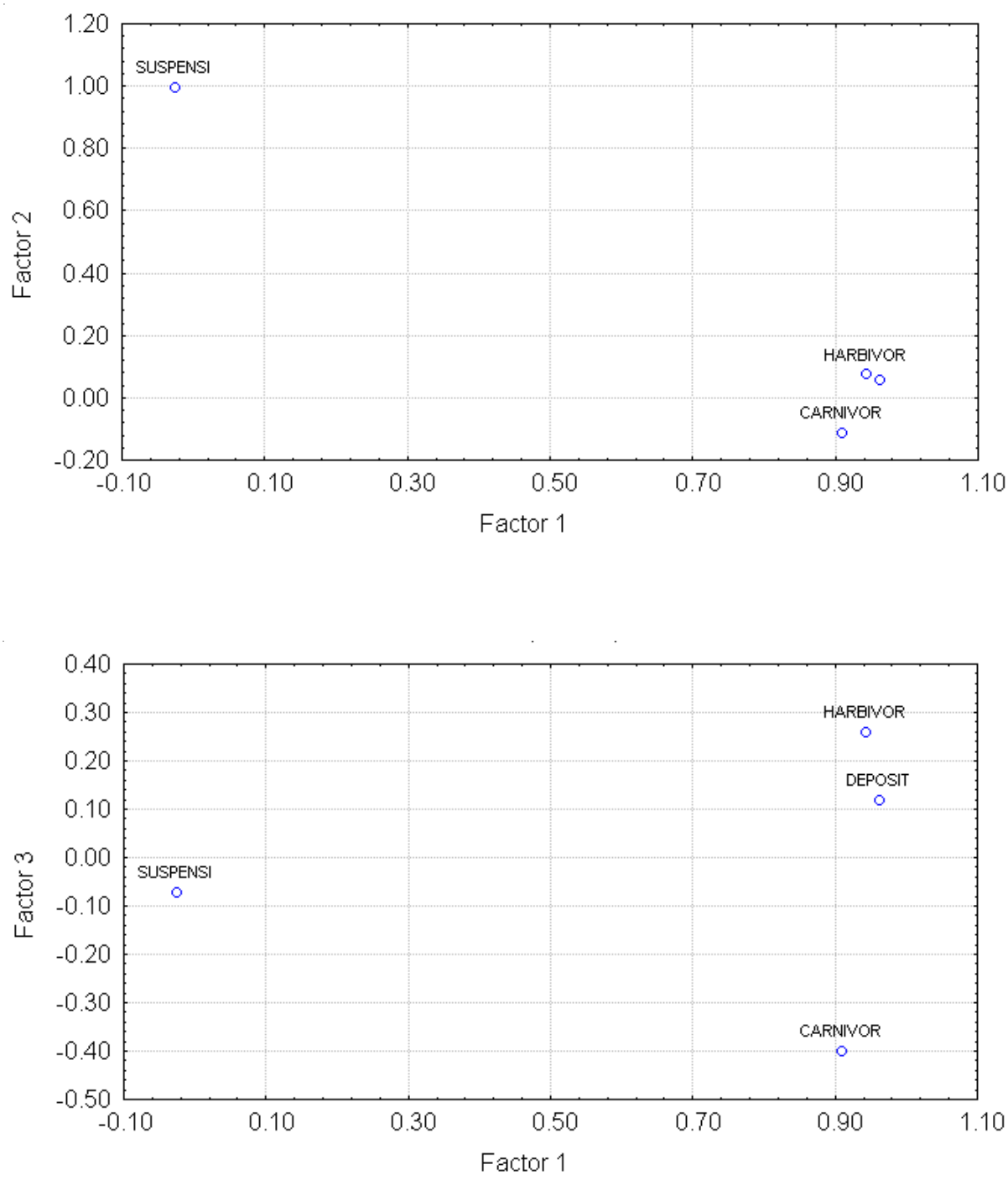

Fig. 7 - PCA results (first, second and third axis loadings) for Carrapateira trophic group abundances.

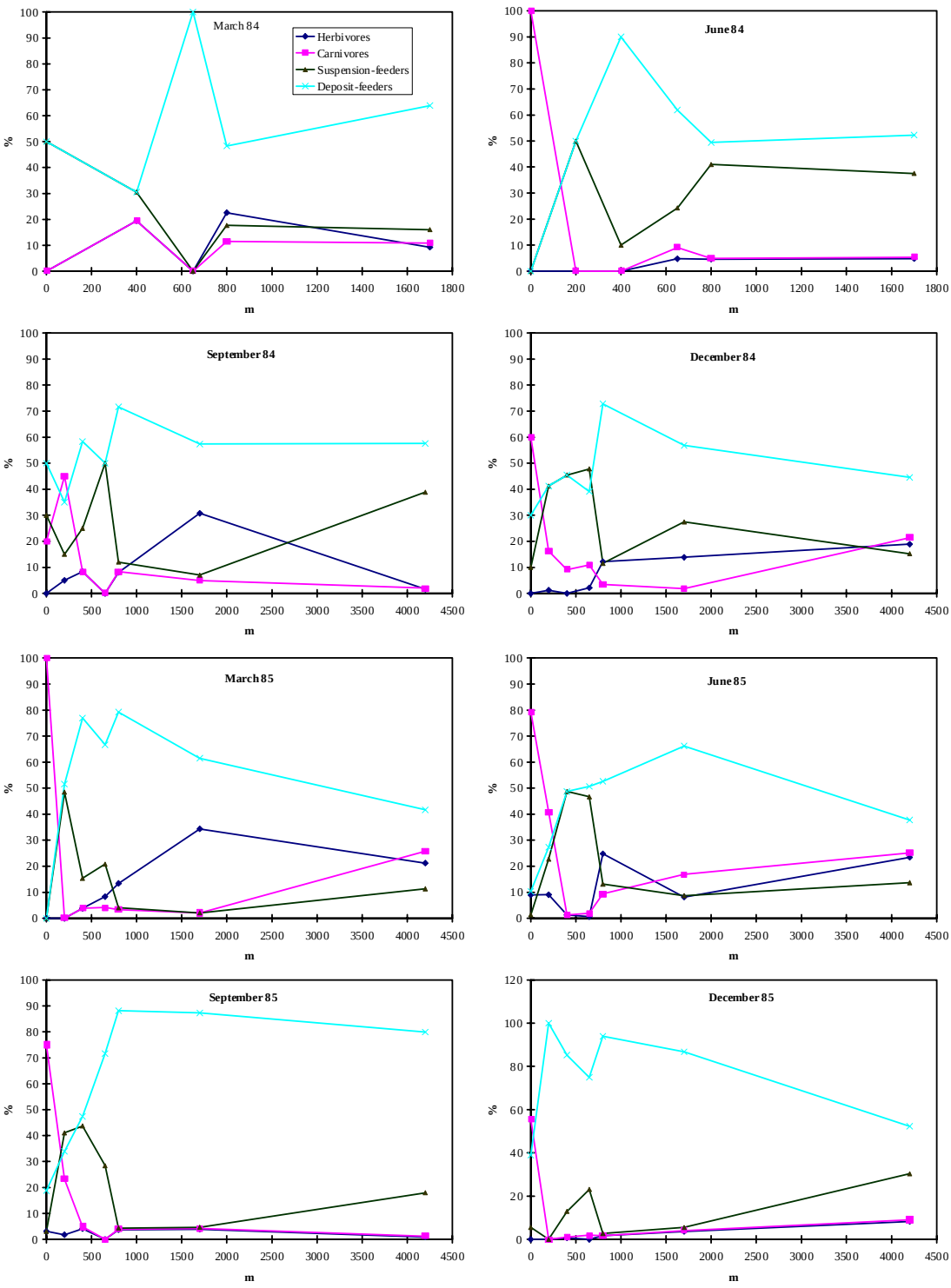

Fig. 8 - Percent importance of the herbivores, carnivores, suspension and deposit-feeders as a function of distance from the sea in Odeceixe.

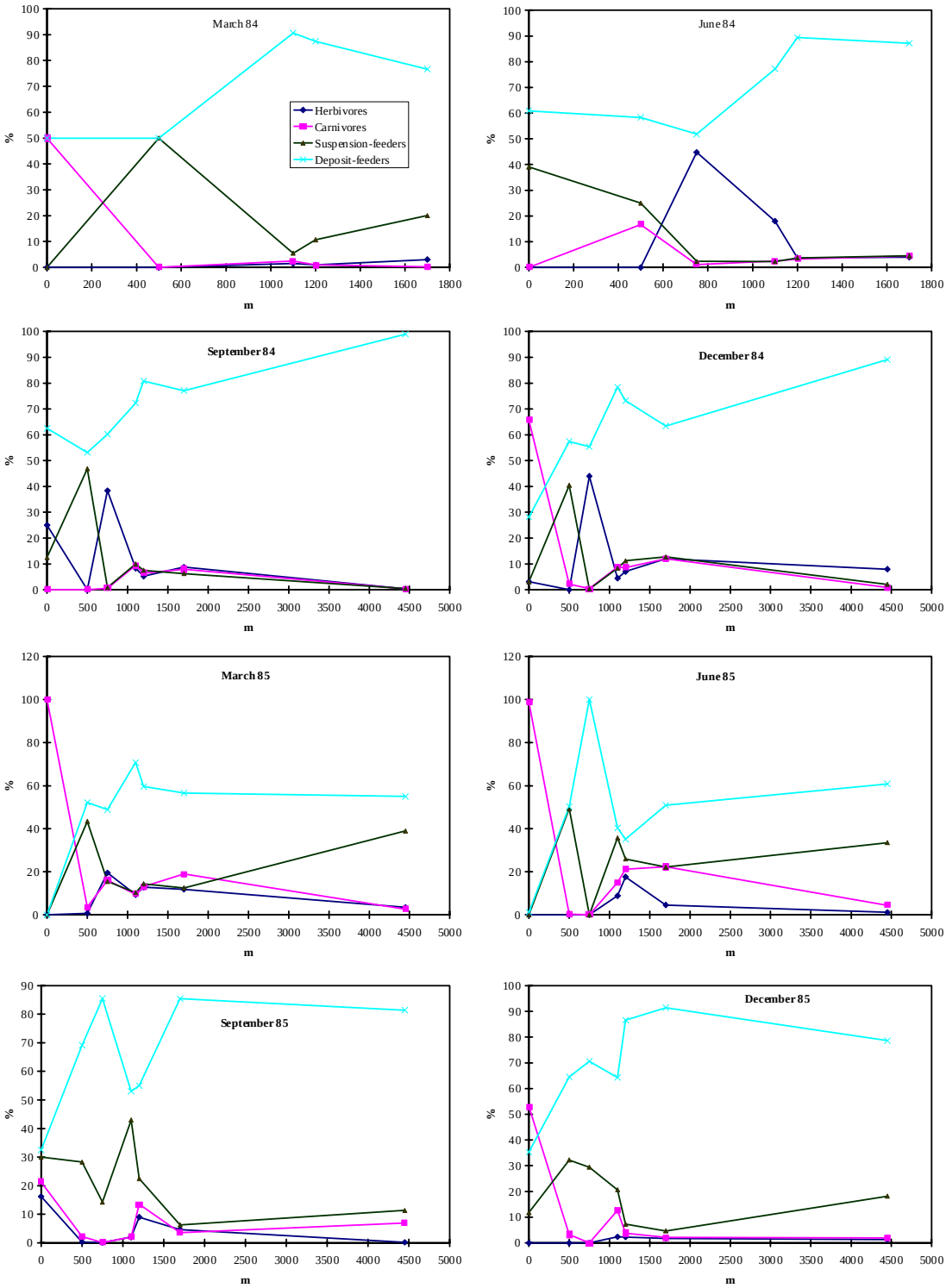

Fig. 9 - Percent importance of the herbivores, carnivores, suspension and deposit-feeders as a function of distance from the sea in Aljezur.

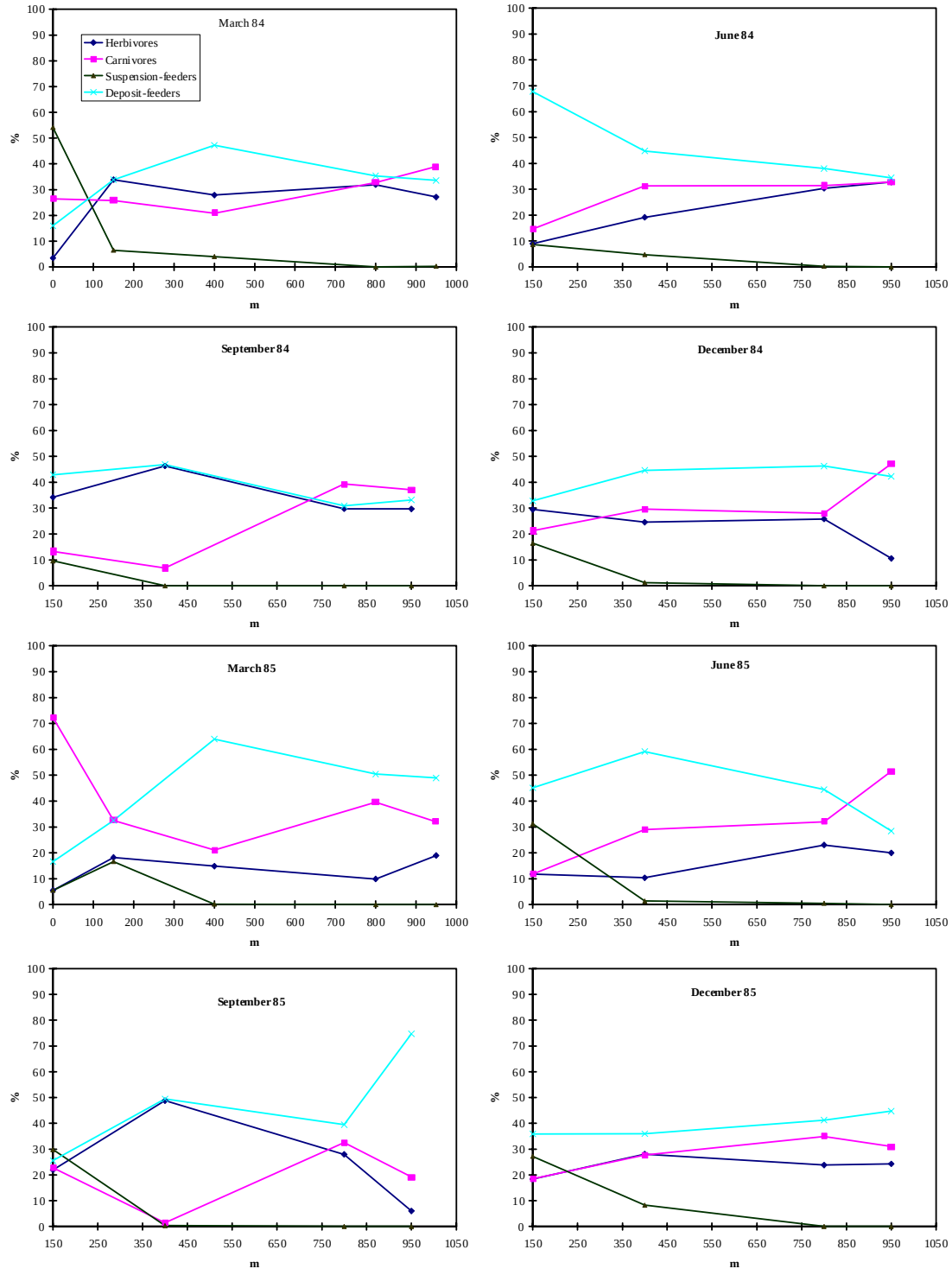

Fig. 10 - Percent importance of the herbivores, carnivores, suspension and deposit-feeders as a function of distance from the sea in Carrapateira.

During all the other sampling campaigns a different result was observed at Carrapateira. St. 11 was not sampled because of the presence, at its location, of a sand barrier closing the river mouth. The suspension-feeders showed maximal preponderance at the stations nearest to the sea, the carnivores on the more upstream stations and the deposit-feeders did not follow any particular trend. The obtained results suggest that outside of the March 1985 situation (open to the sea), the pattern observed for the variation of the different functions in the Carrapateira system was not as defined as those seen for the Odeceixe and Aljezur systems.

DISCUSSION

The maximal percentage of the trophic groups at different stations along the estuarine/lagoonal gradient, is in accordance with the opposing scores in the secondary axes of the PCA analysis, on log transformed abundance data. The presented results are not easily comparable with those obtained in other works, because different authors used different mesh diameter sieves to separate the macrofauna, and some expressed their results in biomass instead of numerical abundance. In spite of these differences, the observed patterns seem to agree, at least partially, with those referred by other authors (SANDERS, 1958; CARRIKER, 1967; RHOADS & YOUNG, 1970; PEARSON, 1971; GRAY, 1981; JARAMILLO *et al*., 1984; CANCELA DA FONSECA, 1989; MAZE, *et al*., 1993; PAIVA, 1993), emphasising the existence of gradients of trophic functions along physical gradients.

The fact that the trophic function "carnivores" reach its maximal proportion at the Odeceixe, Aljezur and March 85 Carrapateira river mouths, where the organic inputs are low and the turbulence highest due to wave action and tidal currents, are in accordance with CARRIKER (1967), PEARSON (1971) and PEARSON & ROSENBERG (1978).

Concerning the "functional suspension-feeder individuals", their expectable higher preponderance is in stable sandy sediments away from the maximum of the deposit-feeders. This was observed in all three systems and is in agreement with SANDERS (1968), RHOADS & YOUNG (1970), JARAMILLO *et al*. (1984) and MILLET & GUELORGET (1964). This may be due to: i) competition and mutual exclusion or both, as suggested by RHOADS & YOUNG (1970) in their amensalism hypothesis; ii) suspension-feeding activities may not be functional in very fine sediments submitted to resuspension, that may collapse their systems of food capture, as it happens in estuaries due to the "turbidity maxima" zone; iii) furthermore, the pattern of distribution of carnivores and suspension-feeders along these gradients may be related with their metabolism: these groups need higher concentrations of dissolved oxygen (CHASSÉ, 1972) which in these systems are usually found in clean sands, with lower levels of organic matter and high levels of pore water circulation near the sea inlets.

The high percentage of "functional deposit-feeders" is expected in fine

sediments with high organic matter content (SOKOLOVA, 1972; PEARSON & ROSENBERG, 1978; JARAMILLO *et al.*, 1984; LOSOVSKAYA, 1984; MURINA, 1984; AMBROGI *et al.*, 1989; CANCELA DA FONSECA, 1989; VAN DEN BRINK & VAN DER VELDE, 1991; MILLET & GUELORGET, 1994), as was observed at Odeceixe and Aljezur.

When an established sea→freshwater gradient exists, a general trend in the spatial distribution of the proportion of each trophic group can be suggested (Fig. 11), at least for carnivores, suspension-feeders and deposit-feeders. The response of the Carrapateira macrobenthic communities to the opening to the sea in March 1985, followed the above described pattern, which seem to be related with a homeostatic process. This apparently predictable pattern probably represents the best way the communities can adapt to exploit the existing resources under the influence of the environmental gradients established by tidal currents and fluvial discharge.

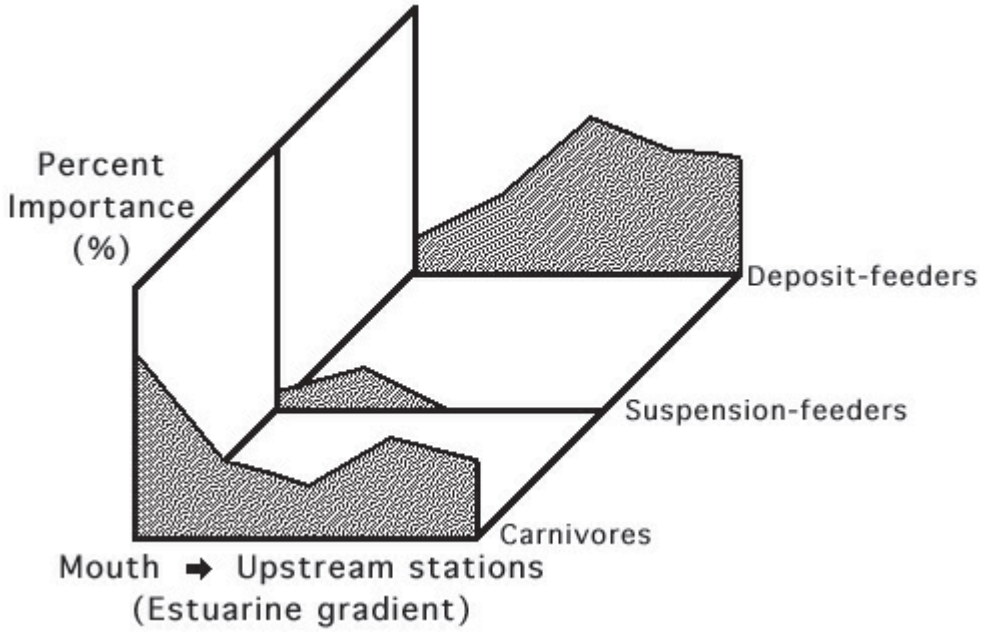

Fig. 11 - Percent importance of the carnivores, suspension and deposit-feeders along the estuarine gradients of Odeceixe, Aljezur and Carrapateira (March 1985). The plot shows the general trend obtained from the succession of peaks observed.

The results for Carrapateira in March 1985 clearly show the determinant role of the opening to the sea and the associated hydrodynamics on the establishment of the observed patterns. Moreover, it seems to confirm their predictability. Similar results have also been described for another Portuguese coastal lagoon (St. André lagoon), after the opening to the sea of its inlet channel (CANCELA DA FONSECA, 1989; DUARTE *et al.*, 1990).

Based on the trophic-dynamic aspects of ecology (LINDEMAN, 1942) and by analogy to the succession theory, the terminal sections of these small rivers, where the carnivores and the suspension-feeders reached their maximal proportions, may be viewed as oligotrophic ends. In this sense, the upstream stations, where the deposit-feeders have higher relative abundances, should correspond to eutrophic ends (PEARSON & ROSENBERG, 1978). Considering the results obtained in this study, there seems to be a shift from grazing to detritus pathways from the mouth of the rivers to the upstream stations. The study of the food webs along this type of estuarine/lagoonal gradients by means, for example, of immunological methods (FELLER *et al*., 1979) could also be used to test this hypothesis.

The sedimentary homogeneity and low organic matter content of Carrapateira sediments disfavour the existence of clearly distinguishable oligotrophic and eutrophic ends. However, deposit-feeders are usually dominants in the stations with higher macrophyte biomass. It can be assumed that these stations correspond to a more eutrophic area inside the lagoon, in opposition to the inlet area where carnivores present a higher numerical importance following the connection to the sea (March 1985). Based on our functioning hypothesis stated above, the opening of the lagoon to the sea could be interpreted as an introduction of a new oligotrophic area with the establishment of a community where the trophic function "carnivores" have their maximal proportion.

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