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Sipunculans and echiurans from the deep Angola Basin

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Abstract

Sipunculans and echiurans collected by the “DIVA 1” expedition by RV *Meteor* (Cruise M48/1) to the deep-sea bottom of the Angola Basin are recorded. Seven species from five genera and two separate phyla are recognized; only the echiuran *Pseudoikedella achaeta* has not been recorded hitherto in the southern sector of the Atlantic Ocean. A gradient analysis using redundancy analysis (RDA) under the CANOCO package indicates the existence of a neat latitudinal gradient of sipunculans along the Angola Basin from the southernmost stations towards the northern ones. The local abundance of abandoned horny tubes of polychaetes at some of the sampling sites of the northernmost stations explains the dense aggregations of *Nephasoma diaphanes*. This species exhibits an opportunistic lifestyle inside empty polychaete tubes on the abyssal plains of the Angola Basin.

Keywords: Angola Basin, Atlantic Ocean, deep-sea, Echiura, gradient analysis, Sipuncula

Introduction

The “DIVA 1” (=BioDiversity in the Atlantic) project is the first in a series of expeditions dedicated to the study of benthic diversity on the deep-sea floor of the Atlantic Ocean. The first cruise was devoted mainly to surveying changes in biodiversity along large-scale transects of hundreds of kilometres in the abyssal bottoms of the Angola Basin. An intensive study in this area was carried out in July 2000 by the German R/V *Meteor* during its cruise M48/1 under the direction of Dr M. Türkay (Forschungsinstitut Senckenberg, Frankfurt am Main).

Sipunculans and echiurans are small phyla (about 150 species each) of coelomate, protostomous unsegmented worms which are distributed worldwide throughout all oceans. Close to the sampling area Wesenberg-Lund (1963) reviewed the known species of these phyla in the waters off South Africa. Stephen and Cutler (1969), Cutler and Cutler (1987), DattaGupta (1981), and Saiz-Salinas (1988) subsequently contributed additional data to the knowledge of this fauna. The majority of these works deal with sipunculans and echiurans collected from shallow waters. That is why the present material, coming from depths of more than 5000 m, is of particular interest to taxonomists and ecologists.

The objective of the expedition was to reveal changes in biodiversity along a large-scale transect in the abyssal bottoms of the Angola Basin. This paper is a contribution to the

general objectives of the research based on the analysis of a fraction of the fauna collected: the taxocoenoses of sipunculan and echiuran worms.

Material and methods

Study area

The area investigated (Figure 1) is located in the South Atlantic Ocean, about 500–1000 km off the coasts of Angola and Namibia. The area was divided into six major working zones in an attempt to reproduce a latitudinal gradient across the abyssal bottoms of the Angola Basin. A total of 35 benthic sites was sampled in all the six working areas using different gear: a box-corer (USNEL, spade corer, 50 × 50 cm) for macrofauna; a multicorer (12 cores of 10 cm diameter) for nano- and meiofauna; an epibenthic sledge for meio- and macrofauna; and an Agassiz trawl for megafauna. Table I lists the stations for those sites where sipunculans or echiurans were found, with data on depths and locations.

Systematics

Identification was mainly based on the monographs by Stephen and Edmonds (1972) and Cutler (1994). The classification and terminology of Gibbs and Cutler (1987) and Edmonds (2000) are used here for sipunculans and echiurans, respectively. Detailed descriptions and synonymies of the species identified in this report have been omitted, but in pertinent cases a reference to a reliable description has been given. The material examined can be found in the collection at the Forschungsinstitut Senckenberg in Frankfurt am Main (Germany).

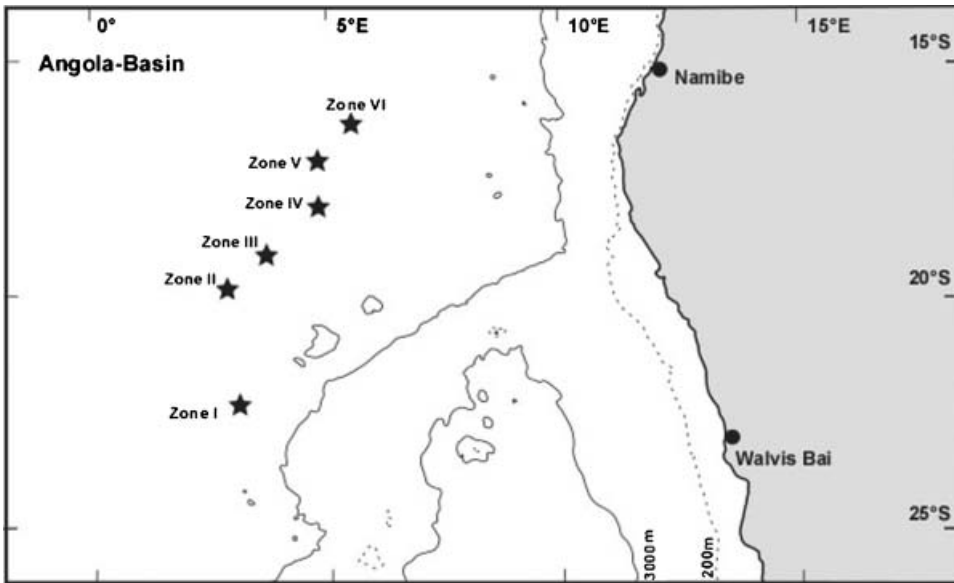


Figure 1. Sipunculan and echiuran collecting stations for the “DIVA 1” expedition to the Angola Basin (South Atlantic Ocean).

Table I. Data summary of sipunculan and echiuran fauna from the abyss of Angola Basin.

WZ	Gear ^a	Station no.	Latitude S	Longitude E	Depth (m)	Tubes ^b	Taxa ^c			
I	EBS	318	22°18.7'–22°20.1'	3°17.7'–3°18.4'	5123–6	0	2 N aby	2 N dia	2 O ste	
I	AT	319	22°22.6'–22°26.3'	3°20.2'–3°21.6'	5117–26	0	4 N dia	1? Ps ach		
I	AT	321	22°20.6'–22°23.6'	3°27.0'–3°27.9'	5126–21	0	5 N dia	1 S fla		
II	AT	327	19°59.2'–20°07.5'	3°00.9'–3°07.9'	5448–39	0	2 N dia	1+1? S fla		
II	EBS	328	19°58.9'–19°59.9'	2°54.1'–2°53.3'	5450–3	0	1 N aby			
III	AT	333	19°12.9'–19°17.4'	3°48.6'–3°52.2'	5423–6	1	4 N aby	1 N dia		
III	AT	334	19°12.5'–19°19.8'	3°49'–3°55.6'	5425–7	1	17 N aby	1 N dia		
IV	AT	337	18°18.9'–18°24.6'	4°42.7'–4°45.1'	5393–2	2	28 N aby	28 N dia		
IV	EBS	338	18°18.1'–18°20.8'	4°39.9'–4°38.6'	5395–8	0	3 N aby	1? N dia		
IV	AT	339	18°19.4'–18°25.3'	4°42.1'–4°44'	5395–2	4	8 N aby	14 N dia	10+1? A mur	
IV	EBS	340	18°17.3'–18°19.4'	4°41.2'–4°41.9'	5394–6	4	32+3? N aby	5 N dia	1? S fla	
V	GKG	341/4	17°08'–17°07.9'	4°42'	5418–9	0	1 N dia			
V	GKG	341/8	17°08.1'	4°41.9'	5419	0	1 N dia			
V	AT	343	17°07.5'–17°11.6'	4°42.9'–4°45.9'	5415	2	1 N aby	6 N dia	1 S fla	1+1? A mur
V	EBS	344	17°04.9'–17°07.5'	4°40.8'–4°42.3'	5420–15	3	35 N aby	3 N dia	2 juv ? S fla	
VI	GKG	345/7	16°17'	5°27'	5390	0	1 N fla			
VI	AT	347	16°14'–16°20.4'	5°26.7'–5°26.8'	5389–7	2	218+1? N dia	5 N fla	2 A mur	1 S fla
VI	EBS	348	16°17.1'–16°19.3'	5°27.2'–5°27.3'	5387–9	3	7+1? N aby	14+1? N dia	1+1 juv A mur	1? S fla
VI	AT	349	16°14.8'–16°24.7'	5°24.7'–5°26.2'	5389–8	2	920 N dia	2 N fla	6 A mur	
VI	EBS	350	16°13.3'–16°14.9'	5°26.7'–5°26.8'	5389	3	3 N aby	8 N dia	1 Ps ach	
VI	AT	351	16°25.2'–16°32.2'	5°27.4'–5°27.1'	5385–7	2	1 N aby	289 N dia	3 N fla	1 S fla

^aType of gear used: AT, Agassiz trawl; EBS, epibenthic sledge; GKG, box-corer (the box number is indicated after the slash). ^bCodes for tubes: 0, no tubes; 1, burrows in pumice stone; 2, horny abandoned chaetopterid tubes; 3, conchiferous tubes; 4, simultaneous presence of items 2 and 3 in the sample. ^cSpecies names: N aby, *Nephasoma abyssorum abyssorum*; N dia, *N. diaphanes*; N fla, *N. flagriferrum*; O ste, *Onchmesoma steenstrupii steenstrupii*; A mur, *Apionsoma murinae*; S fla, *Sluiterina flabellorhynchum*; Ps ach, *Pseudoikedella achaeta*.

Statistical analyses

The relationships between the faunal pattern and some environmental variables measured on the field were analysed using the multivariate CANOCO procedure proposed by ter Braak (1988, 1990). This multivariate method allows the identification of a subset of environmental parameters that correlates best to the biotic structure and may thus be assumed to strongly affect the taxocoenoses. Thus, a data matrix with sipunculan and echiuran species in rows and sampling sites in columns was constructed from the data shown in Table I. The environmental information available consists of several abiotic variables such as: depth of samples taken, the type of gear (dredge) used in the sampling, the presence or absence of biological remains (tubes, shells, tests, etc.) in the samples, and the working zones (WZ) from I to VI which correspond to six spots of intensive sampling where the different stations were located.

Canonical correspondence analysis (CCA) and redundancy analysis (RDA) were performed to assess the relationships between faunal distributions and the whole set of abiotic variables sampled in the field. The forward-selection option was used to determine the minimal set of abiotic parameters that could explain the largest amount of variation in the faunal data. At each step, the statistical significance of the environmental variable added in the course of the forward selection was tested by means of a Monte Carlo permutation test. Variables were taken to be significant if the permutation test derived $P \leq 0.05$.

The multivariate analyses were carried out using version 3.1 of the CANOCO computer program (ter Braak 1988, 1990), whereas plots were made using CANODRAW 3.0 (Smilauer 1992). To investigate the association between faunal and abiotic variables Spearman's coefficient of rank correlation was used.

Results*Systematics*

The sipunculan and echiuran fauna consists of seven species arranged in five genera and two separate phyla. Table I lists the number of records of all species in the different sampling sites under investigation. Each station number is preceded by two letters indicating the type of gear used: AT, Agassiz trawl; EBS, epibenthic sledge; GKG, box-corer (the box number is indicated after the slash).

Nephasoma abyssorum abyssorum (Koren and Danielssen, 1876)

Material. Sta. EBS no. 318, two; Sta. EBS no. 328, one; Sta. AT no. 333, four; Sta. no. 334, 17; Sta. AT no. 337, 28+fragments; Sta. EBS no. 338, three; Sta. AT no. 339, eight+fragments; Sta. EBS no. 340, 32+3?; Sta. AT no. 343, one+fragments; Sta. EBS no. 344, 35; Sta. EBS no. 348, seven+one?; Sta. EBS no. 350, three; Sta. AT no. 351, one.

Description. Trunk 1.5–10 mm long and 0.4–1 mm wide. Introvert 2–4 mm in length and 0.2–0.5 mm in width. Skin smooth, thicker at the posterior end of the trunk. Its surface is marked by small skin bodies, elliptical in shape, 7–12 μm in diameter at the trunk end. Hooks 20–40 μm tall are scattered. Its shape in side-view is rather characteristic with a cylindrical thickness on its convex edge and a lateral flattening on its concave side. Two retractors attached in the trunk.

Remarks. The smooth and cylindrical trunk without papillae and the shape of the hooks help in the identification of the species. In several sampling sites (nos 318, 333, 334, 337–340, 343, 344, 348, 350, 351) it occurs with the common *N. diaphanes* from which it is easily differentiated by the lack of papillae under the microscope. Some specimens have been found in tubes made of shell remains (nos 339, 340, 344) and also in burrows inside small pumice stones (no. 334). This is a common species at bathyal and abyssal depths of the north-east Atlantic and it has been previously recorded from the area by Cutler and Cutler (1987) at 2992–5124 m depth.

***Nephasoma diaphanes* (Gerould, 1913)**

Material. Sta. EBS no. 318, two; Sta. AT no. 319, four; Sta. AT no. 321, five; Sta. AT no. 327, two; Sta. AT no. 333, one; Sta. AT no. 334, one; Sta. AT no. 337, 28; Sta. EBS no. 338, one? fragment; Sta. AT no. 339, 14+fragments; Sta. EBS no. 340, five; Sta. GKG no. 341/4, one; Sta. GKG no. 341/8, one; Sta. AT no. 343, six+fragments; Sta. EBS no. 344, three; Sta. AT no. 347, 218+one?; Sta. EBS no. 348, 14+one?; Sta. AT no. 349, 920+fragments; Sta. EBS no. 350, eight; Sta. AT no. 351, 289+fragments.

Description. Trunk 1.2–50 mm long and 0.5–2 mm wide. Introvert 2–24 mm in length and 0.2–1.5 mm in width. Scattered hooks, 20–60 µm tall. Digitiform papillae 15–30 µm in height at the trunk end. Large specimens with brown pigmented papillae up to 100 µm in diameter covering the posterior half of the trunk. In some everted introverts lobes instead of tentacles could be observed. Two retractors originate near the middle or posterior third of the trunk. One specimen coming from Sta. AT 349 lacks hooks.

Remarks. A cylindrical appearance and a trunk covered by papillae fits the description of this species in a broad sense. Diagnostic for the species is the reduction of tentacles to lobes, but unless the introverts are fully everted, it is practically impossible to assert this character with thin introverts and preserved material. In this way, identifications were achieved under the specific level. Many specimens have been found in abandoned tubes of polychaetes (nos 337, 339, 340, 343, 347, 349, 351) developing large and brown papillae up to 100 µm in diameter. Other few specimens were found inside a sponge (nos 347, 349) and inside an abandoned scaphopod shell (no. 350).

Nephasoma diaphanes has been recorded as a cosmopolitan, deep-water species (Cutler 1994). Similar to our findings, Cutler and Cutler (1987) have previously recorded the species inside polychaete tubes and at abyssal depths.

***Nephasoma flagriferum* (Selenka, 1885)**

Material. Sta. GKG no. 345/7, one; Sta. AT no. 347, five+fragments; Sta. AT no. 349, two; Sta. AT no. 351, three.

Description. Trunk 85–105 mm long. Trunk width: 2–4 mm. Introvert a little shorter. Its width 2 mm. Tail of 4–10 mm long. Bladder-like papillae around the posterior end, about 0.5 mm in diameter. Hooks absent. Two retractor muscles originate in the anterior-middle third of the trunk. Nephridiopores 1 mm in front of the anus.

Remarks. This species is distinctive because of the presence of a tail at the end of the trunk. The lack of hooks and the presence of bladder-like papillae along the posterior part of the trunk distinguish this species from other tailed *Nephasoma*. The species is mainly known from bathyal and abyssal bottoms of the eastern North Atlantic Ocean. It has been found near the investigated area by Cutler (1977) in the Gulf of Guinea at abyssal depths.

***Onchnesoma steenstrupii steenstrupii* Koren and Danielssen, 1876**

Material. Sta. EBS no. 318, two.

Description. Trunk 2–4.5 mm long and 1–2 mm wide. Introvert 3–5 mm in length and 1 mm in width. Pyriform in appearance with the posterior end finished in a blunt point. Over the surface of the trunk are conspicuous small wart-like papillae. Several longitudinal keel-like structures on the end of the trunk. A single retractor originates from the end of the trunk.

Remarks. The presence of small papillae covering the surface of the trunk and the keel-like structures on the posterior end of the trunk are diagnostic for this species. The species is common in the North Atlantic Ocean and is known also in the South Atlantic, Indian and Pacific Oceans at depths of 0–2990 m. It has been found previously in the investigated area by Cutler and Cutler (1987), but at bathyal depths. Finding our specimens at 5126 m extends the vertical known range of this species to abyssal depths.

***Apionsoma murinae* (Cutler, 1969)**

Material. Sta. AT no. 339, 10+one?; Sta. AT no. 343, one+one fragment; Sta. AT no. 347, two; Sta. EBS no. 348, one+one juvenile; Sta. AT no. 349, six.

Description. Trunk 1.5–15 mm long and about 1 mm wide. Introvert 4–20 mm in length (up to three times longer than trunk) and about 0.3 mm in width. Skin smooth and thick mostly, translucent in some parts. Scattered ovoid papillae up to 0.1 mm in diameter over the middle part of the trunk. Large mammiform papillae up to 0.2 mm in diameter are located at the posterior end of the trunk. Hooks not observed since the apical part is missing. Four retractors originate in the central or posterior third of the trunk. Bilobed nephridia (no. 339) in some specimens dissected, others unilobed (nos 347, 349). Nephridiopores are a little in front of anus.

Remarks. The presence of an introvert longer than the trunk and large papillae over the trunk are diagnostic for *A. murinae*. Cutler (1969) recognized two subspecies based on the presence/absence of a secondary lobe on the nephridia. Since conspicuous lobes have not been observed in all the dissected material and the external characters to distinguish subspecies are problematical, it seems more advisable to identify the specimens to specific level. The species is widespread in cold waters (up to 5260 m depth) across the northern Atlantic and down to 15°S. It has been previously recorded north to the investigated area by Cutler and Cutler (1987).

Shuiterina flabellorhynchum Murina, 1976

Material. Sta. AT no. 321, one; Sta. AT no. 327, one+one?; Sta. EBS no. 340, one?; Sta. AT no. 343, one; Sta. AT no. 347, one+fragment; Sta. EBS no. 348, one?; Sta. AT no. 351, one.

Description. Trunk 9–70 mm long and 3–30 mm wide. Proboscis lacking, in a few specimens the basal part preserved. Ventral setae absent. Colour beige. Skin smooth. Translucent in the middle of the trunk, more opaque and contracted at both extremes. Trunk cavity with long intestine filled with muddy balls. Single gonoduct on the left side of the nerve cord, with basal gonostome connected by a long stalk. Some specimens (from nos 344, 348) are referred with doubt since gonoducts were not observed. Anal vesicles sac-like with numerous, thin, unbranched tubules on their surface.

Remarks. This species is distinctive because of its single gonoduct with a basal gonostome and because of the absence of setae. Unfortunately, the bifid/single proboscis could not be ascertained in any of the collected specimens. The species is known mainly from Antarctic waters at depths of 2240–6070 m (Murina 1976; Saiz-Salinas et al. 2000). It has been also recorded in the Atlantic near the Cape Verde Islands at 5880 m (DattaGupta 1981). Therefore the present records seem to be in the middle of the distribution of the species.

Pseudoikedella achaeta (Zenkevitch, 1958)

Material. Sta. AT no. 319, one; Sta. AT no. 327, one; Sta. EBS no. 344, two juveniles; Sta. EBS no. 350, one.

Description. Trunk 9–30 mm long and 3–6 mm wide. Proboscis missing. Ventral setae absent. Opaque and contracted in the anterior part of the trunk, whereas translucent in the posterior part. Internally about 20–30 bands of longitudinal musculature could be observed in the contracted part of the trunk. A single gonoduct with terminal gonostome. Paired anal vesicles long, thin, and tubular without ramifications.

Remarks. The general appearance of the worms, and especially the single gonoduct with a terminal gonostome, show these specimens belong to *Pseudoikedella achaeta*. Most of the previous records of the species came from the North Pacific and the Tasman Sea at depths of 3450–5540 m (Zenkevitch 1958, 1966; Zenkevitch and Murina 1976). Murina (1978) and Saiz Salinas et al. (2000) reported further specimens from Antarctic waters at 1300–3490 m. The species has been recently recorded in the North Atlantic by Biseswar (2005), therefore this finding is an extension of its range towards the deep waters of the South Atlantic.

Gradient analysis

All ordination methods and their constrained counterparts were performed by using the CANOCO package with the species list and the four abiotic variables investigated (working zone, type of dredge, depth of the samples, cryptic life inside tubes). Methods based on the linear response model (PCA and RDA) perform better than those that rely on the unimodal response (CA, CCA). RDA is especially recommended when the samples are representative

of a narrow environmental gradient and taxa appear to respond in a linear fashion to the environmental gradients. The first two RDA axes capture 52% of the cumulative variance of the faunal data, a slightly larger proportion of the variance than is explained by both CCA and detrended CCA. Forward selection and unrestricted Monte Carlo permutation tests indicate that only two (WZ, dredge) of the four abiotic variables previously introduced make statistically significant contributions to explaining the variance in the faunal data. The most significant of these is WZ, which captures 34% of the total variance explained by the whole set of abiotic variables, followed by type of dredge (22%). A Monte Carlo permutation test of the trace statistics, which gives an overall test of the effect on the faunal data of the two variables selected as active, resulted in a *P* value of 0.16.

The result of RDA, incorporating the two forward-selected abiotic variables, is given in Table II and illustrated in Figure 2 as a sites–indicator taxa–abiotic triplot. Two neat latitudinal gradients (EBS and AT gradients) from the right to the left of the plot are revealed for each type of dredge used in this faunal survey. The first abiotic variable, working zone, arranges all the sampling sites from the south to the north of the Angola Basin, whereas the type of dredge separates the fauna well according to the different sampling procedure. The importance of the two forward-selected abiotic variables is shown by their corresponding long vectors in the plot of Figure 2.

Simultaneous plots of species in the ordination diagram of Figure 2 reflect their preferences with respect to sampling sites and abiotic vectors. From this plot prospective indicator taxa could be identified that might be sensitive to some sampling sites. Again, the length of the species arrows indicates the importance of the species in the final faunal survey. Thus, most species move along axis 1, such as *Nephasoma diaphanes*, *N. flagriferum*, *Apionsoma murinae*, and *Onchnesoma steenstrupii steenstrupii*. The reasons are different, for example the first species, *N. diaphanes*, is ubiquitous throughout all WZ, but locally abundant in the sampling sites of WZ VI. *Nephasoma flagriferum* is only present in WZ VI, whereas *Apionsoma murinae* was only collected at different sites of WZ IV, V, and VI. *Onchnesoma steenstrupii steenstrupii* also has a long arrow in the final plot of Figure 2, but along the positive part of axis 1. This indicates its preference for sampling site no. 318 which was sampled by the EBS dredge. Only *N. abyssorum abyssorum* showed preferences along the positive part of axis 2 (Figure 2), indicating its ubiquitous presence in all WZ with local abundant peaks at some sampling sites of WZ III, IV, and V. Echiuran species are quite rare and occasional in the faunal survey and do not exhibit any indicator value in the final plot.

Spearman's rank correlation coefficients and Type I error probabilities between the spatial distribution of the species identified and the abiotic variables investigated are presented in Table III. Only two abiotic parameters were significantly correlated with relatively few species of the faunal survey. WZ is significantly correlated with those species

Table II. Summary statistics for the first four axes of RDA, with 18 sites, seven species and two forward-selected abiotic variables.

Axes	Axis 1	Axis 2	Axis 3	Axis 4	Total variance
Eigenvalues	0.49	0.03	0.29	0.10	1.00
Species–environment correlations	0.81	0.42	0.00	0.00	
Cumulative percentage variance					
of species data	49.7	52.2	80.9	90.9	
of species–environment relation	95.2	100	0.00	0.00	
Sum of all unconstrained eigenvalues					1.0
Sum of all canonical eigenvalues					0.52

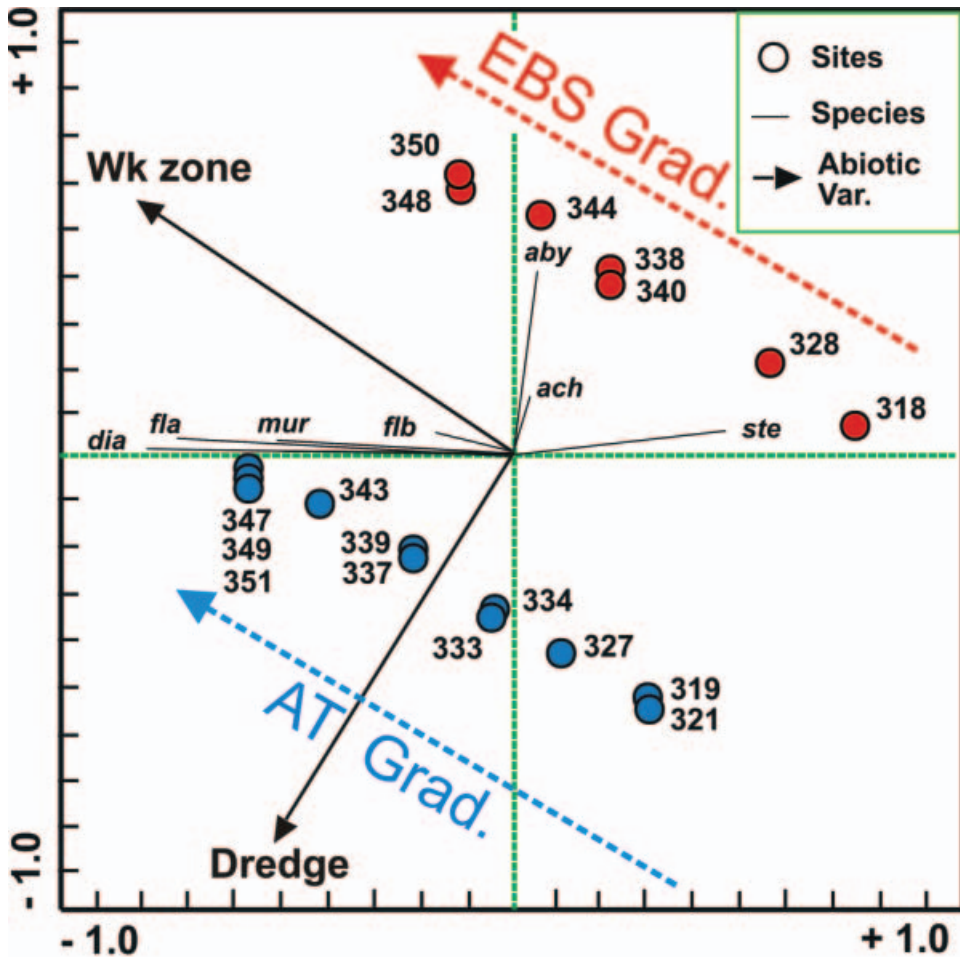


Figure 2. Triplot of the RDA ordination analysis showing the relationship among identified species, sampling sites, and the two significant selected abiotic variables (Dredge, type of dredge employed; Wk zone, working zone). Species: aby, *Nephasoma abyssorum abyssorum*; ach, *Pseudoikedella achaeta*; dia, *N. diaphanes*; fla, *N. flagriferum*; flb, *Sluiterina flabellorhynchum*; mur, *Apionsoma murinae*; ste, *Onchmesoma steenstrupii steenstrupii*.

that move along the negative part of axis 1 in the ordination plot, suggesting the existence of a latitudinal gradient across the Angola Basin. On the other hand, only one species of sipunculans, *Nephasoma diaphanes*, is positively correlated with the availability of horny void tubes of polychaetes, which are remarkably abundant in the sampling sites of WZ VI.

Table III. Spearman's rank correlation coefficients (r_s) and Type I error probabilities ($P > \alpha$) between the species distribution and different abiotic parameters. Species are listed in descending order of correlation coefficient values.

Species	Abiotic parameter	r_s	P
<i>Nephasoma diaphanes</i>	Working zone	0.69	0.0044
<i>Nephasoma flagriferum</i>	Working zone	0.57	0.0191
<i>Nephasoma diaphanes</i>	Void tubes	0.53	0.028
<i>Apionsoma murinae</i>	Working zone	0.52	0.03

Discussion

The faunal survey of sipunculan and echiuran taxocoenoses was carried out as part of a larger study of the deep-sea benthos along the Angola Basin. About 1700 specimens of this fauna were collected, of which only 12 specimens were from the phylum Echiura. The greater part of the Angola Basin consists of soft bottoms inhabited by a sipunculan population composed almost entirely of *Nephasoma diaphanes*. The results of the box-corer (GKG) show extremely low levels of sipunculan abundance in the abyss of the area investigated. Only three of the 19 boxes deployed collected one specimen per box, indicating areas of extremely low density of sipunculans in quantitative terms (one specimen per 0.25 m²). By contrast, trawls were more successful in collecting sipunculans. One trawl (no. 349) was exceptionally productive, since it yielded almost 1000 individuals of *Nephasoma diaphanes* from a single haul. Comparing the low figures of the box-corer samples with those of the trawls, we can infer the existence of dense aggregations of sipunculans in bottoms where empty polychaete tubes are available for the cryptobiotic lifestyle of this sipunculan species. This indicates an opportunistic distribution of sipunculans with a contagious or gregarious pattern in those sampling sites of the northernmost WZ VI.

The number of species of sipunculans obtained in this study is relatively low, but is in general consistent with the relative poverty of abyssal sipunculan fauna as characterized by Murina (1975, 1977, 1984). In her bathymetrical analysis of sipunculans in all world oceans this author was able to list only five endemic abyssal species, whereas a further 18 species could penetrate the abyss from shallower depths. The species collected in this study all belong to this last category, i.e. eurybathic species. It is worth mentioning that *Onchnesoma steenstrupii steenstrupii* has been recorded in this study from deeper (5126 m) than previously recorded in the Atlantic Ocean according to the review of Murina (1993).

In terms of horizontal distribution, almost all of the species have geographical ranges that are known to encompass the survey area or might be expected to do so. The only exception is the record of the echiuran *Pseudoikedella achaeta*, which has been found for the first time in the South Atlantic abyss, although it was previously known from the Antarctic and the North Atlantic (Biseswar 2005). Minor but interesting expansions towards the South Atlantic from the Cape Verde Islands and the Guinea Basin are noted in the echiuran *Shuiterina flabellorhynchum* and the sipunculan *Nephasoma flagriferum*, respectively.

The differences in faunal composition between sampling sites are likely to reflect gradients in both physical conditions and food factors. Physical factors such as the availability of empty polychaete tubes are of primary importance for some sipunculan species which are able to exploit cryptic habitats inside abandoned shells of molluscs and worm tubes (Murina 1984). This has been confirmed in this study by a correlation analysis with the most abundant species, *Nephasoma diaphanes*, which is known both to live freely, making burrows in sediments, and to seek protective shelter in discarded mollusc shells, empty polychaete tubes, or foraminiferan tests (see compilation in Saiz Salinas (1993)). On the other hand, the additional influence of latitude as indicated by the analysis of the sipunculan taxocoenoses may reflect the effects of other unmeasured variables such as food supply, not only at the time of sampling but also during previous periods of sampling. In this study, three species of sipunculans, *N. diaphanes*, *N. flagriferum*, and *Apionsoma murinae*, show significant correlations with WZ. The existence of a better food supply in some sampling sites along WZ is envisaged by the general study of Kröncke and Türkay (2003), who measured higher total organic carbon and chlorophyll *a* contents in the surface of the sediments of WZ IV–VI than in the southern WZ I–III. They infer lower food

availability in the southern areas than the northern. The differences are caused by the Angola–Benguela upwelling, which separates two oceanographic regimes pumped, respectively, by the warm South Equatorial Counter Current in the north and the cold Benguela Oceanic Current in the south. North of this water front, which crosses the transect investigated in the middle of the six working zones, the Angola Basin is quite productive, whereas south of the front the bottoms are more oligotrophic. However, the existence of dense beds of abandoned polychaete tubes on the bottoms of the northernmost sampling sites may be the result of pulses of catastrophic events during earlier previous periods, which could have brought about a large-scale demise of tubicolous polychaetes. Once the polychaete tubes were empty, the sipunculans found an additional habitat in which to settle provided that there was enough food to maintain large numbers of individuals.

In conclusion, there exists a latitudinal gradient of sipunculans from southern areas to northern areas of the Angola Basin as revealed by the ordination analysis. Their assemblage structure is significantly related to WZ, from low abundances in the southern areas towards dense aggregations in the northernmost area. This has been related to the availability of empty polychaete tubes which provide suitable shelter for the cryptobiotic lifestyle of *Nephasoma diaphanes*. Also a better nutrient supply to the benthos in the northern working areas of the Angola Basin as quantified by Kröncke and Türkay (2003) contribute to the existence of patches of high abundances of this sipunculan species.

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