



Feeding Ecology of *Nereis diversicolor* (O.F. Müller) (Annelida, Polychaeta) on Estuarine and Lagoon Environments in the Southwest Coast of Portugal

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Abstract. The feeding ecology of *Nereis diversicolor* (O. F. Müller, 1776) (Annelida: Polychaeta) was studied over 14 months at three estuarine-lagoon systems of the Southwest coast of Portugal (Odeceixe, Aljezur and Carrapateira). The analyses of digestive tract revealed that diet change according to site, period of the year and individual sizes. There are no differences in the digestive contents between sexes. In all sampling stations a total of thirty items were found, but only five shown an occurrence superior to 1%. These were: mucus (56.3%), sand (17.6%), vegetable detritus (10.7%), Nereididae (7.7%) and *Corophium* sp. (1.8%). *N. diversicolor* was detected in all sampling stations with a filter-feeding behaviour, although in Carrapateira there is evidence of slightly higher carnivore behaviour than in Odeceixe and Aljezur. Mucus (a food complex including organic matter, bacteria, fungi and phytoplankton) was the main gut content.

Key words: Seaworms, “common ragworm”, feeding behaviour, diet, brackish environments.

Resumo. Ecologia Alimentar de *Nereis diversicolor* (O.F. Müller) (Annelida, Polychaeta) em Ambientes Estuarino-Lagunares da Costa Sudoeste de Portugal. A ecologia alimentar de *Nereis diversicolor* (O.F. Müller, 1776) (Annelida: Polychaeta) foi estudada num período de 14 meses em três sistemas estuarino-lagunares da costa Sudoeste de Portugal (Odeceixe, Aljezur e Carrapateira). A análise do conteúdo digestivo revelou uma variação da dieta de acordo com os locais estudados, época do ano e com o tamanho dos indivíduos. Não houve diferenças nos conteúdos de machos e fêmeas. Foram encontrados em todas as estações amostradas um total de trinta itens, mas apenas cinco revelaram uma ocorrência superior à 1%. Estes foram: muco (56.3%), areia (17.6%), detritos vegetais (10.7%), Nereididae (7.7%) e *Corophium* sp. (1.8%). *N. diversicolor* evidenciou hábitos filtradores, em todas as estações amostradas embora na Carrapateira tenham sido detectadas percentagens de carnivoría ligeiramente superiores às encontradas em Odeceixe e Aljezur. O principal conteúdo do tracto digestivo foi o muco (complexo alimentar que aglutina matéria orgânica, bactérias, fungos e fitoplâncton).

Palavras-chave: Poliquetas, “minhocas-da-pesca”, comportamento alimentar; dieta, sistemas salobros.

Introduction

The polychaeta *Nereis diversicolor* (O. F. Müller, 1776) is widely distributed in estuarine and lagoonal habitats from North Africa to the North of Europe (Mettam 1979, 1981, Gillet 1993). The species shows high physiological tolerance to extreme variations in environmental factors, and can grow

and reproduce in different sediment types and in stressed environments (Bartels-Hardege & Zeeck 1990, Cheggour *et al.* 1990, Miron & Kristensen 1993, Zubillaga & Salinas 1997, Scaps 2002).

It not only adapts well to a variety of environments, but also its feeding habits are quite generalist. *N. diversicolor* has a wide capacity

regarding the size of food it feeds upon, which ranges from micro and macrozoobenthos, diatoms, to fragmented organic matter including detritus (Gorke 1971, Reise 1979, Witte & Wild 1979, Smith *et al.* 1996, Lucas & Bertru 1997). This species can also use different strategies to capture its food: i) deposit feeding, capturing its food on the sediment surface and around the gallery (Esselink & Zwarts 1989, Esnault *et al.* 1990); ii) suspension feeding, releasing a web of mucus in the gallery and through dorsal-ventral movements, it generates a continuous current capturing the phytoplankton in the web to be ingested afterward (Harley 1950, Well & Dales 1951, Riisgård 1991, Vedel 1998). It adopts this feeding strategy when the water column presents a high concentration of phytoplankton (Vedel & Riisgård 1993); iii) herbivore, it is able to ingest parts of algae and aquatic macrophytes (Olivier *et al.* 1996, Hughes *et al.* 2000); iv) carnivore, playing an important role in the structure of brackish water ecosystems, because it acts as a predator of different bottom fauna species (Rönn *et al.* 1988). These strategies seem to be related to food availability and quality, presence or absence of predators, tidal height and season (Esselink & Zwarts 1989, Masson *et al.* 1995).

Nereis diversicolor, searched as live food or bait by aquaculture and sport fishing activities, is also an important species to the structure of the food webs of another lagoonal environment of Portuguese Southwest coast (Cancela da Fonseca 1989, Bernardo 1990). As a part of a research project dealing with the biology and ecology of this species (Fidalgo e Costa *et al.* 1998, Fidalgo e Costa *et al.* 2002), the analysis of the monthly variation of its digestive tract contents was carried out in order to assess its feeding patterns and so, its trophic position in the wild. In addition the type of food ingested by the different size classes, as well as by different sexes, was also investigated.

Materials and Methods

Study Area

The studied sites are located inside a natural protected area (the Sudoeste Alentejano and Costa Vicentina Nature Park – PNSACV), in which they constitute vital habitats for many species, much of them aquatic birds. It is also one of the best preserved coastal areas in Europe with high landscape, geological and biodiversity richness (Silva e Costa *et al.* 1983). The sampling stations were established at the lower part of Odeceixe (ODX), Aljezur (ALZ) and Carrapateira (CAR)

estuaries (Figure 1), with water basins of about 250, 200 and 110 km² respectively, which partially drain the Western part of Southwest Portugal. According to Day *et al.* (1987), these types of brackish environments, although representing a great geomorphological diversity are from an ecological point of view lagoon-estuarine ecosystems.

The sampling stations (two for Odeceixe, three for Aljezur and for Carrapateira) have the highest occurrences of *N. diversicolor* according to previous studies conducted in those systems (Magalhães *et al.* 1987, Magalhães 1988). To facilitate the statistical work and also to keep the initial goal of comparing the different brackish environments, it was decided to combine and analyse all data per sampling site (ODX, ALZ and CAR) with no specific reference to the sampling stations, within each site. These are arranged in a North-South geographic position in which ODX is the sampling site located further north and CAR the sampling site further south. The distance between these two areas is approximately 35 km.

Field and laboratory work

Monthly data on rainfall, water salinity, near sediment salinity and temperature, and sediment organic matter, chlorophyll *a* and phaeopigments were obtained to characterize the environmental conditions of each site. Salinity and temperature values were measured *in situ* at each station. Surface and near sediment salinity values were obtained in order to evaluate fresh water inputs.

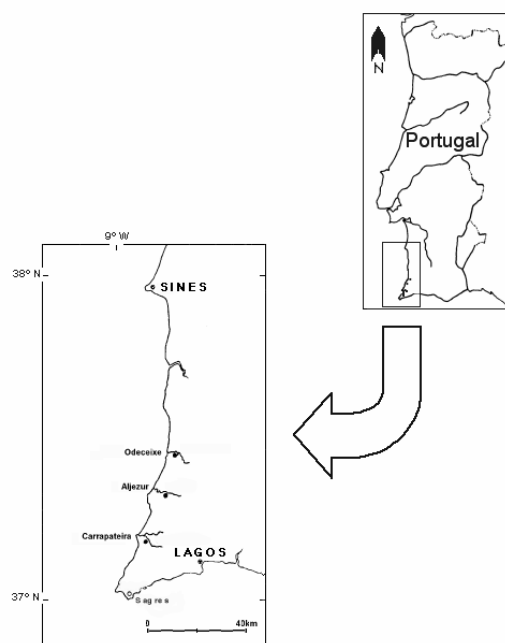


Figure 1 – Map of Portugal and the southwestern coast showing the sampling sites (black dots).

Rainfall values were obtained from the National Meteorological Institute and General Administration of Natural Resources. Organic matter, chlorophyll *a* and phaeopigments of sediment were determined on the top centimetre of sediment samples obtained in each station with a 5 cm diameter corer and were frozen until laboratory analysis (Fidalgo e Costa *et al.* 2002).

All specimens of *N. diversicolor* used in this work were collected between April 1993 and May 1994: i) at low tide in the sublittoral fringe (the upper subtidal layers in a tidal environment) at the lower part of ODX and ALZ; ii) in the sublittoral area (the upper submerged layers in a non-tidal environment) of CAR, in a small coastal lagoon formed by the partial closing of a sandy barrier near the beach. For each station, a total sampling area of 0.1m² was obtained by five sub-samples of 30 cm depth, using a 0.02 m² hand corer. The samples were then sieved through a 0.5 mm square mesh and the remaining fraction was kept in 10% formalin buffered with borax. In the laboratory, samples were washed in order to extract the excess of formalin and sediment. The remainder was dipped into a saturated saccharose solution, which separates the organic from the inorganic matter by flotation (Cancela da Fonseca 1989, Caron *et al.* 1993). All samples were then kept in 70° alcohol (Möller 1985).

Some of the captured animals were too small to be dissected while others had no digestive tract contents due to damages during sampling. Therefore the guts of 3000 animals were observed but, from these, 907 (30%) had any content (220 in ODX, 460 in ALZ and 227 in CAR).

All individuals were measured, based on the length of L₃ (length of prostomium, plus peristomium and 1st chaetiger) according to Gillet (1990, 1993). This measure presented the best correlation with the biomass (Fidalgo e Costa *et al.* 1998) being a good conversion factor (dry weight (mg) = 1.982 (L₃, mm)^{3.479}, N=259, r²=0.914, p<0.001). All measurements were performed using a camera lucida and digitising table (Houston Instruments HiPad) linked to a PC. For the practical purposes of this study, and according to the previous results on cohort analysis (Fidalgo e Costa *et al.* 1998), three basic sizes were established (small (S1), medium (S2) and large (S3)), being represented by a L₃ measure, respectively, of [0.3, 1.5 mm], [1.5, 3.0 mm] and [3.0, 4.5 mm].

The collection of digestive tract content was done after opening individuals with iris scissors, from the first to the last chaetiger. The material was then placed in a Petri dish and observed with a

binocular stereomicroscope and, when necessary, a compound microscope. The identification of the found food items was narrowed down to the lowest possible taxonomic level. Due to the conditions of gut material, we chose to represent individual results as percentage of occurrence. For each month the data were analysed as frequency of occurrence according to the following formula:

$$\frac{\text{number of digestive tract with a certain item}}{\text{number of digestive tract with the observed content}} \times 100$$

Sex was determined when the individuals were opened to extract out the tract contents. Observation of the oocytes and the sperm plates was performed using binocular microscopes and the total sex ratio found in ODX, ALZ and CAR was always female biased, being, respectively, 1:2.9, 1:3.1 and 1:4.1 (Fidalgo e Costa, 2003).

From sediment samples, pigments were extracted with 90 % acetone during 24 h in darkness at 4° C, and subsequently centrifuged. Chlorophyll *a* (surface Chl *a* is generally used as an index of microphytobenthos biomass) and phaeopigments were determined spectrophotometrically by the method of Lorenzen (1967) adapted by Plante-Cuny (1974) and results expressed as mg m⁻².

The organic matter content of the superficial layer of sediment was estimated through the loss on ignition, a method that, according to Duck (1986), provides a close estimate of the total organic matter expressed in g m⁻².

Data analysis

The proportions of different food items ingested per individual were compared between the sexes using T-tests and among size classes (large, medium, small) using one-way ANOVA (each food item was analysed separately). In both cases the variables conformed to the assumptions of parametric statistics of normality and homogeneity of variances was investigated by normal probability plots and Levene's test respectively (Zar 1984, Underwood 1997).

For the statistical analysis of seasonal effects and due to the scarcity of gut contents in some months, the data from the different months were merged into four seasons: spring (April and May 1993; March, April and May 1994), summer (June, July and August 1993), autumn (September, October and November 1993) and winter (December 1993; January and February 1994).

Spatial (Odeceixe vs. Aljezur vs. Carrapateira) and seasonal (Spring vs. Summer vs. Autumn vs. Winter) effects in the proportion of food

items ingested were investigated using two-way ANOVA after transforming the data (arc-sin of the square root) to match the assumptions of ANOVA (Underwood 1997), followed by planned comparisons to identify the significant differences in the same site along different seasons or among the three sites in the same season (Zar 1984, Underwood 1997). A similar analysis (i.e. two-way ANOVA followed by planned comparisons) was performed for the abiotic factors measured. Of the abiotic factors, only salinity and temperature values were log-transformed to meet the assumptions of ANOVA (Underwood 1997). In order to evaluate which groups differed significantly from each other *post-hoc* HSD tests for samples with different sizes were used with a p-level of 0.05. All descriptive statistics were expressed as mean \pm standard error of the mean. All statistical tests were performed using software package Statistica for Windows v. 5.0, from Statsoft.

Results

Abiotic factors and phytopigments

Monthly water temperature values showed a variation according to the normal annual behaviour of this parameter (Figure 2). The ANOVA revealed an effect of the sampling site ($F_{2,99} = 30.76$, $p < 0.001$) and of the season ($F_{3,99} = 77.50$, $p < 0.001$). Significant differences on temperature stress a site effect with CAR presenting the highest value and ODX the lowest (ODX: 15.6 ± 0.52 °C, $n = 42$; ALZ: 17.5 ± 2.07 °C, $n = 42$; CAR: 19.5 ± 0.62 °C, $n = 28$) (post-hoc HSD test, $p < 0.05$). There is also an effect caused by seasonality (Spring: 21.3 ± 2.1 °C, $n = 40$; Summer: 21.6 ± 0.7 °C, $n = 24$; Autumn: 15.7 ± 0.5 °C, $n = 24$; Winter: 13.7 ± 0.3 °C, $n = 24$ - post-hoc HSD test, $p < 0.05$).

Salinity values reflect tidal influence, rainfall and river flow, which is observed through constant stratification throughout the year (Figure 2), especially in spring and winter at sites ODX and ALZ. ANOVA undoubtedly shows an effect of the sampling site ($F_{2,99} = 10.14$, $p < 0.001$) due to differences in bottom salinity between CAR (15.0 ± 1.2 , $n = 42$) and the other sampling sites (ODX - 31.8 ± 0.89 , $n = 28$; ALZ - 30.0 ± 2.8 , $n = 42$) (post-hoc HSD test, $p < 0.05$).

Sediment chlorophyll *a* reveals temporal variation ($F_{3,100} = 3.46$, $p = 0.02$), associated with the amount of fresh water brought by rain and in particular by the continental runoff that penetrates the system (Figure 3A). Significant variations occurred between summer (59.8 ± 9.90

mg.m^{-2} , $n = 24$) and winter (113 ± 17.6 mg.m^{-2} , $n = 24$) (post-hoc HSD test, $p < 0.05$).

The chlorophyll degradation represented by phaeopigment values (Figure 3B), emphasise when (months) and where (sites) accumulation of detritus of plant or microalgae cell occur. The ANOVA showed only a site effect ($F_{2,100} = 7.97$, $p < 0.001$).

The sediment organic matter (Figure 3C) is related to grain size composition in the different sampling sites. The ANOVA showed no significant differences between sites ($F_{2,100} = 2.19$, $p = 0.12$) and season of the year ($F_{3,100} = 0.60$, $p = 0.62$).

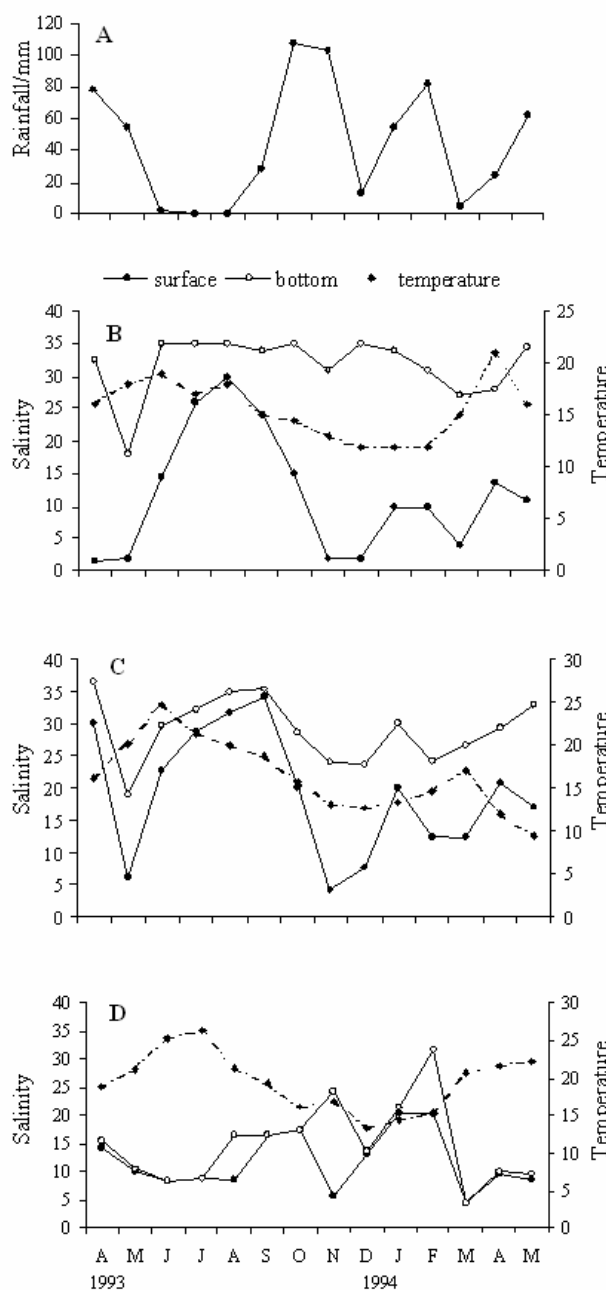


Figure 2 – Monthly rainfall on the south-western coast of Portugal (A). Monthly values of salinity (surface and bottom) and temperature in ODX (B), ALZ (C) and CAR (D).

Spatial and seasonal diet variations

A total of 30 items were found in gut contents for all sampling sites (Table I). However, from this total only five showed a frequency of occurrence higher than 1%. These items were: mucus (56.3%), sand (17.6%), vegetable detritus (10.7%), Nereididae (7.7%) and *Corophium* sp. (1.8%).

The results for feeding habits of *N. diversicolor* in all sampling stations clearly show the ingestion of various food items, with differences in occurrence of these items between sites and during the year (Figure 4).

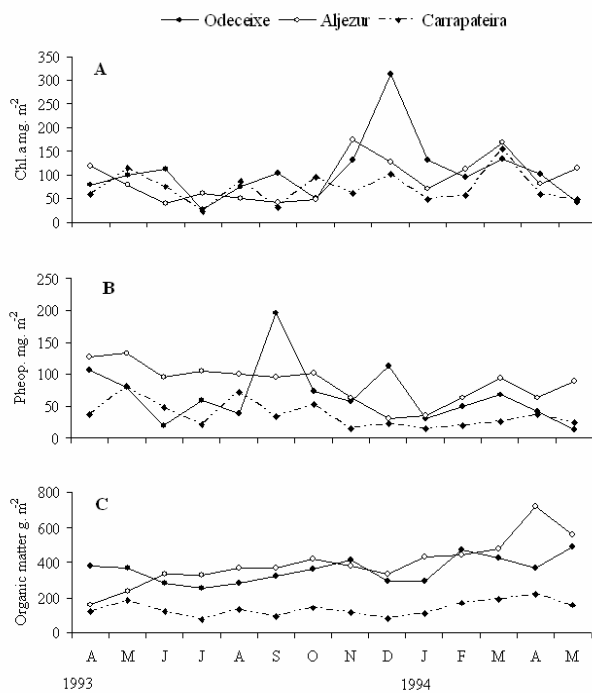


Figure 3 – Sediment values of chlorophyll *a* (A), pheopigments (B) and organic matter content (C) in ODX, ALZ and CAR during the sampling period.

ANOVA showed an effect of sampling site ($F_{2,895} = 4.65$, $p = 0.001$) and of the season ($F_{3,895} = 3.10$, $p = 0.03$) on the percentage of mucus. There was also an effect of the interaction between the two independent variables ($F_{6,895} = 2.33$, $p = 0.03$), showing that mucus seems to be the most important item during spring/summer periods, mainly in what concerns ODX and CAR. The effect of sampling site is due to differences between CAR (50 ± 2.37 %, $n = 227$), with more lagoonal characteristics, and the two remaining sampling sites (ODX: 61.3 ± 2.17 %, $n = 220$; ALZ: 56.8 ± 1.54 %, $n = 460$) (post-hoc HSD test, $p < 0.05$). On the other hand, the effect of season was determined by the differences between winter (47.7 ± 3.01 %, $n = 156$) and the other three seasons of the year (spring: 58.4

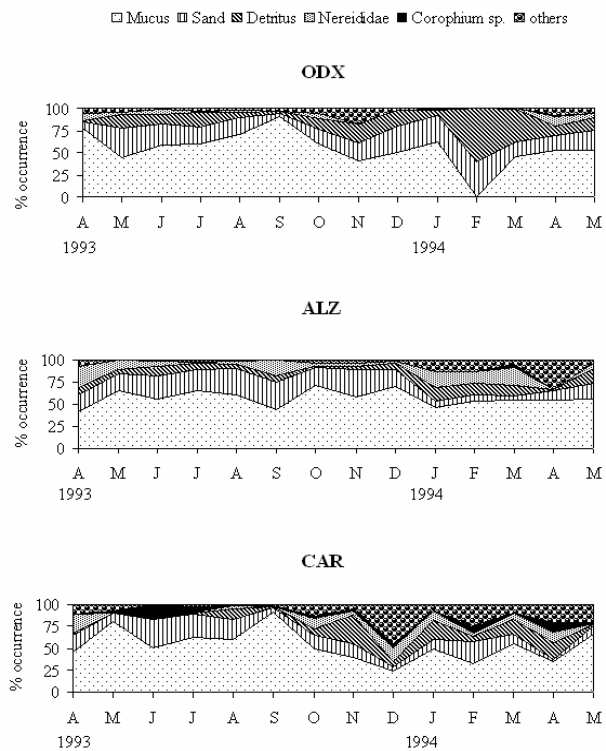


Figure 4 – Different items ingested by *N. diversicolor* in all sampling stations clearly showing the ingestion of various food items, with differences in occurrence of these items between sites and during the year.

± 1.68 %, $n = 383$; summer: 59.5 ± 2.0 %, $n = 205$; autumn: 58.6 ± 2.84 %, $n = 163$) (post-hoc HSD test, $p < 0.05$). The interaction effect was due to differences between autumn and summer in CAR, and between CAR and ALZ in winter (post-hoc HSD test, $p < 0.05$).

There were no significant differences between sampling sites concerning the amount of ingested sand ($F_{2,895} = 1.60$, $p = 0.20$). However for this variable, noteworthy differences related to season ($F_{3,895} = 5.06$, $p = 0.002$) and interaction ($F_{6,895} = 4.64$, $p < 0.001$) were confirmed by ANOVA. In summer *N. diversicolor* ingested a higher percentage of sand (22.1 ± 1.79 %, $n = 205$) than in spring (15.0 ± 1.18 %, $n = 383$) (post-hoc HSD test, $p < 0.05$). The effect of the interaction is due to differences between ODX and ALZ in autumn ($p = 0.004$), ALZ between spring and autumn ($p = 0.004$) and ALZ between winter and autumn ($p = 0.002$) (post-hoc HSD test, $p < 0.05$).

ANOVA results showed, for vegetable detritus, that there were no differences between sampling sites ($F_{2,895} = 1.95$, $p = 0.14$), seasons ($F_{3,895} = 0.35$, $p = 0.79$) and also interaction between them ($F_{6,895} = 1.23$, $p = 0.27$).

Larvae, parapods and bristles of *N. diversicolor* as well as some other Nereididae were found in the samples suggesting cannibalistic behaviour. The ANOVA showed a non significant

Table I – Gut content of *N. diversicolor* (%) in the whole sampling stations (main items in bold).

Gut Contents	%
mucus	56,33
Total Sediment	17,64
sand	17,56
mud	0,08
Vegetable detritus	10,68
Total Polychaeta	7,92
Nereididae	7,68
Spionidae	0,07
Capitellidae	0,03
Polychaeta (unidentified)	0,14
Total Crustacea	4,64
Cirripedia	0,01
<i>Cyprideis</i> sp.	0,91
Ostracoda (unidentified)	0,19
Copepoda	0,02
<i>Cyathura carinata</i>	0,44
<i>Sphaeroma hookeri</i>	0,33
Anthuridae	0,08
Isopoda (unidentified)	0,18
<i>Corophium</i> sp.	1,76
<i>Gammarus</i> sp.	0,01
Amphipoda (unidentified)	0,29
Crustacea (unident. remains)	0,44
Others	2,79
Foraminifera	0,27
Hydrobidae	0,71
Gastropoda (unidentified)	0,01
Bivalvia	0,01
Acari	0,01
Chironomidae	0,78
Insecta (unidentified)	0,10
unidentified	0,91

marginal effect for the sampling sites ($F_{2,894} = 2.70$, $p = 0.07$) and a non significant effect for the season of the year ($F_{2,894} = 1.84$, $p = 0.14$). Although, the same analyses revealed a significant effect of the interactions between variables ($F_{6,894} = 2.77$, $p = 0.01$), due to differences between CAR in spring and in winter (post-hoc HSD test, $p < 0.05$).

ANOVA indicates that there was a significant effect away from the sampling sites ($F_{2,895} = 20.7$, $p < 0.001$) on the percentage of *Corophium* sp. found in the digestive tract of *N. diversicolor*. This effect is due to the fact that CAR (5.4 ± 1.19 %, $n = 227$) is higher than ODX and

ALZ (0.02 ± 0.02 %, $n = 220$; 0.8 ± 0.32 %, $n = 460$) (post-hoc HSD test, $p < 0.05$). There was also an effect of the interaction between the sampling station and season ($F_{6,895} = 2.23$, $p = 0.04$), due to differences between CAR and ALZ in winter. (post-hoc HSD test, $p < 0.05$).

There was a clear trend for the increment of the item “other” (other crustaceans, other polychaetes and different animal groups found in small quantities - cf. Table I) in the rainy seasons (autumn, winter and spring – cf. Figure 2A), mainly at ALZ and CAR (Figure 4). The slight increase in this item in ODX (November and April 1994 - see Figure 4) was due to the presence of the ostracod *Cyprideis* sp. and the isopod *Cyathura carinata*. ALZ showed a little bit higher species richness than ODX, attributable to the presence of almost completely digested and unidentifiable crustaceans. Samples from the family Anthuridae (mainly *Cyathura carinata*), *Sphaeroma hookeri*, and Chironomidae larvae were also found at this site. In December 1993, February 1994 and April 1994 (see Figure 4), and in comparison with other sampling sites a representative amount of unidentifiable parts of crustaceans other *Cyprideis* sp., *Cyathura carinata* and *Sphaeroma hookeri*, were observed in CAR. Also remarkable was the wide presence of Chironomidae larvae in this sampling site.

Figure 5 shows the contents for each site and also a graph formed by the whole of the sampling sites. All crustaceans and polychaetes found were grouped for all sampling sites as well as gastropods and insects were also grouped for ALZ and CAR, respectively, to emphasise their consumption by *N. diversicolor*. The analysis of this figure makes clear the main gradients found in the diet of this species from ODX (the northern sampling site) to CAR (the southern sampling site): i) sand and mucus decrease from ODX to CAR; ii) an increased predation on crustaceans and polychaetes from northern to southern sampling sites; iii) gastropods and insects were relevant in the diet respectively, in ALZ and CAR.

Body size and sex effects on diet

Only mucus ($F_{2,904} = 5.26$, $p = 0.005$) and sand ($F_{2,904} = 6.37$, $p = 0.002$) showed a significant difference between the three sizes studied (S1, S2 and S3) (post-hoc HSD test, $p < 0.05$). Smaller individuals (S1) ingest a higher quantity of sand ($S1 < S2 = S3$) and a lower quantity of mucus ($S1 > S2 = S3$). The feeding strategies have changed between S1 and S2 / S3 size classes, ingesting the latter higher quantities of mucus (see Table II). There were no significant differences in food contents between males and females (Table III, T-test for each food item, $p > 0.05$).

Table II – Comparison (ANOVA) of gut contents of *N. diversicolor* (%) separated in different size classes: (S1) small, (S2) medium and (S3) large.

	S1		S2		S3		F2,904	p
	n	avg. ± se.	n	avg. ± se.	n	avg. ± se.		
Mucus	344	51.9 ± 1.90	542	58.8 ± 1.40	21	66.1 ± 7.05	5.26	0.0053
Sand		21.2 ± 1.52		15.5 ± 0.98		10.7 ± 4.78	6.37	0.0017
Detritus		8.9 ± 1.02		11.1 ± 0.80		10.4 ± 2.57	1.48	0.23
Nereididae		8.15 ± 1.33		7.47 ± 0.90		5.74 ± 3.71	0.22	0.79
<i>Corophium</i> sp.		2.74 ± 0.75		2.17 ± 0.33		0.71 ± 0.70	2.5	0.08

Table III – Male and female *N. diversicolor* gut contents (%).

	♂ (n=62)		♀ (n=159)		t	p
	avg ± se.	avg ± se.	avg ± se.	avg ± se.		
Mucus	63.0 ± 4.3	58.5 ± 2.8	0.85	0.40		
Sand	11.7 ± 2.6	12.6 ± 1,7	-0.28	0.78		
Detritus	9.92 ± 2.4	11.1 ± 1.6	-0.40	0.69		
Nereididae	5.9 ± 2.4	7.9 ± 1.9	-0.60	0.55		
<i>Corophium</i> sp.	1.4 ± 1.3	2.5 ± 1.1	-0.61	0.54		

Discussion

Nereis diversicolor worms with the digestive tract completely empty were found in the study area. Two main explanations may be used for these results: i) for southern sites, namely CAR, the increase of predatory activity showed a large number of worms with only few unidentifiable remains on the gut contents, pointing out Gaston (1987) statement that empty digestive tracts can reveal a predatory feeding strategy, in which digestion is completed more quickly, as opposed to digestion of vegetable matter rich in cellulose; and ii) the existence of a noticed continuous reproductive activity throughout the year (Fidalgo e Costa *et al.* 1998), in which the gut was reabsorbed and feeding ceased, as observed for this species and other Nereididae during its sexual maturity period (Golding 1987, Golding & Yuwono 1994, Last & Olive 1999).

Mucus, the most frequent item found in the digestive tracts, is not by itself a food item; it is an aggregation complex of organic matter, bacteria, fungi, phytoplankton and microphytobenthos. Differences in the amount of mucus present in the contents between CAR and the remaining sample sites was certainly based on its less eutrophic state (Cancela da Fonseca *et al.* 2001a). The scarcity of phytoplankton in the bottom water caused by occasional stratification (Figure 2), and/or by the insufficient renewal promoted by the tidal effect, while the connection to the sea in this site is reduced (Cancela da Fonseca *et al.* 2001b,

Fidalgo e Costa *et al.* 2002) was also another explanation for this result. It is known that *N. diversicolor* acts as an active filter-feeder through the production of a mucus net, when there is a higher predation risk and/or the amount of suspended particles is high (Esselink & Zwarts 1989, Vedel & Riisgård 1993, Masson *et al.* 1995). When it is submerged, this feeding strategy may be more

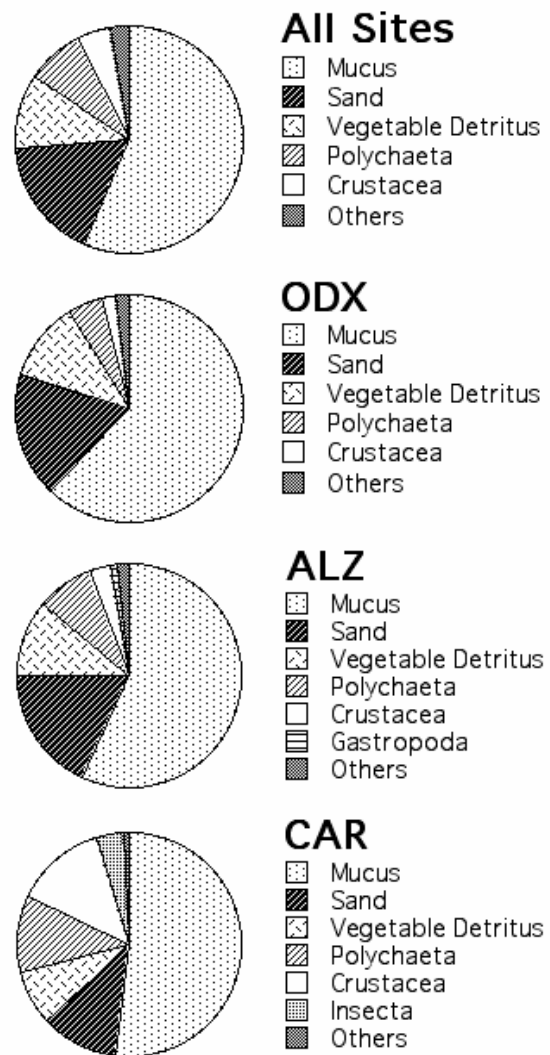


Figure 5 – Main gut contents of *N. diversicolor* (%) in the whole sampling stations and in each station separately.

effective (Harley, 1950, Wells & Dales, 1951, Esselink & Zwarts, 1989, Vedel, 1998). In CAR, with its frequent lack of tidal effect, due to its lagoonal properties (except in November 1993 when a rupture of the sand barrier occurred), a higher quantity of mucus was expected. But in this site *N. diversicolor* increases a carnivore strategy, partially abandoning filtering through the mucus net. This fact can be explained by i) the reduced quantity of particulate material in the water column, or ii) a favorable new feeding option as the capture of crustaceans and insect larvae.

The fact that the mucus ingestion and the aggregated food items increases at the time that the ingestion of sand decreases (Table II), may be due to an ontogenetic change in feeding habits. Small individuals, with small burrows, acquire detritivorous habits feeding more frequently on the surface of the sediment. Possibly this strategy is due to the inability of obtaining enough food through filtration due to the reduced dimensions of its mucus net or to difficulties in bringing enough water inside the gallery through dorsal-ventral pumping movements. On the other hand, larger individuals with a better physical condition are capable of building deeper galleries and pumping higher quantity of water (Esselink & Zwarts, 1989).

Sand was observed frequently in the digestive tract contents of *Nereis*, which swallows large amounts of sediment in sweep-and-plough food-searching strategy. This item may also have been overvalued once it was extremely persistent in the digestive tract, due to the fact that it is not attacked by the digestive processes like the other mentioned items. Like mucus it shows microalgae glued to its surface (mainly diatoms), but also meio and microfauna existing in the interstitial space (Lucas & Bertru, 1997, Tita *et al.* 2000). For all sampling sites, the differences found can be narrowed down to seasonal differences that follow the torrential character of the southern Portuguese rivers in which the studied areas are included (Magalhães *et al.* 1987, Fidalgo e Costa *et al.* 2002) and, consequently, a greater or lower sediment carriage from terrestrial or marine origins. These seasonal changes are strongly evident in ODX and ALZ, and in CAR they present only very low amplitudes (Fidalgo e Costa *et al.* 2002). Frequently that changes include also a seasonal contribution of particulate organic matter (OM) brought by continental runoff (Magalhães *et al.* 1987). So, when the OM amount is higher one may expect that *N. diversicolor* adopt a predominantly filter-feeding behaviour, reducing the amount of sand ingested. On the other hand a reduced organic flow may increase

ingested sand as it was found in CAR sampling site. These statements were supported by the work of several researchers that have already pointed out the effect of sediment dynamics, induced by different degrees of hydrodynamics and even by bioturbation, on the superficial layers in which *N. diversicolor* feeds on (Tamaki 1987, Meadows *et al.* 1990, Turner *et al.* 1995, Mclachlan 1996).

Comparisons of chlorophyll *a* and phaeopigment levels (Figure 3 A and B) with the percentages of sand or mucus ingested (Figure 4) did not allow the establishment of a comprehensive pattern. This is possibly due to the fact that the distribution and abundance of several species of microalgae are controlled by a number of interdependent factors (Cadée & Hegeman 1974, Pomeroy *et al.* 1981, Zedler 1982). In fact values of ODX, ALZ and CAR sediment chlorophyll *a* (as an indicator of microphytobenthos biomass) strongly correlates to rainfall, indicating a dependence of this environmental variable (Fidalgo e Costa *et al.* 2002). As it was also concluded the variation of the ratio between chlorophyll *a* and phaeopigments emphasize that the chlorophyll *a* increase was due to an *in situ* production of microalgae cells (Fidalgo e Costa *et al.* 2002). Nevertheless these details reinforce the above interpretation about sand ingestion because it is supposed that a peak in chlorophyll *a* (related to runoff) stimulate filtration instead of sediment ingestion behaviors. Nevertheless it was difficult to interpret our feeding results based only on a phytopigments dataset, referred only to one sampling day per month.

Detritus has an important role as a food source both in the freshwater and marine benthic communities. It is made up of all kinds of biogenic materials such as bacteria, protozoa, micro and macroalgae, parts of vascular plants in various degrees of decomposition, which may contain energy to be used by the species consumers (Tenore, 1977, Hansen & Kristensen, 1998). In the study area, *N. diversicolor* used detritus as a food source in all sampling stations, especially vegetable detritus such as algae, roots, and parts of the macrophyte *Ruppia* sp. The sampling sites revealed variations in the percent occurrence of ingested vegetable detritus which increased with precipitation (Figures 2A and 4), that may be related with the detritus amount inside a system, with a more torrential character (Magalhães *et al.* 1987). In ODX, it was observed that the occurrence of mucus have decreased with the augmented ingestion of vegetable detritus (Figure 4) contrarily to ALZ where this ingestion have no influence on mucus amounts. In CAR, the rise in the consumption of vegetable detritus started

also with rainfall rise (Figure 4). For this site, November 1993 was the single month where the total emptying of the lagoon occurred, remaining only a few puddles. During the following period filter-feeding was difficult due to the small amount of water available and so *N. diversicolor* fed on remains and roots of *Ruppia* sp. as an alternative. The decomposition of these macrophytes occurred as a result of their emergence and exposure to the sun. The increase in the vegetable remains consumed in the winter and at the beginning of spring seems to be caused by their transport to the system by the frequent rains during these seasons (e.g. Figure 2A).

The digestive contents of *N. diversicolor* in the present study confirm the results of previous studies (Mcintosh 1907, Bogucki 1953), which suggest cannibalistic behavior in this species. It showed continuous reproduction in the three systems studied, with a recruitment peak in early autumn, reaching annual averages of 1126 ind.m⁻² in ODX, 957 ind.m⁻² in ALZ and 337 ind.m⁻² in CAR (Fidalgo e Costa *et al.* 1998). For this reason the presence of larvae and juveniles in the gut contents was frequent at almost all sites (Figure 4). The larvae, juveniles and parts of individuals found in the gut contents suggest that cannibalism follows the life cycle of this species and showed a slightly increase after the referred early autumnal peak of larva with the growth of juveniles and the beginning of an active free benthic life (Fidalgo e Costa *et al.* 1998).

Feeding on the surface of the sediment has been observed in wild and under laboratory conditions (Fidalgo e Costa *et al.* 2000) and it varies according to quantity of food available. This practice is considered as a complement to filter-feeding due to the predation risks it involves (Masson *et al.* 1995). This feeding strategy may also be facilitated by the absence of predators of *N. diversicolor* such as *Carcinus maenas*. The lack of this active predator of *N. diversicolor* (Cancela da Fonseca, 1989) in this lagoon was mentioned by Magalhães (1988) and confirmed during the present study. Due to the apparent lack of predators, *N. diversicolor* could promote prolonged feeding journeys outside of the burrows, which together with gallery digging, favors the sediment turnover making it easier to find prey. *Corophium* sp. was one of the preys frequently observed in the intertidal environment of all sampling stations. In ODX and ALZ with abundant presence of *C. maenas*, there was no significant predation on crustaceans. However in CAR there was active predation of *Corophium* sp. during the study period, which can be confirmed by the pieces and whole individuals found in the digestive content (Figure 4). In lagoonal environments such as CAR,

and according to Jensen & André (1993) even the juvenile *N. diversicolor* have a negative effect on the juvenile *Corophium volutator*, above all in extraordinarily lentic lagoons, which is the case of this lagoon.

In the future, it would be interesting to verify a trade-off between food preferences and predation risk in the laboratory. It would also be interesting to determine in the field how predation affects the population structure of this species.

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