Benthic Communities in Waters off Angola

- Master Thesis Marine Biology -

By

Gesine Lange

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1st supervisor:

Dr. Michael Zettler

Leibniz-Institut für Ostseeforschung Warnemünde
Biologische Meereskunde
Seestraße 15
D-18119 Rostock
Phone: +49 381 5197 236
Fax: +49 381 5197 440
E-Mail: michael.zettler@io-warnemuende.de

2nd supervisor:

Dr. rer. nat. Wolfgang Wranik

Universität Rostock
Institut für Biowissenschaften
Albert-Einstein-Str. 3b
D-18051 Rostock
Phone: +49 381 498 6060
Fax: +49 381 498 6052
E-mail: wolfgang.wranik@uni-rostock.de

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Zusammenfassung

Der Schelf vor der Küste Angolas wurde in den Jahren 2004 und 2011, während Forschungsreisen des Leibniz-Instituts für Ostseeforschung, beprobt und auf die Zusammensetzung seiner makrozoobenthischen Gemeinschaften untersucht. Insgesamt wurden 89 Benthosproben, an 42 Stationen, aus jeweils unterschiedlichen Wassertiefen zwischen 19 und 340 m genommen. Der Beprobungsraum erstreckte sich von der, zu Angola gehörenden, Cabinda Provinz (ca. 5° S) bis zur namibianischen Grenze (ca. 17° S). Innerhalb dieses Areals variierte die Temperatur des Bodenwassers zwischen 13,6° C im Süden und 20,1° C im Norden. Unterschiedliche Sedimentbeschaffenheiten wurden festgestellt. Im gesamten Untersuchungsgebiet wurden 893 verschiedene Arten gefunden. In den Greiferproben konnten 618 Arten ausgemacht werden, von denen 36 % zu den Polychaeten gehörten. Die Crustaceen machten 33 % der Diversität aus. Ihnen folgten Mollusken (20 %), „Andere“ (8 %) und Echinodermaten (3 %). Mit 95 Arten war Station 121 (7,8° S) am artenreichsten. Weiterhin zeigten die Stationen Be71 (9,4° S), SU5 (9,5° S) und Na5 (15° S) mit circa 70 Arten eine hohe Diversität. Station BE9 (13,9° S) wies mit 11 verschiedenen Arten die geringste Diversität auf. In den Dredgeproben wurden insgesamt 579 unterschiedliche Arten bestimmt. Hier stellten die Crustaceen die dominanteste Gruppe (36 %) dar. Polychaeten machten 27 % der Gesamtdiversität aus. Ansonsten stimmten die Ergebnisse der Dredgeproben, hinsichtlich der Artenvielfalt, mit denen der Greifer überein. Die mit Hilfe des Shannon Index ermittelten Diversitätswerte, lagen für einen weiten Bereich des Schelfs (7° S bis 15° S) über 3,5 und teilweise sogar über 4,5. Polychaeten (65 %) dominierten klar die Abundanzen des Makrozoobenthos vor Angola. Die Station mit der höchsten Abundanz war Station Na5. Hier traten 34396 Individuen/m² auf. Station 70 (9,4° S) hingegen zeigte mit 170 Individuen/m² die geringste Abundanz. Die Biomassen variierten zwischen 4,8 g/m an der Station 87 (7,2° S) und 427,7 g/m an der Station KU3, welche an der Grenze zu Namibia liegt. Die Biomassen der Stationen im Süden Angolas, vor allem im Bereich der Kunene-Mündung, an der Grenze zu Namibia, wurden maßgeblich von den Mollusken bestimmt. Die hier beobachteten Schlüsselarten, welche sowohl Biomasse als auch Abundanzen dominierten, waren die Schnecken *Nassarius vinctus* und *Nassarius angolensis*, sowie die Muschel *Nuculana bicuspidata*. In dieser Region war außerdem die starke Präsenz der Polychaeten *Cossura coasta*, *Diopatra neapolitana capensis* und *Galathowenia* sp. auffällig. Die letzteren beiden wurden auch vermehrt in weiter nördlichen Gebieten gefunden. Der Polychaet *Chaetozone setosa* trat auffallend häufig vor Sumbe, Lobito und Namibe auf. Andere Arten, wie die Polychaeten *Paraprionо pinnata* und *Prionospio* sp. sowie der Amphipode *Ampelisca* sp. waren entlang des gesamten angolanischen Schelfs stark vertreten. Hinsichtlich der Gesamtdiversität dieses Schelfgebietes konnte festgestellt werden, dass kein latitudinaler Gradient erkennbar ist. Stattdessen wurden Schwankungen der Artenvielfalt mit Peaks an verschiedenen Breitengraden beobachtet. Vermutlich beeinflussen die unterschiedlichen Sedimentqualitäten die Biodiversität des jeweiligen Standortes. So waren beispielsweise schlickige und schillhaltige Substrate mit Diatomeen in der Regel artenreich. Die vergleichsweise geringen Artenzahlen im äußersten Süden Angolas lassen sich wahrscheinlich auf die dortigen, niedrigen Sauerstoffgehalte (≤ 1 ml/l) zurückführen, die nicht von allen Arten toleriert werden. Dementsprechend sind die Abundanzen und Biomassen der Organismen, die an diese Lebensbedingungen angepasst sind, hoch.

Summary

The shelf off Angola was sampled during a research cruise of the Leibniz Institute for Baltic Sea Research Warnemünde in 2004 and 2011. The samples were analyzed with regard to composition of macrozoobenthic communities. A total of 89 benthos samples were taken at 42 stations with different water depths ranging from 19 to 340 m. The sampling area extended from the Cabinda Province (about 5° S) to the Namibian border (approx. 17° S). Within this area the temperature of the bottom water varied between 13.6° C in the south and 20.1° C in the north. Different sediment textures were observed. 893 different species were found in the whole of the investigated area. 618 species were identified in the grab samples and 36 % of them were polychaetes. Crustaceans contributed 33 % to the diversity. They were followed by mollusks (20 %), “other” (8 %) and echinoderms (3 %). Station 121 (7.8° S) was the most species-rich one with 95 taxa. Furthermore, the stations Be71 (9.4° S), SU5 (9.5 ° S) and Na5 (15° S) showed a high diversity with about 70 species. Station BE9 (13.9° S) with 11 different taxa revealed the lowest diversity. A total of 579 species were determined in the dredge samples. Crustaceans presented the most dominant group (36 %) in this case. Polychaetes amounted to 27 % of the total diversity. Apart from this, the results of the dredge samples were consistent with the results of the grab samples in terms of species diversity. The diversity values, which were calculated by means of the Shannon index, were above 3.5 and in some cases even above 4.5 for a wide range of the shelf. Polychaetes (65 %) clearly dominated the abundances of benthic invertebrates off Angola. The station with the highest abundance was station Na5 with 34396 individuals/m². Station 70 (9.4° S), however, showed the lowest abundance with 170 individuals/m². The biomasses varied between 4.8 g/m² at station 87 (7.2° S) and 427.7 g/m² at station KU3, which is located at the border of Namibia. The biomasses of the stations in the south of Angola, particularly in the area of the Kunene River estuary at the border to Namibia, were significantly characterized by mollusks. The key species observed on-site, dominating both abundance and biomass, were the snails *Nassarius vinctus* and *Nassarius angolensis* as well as the clam *Nuculana bicuspidata*. The strong presence of the polychaetes *Cossura coasta*, *Diopatra neapolitana capensis* and *Galathowenia* sp. in this region was also conspicuous. The latter two species were also increasingly found in more northern areas. The polychaete *Chaetozone setosa* occurred remarkably frequently near Sumbe, Lobito and Namibe. Other species, such as the polychaetes *Paraprionospio pinnata* and *Prionospio* sp. as well as the amphipod *Ampelisca* sp., were strongly represented along the entire Angolan continental shelf. Regarding the overall diversity of the shelf no latitudinal gradient could be detected. Instead, fluctuations in species diversity with peaks at different latitudes were revealed. Biodiversity is probably affected by the different sediment qualities of the respective location. Silty substrates with small shell fragments and diatoms, for instance, are usually rich in species. The comparatively small numbers of species in the most southern part of Angola are probably caused by the prevailing low oxygen levels (≤ 1 ml/l) that cannot be tolerated by all species. Correspondingly high abundances and biomasses occurred among organisms that are adapted to this environmental condition.

1 Introduction

Oceans cover about 70 percent of our planet. Especially since the 19^{th} century, probably as a consequence of the increasing use of the seas, our knowledge about the oceans has significantly improved. This also includes the so-called benthal.

The benthal comprises the bottom and the edge of the sea (Sommer, 2005) mainly consisting of sediments. Marine sediments which comprise a range from coarse mobile particles to clay (Gray, 1974) play an important role as they are one of the largest habitat types on earth. They cover over 80 percent of the ocean floor and provide a habitat for animals living attached on the substrate surface (epifauna) or buried in the soft bottom (infauna). All sessile and motile organisms of the benthal are collectively called benthos. The epifauna represents spatially the minor part of the benthic organisms by occupying less than 10 percent of the entire sea floor area. Large numbers of epifaunal species are found in very shallow water, particularly in intertidal zones with many micro-environments. These animals are associated with rocks, stones, shells and plants while the infauna lives buried in soft sediments like mud and sand using the surface layers of the three-dimensional sea bottom. Infaunal communities occupy more than half of the global surface and are fully developed below the intertidal zone (Thorson, 1957).

All in all, the benthic biomass is dominated by macrofaunal invertebrates. Macrobenthos means organisms, which are larger than 1 mm (Sommer, 2005). The dominant invertebrates of the benthal are different species of polychaetes, crustaceans, echinoderms and mollusks. All these organism groups are well-adapted to the benthic environment. The animals influence this environment significantly with their occurrence. They have a main impact on the structure of the surrounding sediment (Lenihan & Micheli, 2001). Many benthic organisms can be considered as ecosystem engineers because they change the availability of resources for other organisms directly or indirectly by modifying the physical conditions (Jones et al., 1994). The soft-sediment animals cause bioturbation through motion, oxygenation and food acquisition. Due to these processes, the animals become essential for other organisms, since they build habitats for smaller species, recycle nutrients, detoxify pollutants and increase the exchange of matter on the seabed as well as between sediment and water (Zettler et al., 2009; Menot et al., 2010).

Another function of macrozoobenthos relevant to the ecosystem is its importance as a trophic link, especially in coastal areas. Generally, it represents an important food source for birds and fish.

It must be considered that abundance, biomass and diversity in benthic animal communities vary enormously with time and space while reflecting the prevailing environmental conditions. Since the Convention on Biological Diversity in Rio de Janeiro in 1992, the aspect of biodiversity and its global variations has gained in political importance over the last two decades and became the focus of human attention, leading to numerous investigations on diversity.

Biodiversity can be defined as the variety of life on earth and the natural pattern it forms (OSPAR Commission, 2010). A major part of it is the species diversity of communities within an ecosystem. The role of biodiversity was discussed for a long time but now it is clear known to be important for proper functioning of marine ecosystems and functioning of global ecosystems at all. A high diverse system has a greater resilience against intrusions (world oceans review, 2010). Biological diversity has also a high value for human regarding ethical, esthetic and economic reasons. These led to a permanent risk of marine overuse and exploitation. Many ecosystems, habitats and species are sensitive to pressure from human activities. This is reflected in the fact that global diversity has declined in recent years. With the decrease of species, communities may become instable. It is necessary to get an overview of community structures and its possible changes to asses which factors influence or harm a biological community. Statements of status, distribution and changes in diversity are the basis for biodiversity conservation.

Several studies on global biodiversity revealed that there is an obvious gradient of increasing species diversity from poles to the tropics in the terrestrial realm. The increase of biodiversity with decreasing latitude is a fundamental concept in terrestrial ecology (Clarke, 1992; Ellingsen & Gray, 2002; Hillebrand, 2004; Konar et al., 2010). Opinions about a similar diversity gradient in the ocean varied over the years and the research results are still ambiguous (Renaud et al., 2009). Clark (1992) noted that it is usually assumed that a similar loss of species from low to high latitudes is traceable in the sea. The author furthermore mentions that the increasing species richness toward the tropics was found for hard-substratum epifauna, bivalves and gastropods. However, the species number of the soft-bottom inhabiting infauna was broadly the same for arctic, temperate and tropic latitudes. Also Hillebrand (2004) said that the sediment fauna is an exception in the global diversity gradient. Although some marine groups show a strong latitudinal gradient a convincing evidence for a general biodiversity decline toward the poles is missing. Global patterns of marine biodiversity are doubted to be as consistent as terrestrial ones. Hillebrand (2004) further explicates that, on average, significant latitudinal gradients for marine organisms exist. However, these gradients differ in habitat type, region and organism group. Thus, it seems to be unlikely that latitude is the ultimate cause of the marine diversity gradient.

In terrestrial systems changes in temperature are likely to be the crucial factor for determining the global diversity gradients. In the marine milieu there are a number of other local and large-scale factors that have a greater influence on biodiversity than temperature, whose variations over a certain distance are not as great as on land. Latitudinal trends in the ocean are driven by mechanisms like large-scale oceanographic conditions, e. g. the global conveyer belt and currents systems. Physical differences between neighboring water masses are strongly involved in the formation of zoogeographical boundaries (Longhurst, 1958). Furthermore, local abiotic features like substrate, sediment grain size, salinity, oxygen availability, currents and upwelling as well as freshwater- and nutrient input influence marine diversity as well. Last but not least it has to be mentioned that also biological factors have an important impact on biodiversity. These are primary production rates, local assemblages of herbivores and predators, dispersal mechanisms, prevalence of larval stages with differing dispersal ranges and speciation rates (Konar et al., 2010). Particularly, larval stages of benthic organisms are an important factor concerning species distribution and thus the species composition and richness in a region. Benthic organisms with free living planktonic larvae are able to spread farther than those without pelagic larvae. In this connection, larger-sized species generally reach a greater dispersal (Scott et al., 2012). The life-average of pelagic larvae in case of the most frequent macrozoobenthos (polychaetes, mollusks and echinoderms) is approximately three weeks before settling on the sea bottom. This is valid for cold- as well as warm-water species. The settling depends on substratum, light conditions and salinity. Due to locality, current system and varying food availability during the pelagic stage the colonization success shows large fluctuations in year and season (Thorson, 1957; Moore, 1958). As a result, biodiversity of benthic communities is variable, too. Le Loeuff & von Cosel (1998) demonstrated the dependence of benthic biodiversity on the substratum. According to them marine biodiversity increases only conditionally with decreasing latitude. The choice of sediment is essential for the distribution of benthic organisms (Longhurst, 1958) and depends on grain size, organic matter, microbiological assemblages and trophic interactions (Snelgrove & Butman, 1994).

This study deals with benthic communities of the Angolan continental shelf. Their biodiversity and composition is subjected to the conditions mentioned before. Although benthic shelf diversity was globally investigated by several authors (Longhurst, 1958; Gray, 1994; Le Loeuff & Intès, 1999; Bergen et al., 2001; Ellingsen & Gray, 2002; Clarke et al., 2004; Joydas & Damodaran, 2009; Oliver et al., 2011) concrete information about benthos off Angola are lacking.

This is the first study concentrating on coastal macrozoobenthos of the whole Angolan continental shelf with such a large sample size. The objective of this study is to give an informative overview of species composition and distribution in benthic communities. It will be shown whether the assumption of the north-south-gradient in biodiversity is also valid for waters off Angola.

2 Material and Methods

2. 1 Study Area

The Angolan coastline is about 800 nautical miles (approximately 1482 km) long. The continental shelf and upper slope of Angola extends from about 5° S to 17° S. Thus, the area has a tropical climate in the north and a temperate climate in the south leading to a zoogeographic boundary along the Angolan coast that separates tropical fauna of Guinean origin from temperate fauna of the Benguela upwelling system.

The northern part of the region can be typified by a shallow and pronounced thermocline from January to April. Its upper boundary is at about 10 m depth and becomes deeper towards the south where it reaches a depth of 25 to 50 m. The halocline of the northern area is also very sharp (Bianchi, 1992). Main reasons for this are the increased rainfall at this season and the runoff from the Congo River, whose outflow generally produces low salinity (Wauthy, 1977). The upper water layers with a thickness ranging from 30 to 40 m consist of equatorial water with low salinity, high temperature and oxygen levels from above 2 ml/l to 100 m depth. At the shelf edge, oxygen content declines slightly over 1 ml/l. There is a prominent thermocline at depth ranging from 25 to 50 m till Benguela. The surface temperature reaches 28 ° C and decreases gradually southward. Bottom temperature to 50 m can exceed 20° C from Cabinda to Lobito (Bianchi, 1992). A study of Monteiro & van der Plas (2006) revealed that bottom temperatures on the Angolan shelf at Lobito ranged from 14 to 18° C over a period from 1994 to 2003 while surface temperatures varied between 21 and 29° C. It is further depicted that salinity at the same location and the same period is relatively constant at 35.5 and 35.6 respectively. However, surface salinity changed significantly over the years from 33 to 35.8. Oxygen contents varied mostly between 1 and 2 ml/l at the bottom except for oxygen minimums (0.5 to1 ml/l) in the years 1997 and 2002. The oxygen values at the surface were comparably high with a range from 3 to 6 ml/l (Fig. 1).

The southern shelf from Tombua to Cunene is a frontal system and a convergence zone between the Angola Current and the Benguela Current (Bianchi, 1992). South Angola is characterized by nutrient-rich, clear and agitated water. The surface shelf water has an oxygen saturation of 60 percent because of active upwelling of oxygen depleted water (Mohrholz et al., 2008). Also Le Loeuff and von Cosel (1998) stated that there is periodical upwelling of cold and salty water off Angola. It is suggested that upwelling here is no Ekman-upwelling because it occurs at times when favorable winds to upwelling are extremely weak (Bianchi, 1992).

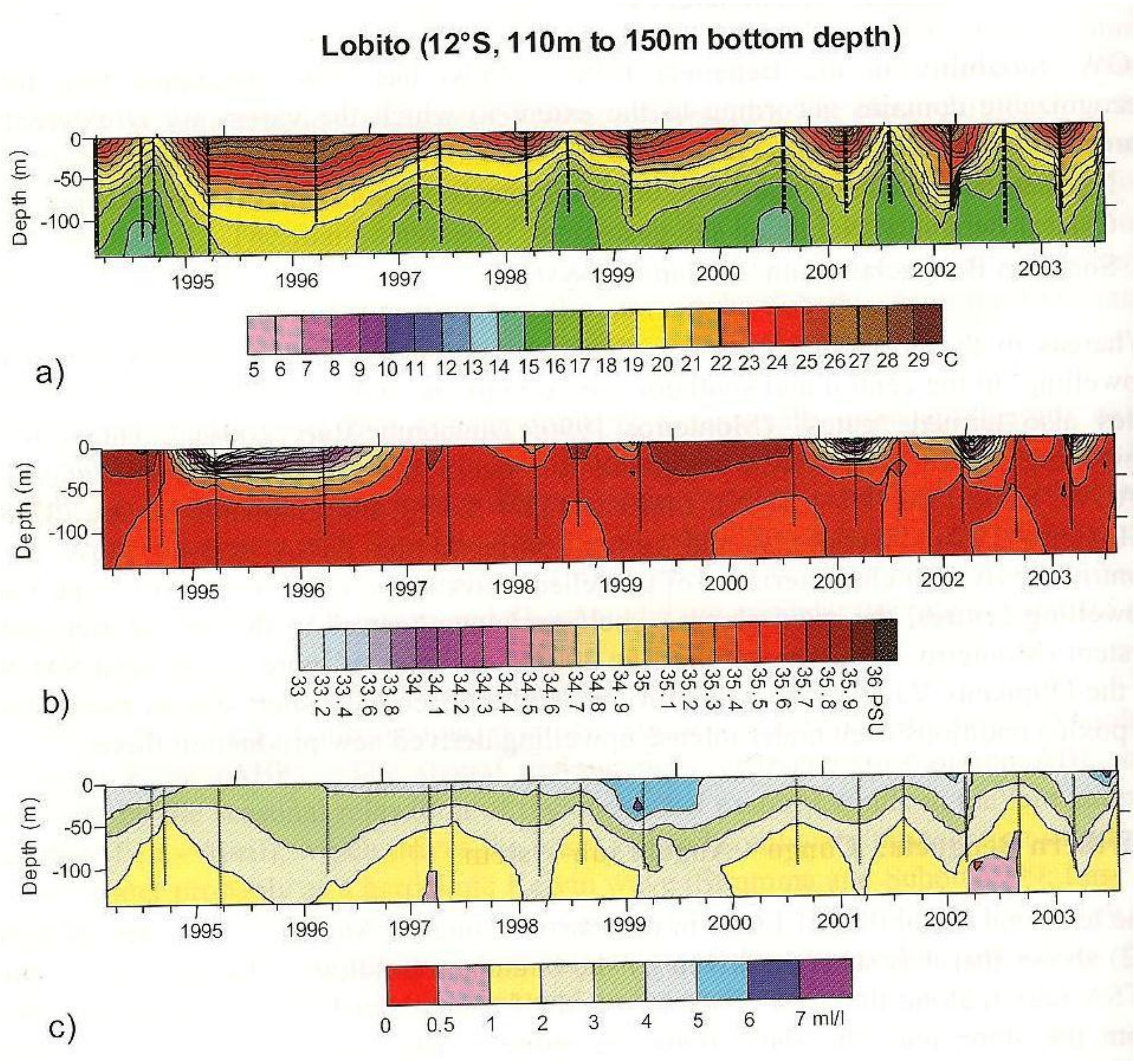

Fig. 1: a) temperature, b) salinity, c) oxygen on the Angolan shelf at Lobito (12° S) to 150 m depth (Monteiro & van der Plas, 2006)

As stated above, ocean currents affect biodiversity enormously. They influence temperature, salinity and oxygen saturation and are able to drift larvae away. The African west coast south of the Equator and consequently the Angolan shelf is strongly affected by the Angola-Benguela current system.

Angola is dominated by the South Equatorial Counter Current, the Equatorial Under Current (Fig. 2), the circulation around the virtually seasonal Angola Dome and the Angola Current (Steele et al., 2009). The latter is formed by the Guinea-Congo Under Current and the South Equatorial Under Current and it is also the eastern boundary of the Angola gyre, driven by the South Equatorial Countercurrent and centered offshore around 1° S and 4° E (Monteiro & van der Plas, 2006; Hogan et al., 2012). The cyclonic Angola gyre (Fig. 2) transports South Atlantic Central Water. The residence time of this water mass within the gyre is about 50 years. Continuous remineralisation of organic matter generates an oxygen loss and an increase in nutrients. Hence, the Angola gyre has a high primary production and therefore a high zooplankton biomass (Blackburn, 1981). High productivity is maintained by additional nutrient input from the Congo River and by open ocean upwelling in the Angola gyre (Mohrholz et al., 2008). Off Angola the southward-flowing Angola Current (Fig. 2) is found between the surface and 200 m. This coastal current reaches speeds of 70 cm/s at the surface and 88 cm/s at the subsurface (Steele et al., 2009; Schmidt & Eggert, 2012). It transports tropical warm water that is oxygen-saturated, poor in nutrients and has a high salinity over 36 (Lass et al., 2000; Bochert & Zettler, 2012).

The so-called source of the Angola-Benguela system is the upwelling system off Namibia south of Angola. It is one of the largest upwelling regions of the world. It gives direction and strength to surface currents and influences regional atmospherically conditions. Upwelling water is cold and rich in nutrients, which generates high production and also high biomass. The cold Namibian upwelling water is permanently pushed north-westward by regional south-east-winds forming the Benguela Current (Bochert & Zettler, 2012). This current is also a part of the South Atlantic subtropical gyre and driven by large-scale wind patterns and thermohaline forcing (Fennel, 1999). The Benguela Current runs parallel to the coastline from circa 15° S to 35° S and moves offshore approximately at the mouth of the Kunene River, forming the border between Angola and Namibia. In the process the current reaches speeds between 10 and 30 cm/s (Steele et al., 2009). It is one of the major eastern boundary currents worldwide and transports cold, less saline and nutrient-rich water masses to lower latitudes (Lass et al., 2000; Lin & Chen, 2002). The cool Benguela Current (Fig. 2) is bounded by warm water regimes, namely the Angola Current in the north as well as the Agulhas Current and the South Atlantic Current in the south (Steele et al., 2009; Laudien, 2002).

At about 15° S near the Angola-Namibia border is a confluence of the Angola Current and the Benguela Current, the so-called Angola-Benguela front (Fig. 2). The contact of the two currents varies over a time from a few years to decades and leads to a change in location of the front. The shifting depends on local meteorology (Hogan et al., 2012). According to Sakko (1998) there is a seasonally movement, too. Also Meeuwis & Lutjeharms (1990) stated this observation. The authors say that seasonal fluctuations of the Angola-Benguela front occur concerning geographical location, width, seaward extent, temperature gradient and surrounding eddy formation. Furthermore, it is described that the front is a result of wind stress, coastal orientation, bottom topography and, as already mentioned, north and south movements of the Angola Current and the Benguela upwelling system. Although the Angola-Benguela front shows variations in its exact location it is a permanent feature at the sea surface in a small latitudinal field ranging from 14° S to 16° S with a 20° C isotherm. Apart from that, the zone shows strong horizontal gradients in temperature and salinity in the upper 50 m. A sharp pycnocline occurs at 30 m depth. The upper mixed layer consisting of water from the Angola Current can reach temperatures above 24° C and a salinity maximum of more than 36.4 apart from the coastal boundary layer influenced by upwelling.

While the coastal boundary is exposed to upwelling, the shelf edge shows strong downwelling between the thermocline (60 m depth) and 500 m depth (Lass et al., 2000).

The Angola-Benguela front can be considered as a transition zone between the oligotrophic tropical ecosystem in the north and the nutrient-rich upwelling driven system in the south with short warm water intrusions of tropical water into the northern Benguela surface water

(Mohrholz et al., 2008). The temperature differences of the warm Angola Current and the cold Benguela current cause greatly variances in composition of successful animals at the Angola-Benguela front. Its occurrence has biogeographically consequences. An example is given by Hogen et al. (2012), saying that there is an isolated ecosystem at the mouth of the Kunene River.

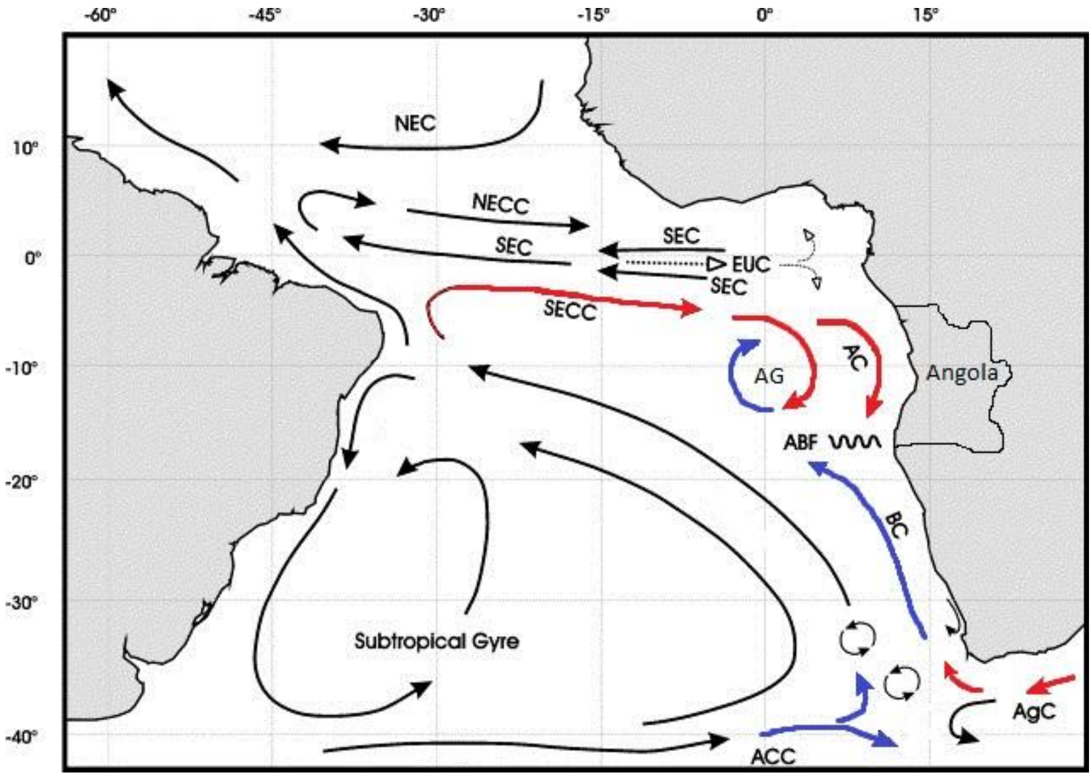

Fig. 2: Marine currents of the South Atlantic Ocean; AG = Angola gyre, AC = Angola Current, ABF = Angola-Benguela front, BC = Benguela Current, AgC = Agulhas Current, SECC = South Equatorial Counter Current, EUC = Equatorial Under Current, SEC = South Equatorial Current, NECC = North Equatorial Counter Current, NEC = North Equatorial Current, ACC = Antarctic Circumpolar Current; drawn by a figure of Zonneveld et al. (2000)

In case of the Angolan continental shelf the northern part of the bottom widely consists of fine to coarse sand. Outside the Congo River estuary, south of Cabinda and north of Luanda silt is found but with interruptions of stones, rocks and corals. The central region of the shelf to Benguela is also characterized by mud and fine to coarse sand (Fig. 3). However, silt and clay dominate large areas. Rocky grounds occur mainly north of Cabo Ledo and off Cabeca da Baleia. The shelf area from Tombua to the Kunene River consists of clay and silt in Baia dos Tigres and has a bottom of fine to coarse sand northwards to Tombua (Bianchi, 1992).

It has to be noted that large coral reef formations, which are hot spots of marine faunistic diversity, are lacking at the Angolan continental shelf. Its absence is possibly due to the low temperatures associated with upwelling water in some regions and periodical strong salinity decrease in other areas (Le Loeuff & von Cosel, 1998).

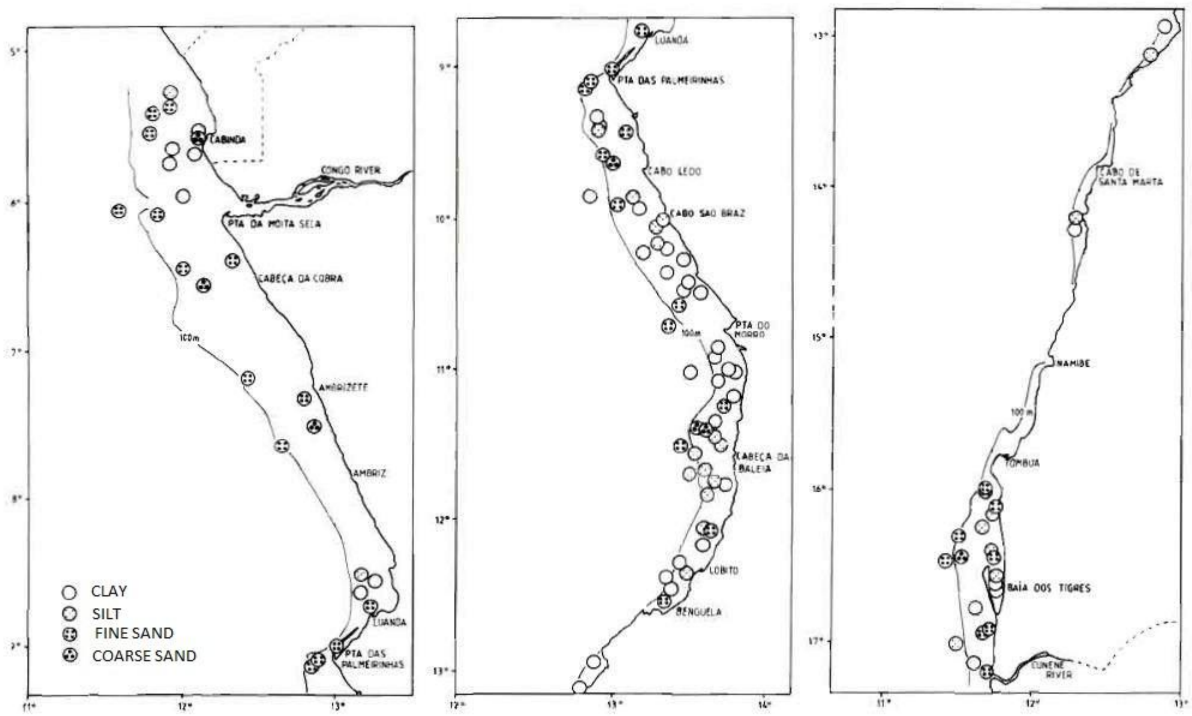

Fig. 3: Location of sample stations described by Bianchi (1992) and their respective sediment types along the Angolan coast; left: northern region of Angola, middle: central region of Angola, right: southern region of Angola

2.2 Sampling

This study is based on the investigation of benthic samples, taken on the continental shelf along the Angolan coast from Cabinda to the northern part of Namibia (Fig. 6) during two research cruises. The first cruise was done with the German research vessel "Alexander von Humboldt" and took place from May 13th till June 2nd 2004. The second one was carried out with the German research vessel Maria Sibylla Merian from July 30th until August 15th 2011. Both ships were in service for the Leibniz Institute for Baltic Sea Research Warnemünde.

Samples were taken with a 0.1 m² Van Veen grab (Fig. 4) at each of 42 stations in a depth ranging from 19 m to 340 m. The sampling effort varied from station to station (table 1 and 2) from 1 single sample to 3 sample replications (hauls 1, haul 2 and haul 3). Then, all hauls were sieved through a 1 mm mesh size sieve. Moreover, dredge samples were taken at each station to get additional information about the biological quality of the appropriate locations. These samples were also sieved through a 1 mm mesh size sieve. The mesh size of the dredge itself (Fig. 5) was 5 mm. The animals were immediately conserved on board by mixing the samples with 4 % buffered formaldehyde.

Environmental variables (salinity, temperature, oxygen content) of the water column near to the sea floor were recorded by means of a profiling CTD-system (Seabird, USA) and a 13-bottle sampling rosette. Oxygen sensors were calibrated by intermediate potentiometric Winkler titration of 3 samples per water column, including the closest position to the sediment. Additionally, sediment samples were taken by a grab to extract the upper surface sediment layer (≤ 20 mm) for analyses of median-size grain (laser particle sizer Cilas 1180L).

The sampled and analyzed stations are summarized in table 1 and table 2 with regard to the number of taken hauls and dredges.

Fig. 4: Van Veen grab (photo: Alexander Darr)

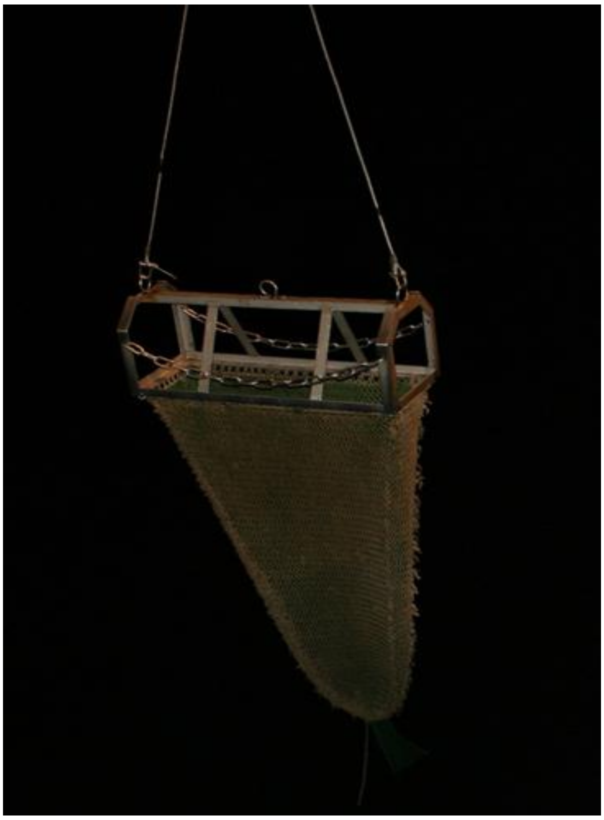

Fig. 5: Dredge (photo: Alexander Darr)

Table 1: Overview of all samples of the year 2004 including the name of the station, the exact location, the sampling date, the depth and the taken number of hauls as well as dredges (indicated by “x”)

station name	latitude	longitude	sampling date	depth [m]	haul 1	haul 2	haul 3	dredge
BE7	-16,993	11,518	13.05.2004	105	x	x	-	x
BE10	-15,001	12,128	17.05.2004	115	x	x	x	-
BE9	-15,008	12,079	17.05.2004	340	x	-	-	-
BE11	-15,129	12,109	17.05.2004	84	x	x	-	-
BE12	-15,181	12,082	17.05.2004	38	x	x	x	x
BE13	-15,293	12,001	17.05.2004	67	x	-	-	x
1	-13,958	12,395	20.05.2004	24	x	-	-	-
2	-13,934	12,397	20.05.2004	20	x	x	-	-
3	-13,934	12,392	20.05.2004	39	x	-	-	-
4	-13,961	12,365	20.05.2004	57	-	x	x	-
5	-13,934	12,369	20.05.2004	125	-	x	-	-
45	-12,088	13,701	23.05.2004	19	x	-	-	-
65	-9,433	13,000	25.05.2004	46	x	x	-	-
66	-9,562	13,100	25.05.2004	20	x	-	-	x
67	-9,432	13,083	25.05.2004	21	-	-	x	-
68	-9,345	13,026	25.05.2004	23	x	-	-	-
70	-9,434	12,917	25.05.2004	75	x	-	-	-
71	-9,437	12,832	25.05.2004	105	x	-	-	-
72	-9,440	12,747	25.05.2004	146	x	-	-	-
76	-7,140	12,275	26.05.2004	108	x	-	-	-
77	-5,725	11,906	27.05.2004	53	x	-	-	-
78	-5,200	11,967	27.05.2004	32	x	-	-	-
87	-7,236	12,767	28.05.2004	27	x	-	-	x
88	-7,235	12,684	28.05.2004	41	x	-	-	x
100	-7,833	13,050	29.05.2004	25	-	-	-	x
101	-7,850	13,009	29.05.2004	47	x	-	-	-
102	-7,866	12,974	29.05.2004	58	x	-	-	-
106	-9,082	12,934	30.05.2004	40	x	-	-	-
107	-9,082	12,949	30.05.2004	36	-	-	-	x
121	-8,755	13,215	02.06.2004	44	x	-	-	-

Table 2: Overview of all samples of the year 2011 including the name of the station, the exact location, the sampling date, the depth and the taken number of hauls as well as dredges (indicated by “x”)

station name	latitude	longitude	sampling date	depth [m]	haul 1	haul 2	haul 3	dredge
Na5	-15,096	12,105	30.07.2011	62	x	x	x	x
BM5	-13,991	12,362	31.07.2011	48	x	x	x	x
LO4	-12,203	13,264	31.07.2011	91	x	x	x	x
LO5	-12,333	13,533	01.08.2011	60	x	x	x	x
SU4	-10,490	13,423	01.08.2011	60	x	-	-	x
SU5	-10,508	13,577	01.08.2011	28	x	x	x	x
Be71	-9,435	12,831	02.08.2011	102	x	x	x	x
LU5	-8,783	13,167	03.08.2011	80	x	x	x	x
KU3	-17,267	11,501	15.08.2011	150	x	x	x	x
Ku4	-17,264	11,615	15.08.2011	102	x	x	x	x
Ku5	-17,262	11,717	15.08.2011	39	x	x	x	x
KU6	-17,151	11,346	15.08.2011	25	x	x	x	x

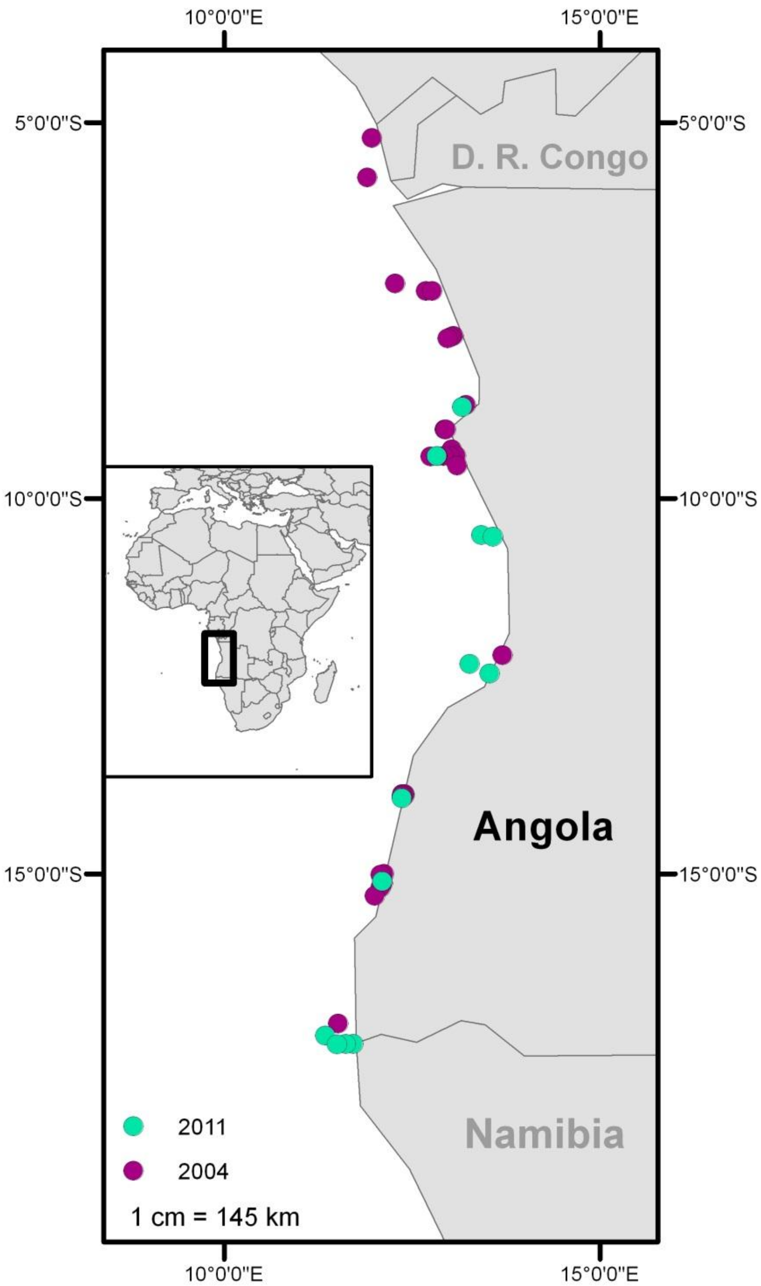

Fig. 6: Map of Angola with marked sampling stations, map by Gesine Lange (created with GIS ArcMap)

2.3 Sample Processing

In the laboratory, the 89 samples were washed through a 0.5 mm mesh size sieve under the fume hood while wearing gloves because of the previous fixation with toxic 4 % buffered formaldehyde. Afterwards, the remaining sediment including the contained animals was observed by means of a stereomicroscope (Leica Wild Type: 479887) with 80-800 x magnification. All organisms were taken out of all samples and were subsequently determined. Several literature and internet sources were used for identifying individuals with the objective to determine the organism to the lowest taxonomic level.

In the following, the used identification literature for the taxonomic main groups is listed:

- Day, J. H. (1969) A guide to marine life on South African shores. A. A. Balkema, Cape Town

Polychaeta:

- Day, J. H. (1967) A monograph on the Polychaeta of southern Africa. Part 1. Errantia. Trustees of the British Museum (Natural History)
- Day, J. H. (1967) A monograph on the Polychaeta of southern Africa. Part 2. Sedentaria. Trustees of the British Museum (Natural History)
- Hartmann-Schröder, G. (1996) Annelida- Borstenwürmer Polychaeta. 2. neubearbeitete Auflage mit 295 Abbildungen. Zoologisches Museum Berlin: Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise 58. Teil

Mollusca:

- Ardovani, R., Cossignani, T. (2004) West African Seashells (including Azores, Meidera and Canary Is.). L'Informatore Picento, Ancona
- Bernard, P. A. (1984) Coquillages du Gabon- Shells of Gabon. Pierre A. Bernard, Libreville-Gabon
- Huber, M. (2010) Compendium of Bivalves. ConchBooks, Hackenheim
- Nicklès, M. (1950) Mollusques testacés marins de la Côte occidentale d'Afrique. Manuels Quest-Africains II. Paul Lechevalier, Paris

Crustacea:

- Barnard, J. L. (1969) The Families and Genera of Marine Gammaridean Amphipoda. Bulletin 271, Smithsonian Institution Press, City of Washington
- Bochert, R., Zettler, M. L. (2010) *Grandidierella* (Amphipoda, Aoridae) from Angola with description of a new species. Crustaceana 83 (10), 1209-1219
- Bochert, R., Zettler, M. L. (2011) Cumacea from the continental shelf of Angola and Namibia with description of new species. Zootaxa 2978, 1-33
- Bochert, R. (2012) Apseudomorph Tanaidacea from the continent shelf of Angola and Namibia with descriptions of three new species. Zootaxa 3583, 31-50
- Corbera, J., Garcia-Rubies, A. (1998) Cumaceans (Crustacea) of the Medes Islands (Catalonia, Spain) with special attention to the genera *Bodotria* and *Iphinoe*. Scientia Marina 62 (1-2), 101-112
- Griffiths, C. (1976) Guide to the benthic marine Amphipods of Southern Africa. Trustees of the South African Museum, Cape Town
- Hayward, P. J., Ryland, J. S. (1990). The Marine Fauna of the British Isles and North-West-Europe Vol. 1 Introduction and Protozoans to Arthropods
- Jones, N. S. (1976) British Cumaceans, Arthropoda: Crustacea, Keys and Notes for the Identification of the Species. Synopses of the British Fauna No. 7. Linnean society of London, Academic press London and New York

- Kensley, B. (1972) Shrimps & Prawns of Southern Africa. Trustees of the South African Museum, Cape Town
- Kensley, B. (1978) Guide to the marine Isopods of Southern Africa. Trustees of the South African Museum, Cape Town
- Lincoln, R. J. (1979) British marine Amphipoda: Gammaridea.
- Manning, R. B., Holthuis, L. B. (1981) West African Brachyuran Crabs (Crustacea: Decapoda). Smithsonian Contributions to Zoology, Number 306
- Reid, D. M. (1951) Report on the Amphipoda (Gammaridea and Caprellidea) of the Coast of Tropical West Africa. Atlantide Report 2, 189-291

The identified specimens were first counted and afterwards weighed with a precision balance (Analytical balance Cubis® MSA225S-000-DA, Sartorius GmbH) to detect the wet weight and thus the biomass. Then, the organisms were put into LSC Vials with 70 % ethanol and a bit of glycerin to preserve them. Also, photos of the most representative species were taken. For that, a microscope (Zeiss Stereo Microscope Discovery V8) with a connected camera (Zeiss Axio Cam ICc 3) was used. The respective camera software is “AxioVision Release 4.8.1 (11-2009)”.

2.4 Data Analysis

All recorded information about the number of taxa; their amount and their wet weight were put into a database, which was used for statistical analysis. The stations 68 and 77 were ignored due to their very low species number, which is probably caused by incorrect sampling. Consequently, 87 samples were analyzed from 40 stations. Abundance [individuals/m²] and biomass [wet weight/m²] were calculated. Standard deviations are missing because of the different sampling effort. Only one sample was taken at some stations (see table 1 and 2). Two multivariate analyses of the benthic community were done with the program “Primer (Version 6)” with the aim to clarify possible similarities within the faunal composition of the sampled habitats. At first, a cluster analysis was accomplished. The data used for this are the abundances for each species of every station. The abundance data were square-root transformed. Due to its low sensitivity upon the occurrence of zeroes in a dataset, the Bray-Curtis index was the distance and similarity measure used. The used link function was a group average linkage. Additionally, an ordination by non-metric multidimensional scaling (MDS) was carried out, also using the Bray Curtis index. Previously; the abundances here were square-root transformed, too.

In this thesis, the Shannon index (H’) is used to ascertain the biological diversity at each sampled station. Indices of species diversity enable the comparability of habitats by giving them a numerical value. There are numerous diversity indices but the Shannon index is the most widely cited one.

In “The Mathematical Theory Of Communication” (Shannon & Weaver, 1949) the following is stated:

“If one is concerned…with a set of *n* independent symbols, or a set of *n* independent complete messages for that matter, whose probabilities of choice are p_1, p_2… p_n, then the actual expression for the information is…$H = -\sum p_i \, log \, p_i$.”

It is explained in their treatise, that *H* is largest when the probabilities of the messages (p_1, p_2… p_n) are equal, i.e. when one is completely free to choose between the messages. If a message is more probable (greater) than the other, then *H* decreases.

The common used Shannon index (*H’*) was derived from this mathematical theory to express interspecific encounters in a complex biological community. In this connection, it is assumed that a more equal distribution among the individuals of various species enables an increasing probability of interactions between the species. Thus, the community is more diverse (Oliver et al. 2011).

So, the Shannon index for each station was calculated with the formula:

$$H' = -\sum p_i \, log_{\,2} \qquad ; p_i = \frac{n_i}{N}$$

n_i …number of individuals of the i-th species

N ... total number individuals

p_i …proportion of individuals of the i-th species in the relevant dataset

3 Results

3.1 Environmental Data

The measurements of the abiotic parameters along the Angolan shelf (table 3) revealed that the benthal off Angola is not uniform everywhere. However, salinity was nearly the same at every measured station ranging from 35.9 to 35.4 with the highest value at the most northern station and the lowest value at the most southern station. Temperature showed greater fluctuations with values varying between 13.6 and 20.1°C but with an obvious trend of a decrease in temperature towards the south. The oxygen content does not show a clear trend within the investigated area but it seems to be more constant in the north. The highest oxygen value of 4.18 ml/l was found at the latitude -13,916 (station 4). The lowest oxygen value of 0.42 ml/l was observed at the latitude -16.993 (station BE7). The sediment differed also at various stations. It varies from silt, which can be found at the Cabinda-region, to gravel and little stones, occurring at station SU4 near Sumbe. Furthermore, the bottom substrate varies among the stations in its amount and size of mollusk shells. The strong differences in sediments are illustrated in figure 7 and figure 8.

Fig. 7: Silty mixed sand with diatoms from station Na5 near Namibe (photo: Alexander Darr)

Fig. 8: Sample from the mouth of the Kunene River with dead shells (photo: Alexander Darr)

Table 3: Abiotic data of the sampled stations (2004 and 2011) including salinity, temperature, oxygen content, grain size and a description of the sediment. The stations are listed according to a north-south-gradient beginning with the northernmost station.

station	salinity	temperature [°C]	oxygen [ml/l]	grain size median [µm]	substrate description
78	35.9	18.5	1.73	33	silt
77	35.7	16,9	2.05	7	silt
76	35.7	16.4	1.68	40	sand
88	35.8	17.8	1.91	no data	sand
87	35.8	18.4	1.89	731	coarse sand
100	35.8	17.8	1.50	74	sand
101	35.8	17.4	1.44	44	silt
102	35.8	17.2	1.51	48	silt
121	35.8	18.2	1.58	no data	silty sand
LU5	35.7	16.5	1.08	7	grey-brown, soft organic silt
106	35.7	17.6	1.47	no data	sand; no ripples
107	35.7	17.2	1.35	no data	sand; no ripples
68	35.7	20.1	3.10	no data	no information
67	35.5	19.7	2.83	no data	no information
65	35.8	18.7	2.21	no data	no information
70	35.8	17.7	1.59	30	sand
Be71	35.7	15.3	1.30	59	firm silty clay; a bit of fine and coarse shell fragments
71	35.7	16.4	1.36	54	silt
72	35.6	15.6	1.17	43	sand
66	35.8	19.3	2.55	356	sand
SU4	35.6	15.7	1.03	no data	suspected densely packed little stones; coarse sand, gravel
SU5	35.7	17.1	2.30	58	tough silty fine sand with diatoms and fine shell fragments
45	35.7	18.1	1.37	62	silt
LO5	35.7	16.3	1.04	14	soft brown-grey silt
LO4	35.5	15.1	0.95	66	tough grey silty clay; fine shell fragments
2	35.7	17.2	2.04	no data	fine sand
3	35.5	15.4	0.80	no data	coarse shells; very coarse calcareous material (biogenically)
5	35.5	15.4	0.80	14	sandy silt
1	35.7	17.2	2.04	no data	fine sand
4	35.7	18.8	4.18	379	coarse sand
BM5	35.7	16.5	1.36	87	dark grey silty fine sand
BE10	35.6	15.8	0.77	no data	no information
BE9	35.7	17.4	2.67	no data	no information
Na5	35.6	16.1	1.28	14	silty mixed sand with diatoms; shell fragments; first 3 cm brown oxidized, below grey-black colored
BE11	35.6	16.0	0.92	no data	silt
BE12	35.6	16.2	0.88	no data	no information
BE13	35.6	15.9	0.80	no data	no information
BE7	35.4	13.6	0.42	no data	silt
KU6	35.5	14.5	1.00	21	organic black silt; debris; H_2S
Ku5	35.5	14.5	0.82	23	soft black silt; 2 mm brown cover; very strong H_2S
Ku4	35.5	14.5	0.66	18	soft dark brown/black silt; very strong H_2S
KU3	35.4	13.7	0.83	60	sandy silt; H_2S

3.2 α-Diversity

3.2.1 Grab Samples

In all hauls taken along the Angolan shelf a total number 618 species of benthic invertebrates (see appendix) were counted. These species were divided into five taxonomic main groups (Crustacea, Polychaeta, Echinodermata, Mollusca and others). Their species number and their percentage are shown in table 4 and figure 9.

Table 4: Total species number and percentage of the taxonomic main groups

Crustacea	206	33 %
Polychaeta	221	36 %
Echinodermata	20	3 %
Mollusca	123	20 %
others	48	8 %

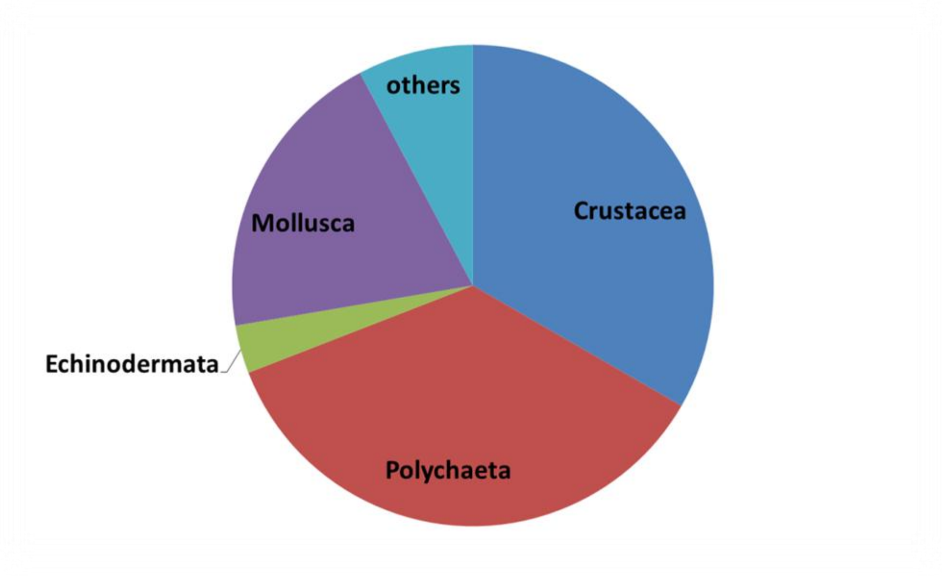

Fig. 9: Taxonomic composition of diversity in the studied area (n= 618)

The macrozoobenthic community in waters off Angola is dominated by polychaetes and crustaceans. The most species-rich main group and thus the group with the highest biodiversity are the polychaetes. With a total number of 221 different species they represent 36 % of the community. They are closely followed by crustaceans consisting of 206 species, which constitute 33 % of the whole community. Mollusks are also a significant part of the Angolan macrozoobenthos. 123 mollusk species, making up 20 % of all counted species, were found. Echinodermata and the remaining species summarized as “other” rather play a minor role in diversity. Echinoderms are the least divers group consisting of 20 species.

The constituted taxonomic main groups comprise various lower taxonomic levels like classes and orders, which are also not equal represented in their species number. Considering the crustaceans (Fig. 10), it is obvious that the order of Amphipoda with 97 species provides almost half of the diversity of this group. They are followed by the decapods with only 46 species, cumaceans with 24 species, isopods with 22 species and tanaidaceans with 8 species. 9 other species could be detected including specimens of Leptostraca, Maxillopoda, Mysida, Stomatopoda and Euphausiacea. The major part of the mollusk diversity (Fig. 11) consists of gastropods having 75 identified species. They are followed by bivalves with 44 different species. Just 3 mollusk species which are neither gastropods nor bivalves were observed. Echinoderms are the group with the fewest species. Their diversity is dominated by Ophiuroids containing 14 species. Holothurians are the second species-rich group with only 3 species followed by asteroids and echinoids, each with 1 species (Fig. 12).

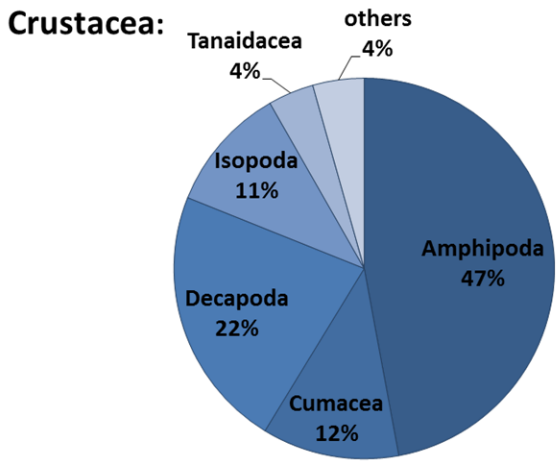

Fig. 10: Percentage composition of crustacean groups (n = 206)

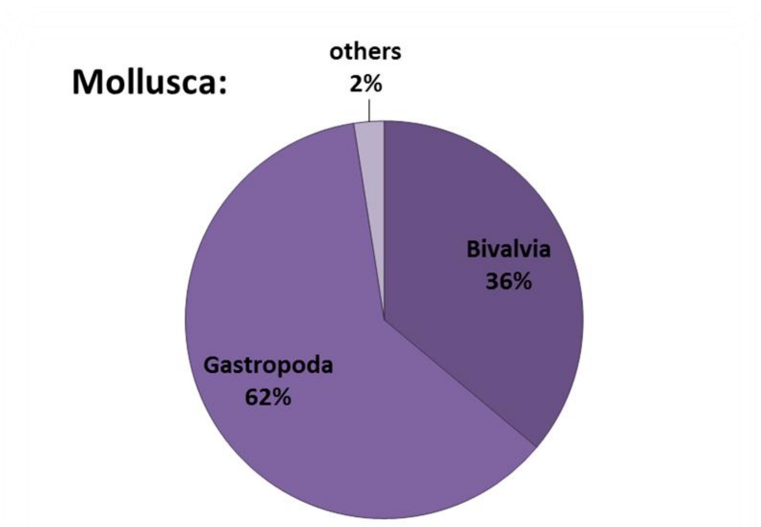

Fig. 11: Percentage composition of mollusk groups (n = 123)

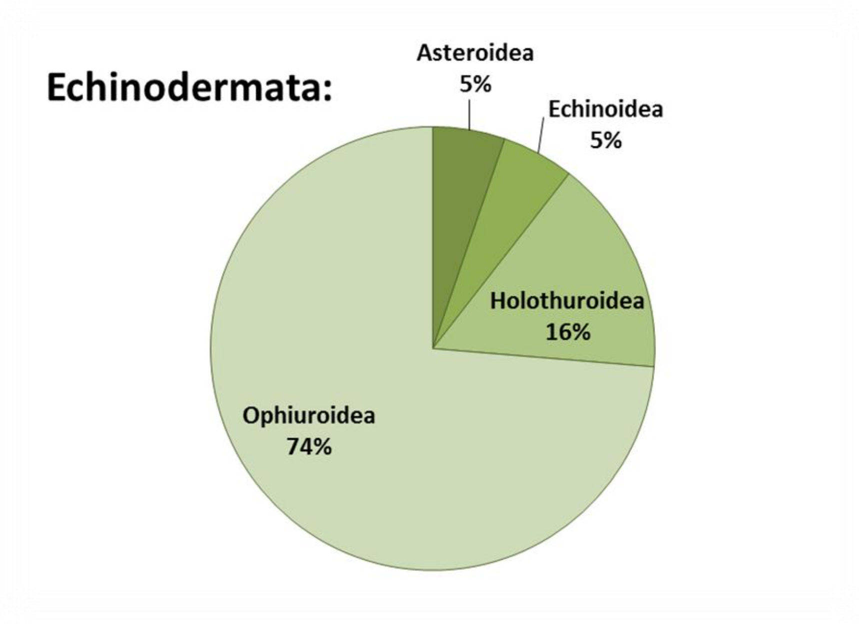

Fig. 12: Percentage composition of echinoderm groups (n = 20)

The most diverse taxon of macrozoobenthos in the investigated area is the class of polychaetes. 49 Polychaetes families were collected from all grab samples along the shelf of Angola. The different species numbers of the most diverse families are shown in figure 13. Spionidae has by far the greatest species number (36 species). They are followed by the family of Cirratulidae with 14 species and the family of Paraonidae with 12 species.

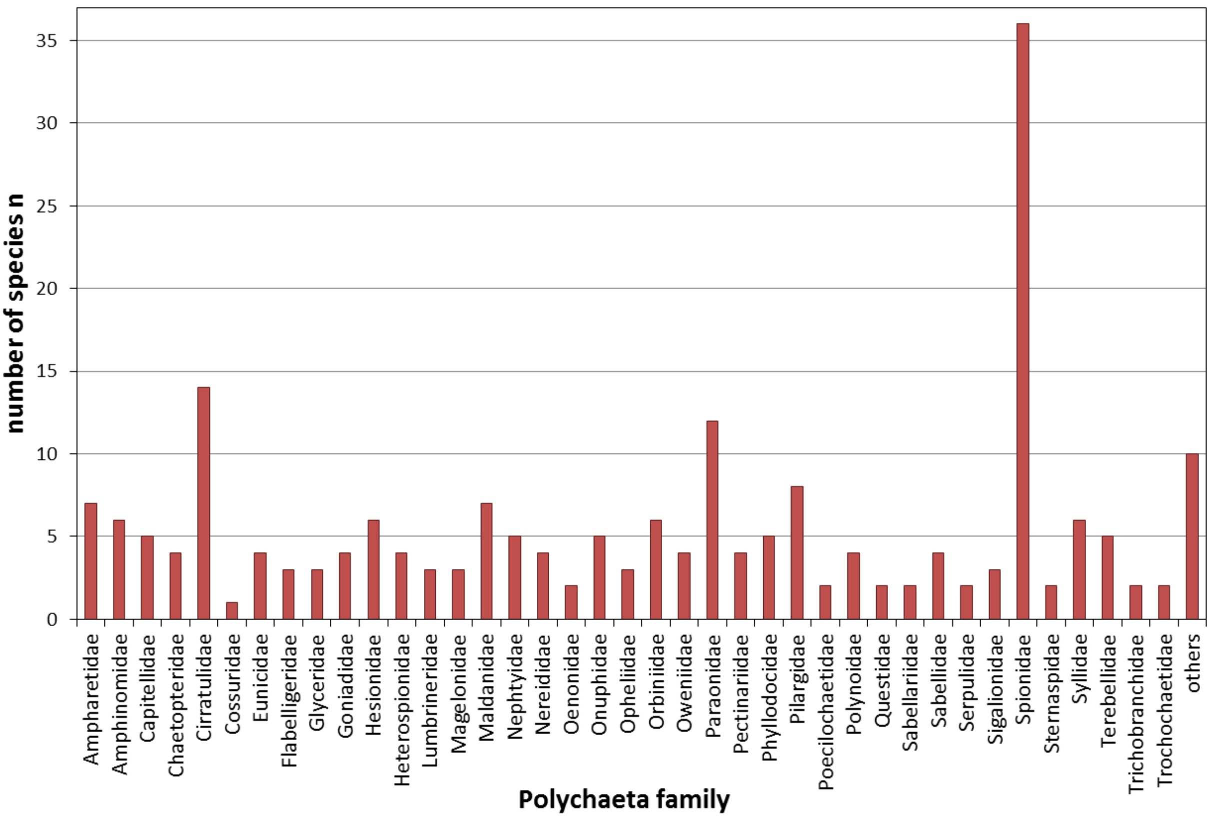

Fig. 13: Species richness of assorted polychaetes families of all grab samples in the studied area

If one considers the total composition of diversity among crustaceans, polychaetes, echinoderms, mollusks and others (Fig. 9), it should be noted that it is not the same at every region. In Cabinda, which includes the two most northern stations, echinoderms are completely absent. In comparison to the taxa's percentages of all samples, the Cabinda-stations show a little greater diversity in mollusks and polychaetes, while the number of crustacean taxa is smaller (Fig. 14). The northern part of the coast of Angola from -7,140 to -9,562 has greater polychaetes diversity than the Cabinda-stations and it is also greater when compared with the percentage of the polychaetes species number of all samples. Furthermore, the crustacean species percentage is greater here than in the both stations off Cabinda but lower relative to crustacean species percentage of the total community. The percentage that mollusks contribute to the community diversity in northern Angola is significantly smaller than in samples off Cabinda as well as in the whole sampled area. In contrast to the Cabinda-stations, echinoderm species occur in the north of Angola from approximately Soyo to the mouth of the Cuanza River. Their percentage of the community agrees with those estimated for the whole waters off Angola. The species assemblage of the sampled stations of North Angola is similar to those of middle Angola including the area from Sumbe to Lobito (Fig. 14). The sampled area from Benguela to Namibe is more diverse in crustacean taxa compared to the already mentioned stations further north and similar compared to the total crustacean proportion. The contribution of polychaetes to the community diversity between Benguela and Namibe is a bit smaller than in the north. However, it is a little greater in comparison to polychaetes contribution to community diversity when all stations are involved. The percentage of echinoderms on the diversity here is similar to the previous regions and reflects the general proportion of echinoderms on the total diversity. In case of mollusks, the percentage on biodiversity is a bit smaller at the region from Benguela to Namibe than at the northward region. Compared with the mollusks proportion on the community diversity of all sampling locations, their percentage in this area is significantly smaller. Moreover, it must be mentioned that the percentage of the group "other" on the diversity is substantially greater within the area off South Angola and the mouth of the Kunene River than within the northern stations (Fig. 14). The taxonomic composition of species richness for the stations near the Kunene River is characterized by an above-average high percentage of mollusks. Except from the Cabinda-stations, which have a little bit higher mollusk percentage, all other areas show a clearly smaller proportion of mollusks. However, proportion of crustaceans and echinoderms on diversity of the stations in vicinity of the Kunene River is lower than in other sampled areas. The number of polychaetes species provides nearly the half of the biodiversity in the southernmost area, like it is more or less valid for all investigated areas along the Angolan coast (Fig. 14). Concrete percentage values for all regions are given in table 5.

Table 5: Percentages of taxonomic main groups on the diversity of certain areas from North- to South Angola

region	Crustacea	Polychaeta	Echinodermata	Mollusca	others
Cabinda	23 %	45 %	0 %	27 %	5 %
Soyo to Luanda	28 %	51 %	3 %	11 %	7 %
Sumbe to Lobito	29 %	51 %	3 %	12 %	5 %
Benguela to Namibe	32 %	44 %	3 %	9 %	12 %
Kunene River mouth	16 %	48 %	1 %	24 %	11 %

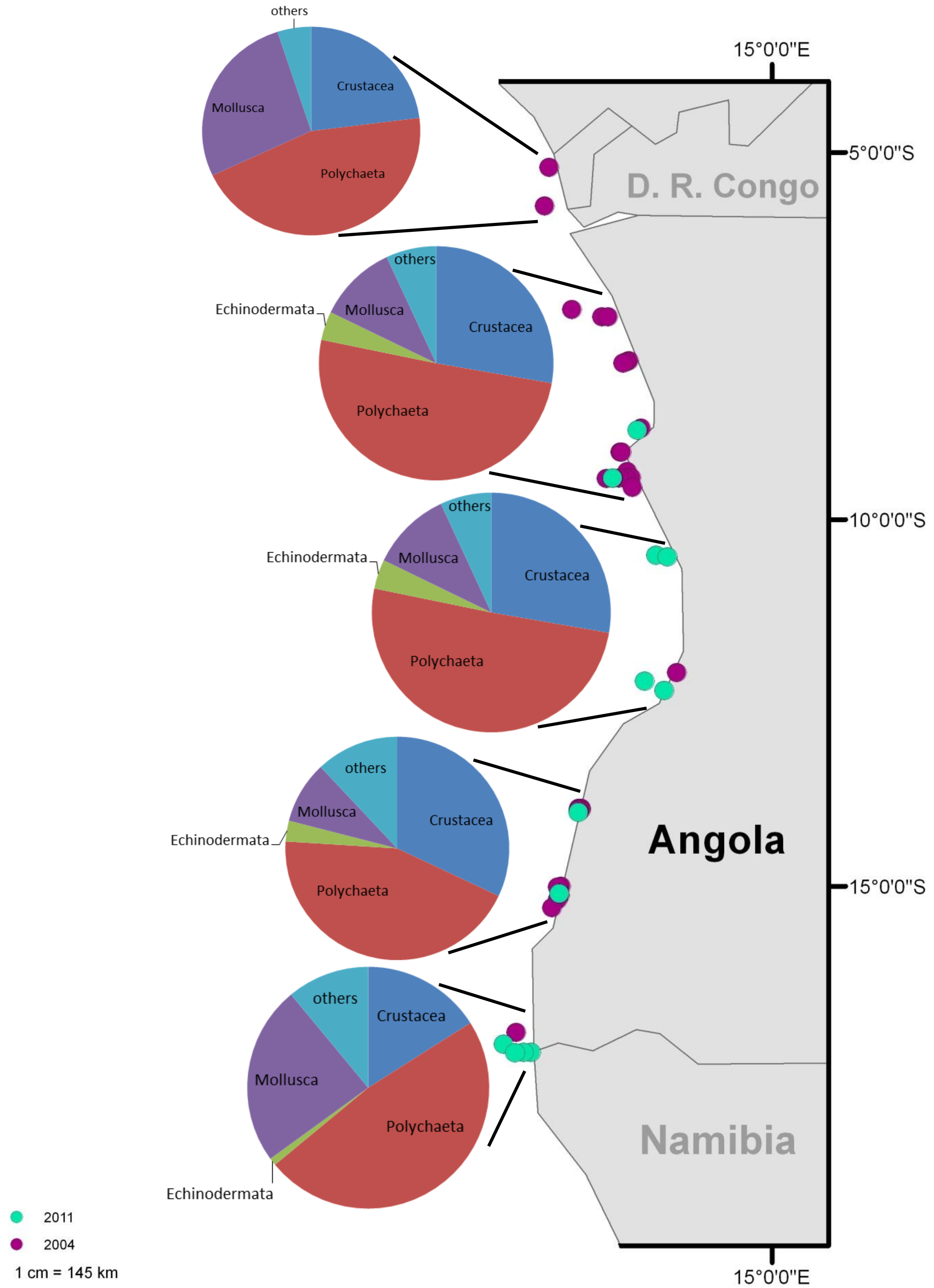

Fig. 14: Percentage of taxonomic main groups on the diversity of certain areas along the Angolan coast (based on grab samples)

In the following the counted species number of the main groups and the total species number are given for all grab samples at every station. The stations are listed in sequence of a latitudinal gradient beginning with the northernmost station off Cabinda and ending with the southernmost station off the Namibian border.

Table 6: Species number of the taxonomic main groups and total species number of every grab sample

station_haul	Crustacea	Polychaeta	Echinodermata	Mollusca	others	total
78_1	4	7	0	3	0	**14**
76_1	2	12	0	2	0	**16**
88_1	12	21	0	5	1	**39**
87_1	6	10	1	5	2	**24**
101_1	6	12	1	3	4	**26**
102_1	6	17	2	3	1	**29**
121_1	43	24	7	13	8	**95**
LU5_1	8	18	0	2	4	**32**
LU5_2	5	10	1	4	3	**23**
LU5_3	3	18	0	4	2	**27**
106_1	8	12	1	3	1	**25**
67_1	2	14	0	1	1	**18**
65_1	11	21	1	3	1	**37**
70_1	2	6	1	2	1	**12**
Be71_1	16	37	2	9	7	**71**
Be71_2	13	27	3	2	2	**47**
Be71_3	9	28	1	3	3	**44**
71_1	3	13	0	2	1	**19**
72_1	4	11	0	1	1	**17**
66_1	4	13	1	1	1	**20**
SU4_1	11	22	1	2	5	**41**
SU5_1	17	34	1	13	5	**70**
SU5_2	14	39	1	11	7	**72**
SU5_3	19	30	1	12	6	**68**
45_1	21	24	0	8	3	**56**
LO5_1	9	24	0	3	2	**38**
LO5_2	8	26	1	2	2	**39**
LO5_3	8	23	0	4	3	**38**
LO4_1	12	22	2	7	4	**47**
LO4_2	8	18	2	4	4	**36**
LO4_3	14	20	2	3	2	**41**
2_1	9	8	2	2	0	**21**
3_1	10	23	1	2	1	**37**
5_1	8	12	1	6	0	**27**
1_1	8	20	3	5	1	**37**
4_1	12	13	4	6	0	**35**
4_2	12	11	1	1	0	**25**
BM5_1	19	36	1	8	3	**67**
BM5_2	12	26	1	3	5	**47**
BM5_3	20	31	1	3	4	**59**
BE10_1	15	23	1	3	0	**42**
BE10_2	6	18	0	4	0	**28**

BE10_3	10	21	0	2	0	**33**
BE9_1	2	7	0	0	2	**11**
Na5_1	19	34	1	3	6	**63**
Na5_2	16	37	1	4	4	**62**
Na5_3	16	43	2	11	5	**77**
BE11_1	4	21	1	4	4	**34**
BE11_2	3	13	1	2	1	**20**
BE12_1	22	21	3	1	6	**53**
BE12_2	14	11	2	4	6	**37**
BE12_3	10	7	1	0	4	**22**
BE13_1	25	7	2	4	9	**47**
BE7_1	0	6	0	5	1	**12**
BE7_2	4	8	0	5	1	**18**
KU6_1	5	13	1	7	2	**28**
KU6_2	8	21	1	14	4	**48**
KU6_3	2	18	1	9	3	**33**
Ku5_1	1	17	0	7	4	**29**
Ku5_2	2	15	0	5	4	**26**
Ku5_3	2	14	0	7	5	**28**
Ku4_1	7	10	0	4	2	**23**
Ku4_2	7	7	0	3	4	**21**
Ku4_3	5	10	0	2	3	**20**
KU3_1	7	11	0	5	3	**26**
KU3_2	5	8	0	8	1	**22**
KU3_3	5	9	0	5	1	**20**

The highest diversity (95 species) were observed at sample 121_1 at the latitude -8,755 (Fig. 15). It has to be mentioned that this station is one of the few, where diversity is significantly dominated by crustaceans. The stations Be71, SU5, BM5 and Na5 also show samples with high numbers of species. Polychaetes are the most diverse group in most samples. Exceptions for this are the samples of station 121, 2, BE12 and BE13, where crustaceans are dominant. The echinoderms are the least diverse group in most samples. They have their species maximum at the sample of station 121. Here, 7 echinoderm species were counted. The least diverse sample is BE9_1 with only 11 species. The exact species number from every sample is listed in table 6.

The trend in diversity shows clear fluctuations in all groups. However, the strongest fluctuations occur in species richness of crustaceans and polychaetes. It is conspicuous that all taxonomic groups have their maximum peak at the sample from station 121 except for the polychaetes, of which diversity maximum is in sample Na5_3. The group with the least variations in species number is the one of echinoderms.

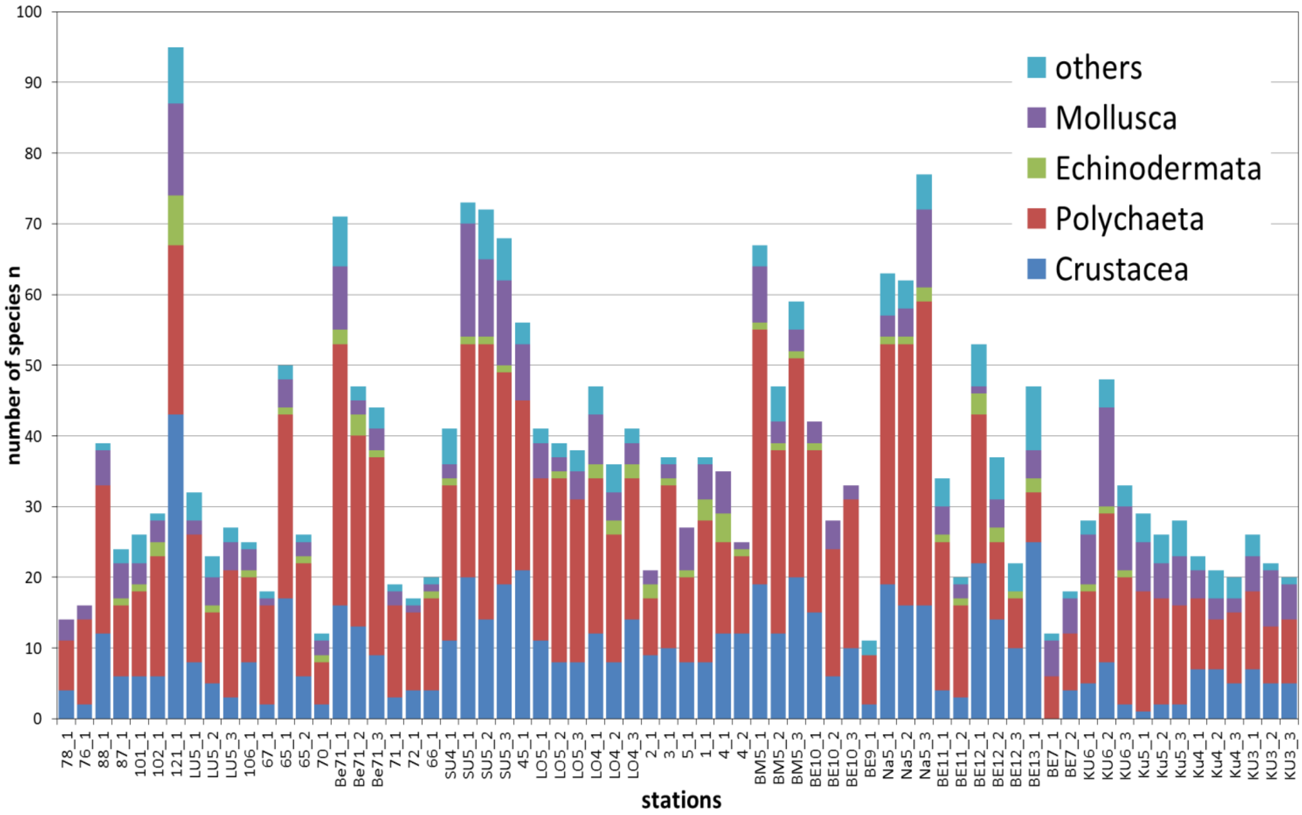

Fig. 15: Species richness of all grab samples. The samples of every station at the abscissa are listed along a latitudinal gradient from north (left side) to south (right side)

3.2.2 Dredge Samples

Additionally, all species from the dredge samples of the Angolan shelf were counted. 579 species were found and were again divided into the same taxonomic main groups as given above (Crustacea, Polychaeta, Echinodermata, Mollusca and others). Their species number and their percentage are shown in table 7 and figure 16.

Table 7: Total species number and percentage of the taxonomic main groups

Crustacea	208	36 %
Polychaeta	157	27 %
Echinodermata	30	5 %
Mollusca	145	25 %
others	39	7 %

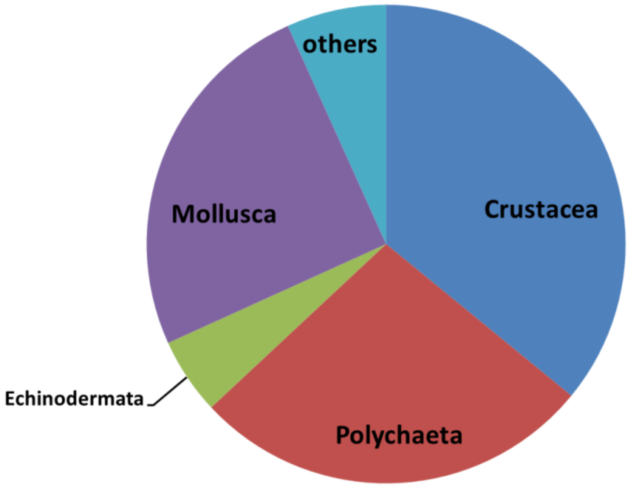

Fig. 16: Taxonomic composition in the studied area (n = 579)

In contrast to the grab samples, species richness of the dredge samples is dominated by crustaceans. With 208 species they provide 36 % of the whole assemblage diversity. They are followed by polychaetes with 157 species. The polychaetes are followed by mollusks. This group has more species compared to the grab samples. Echinoderms are still the least divers group. However, 10 more echinoderm species were found in the dredge samples than in the hauls. With regard to the lower taxonomic levels within the main groups, it has to be mentioned that crustacean's diversity is dominated by decapods (Fig. 17). This is a strong contrast to the grab samples, where the diversity is mainly represented by amphipods. The proportion of diversity among the mollusks is similar to those from the grab samples. However, cephalopods were found (Fig. 18). The echinoderm diversity is also similar split like those from the hauls but with a little greater percentage of holothurians (Fig. 19).

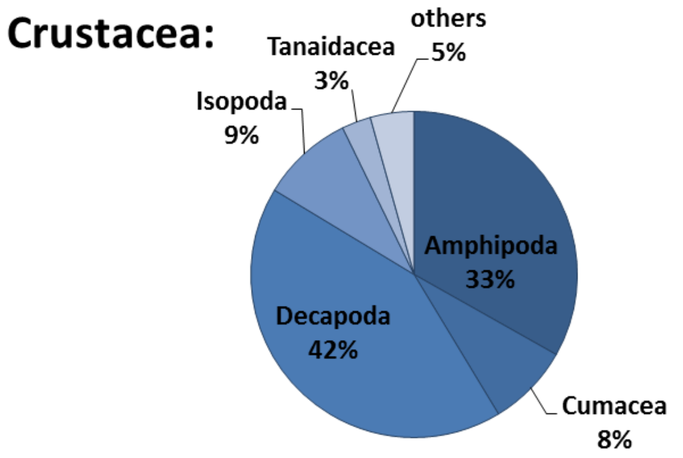

Fig. 17: Percentage composition of crustacean groups (n = 208)

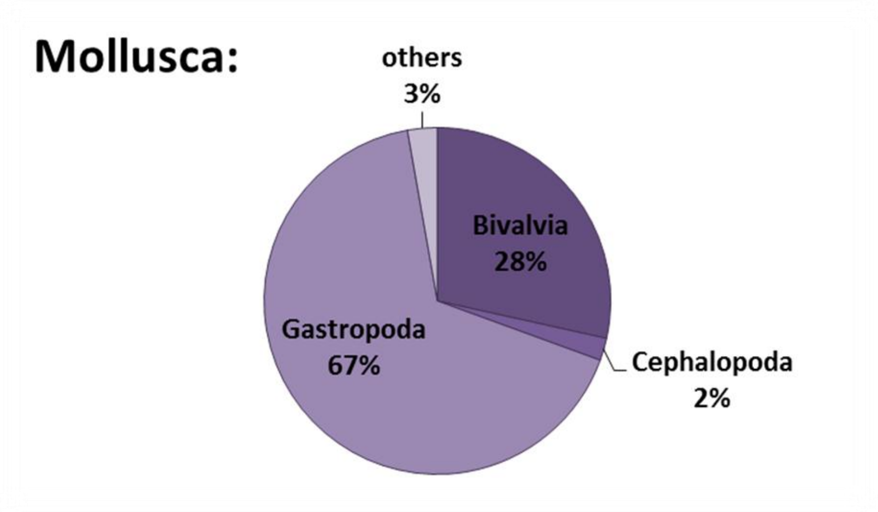

Fig. 18: Percentage composition of mollusk groups (n = 145)

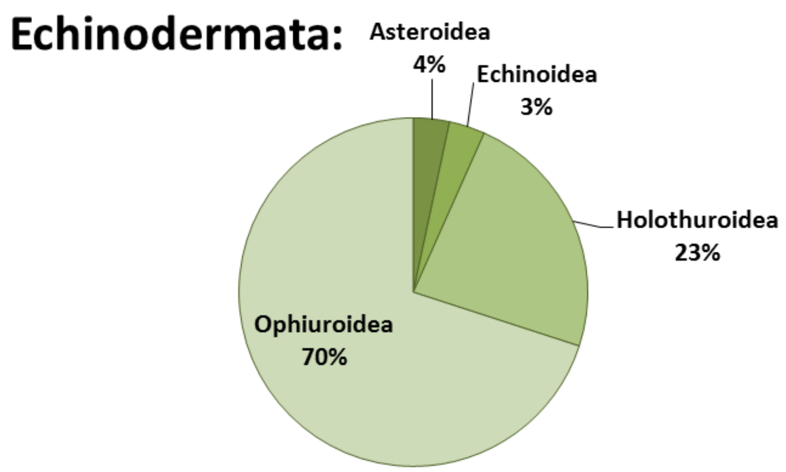

Fig. 19: Percentage composition of echinoderm groups (n = 30)

42 Polychaetes families were found in dredge samples along the coastal waters of Angola. The most diverse familiy are the Spionidae having 20 species (Fig. 20). They are followed by cirratulids with 8 species. Compared with the hauls, most of the polychaetes families from the dredge samples have less species. However, species number of the Nephtydae and the Onuphidae is greater in dredge samples than in the grab samples.

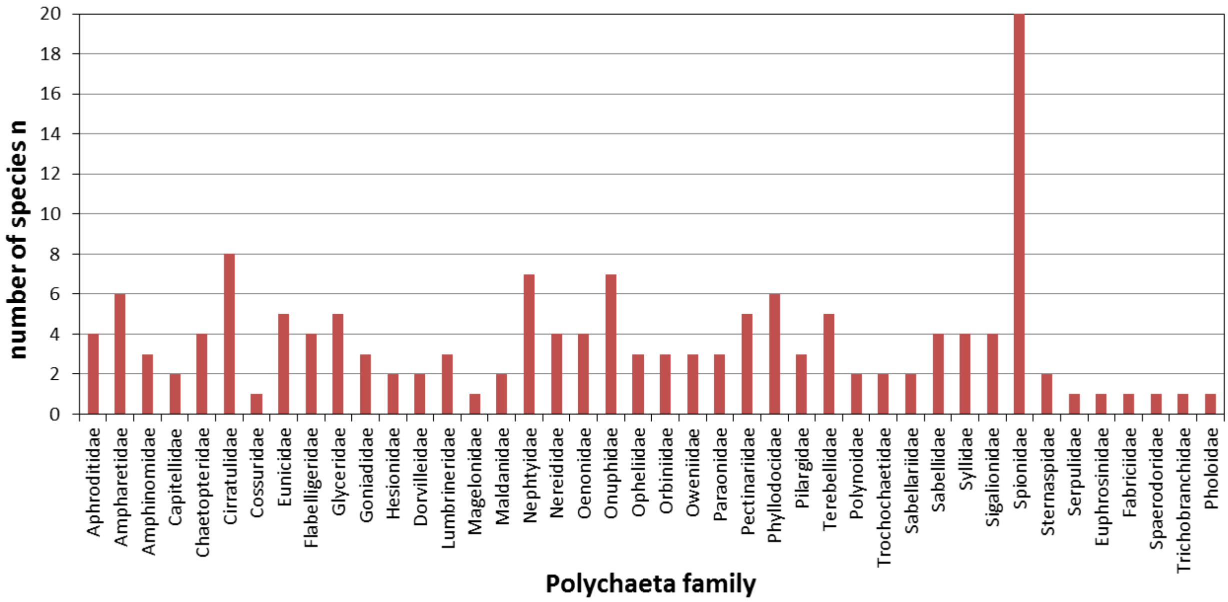

Fig. 20: Species richness of polychaetes families of dredge samples in the studied area

The regional distribution of species number among the taxonomic main groups varies visibly (Fig. 21). Polychaetes percentages on the community diversity are nearly the same at every region and match approximately with the percentage of the total studied area (Fig. 16). This statement can also be made for the crustaceans. Only the area at the latitude of the Congo River mouth shows a significantly decrease in crustacean species. Mollusks have an increasing percentage instead. Echinoderms contribute at least to assemblage diversity. They have their highest percentage (6 %) in the northern region and their lowest percentage on community diversity (1 %) at the southern area. The percentages of all taxonomic main groups at the stated regions are listed in table 8. There are no results for the region of Cabinda, because dredge samples are lacking here.

Table 8: Percentages of taxonomic main groups on the diversity of certain areas from North- to South Angola

region	Crustacea	Polychaeta	Echinodermata	Mollusca	others
Soyo to Luanda	38 %	34 %	6 %	17 %	5 %
Sumbe to Lobito	35 %	29 %	3 %	25 %	8 %
Benguela to Namibe	41 %	32 %	4 %	16 %	7 %
Kunene River mouth	18 %	35 %	1 %	33 %	13 %

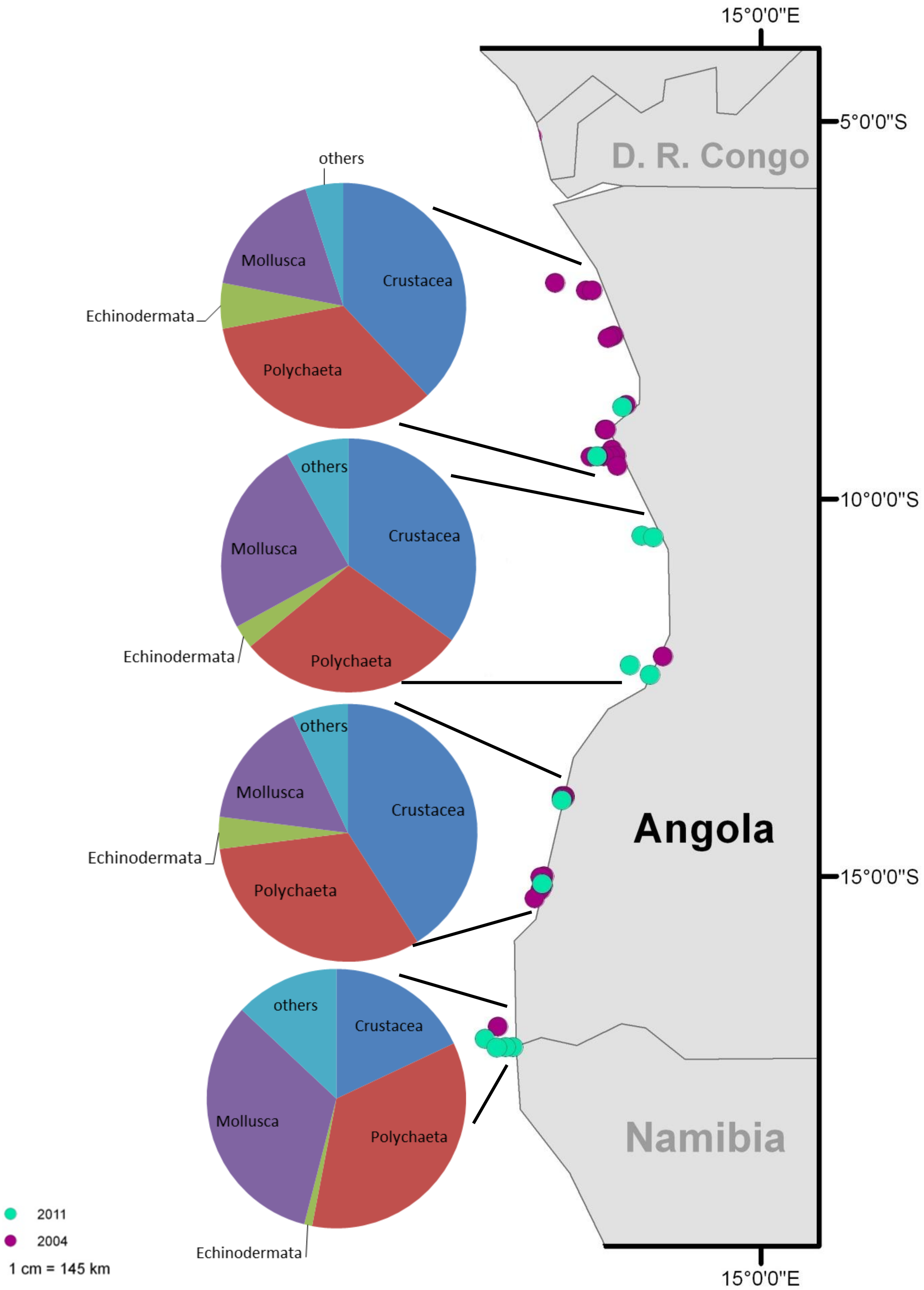

Fig. 21: Percentage of taxonomic main groups on the diversity of certain areas along the Angolan coast (based on dredge samples)

In the following the species number of the main groups is given for every station sampled with a dredge. The stations are listed in sequence of a latitudinal gradient beginning with the northernmost station (south of the mouth of the Congo River) and ending with the southernmost station off the Namibian border.

Table 9: Species number of the taxonomic main groups and total species number at every station sampled with a dredge

station	Crustacea	Polychaeta	Echinodermata	Mollusca	others	total
88	33	17	10	5	4	**69**
87	43	48	7	36	4	**138**
100	21	30	0	4	1	**56**
LU5	21	20	1	19	7	**68**
107	11	6	3	4	1	**25**
Be71	26	24	3	9	4	**66**
66	46	29	10	16	5	**106**
SU4	9	8	1	3	5	**26**
SU5	34	33	1	35	11	**114**
LO5	14	13	2	11	1	**41**
LO4	38	24	4	21	5	**92**
BM5	16	10	1	4	5	**36**
Na5	38	40	1	14	1	**94**
BE12	14	4	1	8	4	**31**
BE13	19	11	5	8	5	**48**
BE7	2	5	0	1	0	**8**
KU6	13	22	1	21	12	**69**
Ku5	4	17	0	11	2	**34**
Ku4	3	5	0	6	2	**16**
KU3	4	2	0	6	1	**13**

The highest diversity was observed at station 87. With a total number of 138 species, its species richness is far above those of the surrounding stations with 69 and 56 species. The least diverse station is station BE7 with 8 species. The both stations located north and south of BE7 show remarkably higher species numbers although they are not as high as at many other stations within the studied area. Stations with above-average diversity in addition to station 87 are the stations 88, LU5, Be71, 66, SU5, LO4, Na5 and KU6. As figure 21 already shows, figure 22 also demonstrates that crustaceans provide the most species at many stations. However, their species number is rather low at the stations near the Kunene River mouth and polychaetes still play a crucial role in biodiversity. Echinoderms are in general the group with the fewest species. The most echinoderm species were found at station 88 and 66. Concrete species numbers of all taxonomic main groups at every station and the total species number of every station is listed above in table 9.

Pronounced fluctuations in diversity are noticeable in all groups especially in crustaceans, polychaetes and mollusks. However, a decreasing trend is recognizable for every group although this trend is low in case of mollusks and the group “others”.

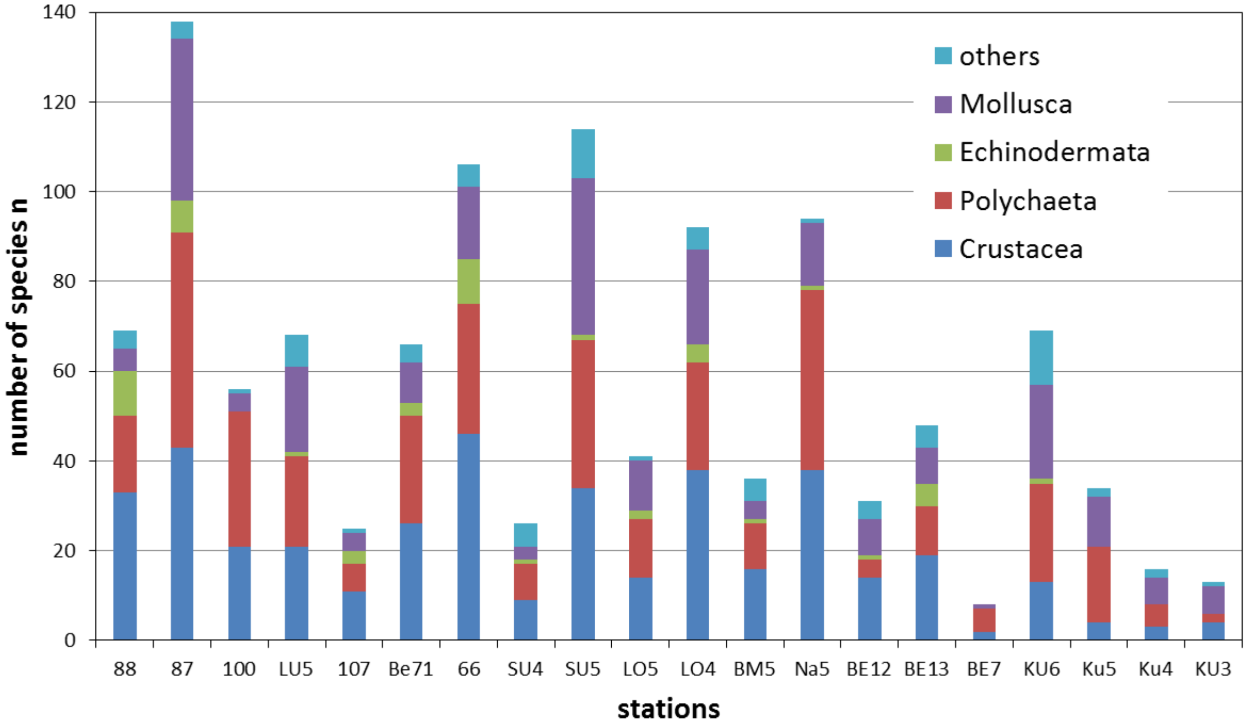

Fig. 22: Species richness at every dredge-sampled station along the Angolan coast. The stations at the abscissa are listed along a latitudinal gradient from north (left side) to south (right side)

3.2.3 Station Approach

Three sample replications (haul 1, 2 and 3) and dredge samples were taken at 12 stations (LU5, Be71, SU5, LO5, LO4, BM5, Na5; BE12, KU6, Ku5, Ku4, KU3). Therefore, it is possible to compare these stations on a real station level instead of just comparing the sample level. The counted species of the taxonomic main groups at each of these stations are shown in table 10 and figure 24. The proportion of the taxonomic main groups is depicted in figure 23. It is similar to the proportion calculated from the grab samples (Fig. 9). Polychaetes dominate the diversity, followed by crustaceans, mollusks and the group "others". The least diverse group is represented by echinoderms.

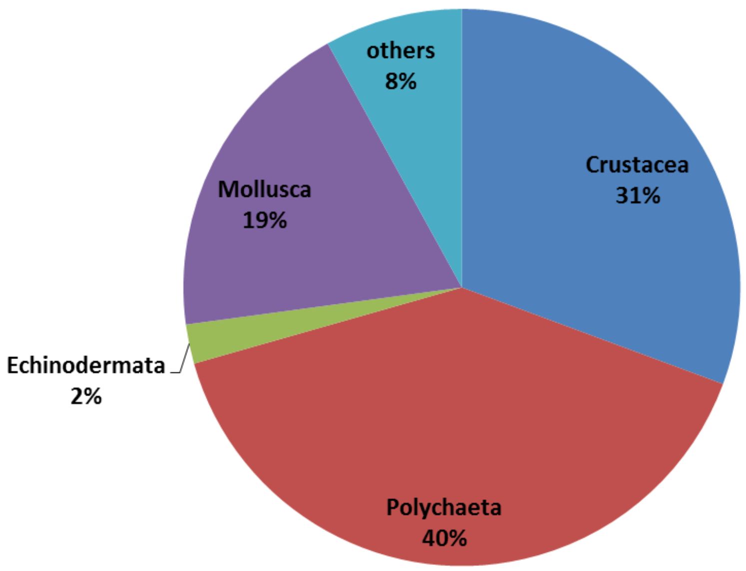

Fig. 23: Taxonomic composition of all stations with 3 hauls and a dredge sample (n = 601)

The most diverse station with 187 species is station SU5 in the middle of the Angolan shelf. It is followed by station Na5 (178 species), located further south. The lowest diversity is observed at the mouth of the Kunene River at the border to Namibia. The species numbers of these stations are ranging between 43 and 60 species. The diversity trends of all taxonomic main groups fluctuate from north to south. However, a decrease in species richness concerning Polychaeta and Crustacea is significant at the southern stations.

Table 10: Species number of the taxonomic main groups and total species number at stations with 3 hauls and a dredge sample. The stations are listed along a latitudinal gradient starting with most northern station.

station	Crustacea	Polychaeta	Echinodermata	Mollusca	others	total
LU5	27	34	2	23	10	96
Be71	22	56	7	18	9	112
SU5	54	72	1	49	11	187
LO5	27	50	2	12	6	97
LO4	44	39	7	24	10	124
BM5	43	57	1	13	10	124
Na5	67	72	4	25	10	178
BE12	44	31	3	13	11	102
KU6	13	22	1	18	6	60
Ku5	6	27	0	16	6	55
Ku4	14	16	0	8	5	43
KU3	14	13	0	15	4	46

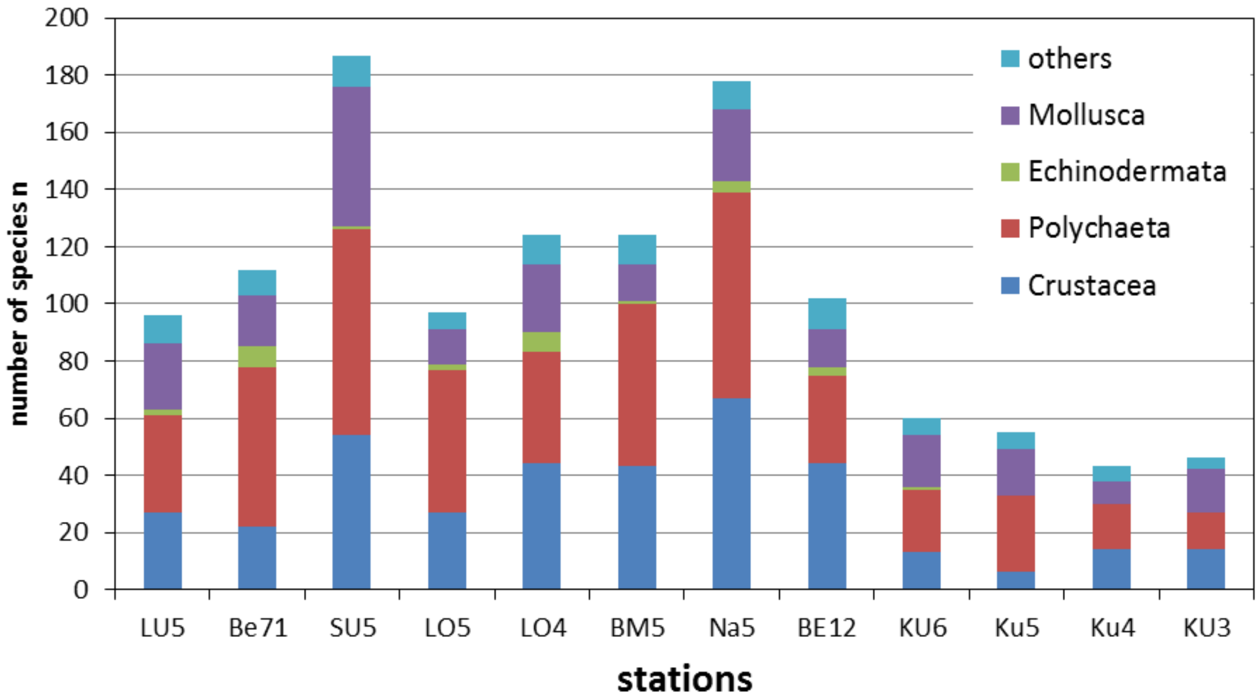

Fig. 24: Species richness at stations with 3 hauls and a dredge sample along the Angolan coast. The stations at the abscissa are listed along a latitudinal gradient from north (left side) to south (right side).

3.2.4 Shannon Index

The Shannon index is the most common index to express biological diversity (Clarke & Warwick, 1994). In this study, it was calculated (see Material & Methods) for all grab samples. The results are presented along a latitudinal gradient starting with the northernmost station in Cabinda (Fig. 25).

Very high diversities with a Shannon index above 4.5 are found at the latitudinal middle of the Angolan shelf. Khan (2006) mentions that the Shannon index seldom is above 4.5. According to the author, values between 1.5 and 3.5 are common. Thus, the waters off Angola have a great biological diversity. However, Cabinda in the north has a little lower diversity. The Shannon index for this sample is below 3.5. The southern stations at the mouth of the Kunene River show also a lower Shannon index ranging between 1.7 and 3.2. Only one sample from this region is above 3.5.

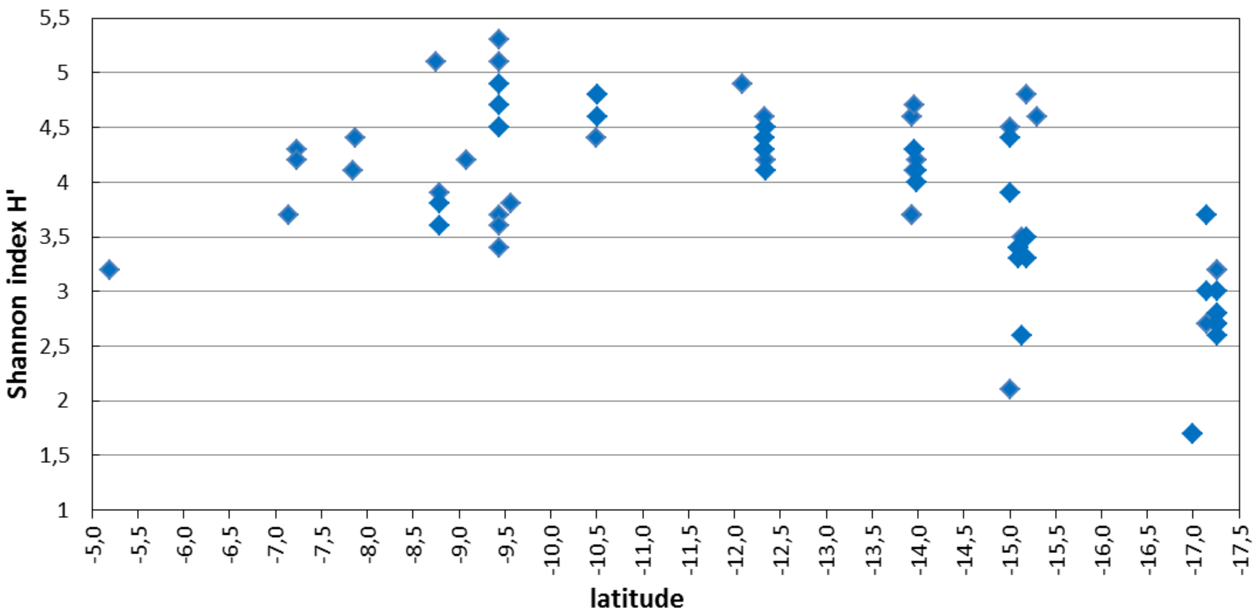

Fig. 25: Diversity (expressed by the Shannon index) along the Angolan coast in a north-south-gradient.

3.3 Community Analysis

Multivariate analyses were done to get information about the similarity levels of the grab samples with regard to species composition. The results of the culsteranalysis are presented as a dendrogramm (Fig. 26). Furthermore, the similarities of the samples are illustrated in a non-metric multidimensional scaling (MDS) plot (Fig. 27).

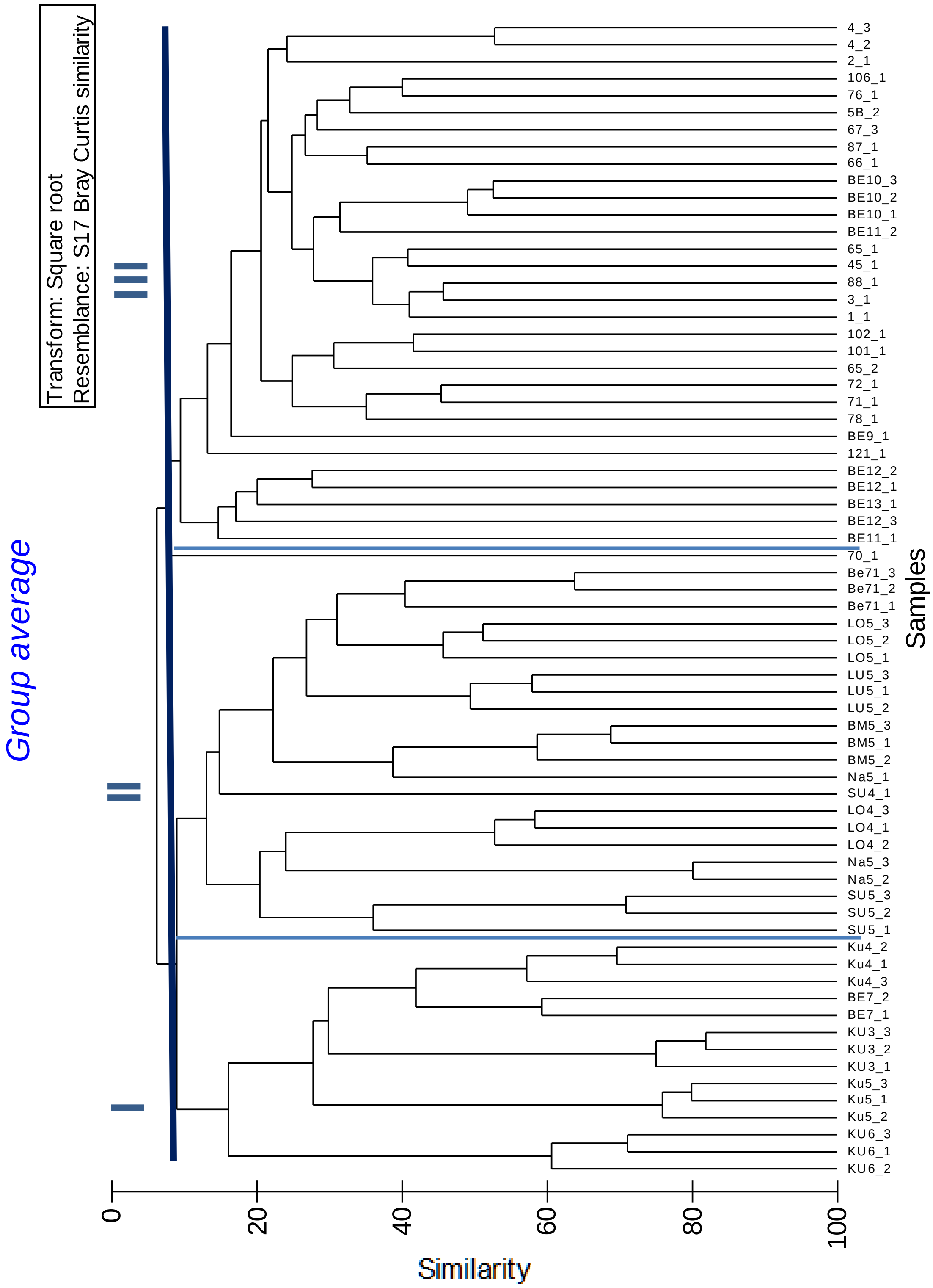

Fig. 26: Hierarchical, agglomerative clustering of macrozoobenthos data of all grab samples

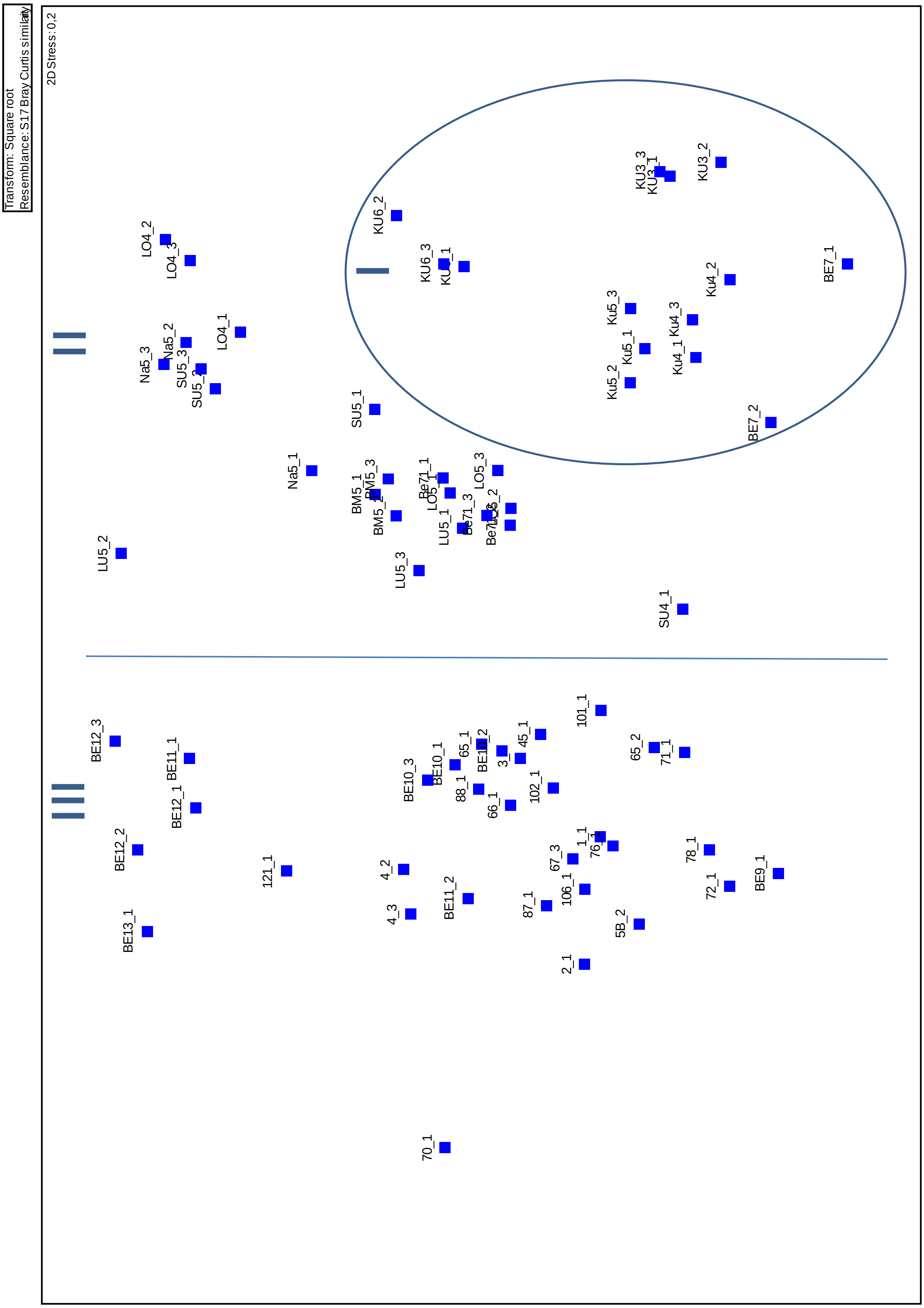

Fig. 27: MDS plot of square root transformed macrozoobenthos data of all grab samples

The dendrogramm shows the formation of 3 clusters with a low similarity of about 10 %. The first cluster mainly contains samples from the mouth of the Kunene River, where the substrate consists of fine silt with low oxygen contents. The second cluster contains samples from nearly all regions of the Angolan shelf except for the most northern and the most southern samples. The sediments of this area are dominated by silt and sand. Generally, a high similarity is recognizable among samples from the same station in the first and the second cluster. Those similarities range approximately between 60 and 85 %. The third cluster mainly includes northern samples that were taken from Cabinda to Luanda as well as southern samples taken between Benguela and Namibe. The similarities of samples from the same station vary in cluster 3 from about 30 to 50 %. Sample 70_1 is an outlier.

Overall, the results of the cluster analysis are supported by the results of the MDS plot. The separation of samples into 3 groups is similar to the 3 clusters formed in the dendrogramm of the cluster analysis. The samples from the mouth of the Kunene River (I) are encircled in figure 27.

3.4 Abundances

This paragraph deals with the numbers of individuals of the stated taxonomic main groups as well as the individual numbers of all stations sampled by a Van Veen grab. Dredge samples are left aside, because this sampling method is purely qualitative.

Individuals of all taxonomic main groups in the whole investigated area were counted and extrapolated to species number per m². Their proportion is shown in figure 28. The abundance of the benthic community in waters off Angola is strongly dominated by polychaetes. They represent far more than half of the total abundance. They are followed by crustaceans having an abundance proportion of 17 %, mollusks, and the group "others". The least abundant group is the group of echinoderms (3 %).

Considering the lower taxonomic levels within the Crustacea, amphipods are the most abundant group. They represent 46 %, followed by cumaceans (21 %), decapods (18 %) and isopods (8 %). The least abundant group of crustaceans is the tanaidaceans with 3 % (Fig. 29). 67 % of the total abundance of mollusks is provided by bivalves. The rest is almost represented by gastropods (Fig. 30). Echinoderm's abundances are dominated by ophiuroids contributing 49 %. They are followed by holothurians (44 %). Asteroids and echinoids have a small proportion on the abundance of echinoderms (Fig. 31).

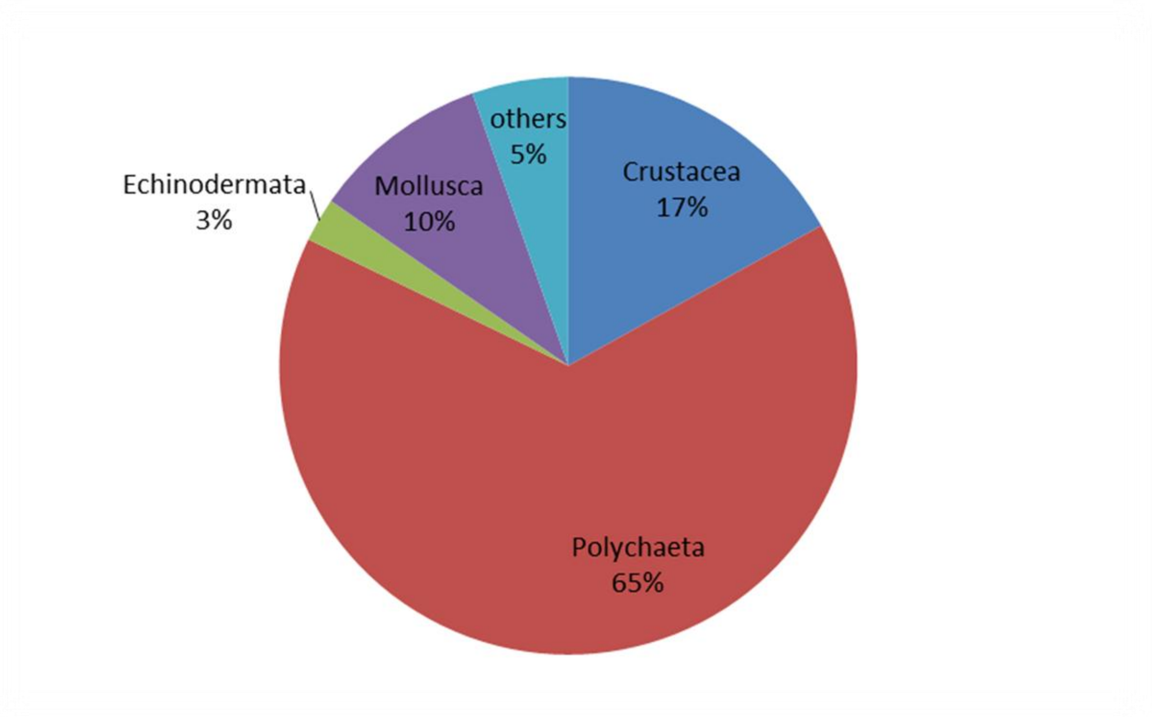

Fig. 28: Abundance percentages of the taxonomic main groups in the whole studied area

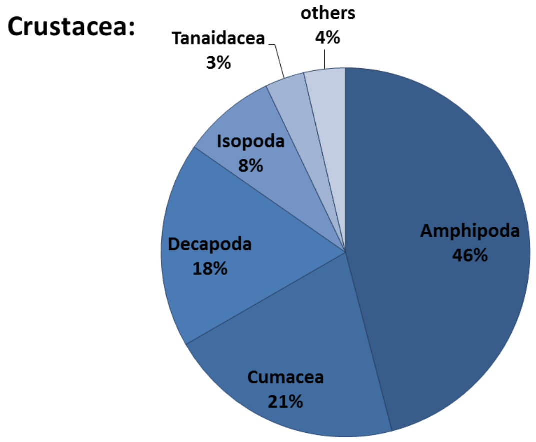

Fig. 29: Abundance percentages of crustacean groups

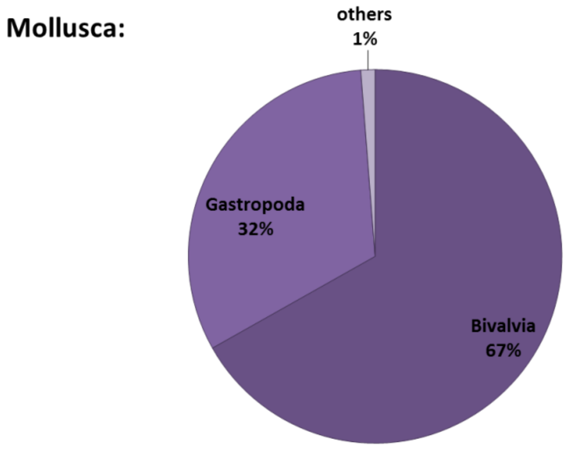

Fig. 30: Abundance percentages of mollusk groups

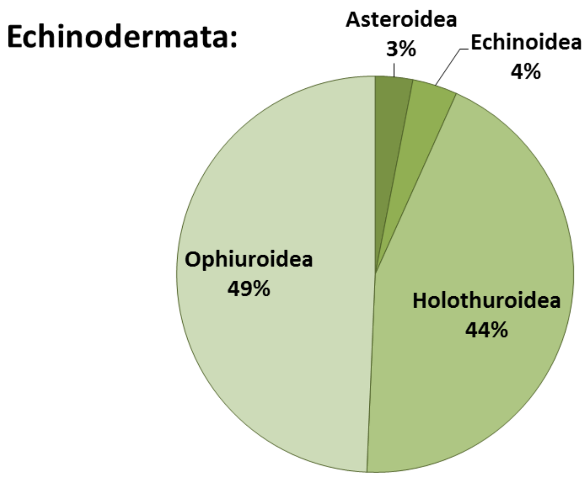

Fig. 31: Abundance percentages of echinoderm groups

The most abundant polychaetes families are the Spionidae with 5700 individuals/m² (Fig. 32). They are followed by Oweniidae (2959 individuals/m²), Paraonidae (2442 individuals/m²) and Cirratulidae (2081 individuals/m²).

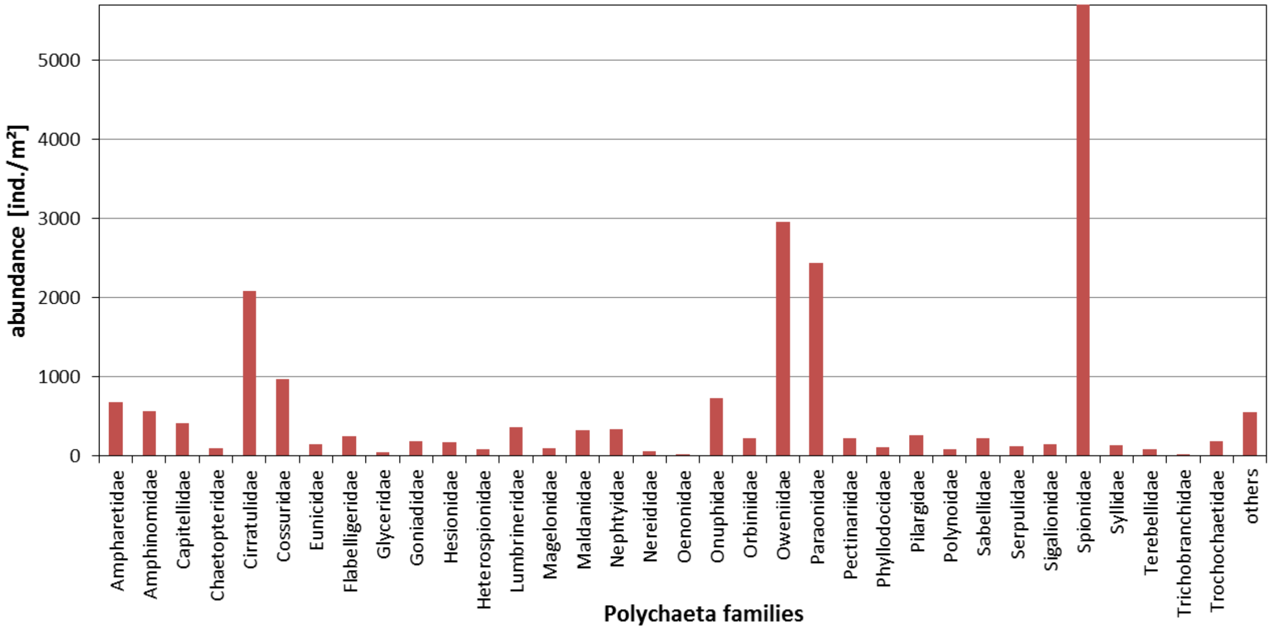

Fig. 32: Mean abundances [individuals/m²] of polychaetes families from 67 grab samples of the studied area

Abundances differ immensely among the taxonomic main groups at different regions. Polychaetes are generally the most abundant group in all regions. They have the greatest percentage (79 %) on community abundance at the region from Benguela to Namibe. The abundance percentage of crustaceans is very different from one region to another. It has its minimum (4 %) at the stations near the mouth of the Kunene River and its maximum (40 %) between Sumbe and Lobito (appropriate latitudes: from -10,490 to -12,338). Mollusks also vary strong regarding their abundance at different stations. They show their highest percentage on community abundance at the mouth of the Kunene River. However, their percentage in the north (Cabinda) is high, too. Echinoderms are the least abundant group. No individuals were found off Cabinda. The highest percentage of echinoderms on the abundance of an assemblage was observed within the area between Soyo and Luanda. This region is located south of Cabinda. The abundance proportions of the taxonomic main groups at 5 stated regions are shown in table 11 and illustrated in figure 33.

Table 11: Abundance percentages of taxonomic main groups at certain areas from North- to South Angola

region	Crustacea	Polychaeta	Echinodermata	Mollusca	others
Cabinda	32 %	41 %	0 %	20 %	7 %
Soyo to Luanda	29 %	49 %	8 %	10 %	4 %
Sumbe to Lobito	40 %	44 %	2 %	7 %	7 %
Benguela to Namibe	13 %	79 %	1 %	4 %	3 %
Kunene River mouth	4 %	63 %	2 %	22 %	9 %

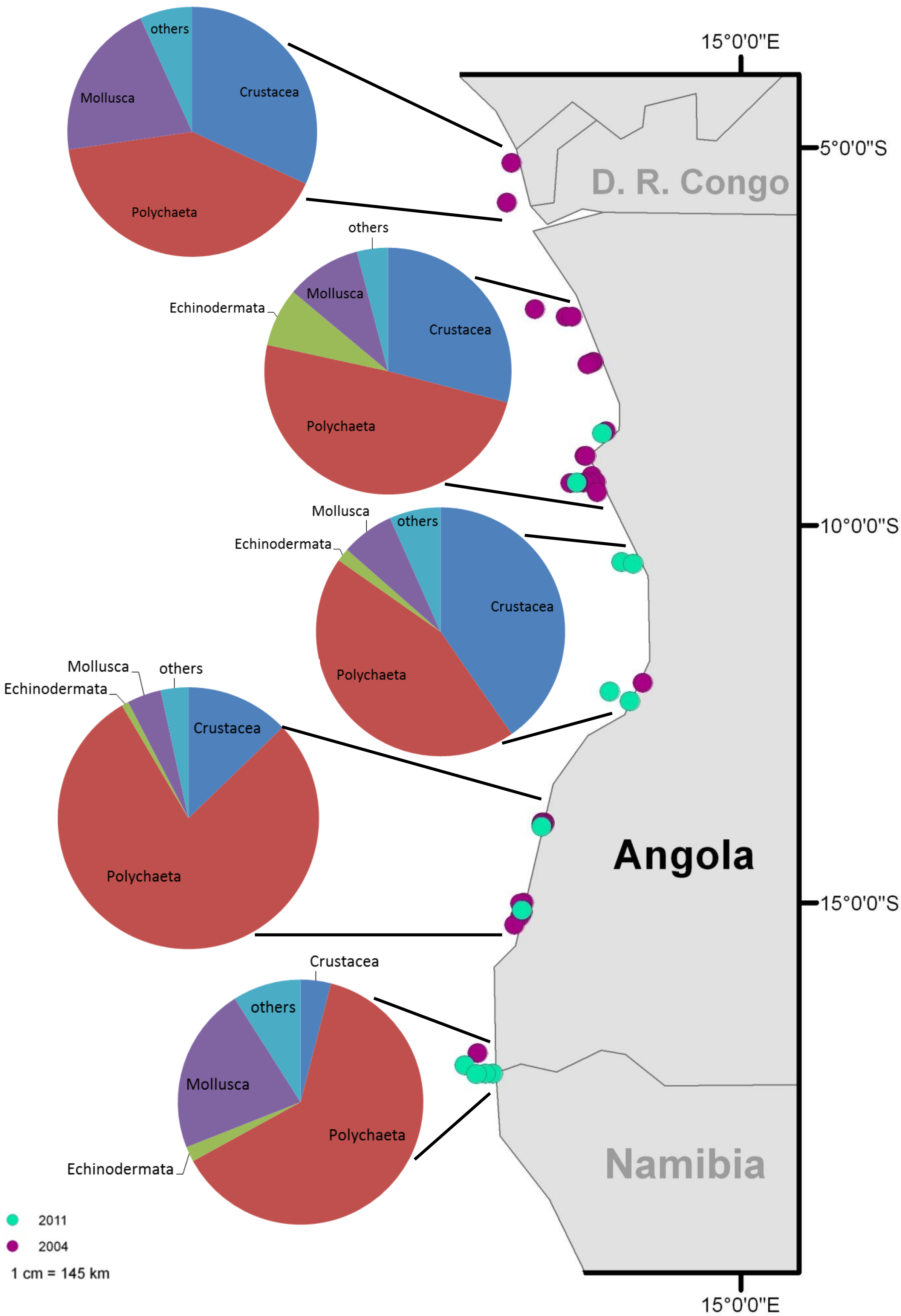

Fig. 33: Percentage of taxonomic main groups on the abundance of certain areas along the Angolan coast

In the following, abundances are shown for all taxonomic main groups and for all stations. Because of the various sample effort at different stations, the calculated abundances [individuals/ m²] were divided by the number of hauls at the respective station (see table 1, 2).

Table 12: Abundances [individuals/m²] of the taxonomic main groups and total abundances [individuals/m²] at every station. The stations are listed in a latitudinal gradient starting with the most northern station.

station	Crustacea	Polychaeta	Echinodermata	Mollusca	others	total
78	130	130	0	70	0	**330**
76	20	330	0	10	0	**360**
88	690	1470	0	390	50	**2600**
87	130	320	60	190	40	**740**
101	240	270	30	30	50	**620**
102	180	440	140	20	40	**820**
121	3980	2570	1330	1160	210	**9250**
LU5	80	723	3	93	136	**1035**
106	90	170	0	60	10	**330**
67	50	570	0	10	10	**640**
65	295	700	15	50	60	**1120**
70	30	90	20	10	20	**170**
Be71	280	1650	40	56	166	**2192**
71	40	520	0	30	20	**610**
72	40	370	0	0	20	**430**
66	90	380	10	10	30	**520**
SU4	710	470	230	20	70	**1500**
SU5	3690	2043	6	713	140	**6592**
45	890	1140	0	150	480	**2660**
LO5	413	893	0	86	163	**1555**
LO4	513	2303	30	90	173	**3109**
2	300	200	80	40	0	**620**
3	340	890	0	50	20	**1300**
5	130	210	230	70	0	**640**
1	220	480	40	250	280	**1270**
4	360	180	35	55	0	**630**
BM5	1326	5516	0	203	510	**7555**
BE10	276	916	10	46	0	**1248**
BE9	20	740	0	0	30	**790**
Na5	1833	31886	20	90	566	**34395**
BE11	175	1865	25	30	160	**2255**
BE12	986	913	30	20	100	**2049**
BE13	1230	400	10	270	250	**2160**
BE7	20	170	0	1255	10	**1455**
KU6	783	12173	656	3100	320	**17032**
Ku5	43	4280	0	1843	2493	**8659**
Ku4	113	263	0	726	6	**1108**
KU3	243	2260	0	1023	13	**3539**

The station with the highest number of individuals per m² is by far station Na5 (34396 individuals/m²), caused by the great abundance of polychaetes. Station Na5 is followed by station KU6 with 17032 individuals/m², station 121 with 9250 individuals/m² and station Ku5 with 8659 individuals/m² (Fig. 34). The total abundances calculated for all other station are below 8000 individuals/m². These stations are additionally shown in figure 35. Significant abundance trends in the studied area are the rise in polychaetes and mollusks in the south.

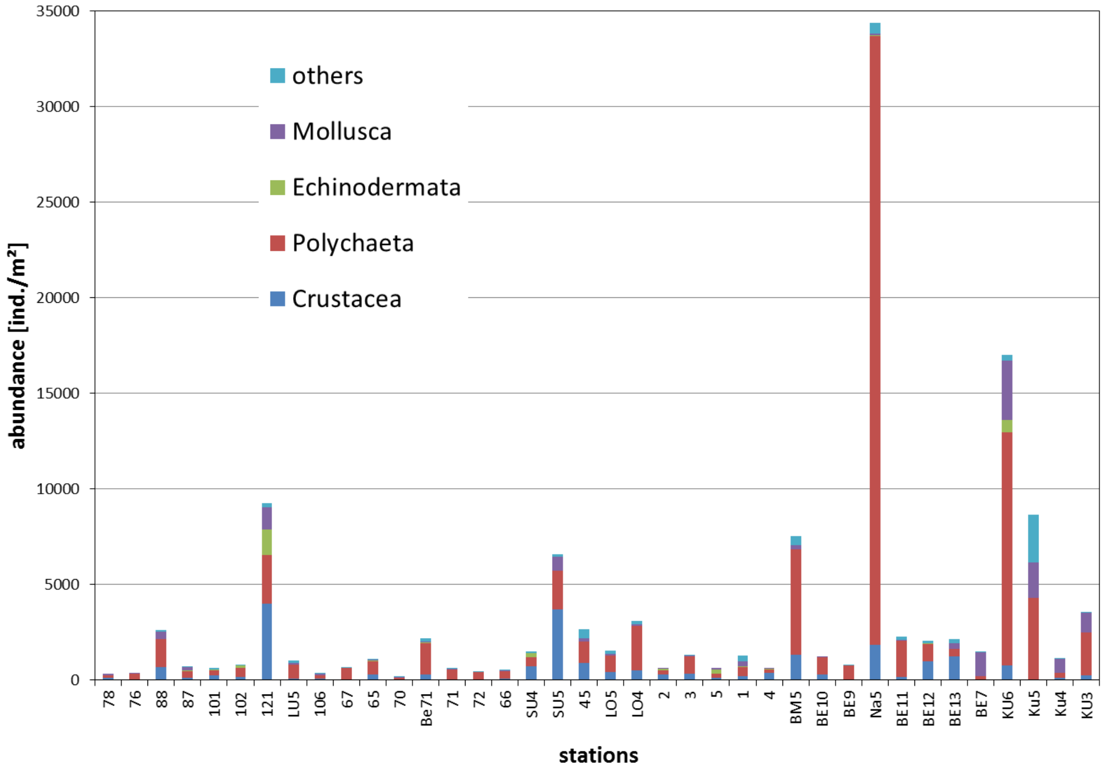

Fig. 34: Abundances at all stations along the Angolan coast from north (left side) to south (right side)

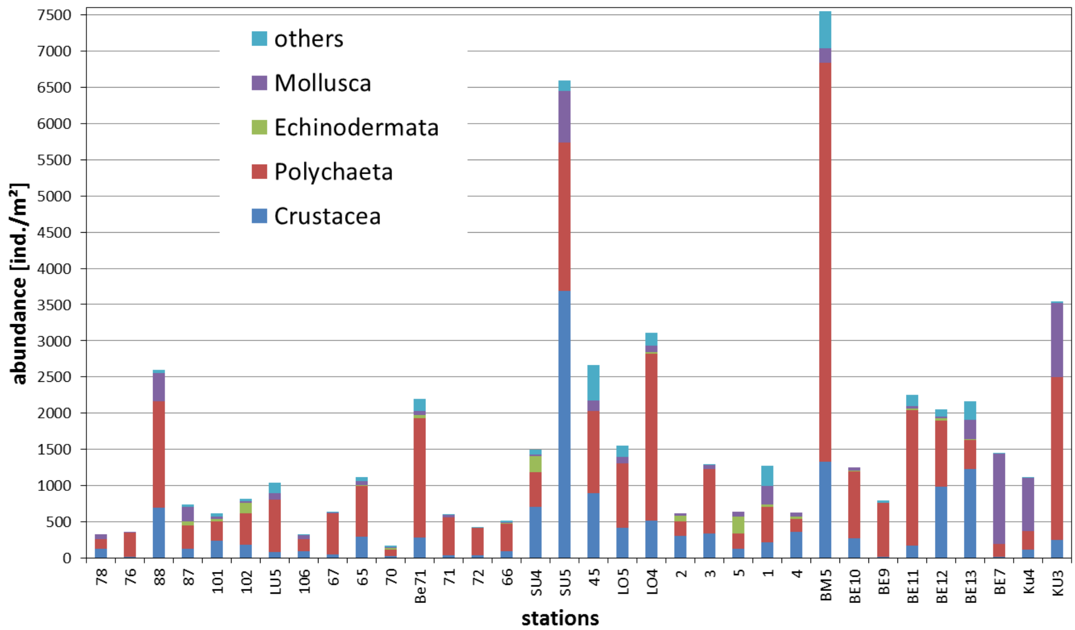

Fig. 35: Abundances at all stations along the Angolan coast from north (left side) to south (right side)

3.5 Biomasses

The wet weight [g] of all taxa from the grab samples were measured at the stations 78, 77, 88, 87, LU5, Be71, 71, 72, SU4, SU5, LO5, LO4, 3, BM5, Na5, BE7, KU6, Ku5, Ku4 and KU3. Subsequently the wet weights were extrapolated to one m². This wet weight [g/m²] expresses the biomass.

The total biomass of the studied area is dominated by mollusks. They contribute 60 % to the whole biomass. With 1 %, echinoderms constitute the smallest proportion on total biomass (Fig. 36).

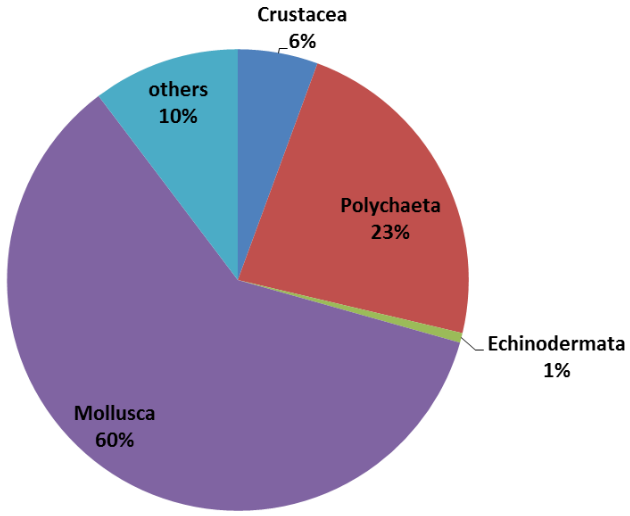

Fig. 36: Biomass percentages of the taxonomic main groups in the whole studied area

The biomass percentages of the taxonomic main groups vary enormous at different areas of the Angolan shelf (table 13; Fig. 37). The percentage of mollusk biomass is extremely high in South Angola, particularly in the region of the mouth of the Kunene River. The biomass percentages of other groups are low in this area. The lowest percentage of mollusk biomass occurs at the area from Soyo to Luanda, while the percentage of Polychaeta biomass is highest here. Echinoderm biomass is negligible small in the external regions. However, they have a noticeable impact on the total proportion of macrozoobenthic biomass from Soyo to Namibe.

Table 13: Biomass percentages of taxonomic main groups at certain areas from North- to South Angola

region	Crustacea	Polychaeta	Echinodermata	Mollusca	others
Cabinda	16 %	10 %	0 %	54 %	20 %
Soyo to Luanda	10 %	59 %	2 %	23 %	6 %
Sumbe to Lobito	17 %	32 %	5 %	44 %	2 %
Benguela to Namibe	1 %	21 %	0 %	75 %	3 %
Kunene River mouth	1 %	5 %	0 %	90 %	4 %

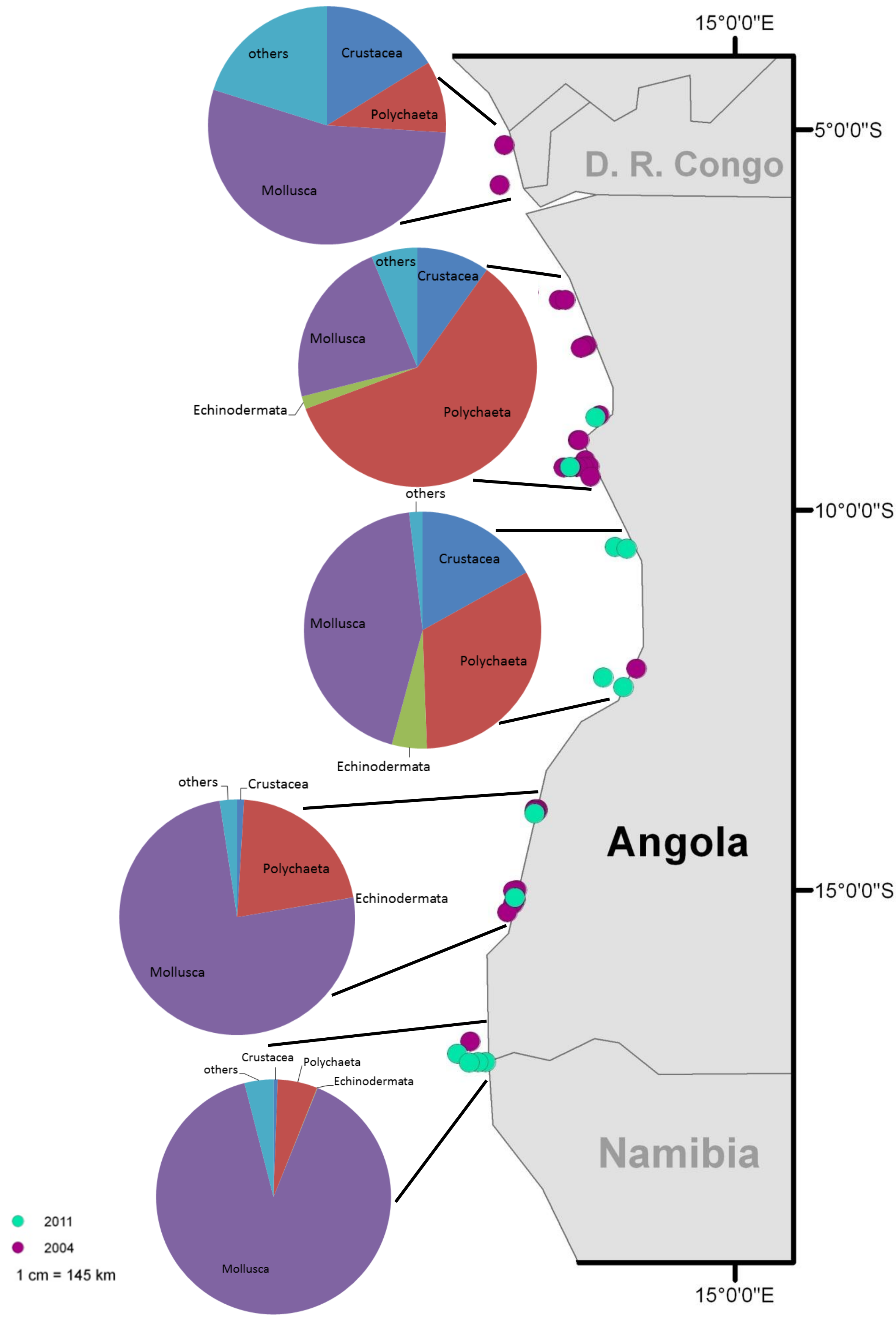

Fig. 37: Percentage of taxonomic main groups on the biomass of certain areas along the Angolan coast

In the following, biomasses (wet weights) are shown for all taxonomic main groups and for all stations. Because of the various sample effort at different stations, the calculated biomasses [g/ m²] were divided by the number of hauls at the respective station (see table 1, 2).

Table 14: Biomasses [g/m²] of the taxonomic main groups and total biomasses [g/m²] at every station. The stations are listed in a latitudinal gradient starting with the most northern station.

station	Crustacea	Polychaeta	Echinodermata	Mollusca	others	total
78	5.9	2.4	0	11.2	0	19.5
88	6.2	154.6	0	8.6	0	169.5
87	0.5	2.9	0.2	1.1	0.1	4.8
LU5	0.9	40.8	0.1	1.3	1.3	44.3
Be71	9.7	9.9	6.0	51.7	3.6	80.9
71	1.1	3.8	0	19.7	17.4	42.1
72	17.6	4.5	0	0	0.3	22.4
SU4	2.3	3.8	5.8	0.5	0.1	12.6
SU5	9.9	35.8	0.02	53.4	1.1	100.1
LO5	9.3	4.9	0	1.5	0.2	15.9
LO4	2.7	2.1	1.0	7.7	1.3	14.8
3	0.7	52.2	0	0.2	0.1	53.2
BM5	1.4	9.6	0	1.9	0.4	13.4
Na5	1.8	30.4	0.04	24.3	0.2	56.8
BE7	0.2	1.9	0	305.5	9.8	317.5
KU6	0.7	22.9	0.4	20.5	3.2	47.8
Ku5	0.04	8.1	0	44.5	1.3	54.0
Ku4	0.1	2.1	0	203.3	1.0	206.4
KU3	3.4	7.2	0	393.2	23.9	427.7

Only stations, where the wet weights of all taxa were measured are considered for the biomass analysis. Although some stations have to be omitted, stations from latitudes of the complete Angolan coastal waters are included in the results of biomass. It is demonstrated in figure 38 that the highest biomass (427.7 g/m²) occurs at station KU3, which is the most southern one. A high biomass (317.5 g/m²) is also found at another southern station, the BE7. The high biomasses in the south are caused by the increasing trend in mollusk biomass. The remaining taxonomic groups have more or less similar biomasses at all stations. However, polychaetes biomasses fluctuate a little with a comparatively high peak at station 88. The station with the lowest biomass is station 87 (4.8 g/m²). The exact biomass values for every taxonomic main group as well as for every station are listed in table 14. Furthermore, these values are illustrated in figure 38.

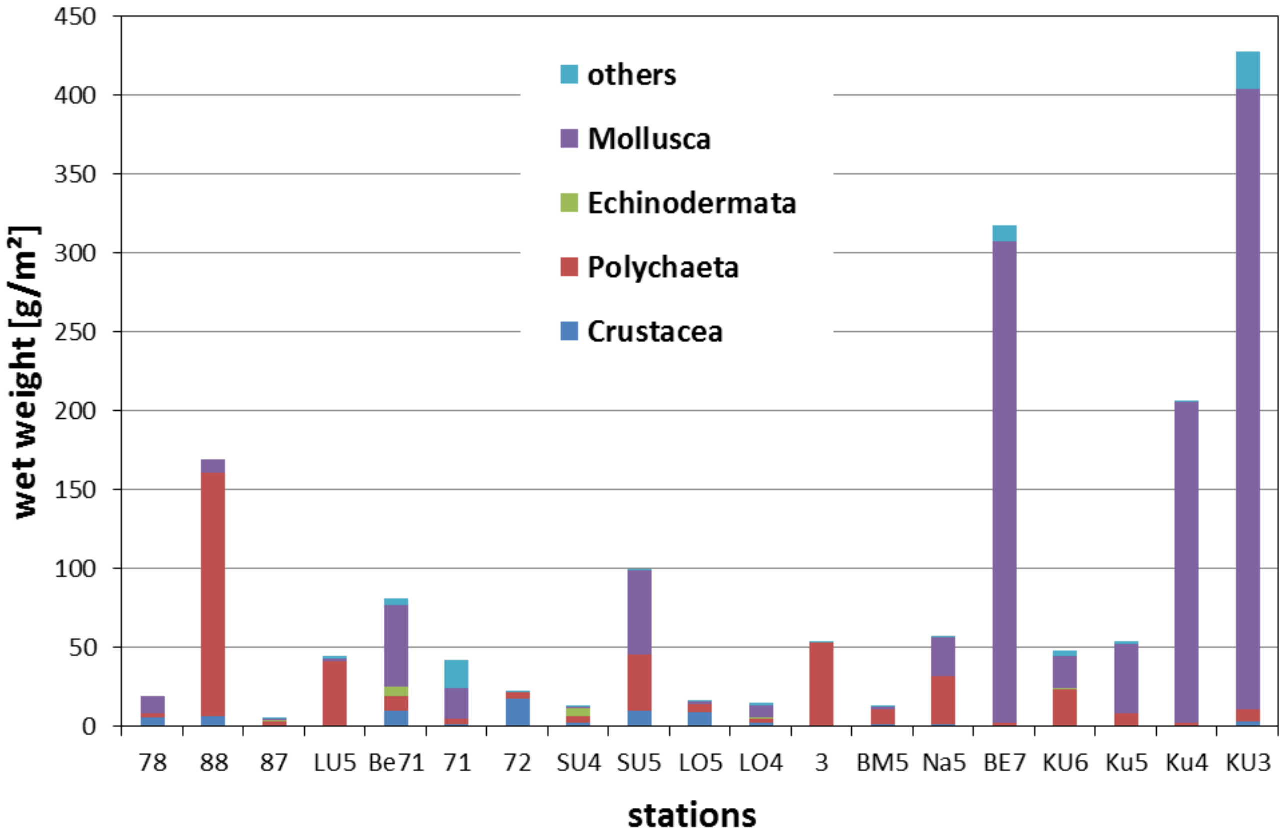

Fig. 38: Biomasses, given as wet weight, of different stations along the Angolan shelf. The stations are listed in a latitudinal gradient from north (left side) to south (right side)

3.6 Characteristics of Key Species

The “key species concept” was established by Paine (1966). Key species can be defined as species which have a disproportionally impact on a community or on a whole ecosystem. These ecosystem relevant effects may depend on the dominance of key species or are much larger than expected from their abundance or biomass (Bengtsson, 1998). Key species can be significantly involved in the control of crucial processes for ecosystem functioning. Consequently, not only information about diversity but also knowledge of the ecology and physiology of key species are important to understand dynamics within an ecosystem.

Some species found on the shelf of Angola are presented in the next paragraph regarding habitat, feeding, reproduction, morphology and distribution. The chosen species show remarkably high numbers of individuals in certain regions.

3.6.1 *Nuculana bicuspidata* (Gould, 1845)

Habitat:

This buried bivalve lives close to the sediment-water interface in organic rich, fine-grained sediments like mud and fine sand. *N. bicuspidata* is a species of the strictly marine family Nuculanidae with a low mobility (Michel et al., 2011). The species were observed in depth from 25 to 150 m in this study.

Feeding:

The shell is a deposit feeder. They feed on the organic surface of the sediment, which is a good adaption to habitats with much detritus (Michel et al., 2011; Bochert & Zettler, 2012).

Reproduction:

Nuculanidae have separated sexes. Species of the genus *Nuculana* produce lecithotrophic larvae with a short pelagic lifetime (Huber, 2010). Concrete information about the reproduction of *N. bicuspidata* are not available.

Morphology:

This white shell is equivalve and elongated (Fig. 39 & 40). The anterior end is rounded while the posterior end is produced and elongated with a deeply grooved surface. The grooves are interrupted at the anterior end by a vertical notch. The hinge plate is strong with two rows of numerous chevron-shaped taxodont teeth (Huber, 2010).

Distribution:

The bivalve occurs in waters of the subtropical and tropical West Africa. Individuals were found from Angola to Mauritania and at the Cape Verde Islands (Kensley, 1985). In this study, the animals were collected from Benguela to the mouth of the Kunene River and near Sumbe.

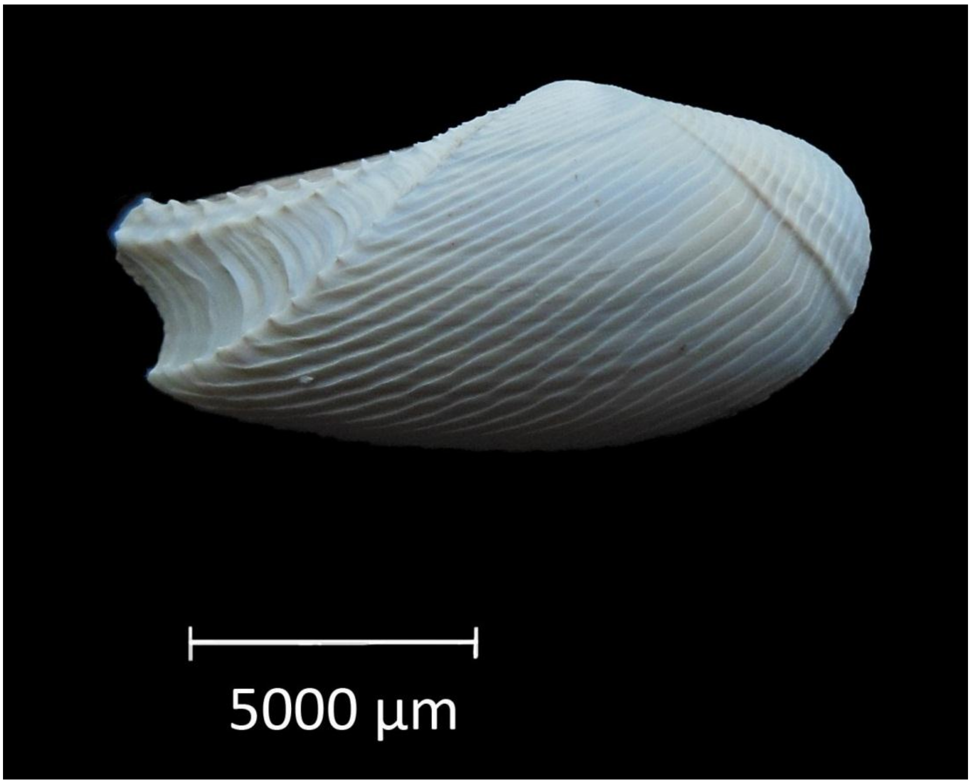

Fig. 39: *Nuculana bicuspidata* (outer side) from station KU6 (photo: Gesine Lange)

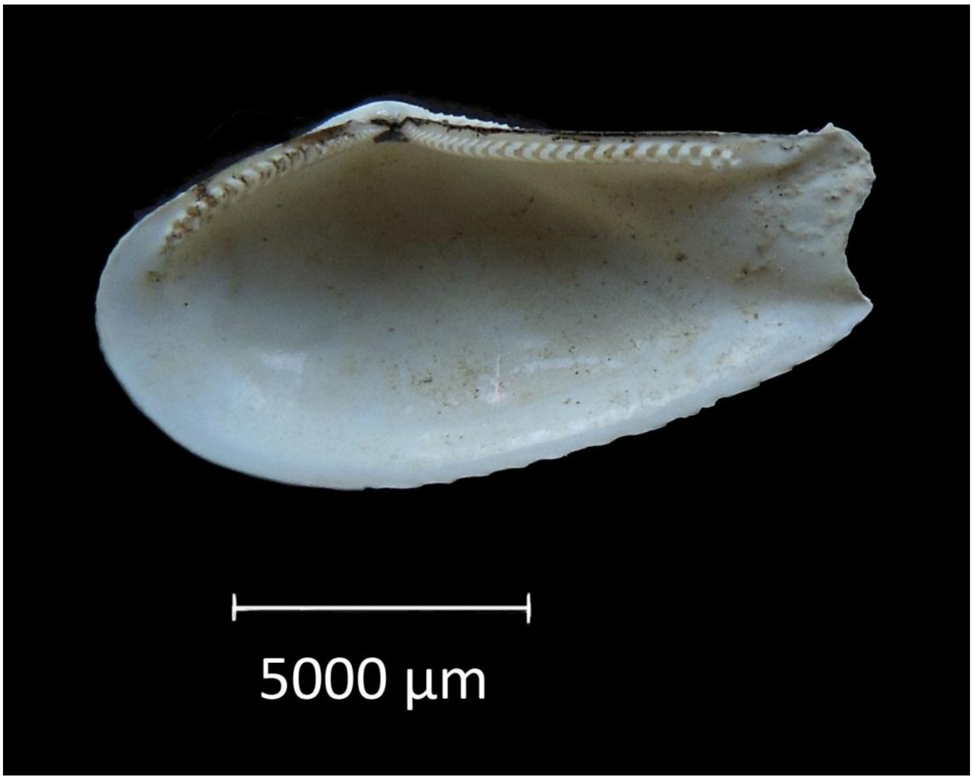

Fig. 40: *Nuculana bicuspidata* (inner side) from station KU6 (photo: Gesine Lange)

3.6.2 *Nassarius* sp.

Several species of the genus *Nassarius* were found in waters off Angola. The most abundant species are *Nassarius angolensis* (Odhner, 1923) and *Nassarius vinctus* (Marrat, 1877). However, many individuals of *Nassarius elatus* (Gould, 1845) were found, too.

Habitat:

Nassariidae are sand-dwelling gastropods, which inhabit the benthal from shallow to deep waters (Ardovini & Cossignani, 2004). *Nassarius*-specimens were found on the Angolan shelf in depth from 25 to 150 m during the research cruises of the Leibniz Institute for Baltic Sea Research Warnemünde in 2004 and 2011. The species *Nassarius vinctus* (Fig. 41) lives on muddy sediment surfaces (Herbert & Compton, 2007), were they are often covered with algae or hydrozoans. Species, which are not living in mud belts, burrow in response to falling tides (Herbert & Compton, 2007).

Feeding:

Nassariidae are carnivorous (Ardovini & Cossignani, 2004). *N. vinctus* is an active scavenger (Herbert & Compton, 2007).

Reproduction:

The fertilization in the genus *Nassarius* is external and takes place annually during March and August. The produced egg capsules are attached on stones. Each of the approximately 6000 capsules contains about 200 eggs. The hatched larvae are pelagic (Moritz, 2012).

Morphology:

The shells of the gastropods are ovate but a bit elongated with colors from yellow to brown, sometimes with whitish patches. They can be smooth as in *N. elatus* (Fig. 42) or pronouncedly ribbed as in *N. angolensis* (Fig. 43) or *N. arcadioi* (Fig. 44). The found species (see appendix) has an inner lip with an inconspicuous parietal callus and a thin outer lip. The rounded aperture is corneous as well as the operculum, which is missing at the collected specimens. Slender siphons, some tentacles around the head and expanded foots are features of members of the Nassariidae (Ardovini & Cossignani, 2004).

Distribution:

Species of *Nassarius* are widespread in the Atlantic Ocean. *N. vinctus* is distributed from London to Namibia (Moritz, 2012) and *N. elatus* is spread from Portugal to Angola. The type locality of *N. angolensis* is Porto Alexandre in Angola (Adam & Knudsen, 1984). Other distribution areas of this species are not published. In this study *Nassarius*-species occurred from Soyo to North Namibia.

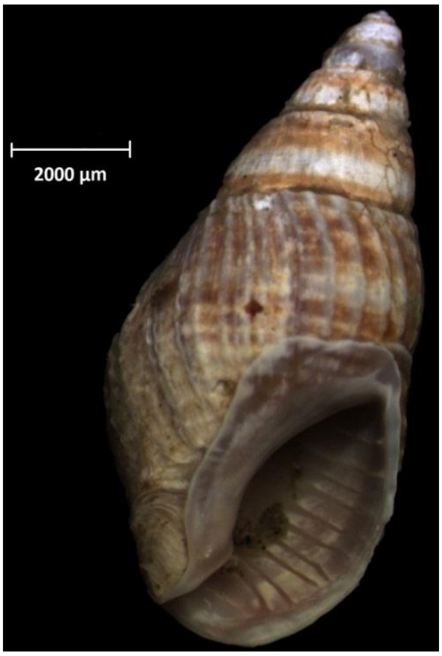

Fig. 41: *Nassarius vinctus* from station KU3

(photo: Gesine Lange)

Fig. 42: *Nassarius elatus* from station SU5

(photo: Gesine Lange)

Fig. 43: *Nassarius angolensis* from station KU6

(photo: Gesine Lange)

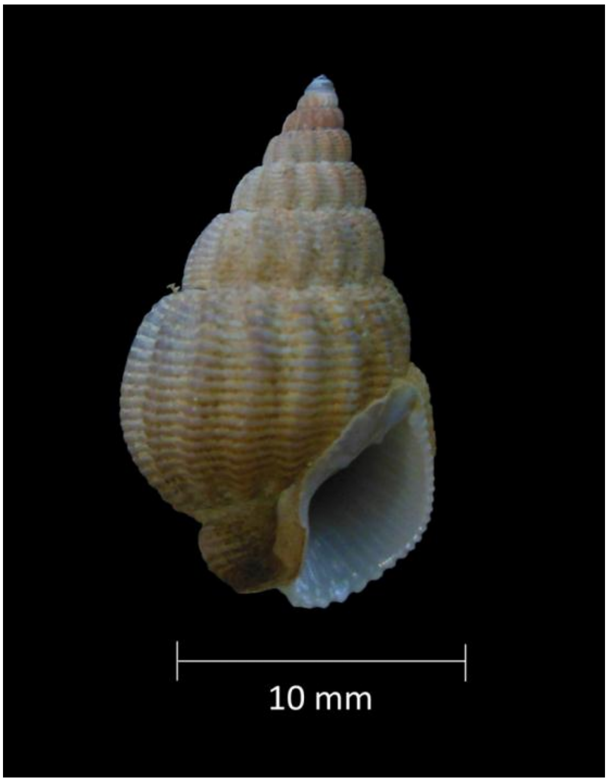

Fig. 44: *Nassarius arcadioi* from station Na5

(photo: Gesine Lange)

3.6.3 *Paraprionospio pinnata* (Ehlers, 1901)

Habitat:

This polychaete of the family Spionidae inhabits the sediment-water interface. The eurytopic animals prefer polyhaline and mesohaline waters, where they mainly occupy muddy areas consisting of 11 to 100 % silt and clay (Dauer et al., 1981). Dauer (1985) mentioned that *P. pinnata* (Fig. 45) prefers fine-sized substrates with 70 to 80 % of particles less than 63 µm and that the species often builds colonies in those areas. Motions on the surface and swimming movements occur in response to physical disturbances (Dauer et al., 1981).

Feeding:

The organisms feed on deposited matter, which they collect at the seafloor surface, using a pair of tentaculate palps (Dauer et al., 1981). If currents are present, the worms collect suspended and resuspended particles, by arching the palps. Simultaneous suspension- and deposit-feeding is possible. Increasing feeding rates described by Dauer (1985) in presence of a particle transporting current support this fact. The palps of the polychaetes have lateral, latero-frontal, frontal and basal transverse rows of cilia groups. The lateral cirri initiate a current flowing toward the palps's frontal surface. Latero-frontal cirri deflect suspended particles in the same area. The frontal cilia transport particles to the pharynx. The basal transverse cilia create an undercurrent in u-shape in combination with the frontal cilia. The latter remove particles that are rejected by the pharynx (Dauer, 1985).

Reproduction:

Recruitment of *P. pinnata* occurs from June to December. Multiple generations were observed during summer. The species produces gamete-clutches consisting of about 6000 eggs. Individuals die after the production of one clutch. The oocytes float freely in the coelomic cavity. Vitellogenesis occurs. Females of *P. pinnata* are suggested to have storage sites, which attract sperms (Mayfiled, 1988).

Morphology:

Large individuals can reach a body length of 60 mm (Day, 1967) and a width up to 1.3 mm with 79 setigers. The prostomium is fusiform with a round anterior end and two pairs of dark-brown eyes, which are seldom visible in adults. Palpi have a basal sheath. Marginal papilla are lacking on the peristomium. Setigers 1-3 bear 3 pairs of large pinnate gills of approximately the same length (Fig. 46). They have 50 to 60 lamellae on the branchial shaft except of its base and its distal tip. 1 or 2 lamellae of triangular plates are found at the proximal region of the branchial shaft. The notopodial postsetal lamellae are subtriangular elongated on setigers 1 to 5 and become smaller and low rounded posteriorly to about setiger 11 (Yokoyama, 2007). They are united across the dorsum and form low ridges from setiger 21 to the middle of the body. Anterior neuropodial postsetal lamellae are prominent, ovate and distally pointed. They become low rounded from setiger 4 and reduced to a low ridge from setiger 9. Hooded neuropodial hooks occur from setiger 9 and reach a maximum of 15 hooks per neuropodium. They are accompanied by an inferior sabre seta (Day, 1967). Individual hooks with 4 pairs of accessory teeth are located above the main fang (Delgado-Blas, 2004). The pygidium has a long medial cirrus and 2 short lateral cirri (Yokoyama, 2007).

Distribution:

The species occurs in the Atlantic from Morocco along tropical West Africa to South Africa (Day, 1967) and from Chesapeake Bay to Florida (Dauer et al., 1981; Dauer, 1985). Along the Angolan shelf, individuals were found near Luanda, Sumbe, Lobito, Namibe and the border between Angola and Namibia. *P. pinnata* is also spread in the tropical Indian Ocean and the Pacific Ocean from West Canada and Japan to Chile (type locality: Talcahuano) as well as New Zealand (Day, 1967).

Fig. 45: *Paraprionospio pinnata* (habitus) from station Na5 (photo: Gesine Lange)

Fig. 46: *Paraprionospio pinnata* (pro-, peristomium; setiger 1-14; gills) from station Na5 (photo: Gesine Lange)

3.6.4. *Prionospio ehlersi* Fauvel, 1928

Habitat:

This spionid polychaete prefers sediments of a lower grain size like mud, sandy mud or muddy sand (Mackie & Hartley 1990; Probert et al., 2001). This assumption is confirmed by investigations of Wakasa Bay (Japan) accomplished by Yokoyama & Hayashi (1980), who found that *P. ehlersi* (Fig. 47) is dominant on mud bottom. The authors also show that the species is dominant on deeper offshore bottoms while it is absent in shallow areas. However, Bigot et al. (2006) discovered great abundances of *P. ehlersi* in intermediate depth ranging from 50 to 100 m. This is consistent with the own observations of the shelf off Angola, where the species occurs in depths from 62 to 92 m.

Feeding:

Generally, Spionidae feed at the sediment-water-interface with 1 pair of tentaculate palps (Dauer et. at, 1981). These palps are ciliated and enable the selection of deposited food particles from the nearby bottom surface. It is assumed that the worms have good discriminatory abilities and select particles on both size and content. Furthermore, spionids are able to move discretely, but they stop motions while feeding (Fauchald & Jumars, 1979).

Reproduction:

A 1:2 sex ration to female were observed in a Japanese population of *P. ehlersi*. Those animals need a certain body size with a peristome width of 0.38 mm or a wet weight of 4.4 mg to mature. Mature specimens containing eggs or sperm occur from April to November. Newly recruited individuals appeared from August to December (Tamai, 1988). Eggs were found within the body cavity of females can reach a size up to 100 µm in diameter (Mackie & Hartley, 1990). *P. ehlersi* produces small meroplanktonic larvae (Schlüter & Rachor, 2001).

Morphology

The worms reach a length up to 20 mm. Their prostomium is anteriorly expanded, posteriorly narrowed and forms an elevated keel between the peristomial folds. 1 to 2 pairs of little eyes and black pigment spots occur. Setiger 1 shows small notopodial and neuropodial lobes (Day, 1967). The peristomium surrounds the prostomium and fuses with setiger 1 (Fig. 48). This creates triangular, well-developed pointed notopodial lamellae (Mackie & Hartley, 1990). 4 pairs of gills are found on setiger 2 to 5. The first one is pinnate; the second and third one is short and smooth. The fourth gill is long, smooth and tapered. They have their maximum size on setigers 3 to 5. Then, they decrease in size. The notopodial lamellae are united by a low membranous ridge. This ridge starts on setiger 5 or 6 and continues for the next 20 to 30 segments (Day, 1967). Neuropodia have multidentate hooded hooks with 2 rows of 6 or 7 secondary teeth above the main fang. Striated internal hoods create a feathering appearance below the main fang. Neuropodial hooks occur on setiger 19 to 21. Hooded hooks also appear in notopodia from setiger 37. These hooks are longer and more slender than the neuropodial hooks. Moreover, there are fewer hooks per ramus (Mackie & Hartley, 1990). The inferior neuropodium has a punctuate sabre seta. These setae start at about setiger 19 to 23 and run onwards. Adult individuals show genital pockets between the neuropodia from setiger 2 to approximately setiger 22. Neuropodia lamellae are rounded and firstly longer than broad. Later, they become oval (Day, 1967).

Distribution:

This species is cosmopolitan. The type locality of *P. ehlersi* is Morocco. Other locations of occurrence are Natal, Mozambique (Day, 1967), Wakasa Bay (Yokoyama & Hayashi, 1980), Mediterranean Sea off France (Sigvaldadóttir, 1998), Canary Islands, South West Africa, North West Atlantic, western Mexico, South East Africa, Red Sea, Indian Ocean, Vietnam, Hong Kong, Australia and Antarctica (Mackie & Hartley, 1990). On the Angolan shelf, the species was found from Lobito to Namibe.

Prionospio steenstrupi Malmgren, 1867 and *Prionospio malmgreni* Claparède, 1869 are other spionid species found in nearly the same area (Sumbe to north Namibia) and similar depths (25 to 92 m). They show high individual numbers (see appendix).

Fig. 47: *Prionospio ehlersi* (habitus) from station LO4 (photo: Gesine Lange)

Fig. 48: *Prionospio ehlersi* (pro-, peristomium; setiger 1-13; gills) from station LO4 (photo: Gesine Lange)

3.6.5 *Galathowenia* sp.

Habitat:

This tube-dwelling polychaetes-genus of the family Oweniidae inhabits depths from 12 to 2500 m. *Galathowenia* sp. (Fig.49) was found off Angola in depth ranging from 25 to 92 m. *Galathowenia kirkegaardi* De León-González & Sanchez-Hernández, 2012 was observed in coastal lagoons, where it dwells in muddy bottoms with high clay content. All other species occur in deeper water of open ocean environments. This genus builds concise tubes from which the animals are difficult to remove. The use of construction materials is selective and varies from grain and sand to foraminifera or sponge spicules (De León-González & Sanchez-Hernández, 2012).

Feeding:

Feeding appendages like they are typical for oweniids are missing in *Galathowenia* except for a pair of lips (Fig.50) (Wlodarska-Kowalczuk & Pearson, 2004). Fauchald & Jumars (1979) assumed that those oweniids feed in a buried position and in the same manner like maldanids feed: by eversion of a sac-like pharynx. However, specimens of the genus were observed while extending their head from the tube and bending the head to sweep the surrounding surface. This is considered as a feeding mechanism to collect particles from the sediment (Wlodarska-Kowalczuk & Pearson, 2004). The structures for the food consumption in oweniids generally indicate high selectivity regarding particle size and composition (Fauchald & Jumars, 1979).

Reproduction:

Carson & Hentschel (2006) observed the reproduction of polychaetes, including oweniids, in the Southern California Bight. They revealed that all found Oweniidae, inclusive one species of *Galathowenia*, namely *Galathowenia pygidialis* (Harman, 1960), produce egg-clutches. Pelagic swimming with a Mitraria stage occurs during the life history of this oweniids. Their dispersal potential is high.

Morphology:

The body of *Galathowenia* is elongated and cylindrical with few segments and reduced parapodia. The concise tubes built by the worms differ from species to species in form and ornamentation. This is helpful to distinguish species. *Galathowenia africana* Kirkegaard, 1959, for example, produces tubes with very small, not overlapping sand grains whereas *Galathowenia oculata* (Zachs, 1923) uses oblong sand grains. *G. kirkegaardi* uses both white sand and sponge spicules. A morphological feature to distinguish species is the number of anal cirri. *G. kirkegaardi* and *G. oculata* have 2 pygidial lobes or cirri. Pygidial lobes are absent in *G. africana*. The presence of eyes was validated for *G. kirkegaardi*, *G. africana* and *G. oculata*.

Distribution:

The genus is distributed at West Africa off Nigeria and Congo (*G. kirkegaardi*, *G. africana*) and at the Boreo-Arctic White Sea (*G. oculata*) (De León-González & Sanchez-Hernández, 2012). *Galathowenia sp.* appears on the Angolan shelf from Sumbe to the mouth of the Kunene River.

Fig. 49: *Galathowenia* sp. from station KU6 in its tube (photo: Gesine Lange)

Fig. 50: Head with a pair of lips of *Galathowenia* sp. in its tube (photo: Gesine Lange)

3.6.6 *Cossura coasta* Kitamori, 1960

Habitat:

C. coasta (Fig.51) is a polychaete of the family Cossuridae that burrows in mud and sand bottoms. It is commonly found in the deep sea but the species also occurs in shallow sediments (Rouse & Pleijel, 2001).

Feeding:

Polychaetes of the genus *Cossura* feed on deposit of the sediment surface by opening their mouth widely and using heavily ciliated buccal tentacles (Rouse & Pleijel, 2001).

Reproduction:

The species has probably separated sexes. There are no further information on reproduction and development of these animals (Rouse & Pleijel, 2001).

Morphology:

The body with 107 segments is up to 15 mm in length (Day, 1967). The prostomium of the species is a blunt cone. Eyes and head appendages are lacking. 2 apodous rings are located behind the prostomium. The ventral mouth opens between these rings. The pharynx is evertable and has a lobed margin. 40 cylindrical setigerous segments appear behind the second apodous ring. Parapodial projections are absent so that setae arise directly from the body sides. Setae arise from 2 fans in posterior segments. Hence, these segment a biramous. The setae of each ramus build 2 rows, with the anterior row of about half the length of the posterior one. All setae are capillaries having flattened blades. Their margin is hispid or spinulose. A conspicuous very long and slender gill arises from the anterior dorsal surface of the middle of setiger 3 (Day, 1963). It is about three-quarters the length of the body. The last few segments have no setae and the pygidium has 3 long filiform anal cirri (Day, 1967).

Distribution:

C. coasta occurs at Japan and South-West Africa (Day, 1967). It was found with a high number of individual (see appendix) in all waters off Angola with the exception of the Cabinda-region.

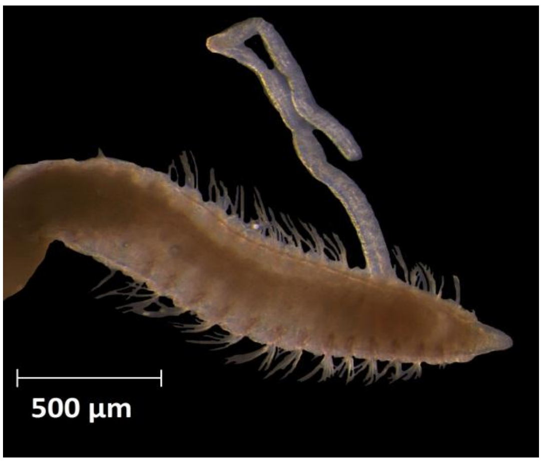

Fig. 51: Anterior part of *Cossura coasta* from station KU6 (photo: Gesine Lange)

3.6.7 *Chaetozone setosa* Malmgren, 1867

Habitat:

C. setosa (Fig. 52) is a polychaete of the family Cirratulidae. It is common on soft-bottoms like mud or sandy mud (Hily, 1987). However, this species does not depend on a certain kind of substrate. They also inhabit gravel, sand with shell fragments and stones, mixed bottoms, silt, reef structures, empty worm tubes and rock crevices. They occur from intertidal zones to the abyssal and are able to tolerate mesohaline salinities (Hartmann-Schröder, 1996).

Feeding:

Hily (1987) claims this polychaetes are small-surface and subsurface deposit-feeders. Fauchald & Jumars (1979) predict that the worms are selective in feeding on deposit by using their palps to collect particles.

Reproduction:

Epitoke sexual stages with elongated dorsal setae at the anterior end occur. Females with mature eggs were observed in May and June (Hartmann-Schröder, 1996). The temporal free-spawning varies in different areas. Hily (1987) suggest that variabilities in recruitment and somatic growth of *Chaetozone* are caused by variations in the benthic environment. The author further suggests that free oocytes in the coelom indicate spawning potential over a long period. 1 or 2 recruitment periods occur in every year. The species has a medium potential for dispersal (Carson & Hentschel, 2006). The longest benthic life time of the animals is about 1.5 year (Hily, 1987).

Morphology:

C. setosa has an elongated body of 70 to 90 segments with a length of 20 to 25 mm. The Prostomium is conical and without eyes (Fig. 53). Setiger 1 bears 2 stout palps at its anterior margin and branchial filaments. The latter arise close above the notosetae and run further to the middle of the body. Capillary setae start also at setiger 1 and appear up to the posterior end. Simple sigmoid acicular hooks occur in the notopodia from setiger 3 onwards and in the neuropodia from setiger 1. Notopodial and neuropodial setae appear mostly as separated bundles. However, they form a dorso-ventral arc of spines at the posterior end. The species has a pygidium with a dorsal anus (Day, 1967). The color of the worms varies from light- or dark-grey over blue-black to brown (Hartmann-Schröder, 1996).

Distribution:

C. setosa is a cosmopolitan species. It was observed in the following areas: Arctic, Greenland, North Carolina, Sweden, Scotland to Morocco, tropical West Africa, Mediterranean, Aden, subantarctic Heard Isles as well as the Pacific from Behring Sea and Japan to California (Day, 1967). In waters off Angola, *C. setosa* is distributed near Sumbe, Lobito and Namibe. Although the species only was found at 3 stations on the Angolan shelf, 767 individuals were counted.

Fig 52: *Chaetozone setosa* (habitus) from station Su5 (photo: Gesine Lange)

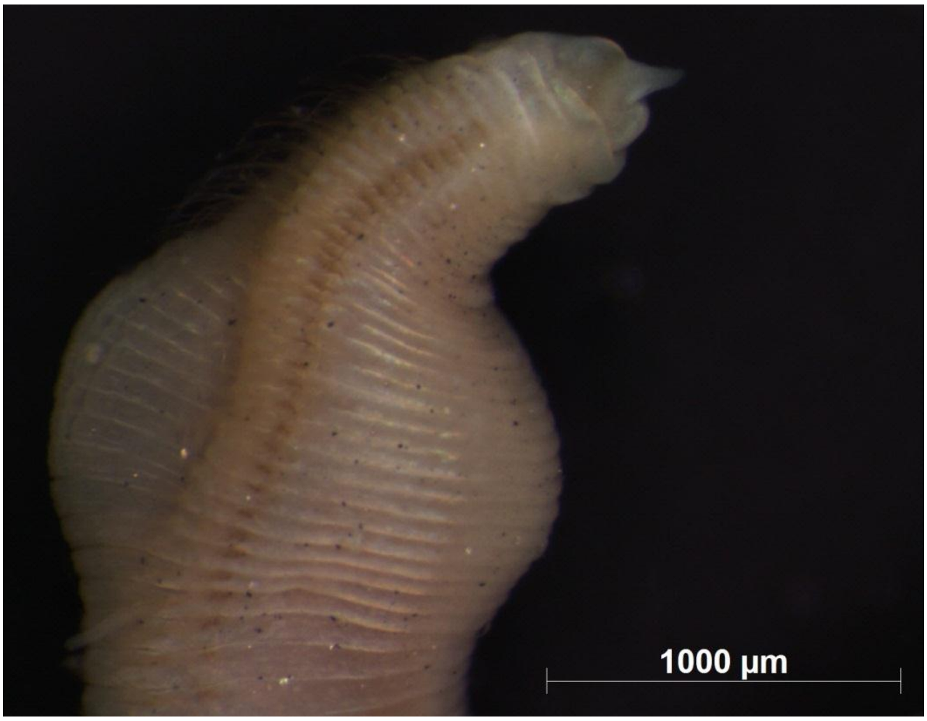

Fig.53: Anterior part of *Chaetozone setosa* from station Su5 (photo: Gesine Lange)

3.6.8 *Diopatra neapolitana capensis* Day, 1960

Habitat:

D. neapolitana capensis (Fig. 54) was found on bottoms that mainly consist of silt during the sampling for this study. It is a subspecies of *Diopatra neapolitana* Delle Chiaje, 1841 (Polychaeta: Onuphidae), which is known from intertidal mudflats and shallow subtidal transitional waters (Pires et al., 2012). The polychaetes inhabit muddy tubes built with a secretion layer to which substrate particle and solid animal parts stick. Tubes of *D. neapolitana capensis* have shell fragments attached near the anterior end (Day, 1967).

Feeding:

Onuphids are in general carnivore scavengers. There are assumptions that the species *D. neapolitana* (Fig. 55) is carnivore and herbivore (Day, 1967; Fauchald & Jumars, 1979).

Reproduction:

D. neapolitana carries gametes in the coelom during the whole year. The number of female oocytes in the body cavity is high from May to August, which is also the spawning period. No release of oocytes is suggested from October to December. The species releases eggs and sperm into the water column. Planktonic lecithotrophic larvae emerge (Pires et al., 2012).

Morphology:

D. neapolitana capensis reaches a length of 80 mm. Frontal antennae are subulate. The median occipital antenna has a ceratophore with 10 to 13 rings. Mandibles with straight tapered shafts occur. The dorsal surface of the peristome is dark brown and the next view segments show 5 short bars. Further, the most of the branchiferous segments show a pair of brown spots. The gills have stout trunks and short filaments. Pseudocompound setae are unidentate or with minute secondary tooth and a less-developed hood. Comb setae with 5 to 12 teeth occur at setiger 12. Acicular setae are bidentate and start at setiger 18 (Day, 1967).

Distribution:

D. neapolitana is a cosmopolitan species known from the Mediterranean, the Red Sea, the Eastern Atlantic Ocean and the Indian Ocean (Rouse & Pleijel, 2001). Day (1967) calls the subspecies *D. neapolitana capensis* endemic for South Africa (Day, 1967). However, it has a wide dispersal range along the Angolan coast but it was not found at Cabinda.

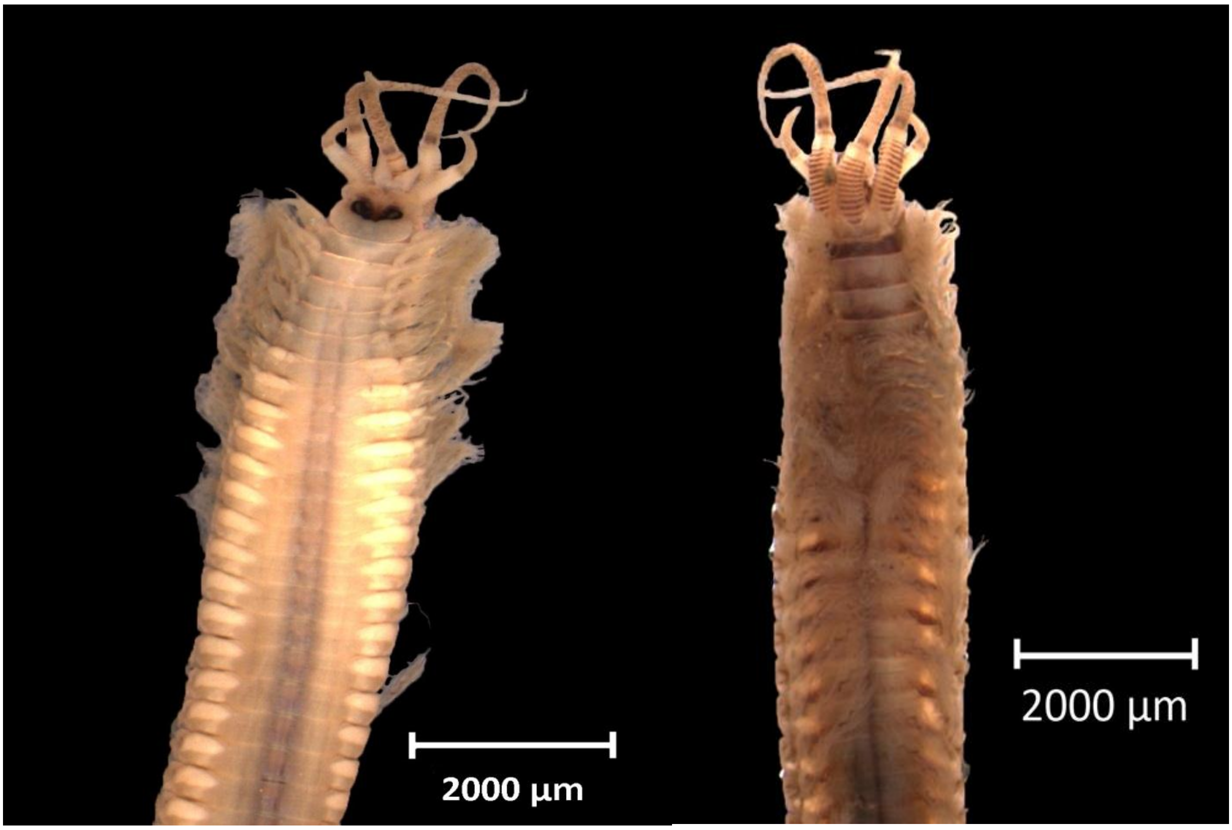

Fig 54: *Diopatra neapolitana capensis* (anterior body) from station KU6; left: dorsal view, right: ventral view (photo: Gesine Lange)

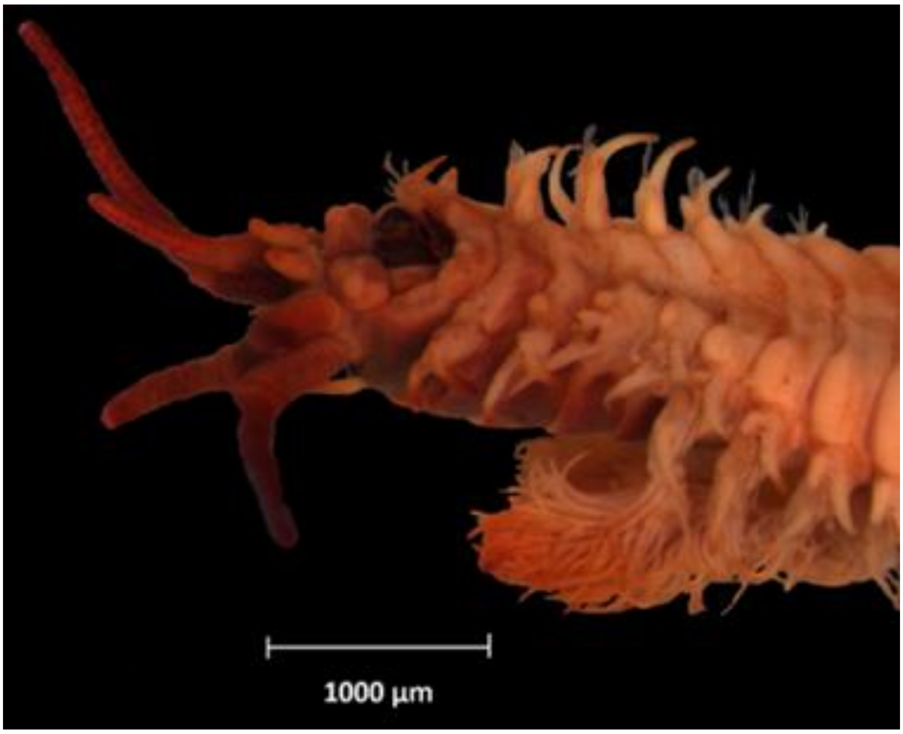

Fig 55*: Diopatra neapolitana* (head and some branchiferous segments) from station KU6 (photo: Gesine Lange)

3.6.9 *Ampelisca* sp.

Ampelisca sp. (Fig. 56, 57) represents the most diverse (7 species) genus of the order Amphipoda (Crustacea: Peracarida) on the Angolan shelf.

Habitat:

Ampelisca is an infaunal burrowing and tube-dwelling genus. It prefers fine sand but also inhabits mud in areas ranging from shallow coastal waters and intertidal zones to abyssal habitats (Hastings, 1981; Anderson, 2005). The genus is typically known from littoral environments (Lincoln, 1979).

Feeding:

These amphipods are detritivorous suspension-feeders. They strain particulate matter with their antennae (Anderson, 2005).

Reproduction:

Amphipods have generally separated sexes. Sexual organs are similar in female and male. They end on a pair of short papillae at the ventral side of pereon segment 5 or 7. Females carry eggs in a marsupium (Stephensen, 1929). Investigations on *Ampelisca brevicornis* (Costa, 1853) at the Isle of Man revealed that this species produces 1 generation per year with a breeding season from May to September. Recruitment starts in July. Mature males were observed from April to August (Hastings, 1981). Poggiale & Dauvin (2001) reported a recruitment period from June to October at the western English Channel. *Ampelisca* has a life span of 1 to 2 years (Nerini, 1984).

Morphology:

The body length of the genus ranges from 13 to 27 mm (Nerini, 1984). The body form is laterally compressed (Hayward & Ryland, 1990). The coxal plate 1 is broad. Distal margins of the plates 1 to 4 have rows of long setae. The posterior margin of the large plate 4 is deeply emarginated. The head is elongated and usually anteriorly truncated. A rostrum is absent. 2 pairs of corneal lenses are common. Both pairs of gnathopods are elongated, setose and with a feebly subchelate dactylus. Pereopod 3 and 4 has a long and broad merus, which is fringed with long plumose setae. Pereopod 4 is larger and more densely setose than pereopod 3. Pereopod 5 and 6 have a broad basis whereas carpus and propodus are very spinose. The dactylus is very small. Pereopod 7 has a very large basis with an obliquely expanded posterior lobe. The propodus is foliaceous and the dactylus is lanceolate. The outer ramus of uropod 1 is often naked. Generally, uropod 1 and 2 are spinose. Uropod 3 is large with foliaceous rami. The telson of *Ampelisca* is elongated and deeply cleft (Lincoln, 1979).

Distribution:

Ampelisca is a cosmopolitan genus containing more than 100 described species. Distribution areas include the North Atlantic, West European coasts, the Atlantic coast of Africa, Natal, the Mediterranean, the Azores as well as the Indian and the Pacific Ocean (Reid, 1951; Lincoln, 1979; Hastings, 1981). Specimens are omnipresent at the Angolan shelf.

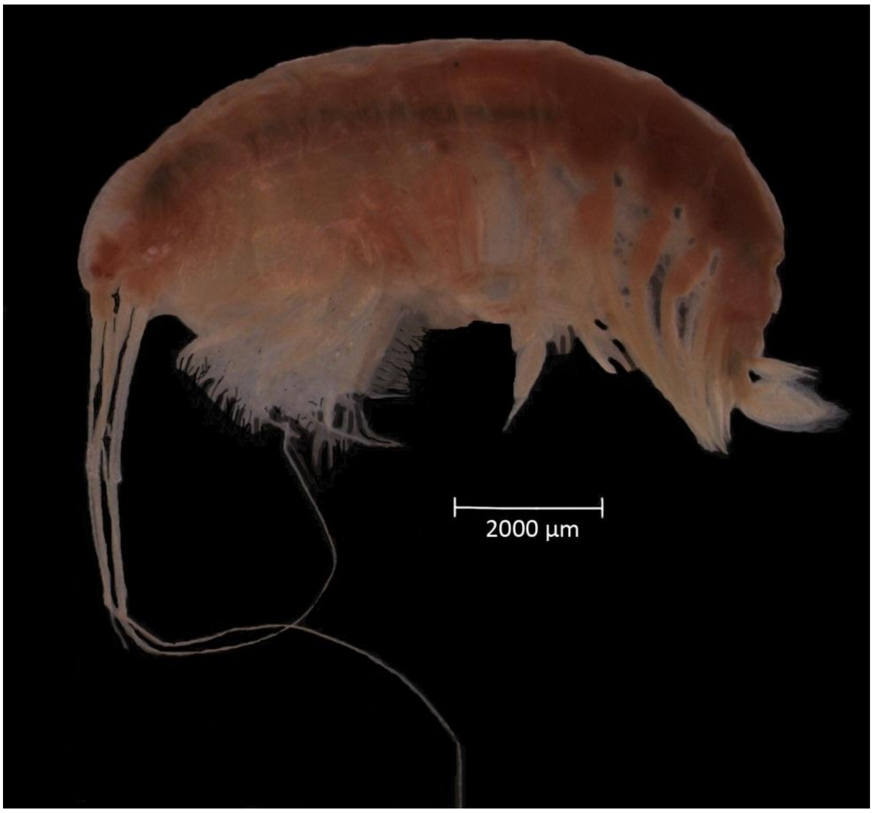

Fig. 56: *Ampelisca* sp. (habitus, left side) from station SU5, pereopod 7 is missing (photo: Gesine Lange)

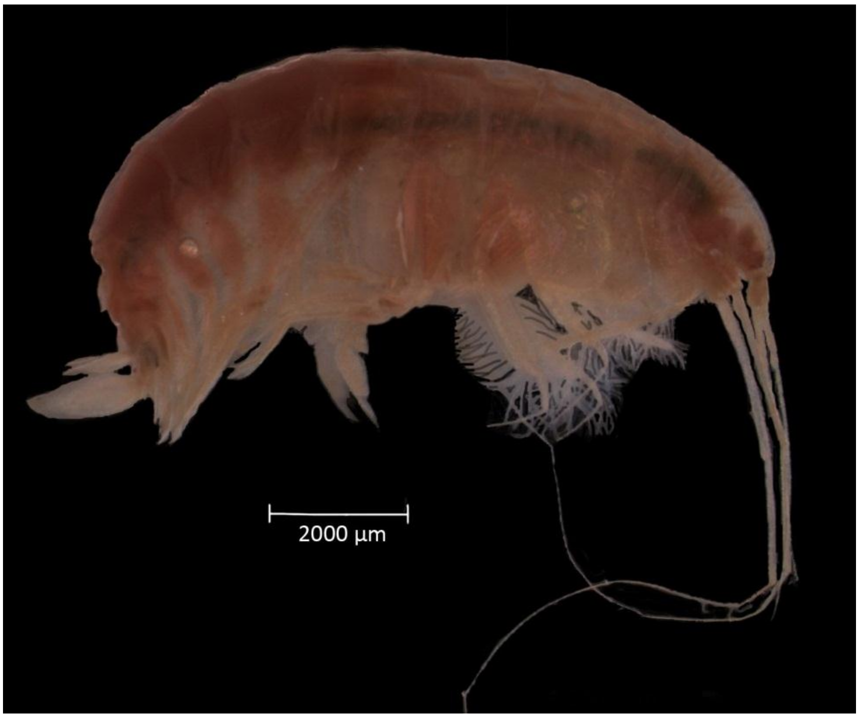

Fig. 57: *Ampelisca* sp. (habitus, right side) from station SU5, pereopod 7 is missing (photo: Gesine Lange)

4. Discussion

4.1 Latitudinal gradient and diversity patterns

In this study, no latitudinal gradient in the diversity of macrozoobenthos was observed. Rather, an alternating diversity trend is evident for the Angolan shelf, which extends from 5° S to about 17° S. Thus, the area is subject to tropical climate in the north. In dependence of the adjacent Benguela upwelling system it is subjected to temperate climate in the south. High numbers of species occur at different locations, for instance, at station 121 (8.7° S), where the number of crustaceans taxa was exceptionally high, at station SU5 (10.5° S) and at station Na5 (15.9° S). A low species number is present at station BE9 (15.0° S) and BE7 (16.9° S). It must be considered that the species number varies in response to the sampling method. Hence, diversity was additionally high in grab samples of station Be71 (9.4° S) and BM5 (13.9° S) while the dredge samples revealed a diversity peak of 138 species at station 87 (7.2° S) that could not be detected in the grab sample of this station. This differences result from the fact that the grab truly intrudes into the sediment whereas the dredge is pulled along the bottom surface. The most striking disparity between grab samples and dredge samples is the higher number of crustaceans taxa in the dredge samples. Thus, it is important to use both sampling methods to get a real impression of the present fauna. Because of the various sampling effort, it was necessary to consider both sampling methods separately. However, there were stations that were samples with both devices (see the Station Approach section). When comparing the species number between stations with the same sampling effort, a peak at station SU5 and Na5 is also present. The assumption that a latitudinal gradient in biodiversity is missing in the waters off Angola is supported by the results of the cluster analysis and the MDS plot, since cluster 1 contains stations from the mouth of the Kunene River while cluster 2 includes stations from the whole studied area apart from the Cabinda Province. Cluster 3 contains samples of the northern part of Angola reaching from Cabinda to Luanda as well as samples from the south of Angola extending from Benguela to Namibe. Additionally, high H' values (4.5 to 5.5) between 9° S and 15.5° S do not indicate diversity increase towards the tropics.

Several other studies also do not reveal a latitudinal increase in marine species richness with decreasing latitude (e.g. Clarke & Crame, 1997). Gray (1994) as well as Ellingsen & Gray (2002) investigated the species diversity of the Norwegian continental shelf. They suggested that the pole-to-tropic gradient is at most weak if it is detectable at all. Generally, the benthic fauna of the European continental shelf is not subject to strong latitudinal diversity trends (Renaud et al., 2009). The same fact is evidenced by Bergen et al. (2001) who investigated infaunal assemblages on the mainland shelf of southern California. The authors state that latitude was not a determining factor for the community composition. The hypothesis of a gradient in marine benthic diversity between high and low latitudes (Sanders, 1968) has been questioned by Kendall & Aschan (1993), who figured out that diversity profiles from the arctic Svalbard, the temperate North East England and the tropic Java are similar.

Latitudinal decline in species richness from the tropics to the poles is often presumed as a fundamental rule in the terrestrial realm (Konar et al., 2010). However, marine conditions differ substantially from terrestrial ones; e. g. in pelagic larvae floating in the water column, oxygen availability, hydrodynamic processes and lower temperature gradients. Hillebrand

(2004) used 198 published marine gradients to assess the validity of the assumption of diversity increase with decreasing latitude for marine environments. He figured out that marine biota show a comparable overall decrease in diversity with latitude. However, strength and slope of the gradient are strongly subjected to regional features as well as features of habitats and present organisms. Latitudinal gradients tend e.g. to be more regular on the northern hemisphere than on the southern hemisphere (Crame, 2000; Ellingsen & Gray, 2002). Clark (1992) also says that the supposed latitudinal diversity decline from tropic areas to polar regions in the sea has to be considered critically. The author references to Thorson (1957), who pointed out that there is a significant diversity increase of the epifauna of hard-substratum towards low latitudes. In contrast, the species richness of soft-bottom organisms does not show noticeable changes in different climate zones. The latitudinal trend in epifaunal species is probably due to the fact that they live in a heterogeneous habitat, which is more exposed to environmental factors than the more homogenous soft-bottom habitat that is inhabited by infaunal species. These burrowing organisms are buffered from spatial and temporal environmental variations (Roy, Jablonski & Valentine, 2000). Thorson's presumption is supported by investigations of Fischer (1960) revealing that the diversity gradient for mollusks along the east and west coast of the USA and Canada was more pronounced for gastropods, which are mainly epifaunal than for lamellibranchs, which include a lot of infaunal species (Warwick & Ruswahyuni, 1987).

The appearance of latitudinal diversity patterns do also depend on the considered taxonomic group. Latitudinal declines in species richness of shallow water benthos have been observed for gastropods and bivalves (Ellingsen & Gray, 2002). Crame (2000) as well as Roy, Jablonski & Valentine (2000) observed latitudinal gradients for bivalves. The latter authors found strong latitudinal diversity gradients for major functional groups of epi- and infauna bivalves in the north-eastern Pacific. They further stated that marine mollusks are the most diverse group of shelf macrobenthos. These assumptions are not in agreement with the presented results from the Angolan shelf. Overall, polychaetes represent the group with the highest species richness, followed by crustaceans. Mollusks are found to be the third-diverse taxonomic group. Their species number is at its highest in the most southern part of the shelf (approx. 17° S) and in the consideration of the grab samples only it is also high in the Cabinda Province (about 5° S). However, this species distribution does not indicate a gradient of species increase with decreasing latitude. This result confirms the findings of Ellingsen & Gray (2002) from the Norwegian Sea regarding the lacking relationship to latitude and the diversity ranking of taxonomic groups. In the studied waters off Angola, no taxonomic main group shows a convincing latitudinal diversity trend. Species richness of the crustaceans is similar along a wide range of the Angolan shelf but with a noticeable decline at the Namibian border in the south. Polychaetes diversity is roughly the same in the entire study area. Less prominent latitudinal changes in polychaetes species richness were also obvious in the study of Joydas & Damodaran (2009) along the shelf in the Arabian Sea at the west coast of India.

The ambivalent global results of latitudinal impact on species richness imply that other environmental variables also influence benthic diversity. Alongi (1989) already mentions that shelf variations are caused by several factors, *inter alia* by gradients in depths and sedimentation. Levin, Gage, Martin & Lamont (2000) correlated water depth positively with species richness in the vicinity of oxygen minimum zones of the Northwest Arabian Sea. In contrast, polychaetes species number along the West Indian shelf appear to decline with increasing depth according to Joydas & Damodaran (2009). The authors noticed a steep decrease of diversity in areas deeper than 150 m. The decrease of benthic standing stocks, including species diversity and abundance, matches the decrease of food supply and increase of water depth due to degradation processes within the water column (Soltwedel, 1997). The analyzed samples of the Angolan shelf were taken mainly in shallower depths between 19 and 146 m. Species-rich samples occur in depth ranging from 28 m (SU5) to 62 m (Na5). The observed diversity varies in samples taken in depth greater than 100 m from relatively high (Be71) to rather low (71; 72; 5; BE7; Ku4 & KU3) species numbers. Station BE9 was the only sample taken in a depth of 340 m. Just 11 species have been detected here, which makes this station the most poor in species. Thus, it seems that the deeper stations tend to be less diverse compared with mid-depths between approximately 30 and 60 m. However, it must be noted that moderate and relatively low species numbers have been also observed in mid-depths. Therefore, it would be inaccurate to claim that depth is the decisive factor for the distribution of diversity in this study. Species increase over similar mid-depths is noticed by Coleman, Gason & Poore (1997) and Bergen et al. (2001). Higher diversity at shallow stations compared to deeper stations is shown for tropical and temperate soft-bottom communities by Warwick & Ruswahyuni (1987). According to the authors, this fact is attributed to the effects of natural-, low-level-, physical disturbances that keep communities in a sub-climax stage. A comparison of coastal and deep-sea benthic diversities by Gray et al. (1997) also reveals that diversity in shallow waters is high, if not higher than in the deep-sea habitats. They found that both deep-sea and coastal habitats transverse a variety of microhabitats. Consequently, sediment heterogeneity is not a satisfactory explanation for high species richness in coastal waters.

It is, however, reasonable to assume that the properties of sediments affect benthic diversity. Bertini & Fransozo (2004) showed that brachyuran crab communities are more diverse in heterogeneous sediments, referring to the assumption that the greater diversity of those sediments is due to its wide variety of microhabitats. Etter & Grassle (1992) assume that sediment particle size diversity plays an important role in the determination of species number within a community. They demonstrate that variability in species diversity seems to be related to changes in sediment characteristics in the western North Atlantic. The authors continue with the reference to other studies that have been documented in shallow water, revealing similar effects of sediment diversity on species diversity. This leads to the conclusion that the influence of sediment particle size may be an ubiquitous feature of soft-sediment communities. The distribution of infaunal macrozoobenthic species has been correlated with sediment grain size in many studies, leading to the presumption of an association between certain animals and specific sediment types. Although lots of species are characteristically associated with a sedimentary habitat their distributions are seldom confined to that environment. Some species show low affinity to any special type of sediment. Hence, one can assume that grain size it not the only sedimentary feature that determines species distribution and that other factors like organic content, microbial assemblages and trophic interactions do also have an impact (Snelgrove & Butman, 1994). The importance of grain size itself for species distribution is demonstrated by feeding mechanisms and passive deposition of settling larvae. Some deposit feeders have been shown to ingest specific grain sizes. Larvae-settling only provides a parsimonious explanation. It depends more on physical characteristics of the larvae, boundary-layer flow and sediment transport regime. The energy profiles of the water flow directly above the sediment-water interface influence not only the larvae dispersal; it also determines particle size of the surficial sediments, which in turn influences the life conditions for adult burrowing organisms. The relationship is: the greater the energy, the higher the velocity, the larger the sediment particles carried away by the water. Effects of wave energy on the bottom are typically greater in shallow waters and decreases with increasing depth (Bergen et al., 2001). A study of Coleman, Gason & Poore (1997) in shallow marine waters south-east off Australia showed that species diversity is highest at the intermediate values of mean grain size in poorly sorted sediments.

The median grain sizes measured on the Angolan shelf ranged between 7 and 731 µm. However, it should be noted that measurements of median grain sizes are lacking for 18 stations. This weakens the ability to draw conclusions about the relationships between the median grain size and species richness. Nevertheless, information about the sediment quality are present. Different substrate types occur along the shelf off Angola. The most stations are characterized by the presence of silt and sand. Station 87 showed coarse sand of the greatest measured grain size (731 µm). The taxa number found in the grab sample of this station is rather low (24 species) while it is high (138 species) in the dredge sample of this station. The difference in species richness between the grab sample and the dredge sample of station 87 is visible for all taxonomic groups. This dissimilarity is possibly due to the fact that coarse-grained regions are generally exposed areas, which are often inhabited only by specialists. On the other hand, there are usually many microhabitats (e.g. macrophytes, stones and other coarse structures) at the sediment surface, which show a greater number of species. These microhabitats can be recorded to a great extent by dredge sampling but not by grab sampling. Only one of the sampled stations (SU4) is characterized by densely packed little stones, coarse sand and gravel. Due to this texture it was not possible to measure the grain size of this station. The observed diversity is moderate in the grab samples and lower in the dredge sample with nearly the same diversity proportion of the taxonomic groups except for a higher percentage of polychaetes in the grab samples. Altogether, the highest diversities could be observed at the stations SU5 and Na5. Both stations are dominated by silt wherein the median grain size differs between 58 µm at station SU5 and 14 µm at station Na5. It is also conspicuous that diatoms and small shell fragments are present at these stations. In addition to the generally organic-rich silt, diatoms represent a food source for benthic organisms. The shell detritus provides protection to the invertebrates and may be a component of tubes of polychaetes e.g. *Diopatra neapolitana*. This can be an explanation for the high diversity as well as for the high abundances that were present at these silt stations, especially at station Na5. Joydas & Damodaran (2009) also observed high abundances (and biomasses) in muddy substrata. However, they found that diversity is higher in sandy substrate. Similar results were achieved for the polychaetes fauna in coral-algal buildup sediments from Brazil by de Santa-Isabel, Peso-Aguiar, de Jesus, Kelmo & Dutra (1998). They recorded highest species richness on carbonate sands and gravels. However, big coral reef formations are absent in the tropical West Africa due to upwelled water with lower temperatures and periodical salinity decreases (Longhurst, 1959; Le Loeuff & von Cosel, 1998). This creates environmental conditions other than in the Brazilian study and thus different diversity patterns are not surprising. Another study from soft bottoms off Brazil (Bertini & Fransozo, 2004) also shows lower diversity of brachyuran crabs in zones associated with predominantly silt-clay sediments. Nonetheless, highest species numbers occur in silt along the Angolan shelf. It can be assumed that the presence of diatoms and shells contributes to these high diversities because there are few silt stations with middle or low species richness. Sand (median grain size > 63 µm) never showed high diversities. It has to be admitted that information about the bottom texture are missing for some stations (see table 3).

Generally, the comparison between diversity in various habitats is difficult due to different sampling procedures and analysis techniques. As stated by Clarke (1992), it should be ensured that the same variables are measured everywhere to compare different areas. It could be helpful to sample in same depths for a better comparison between habitats and to show possible gradients within the region. Further, equal sample effort facilitates the data analysis. It must be considered that stations should be sampled with several replications whenever possible to obtain a representative statistic. Species/area curves are a useful means to find out how many replicate samples give an adequate impression of the bottom fauna in a certain area.

4.2 Remarks on Key Species

The dominating key species among the group of the mollusks on the shelf off Angola, especially in the region of the Kunene River, are *Nassarius* sp. and *Nuculana bicuspidata*. The shelf area at the river mouth is characterized by muddy sediments with strong hydrogen sulfide content, which is caused by oxygen depletion. These results agree with observations of Zettler, Bochert & Pollehne (2009), who showed that *N. bicuspidata* and *N. vinctus* are key species with high biomasses at the fringe of the oxygen minimum zone (OMZ) off northern Namibia. They further say that bioturbation and biopumping of these larger size classes of macrozoobenthos enhances transport processes between the sediment and water. The organisms therefore provide ecosystem relevant functions by changing the sediment properties. Both taxa are able to reduce or increase their biopumping or bioturbation rates as an adaptation to survive in spite of the low and discontinuous oxygen supply (< 0.5 ml/l) in their habitat. OMZ's of other upwelling areas in the world are dominated by small-bodied polychaetes.

The polychaete with the highest abundance at the fringe of the northern Benguela upwelling system is *Cossura coasta*. It is the only observed species of genus *Cossura* on the Angolan shelf. It inhabits all latitudes except for the north (Cabinda Province), but the highest numbers of individuals occur in the south close to the OMZ. This genus is known as a component of other shelf areas with low oxygen conditions, e.g. the Chilean shelf and the East Indian shelf. Also in these regions the composition of benthic faunal communities is characterized by high abundances and low diversity. *C. coasta* comprises most of the macrozoobenthos in the areas of the East Indian shelf with oxygen concentrations below 0.1 ml/l (Levin et al., 2009). So it seems that this species is well-adapted to OMZ's. The long slender dorsal gill of *Cossura* is presumably an adaptation to hypoxic conditions.

Elaborated branchial proliferations as well as associations with hydrogen sulfide consuming bacteria are commonly found for polychaetes of the inner shelf off northern Namibia. Pronounced branchiferous structures are a feature of spionids, onuphids, pectinarids, hesionids, sigambrids and nereids (Levin et al., 2009). The same polychaetes families are found on the Angolan shelf. One of the most abundant species is the spionid *Paraprionospio pinnata*. This species shows the same territorial range along the Angolan coast as *C. coasta*. *P. pinnata* is abundant at many other areas in the world. This annelid represents half of the polychaetes on the Chilean shelf; it colonizes the inner Texas shelf and it is abundant at the West India shelf (Joydas & Damodaran, 2009). The species is highly adapted to oxygen deficiency by its elaborated brachial structures that enhance oxygen diffusion and enzymatic adaptations for anaerobic metabolism (Levin et al., 2009). Thus it is not surprising that the polychaete was observed beneath the OMZ of the North West Arabian Sea (Levin, Gage, Martin & Lamont, 2000). It shows also high numbers of individuals in the OMZ-community off northern Namibia. Moreover, it is frequently observed in Namibian and South African upwelling areas (Zettler, Bochert & Pollehne, 2009).

Many polychaetes that represent key species for waters off Angola are deposit feeders (*C. coasta*, *P. pinnata*, *Galathowenia* sp. *Prionospio ehlersi* and *Chaetozone setosa*). This is a known reaction of ecosystems towards oxygen depletion. Suspension feeders are replaced by deposit feeders in low-oxygen areas and muddy sediments (Joydas & Damodaran, 2009; Levin et al., 2009). The tube-dwelling polychaete *Galathowenia* sp. shows high numbers of individuals in several latitudes of the Angolan shelf but all are characterized by silt. However, oxygen contents vary between 0.8 and 2.3 ml/l. *Prionospio ehlersi* is abundant near Lobito (LO4) and Namibe (Na5). Both stations show low oxygen content (approx. 1 ml/l) and sediments of small grain sizes. The spionid exhibits high dominance in benthic communities of the Oregon shelf and of the East India shelf, especially at regions with oxygen concentrations below 0.1 ml/l (Levin et al., 2009). *P. ehlersi* as well as the key species *Diopatra neapolitana capensis* are able to build and inhabit tubes, where they can hide from predators. They use sediment particles, foraminifera tests, fragments of shells and other animal detritus for tube-building by producing a secretion layer, which adhere to these materials (Moritz, 2012). Consequently, this species shows high numbers of individuals at station SU5 near Sumbe; station Na5 near Namibe and at stations near the mouth of the Kunene River. All of these habitats have a large occurrence of mollusk shells that supports environmental preferences of the polychaetes. Additionally, the sediment at the station SU5 and station Na5 contains lots of diatoms, which represent a food source for benthic invertebrates. *D. neapolitana capensis* furthermore inhabits interstices of *Discinisca* shells that show high abundances and biomasses within the OMZ-community off northern Namibia (Zettler, Bochert & Pollehne, 2009).

Cirratulids dominate various habitats in the world. They dominate, for example, the macrozoobenthic community off the west coast of India (Joydas & Damodaran, 2009) and the area beneath the OMZ of the North West Arabian Sea (Levin, Gage, Martin & Lamont, 2000), mainly in depths between 400 m and 700 m. They are also the most abundant species in various depths of the Sassenfjord, Svalbard (Kendall & Aschan, 1993). With regard to the shelf off Angola, *Chaetozone setosa* is the cirratulid with the highest number of individuals even though the species is only present at three stations (SU5, LO4 and Na5). Although this polychaete is able to inhabit different kinds of substrate e.g. mud, sand, gravel, stones, small shell fragments and empty worm tubes (Hartmann-Schröder, 1996) it seems to prefer silt bottoms with shells on the Angolan shelf. A possible reason for this distribution is the occurrence of mollusks detritus and empty tubes of *D. neapolitana capensis* at station SU5 and Na5, which represent a sheltered habitat for *C. setosa*. It is also possible that the species benefits from the nutrient enrichment by the diatoms. However, these conditions are not given at station LO4.

The most diverse and most abundant amphipod of the shelf off Angola is *Ampelisca* sp. The animals are ubiquitous here. The highest individual numbers were observed at station SU5 and Na5. The abundances at the oxygen-poor area near the mouth of the Kunene River are rather low. Nevertheless, *Ampelisca* could be detected here. The species is also recorded from the oxygen depleted shelf off Chile. Although the genus is not tolerant to severe hypoxia, they seem to be common just prior to hypoxic events (Levin et al., 2009). Another study of Levin, Gage, Martin & Lamont (2000) revealed that *Ampelisca* is abundant within the OMZ of the North West Arabia Sea. It is also mentioned that ampeliscids became dominant in a community on the Texas shelf several months preceding severe hypoxic events. It is suggested that ampeliscids have physiological mechanisms that increase the oxygen uptake and could be sulfide tolerant (Levin, Gage, Martin & Lamont, 2000).

4.3 Benthic invertebrates in waters off Angola: current state of knowledge

Until now, waters off Angola are poorly studied. Although there are several studies on fisheries, zooplankton and meiozoobenthic communities (Strømme & Sætersdal, 1991; Bianchi, 1992; Misund, Luyeye, Coetzee & Boyer, 1999; Binet, Gobert & Maloueki, 2001; Afonso, 2000; Postel, da Silva, Mohrholz & Lass, 2007; Soltwedel & Thiel, 1995; Soltwedel, 1997) little information about the macrobenthic communities are available.

There is another master's thesis (Motitz, 2012) providing a first impression of benthic assemblages along the Angolan shelf. However, the number of sampled stations and the number of observed taxa was significantly smaller than in the present study. Nevertheless, the proportion of the taxonomic main groups in the diversity patterns was similar in both studies. Polychaetes are the most diverse group, followed by crustaceans, mollusks, echinoderms and others when the grab samples and the station approach are considered. If one considers only the dredges, the crustaceans are just as diverse or even more species-rich than the polychaetes in the most regions except for the area at the border of Namibia. The proportion of lower taxonomic levels on the whole diversity and abundance of the Angolan shelf is shown for the first time. Amphipods are the most species-rich group in Angola's coastal waters. All in all, they constitute half of the crustaceans. They are followed by the decapods, cumaceans/isopods and tanaidaceans. Only dredge samples show a higher proportion of decapods. In the rough approximation abundances correlate positively with diversity. The mollusks diversity is dominated by gastropods followed by bivalves. The reverse is applicable for abundances. The least diverse and least abundant group is represented by the echinoderms. More than the halves of the echinoderms species are ophiuroids. They are followed by holothurians, which were more diverse in the dredge samples. Asteroidea and Echinoidea are the least diverse groups along the Angolan shelf. The abundances of echinoderms show patterns similar to their species richness. The highly diverse polychaetes are dominated by members of the family Spionidae in diversity and abundance. Cirratulids are the second-diverse group in the waters west off Angola. Depending on the sampling device the third-diverse groups are Paraonidae (grab samples) or Nephtyidae/ Onuphidae (dredge samples).

The investigation of benthic communities of the Angolan shelf took place in different extent with regard to the geographical location. Three studies exist that deal with macrozoobenthos in the north of the country including Cabinda and Soyo Province (Faria, 2006; "Dr. Fridtjof Nansen" Cruise Report, 2006; "Dr. Fridtjof Nansen" Cruise Report No 4, 2009). The sampling locations of this area are shown in figure 58.

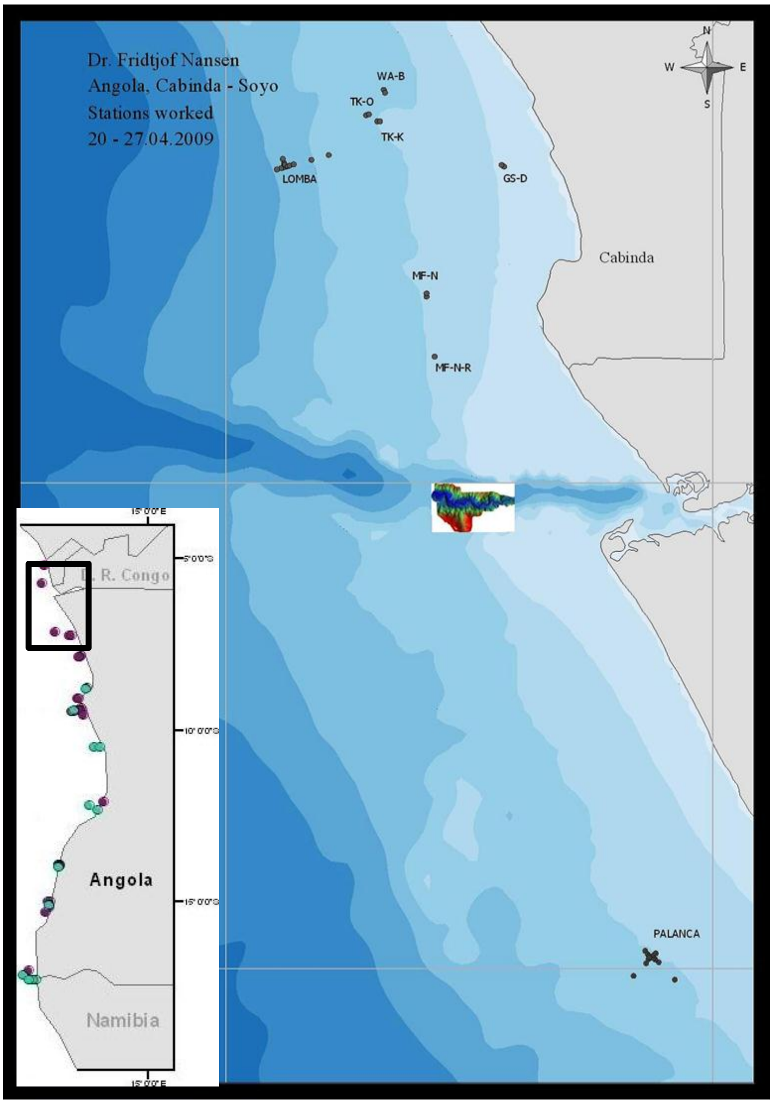

Fig. 58: Map showing all the investigated sites from the "Marine Environmental Survey of Bottom Sediments in Cabinda and Soyo Province, Angola" ("Dr. Fridtjof Nansen" Cruise report No 4/2009)

These studies are a useful addition to the own results because this locality was less represented by samples collected during the research cruises of the Leibniz Institute for Baltic Sea Research Warnemünde (IOW).

The attention to this region is caused by the local petroleum industry, which started in the early 19th century. There is a concern that this oil exploration has a negative effect on marine environment, for instance resulting in the decline in fishstocks and biodiversity. There are also worries about human health problems, decrease in water quality and negative impact on tourism industry.

The region of Cabinda (5° S to 6° S) is a part of the Guinea Current Large Marine Ecosystem. The area shows fine grained sediment and is substantially influenced by the fresh water inflow from the Congo River, which water flow is the second largest in the world. The discharge has an impact on the horizontal and vertical gradients of the temperature and salinity. Additionally, pollutants from big cities along the river, fertilizers from the agriculture and other terrestrial discharges may have an effect on the marine environment. Soyo (6° S to 7° S) is located in the south of the Congo River and is dominated by sandy sediments. The results of the Nansen Cruise Report 2009 revealed that Annelida are the most diverse and most abundant group here. The highest number of taxa (76 and 67) and individuals (404 and 362) occurred in shallow sites, while lowest numbers of taxa (24 and 17) and individuals (58 and 41) were observed at deepest stations during the "Dr. Fridtjof Nansen" cruise in 2009. It was also revealed that lead and copper have an impact on the bottom fauna distribution. A low number of species with few individuals were related to observations of oil in the sediment. Although polychaetes are shown to be most frequent, most of the other taxonomic groups are abundant, too. This was also true for station 78, which is the only analyzed station off Cabinda. However, only 14 species were found here although the sampling depth (32 m) corresponds to those that show higher species numbers according to the Nansen Cruise Report of 2009. The "Dr. Fridtjof Nansen" Cruise Report (2006) also shows results from the shelf off Cabinda between approximately 5.2 ° S and 5.5° S. According to them, annelids are the most abundant and most diverse (45 to 55 taxa) group. Faria (2006) demonstrates that Spionidae are the most abundant family among the polychaetes while Nephtyidae are the most diverse family. The most abundant observed taxa in the area are *Nassarius megalocallus* Adam & Knudsen, 1984, *Prionospio* sp., *Nephtys* sp., *Amphinome rostrata* (Kinberg, 1867), *Lanice conchilega* (Pallas, 1766) and an undetermined brachyuran crab ("Dr. Fridtjof Nansen" Cruise Report, 2006). *Prionospio* sp. is also one of the most abundant taxa in the own observation. All of the other species were not observed in the station off Cabinda during the research cruise of the IOW. Instead *Ampelisca palmata* K.H. Barnard, 1916 is abundant. The Nansen Cruise Report (2006) reveals low species numbers near the platform indicating disturbance of the fauna close to the platform. The H' values for the Cabinda Province vary between 2.8 and 4.7. This agrees with the own calculated H' values (3.2) of this region.

The middle latitudes off Angola are poorly investigated. This study reveals that the whole shelf is dominated by polychaetes with regard to abundance and diversity but their biomass is very variable in different regions. The polychaetes biomass is extremely high in the northern part of Angola from about Soyo to Luanda. This region in influenced by a tropical climate and the warm water of the South Equatorial Counter Current, which contributes to the initiation of the warm Angola Current that influences the hydrology of the whole Angolan coast. The most abundant observed taxa are polychaetes of the family Ampharetidae and Aphroditidae as well as the onuphid polychaete *Diopatra* sp. The species *Diopatra neapolitana capensis* is highly abundant at the station LU5 near Luanda, which is the only big city in this region. South of Luanda, where the Cuanza River discharges, high abundances of Syllidae and undetermined polychaetes could be observed. The overall species diversity at the mouth of the Cuanza River is found to be rather low. Polychaetes biomass shows a significantly decrease from this area to the region further south (from the south of the Cuanza River to the north of Lobito). Mollusks are the group with the highest biomass there. This is caused by high biomasses of the mytilid bivalve *Jolya letourneuxi* Bourguignat, 1877. Nonetheless, polychaetes and crustaceans equally dominate abundances in this area. The stations near Sumbe differ remarkable in abundance and also in diversity. The number of taxa and individuals are significantly higher at station SU5. This is probably explained by the various sediment properties. While station SU4 is characterized by gravel and stones, station SU5 comprises fine silt with diatoms and mollusk shells. The dominant species at station SU5 are the polychaete *Ampharete* sp. and the amphipods *Dyopedos* sp. and *Grandidierella elongata* (Chevreux, 1926). Further south (near Lobito) *Galathowenia* sp. and *Prionospio ehlersi* are strongly represented. Polychaetes are by far the most abundant group in the area between Benguela and Namibe. However, biomasses of this region are even more dominated by mollusks, particularly the bivalve *Nuculana bicuspidata*. Especially station Na5 (near the city Namibe) reveals high numbers of taxa as well as individuals. This station stands out by its extremely high polychaetes abundance (31886 individuals/m²). The taxa that have the greatest share of it are Ampharetidae, Syllidae, *Diopatra* sp., *Galathowenia* sp., *Owenia* sp., *Prionospio malmgreni*, *P. steenstrupi* and Cirratulidae, above all *Chaetozone setosa*. However, other invertebrate groups are also abundant, e.g. *Ampelisca* sp. and *Diastylis* sp.

The border zone between Angola and Namibia is characterized by an increase of mollusks abundance and biomass. The group constitutes 90 % of the total biomass in this region. This area shows special conditions for the structure of benthic communities. Firstly, the Kunene River discharges here. Secondly, this area is influenced by the so-called Angola-Benguela front (ABF), which is generated by the confluence of the warm, oligotrophic, southward flowing Angola Current and the cold, nutrient-rich, northward flowing Benguela Current. Due to this uncommon combination of environmental conditions the area represents an interesting point for biological research. The runoff from the Kunene River does not seem to influence the observed stations significantly. Although the nutrient input from the river causes increasing diversity on the shelf, this biological hot spot is locally restricted to the mouth region (Bochert & Zettler, 2012). Further studies assume that the ABF represents a zoogeographical boundary. Successful organisms at the front show differences in composition due to the temperature variations within both currents (Hogan, Baum & Saundry, 2012). Most species that live immediately south of the Kunene River are adapted to cold temperatures. Moreover, these communities need to tolerate low oxygen contents (< 0.5 ml/l) of the oxygen minimum zones (OMZ) off northern Namibia, which is a part of the Benguela upwelling system, one of the largest upwelling systems in the world. The Benguela OMZ starts directly below the euphotic zone so that fresh organic matter reaches the sediment. This results in high oxygen consumption but it also enables occasionally oxygen replenishment by currents and tides. Such transport dynamics within a gradient system influence the function and the structure of the biological community (Zettler, Bochert & Pollehne, 2009; Bochert & Zettler, 2012; Zettler, Bochert & Pollehne, 2013). The observed overall biodiversity in this region is reduced whereas the species richness of mollusks increases. Instead of the occurrence of many species of different groups, fewer species appear that are characterized by larger body sizes and a high abundance. A strong presence of *Nuculana bicuspidata*, *Nassarius vinctus* and *N. angolensis* was noticeable at the Namibian border. High individual numbers of mytilids, undetermined oligochaetes as well as of the polychaete *Cossura coasta* could be observed, too. These results for mollusks are supported by observations of Zettler, Bochert & Pollehne (2009), who showed that *N. bicuspidata* and *N. vinctus* are key species in the OMZ off northern Namibia. The high abundances of taxa *C. coasta* and Oligochaeta indet. are not confirmed by the authors.

Although this study contributes to our knowledge about the composition of benthic communities on the shelf off Angola further research is necessary. It became apparent during the determination of taxa, that some species of the studied area are not known yet. Considering the fact that the waters off Angola represent a highly diverse region, one can assume that other unknown species occur here. There are, for instance, specimens of the family Apseudidae, the genus *Iphinoe* and the genus *Turritella*, which presumably represent new species. Several species could not be determined to the lowest taxonomic level during the sample processing. Therefore, the actual diversity of the waters off Angola is probably higher than determined in this study. Despite all efforts, some taxa could only be determined up to the family level. This circumstance is due to the lack of identification literature for benthic invertebrates off Angola. Even though some publications about the taxonomic groups are available (Nicklès, 1950; Reid, 1951; Manning & Holthuis, 1981; Rolán & Ryall, 1999; Ardovani & Cossignani, 2004) and there are several new descriptions of species from the Angolan shelf by staff of the IOW (Bochert & Zettler, 2009; Bochert & Zettler, 2010; Thandar, Zettler & Arumugam, 2010; Bochert & Zettler, 2011; Bochert, 2012; Glück, Stöhr, Bochert & Zettler, 2012) comparable evaluations of soft bottom communities from this region are lacking. The only available overall consideration of the Angolan coastal fauna is a publication of Kensley (1973) that is focused on the fauna of rocky shores. Thus, it is not applicable to the offshore soft bottom fauna, which is investigated in this study.

A good knowledge about the species composition within an ecosystem is important for the human use in different ways. Shells of mollusks from mud belts (e.g. *N. vinctus*) are a reliable material for the age dating via radiocarbon analysis (Herbert & Compton, 2007). They also represent a basis for the reconstruction of the conditions over the past climate cycles (Zettler, Bochert & Pollehne, 2013) or they can be used for monitoring of trace metals, because the organisms reflect the environmental conditions. For these reasons and for the conservation of nature itself, a sustainable environmental treatment is of highest importance, especially in the consideration of the current extensive use of marine resources. Biodiversity of an ecosystem can increase the resilience of the system against the human exploitation and the natural disturbances. Hence, understanding the biodiversity and functioning of communities is the basis of the environmental management.

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Appendix

A I- Fauna List

In the following an alphabetical list of all determined taxa from the grab samples is given. Their location, their taxonomic classification and the total number of counted individuals are also stated.

Total number of taxa: 618

<u>Phylum: Annelida</u> (223 species)

taxon	station	total number of counted individuals
Oligochaeta (2 taxa)		**870**
Oligochaeta indet.	70, 88, 101, Na5, BM5, LO5, Ku5	782
Tubificidae	LO4, Na5, KU6	88
Polychaeta (221 taxa)		**22032**
Ampharete sp.	BE11, BE12, BE13, LO4, SU5, Na5, KU6	144
Ampharetidae	1, 3, 45,65, 66, 70, 71, 72, 76, 78, 88, 101, 102, 106, 121, Na5, BM5, LO5, SU4, SU5, Be71, LU 5, Ku5	728
Amphictene sp.	SU5, Be71	27
Amphinomidae	88	1
Aonides cf. *oxycephala*	BE12	4
Aonides sp.	67, BE10, BE11, BE12, BE13, SU5, Na5	36
Aphroditidae	1, 5, 45, 65, 71, 72, 78, 88, 102, 106, Be10, BE11, BE12, BE13, Na5, SU4, LU5	61
Arabellinae?	70, 72	2
Arenicolidae	4, 77	2
Aricidea	88, BE11, BE12	54
Aricidea longobranchiata	SU5, Na5	7
Aricidea sp.	Na5, BM5, LO4, LO5, Be71, LU5	333
Aricidea sp. B	LO5	1
Aricidea sp.(thick)	SU5	3
Aricidea sp. (slim)	SU5	2
Autolytus	4	1
Autolytus sp.	Be71	1
Capitellidae	1, 3, 4, 66, 71, 88, BE10, LO4, Na5, BM5, SU4, SU5, Be71, KU6	642
Capitellidae 2	SU5	2
Caulleriella cf. *bioculata*	KU3	1
Caulleriella sp.	BM5, LO4, KU6, SU5,	44
cf. *Ampharete*	BM5, LO5, SU5, Be71	30
cf. *Amphictene*	Ku5	5
cf. *Aricidea* sp.	SU5	16

taxon	**station**	**total number of counted individuals**
cf. Capitellidae	LO5	1
cf. *Chloeia sp.*	Be71	7
cf. Cirratulidae	LO5	1
cf. *Euclymene* sp.	BM5	1
cf. Hesionidae	Na5	6
cf. *Heteromastus* sp.	Be71, Ku4, Ku5	50
cf. *Onuphis* sp.	BM5	1
cf. *Oxydromus* sp.	BM5	2
cf. Orbinidae	BM5	1
cf. *Phyllamphicteis* sp.	Ku4, Ku5	2
cf. Pontodoridae	Be71	1
cf. Questidae	BM5	1
cf. *Sigambra bassi*	BE11	2
cf. Terebellidae	SU4	2
Chaetopteridae	BE10, BE11, BE12, 2, 4, 45, 71, 76, 102	13
Chaetopterus sp.	LO5, SU5, Be71, Ku5	10
Chaetozone	BE11, 65	3
Chaetozone B	SU5	4
Chaetozone setosa	SU5, Na5, LO4	767
Chaetozone sp.	SU5, Be71, LU5, Ku5	26
Chloeia inermis	Be71	1
Chone sp.	SU5, Na5	15
Cirratulidae	BE7, BE10, BE11, BE12, 1, 2, 3, 4, 5, 45, 65, 66, 67, 71, 72, 76, 87, 88, 101, 102, 106, 121, Na5, BM5, LO4, LO5, SU4, SU5, Be71, LU5, Ku4, Ku5, KU6	1058
Cirratulidae B	5, Ku5	2
Cirratulidae (brown)	121	2
Cirratulidae C	BM5	2
Cirratulidae C (brown/lime tube)	BE10	11
Cirratulidae D	Be71	1
Cirratulus sp.	KU6	1
Cirrophorus sp.	Na5, BM5, LO4, LO5, Be71,	163
Cossura coasta	Na5, BM5, LO4, LO5, SU5, Be71, LU5, KU3, Ku4, Ku5, KU6	2914
Ctenodrilidae	1	1
Diopatra neapolitana capensis	Be12, Na5, SU5, LO4, LO5, LU5, Ku4, Ku5, KU6	915
Diopatra sp.	4, 65, 101, BE10, Na5, BM5, LO5, SU5, Be71	315
Diplocirrus sp.	Na5, SU5	9
Dipolydora coeca	Na5	1
Dorvilleidae	BE12	2
Drilonereis sp.	Be71	1

taxon	**station**	**total number of counted individuals**
Eteone sp.	3, 121, BE10, Na5, BM5, SU4, Be71	25
Euchone?	BE12	10
Euclymene sp.	BE12, BM5, Na5	84
Eulalia sp.	Na5, KU6	3
Eumida sp.	Na5, Ku4	7
Eunice sp.	BE10, Na5,	8
Eunicidae	1, 2, 3, 5, 45, 67, 70, 72, 76, 77, 78, 88, 102, 106, 121, BE9, BE10	97
Euphrosida	121	35
Euphrosine sp.	SU4	3
Exogone sp.	SU4, Na5	14
Fabricia sp.	4, 45, BE11, BM5, SU4, SU5	15
Flabelligeridae	76, BE10, SU5, Na5, LO5	10
Galathowenia sp.	BE11, BE12, LO4, SU5, Na5, KU3, Ku5, KU6	2841
Galathowenia sp. 1	LO4	55
Glycera pappilosa	68	1
Glycera sp.	SU5, Na5	3
Glyceridae	1, 3, 5, 45, 65, 67, 87, 88, 106, 121, BE7, BE10, BE12, BM5, LO5, SU5, Be71, LU5	73
Glycinde kameruniana	KU3	3
Goniada congoensis	Na5	1
Goniada sp.	71, SU5, Be71, Na5, Ku4, Ku5, KU6	160
Goniadidae	Na5	7
Gyptis?	BE12	4
Harmothoe B	LO5	4
Harmothoe C	BM5	1
Harmothoe sp.	BM5, LO5, SU5, Ku4, Ku5, KU6,	48
Hermundura aberrans	45, KU6	4
Hermundura sp.	LO5	1
Hesionidae	67, KU6	3
Heteromastus?	65, BE11, BE12	9
Heterospio angolae	71, 72	22
Heterospio longissima	65, SU5	3
Heterospio nov. spez. 1	65	1
Heterospio sp.	71, Be71, LU5	29
Isolda pulchella	SU5, Na5,	89
Johnstonia clymenoides	Na5	1
Johnstonia knysna	Na5	2
Lanice conchilega	65, BE10, SU5	3
Laonice sp.	LO5	1
Laonice sp. B	SU4	8
Laonome sp.	SU5	2

taxon	station	total number of counted individuals
Levinsenia sp.	KU3	337
Levinsenia gracilis	SU5, LO4	63
Loandalia?	65	2
Lumbrineridae	3, 4, 5, 45, 65, 66, 67, 71, 76, 88, 101, 102, 106, 121, BE10, BE11, Na5, BM5, LO5, SU4, SU5, Be71, LU5, Ku5	327
Lumbrineridae B	BM5	2
Lumbrineris sp.	BE11, BE12, LO4, SU5, Na5, KU3, KU6	358
Lygdamis	65, 121	3
Magelona	45, 76, 102, BE11,	17
Magelona sp.	BE10, BE11, LO4, SU5	36
Magelonidae	BM5, SU4, Be71	10
Malacoceros sp.	SU4	1
Maldanidae	1, 2, 3, 5, 45, 65, 66, 67, 72, 76, 87, 88, 101, 106, 121, BE7, BE9, BE10, BE11, Na5, BM5, SU4, Be71, LU5, KU6	170
Marphysa sp.	Be71	1
Minuspio cirrifera	LO4, Na5, KU6	72
Minuspio sp.	BE12	47
Minuspio?	LO5	1
Nematonereis sp.	BE10	5
Nephtyidae	1, 2, 3, 4, 45, 65, 71, 78, 87, 101, 102, 121, BE7, BE9, BE10, Na5, BM5, LO5, SU4, SU5, Be71, LU5, Ku4, Ku5	213
Nephtyidae?	BM5	2
Nephtys hombergii	Na5, KU3	33
Nephtys lyrochaeta	LO4, SU5, KU6	104
Nephtys sp.	BE7, BE12	6
Nereididae	4, 45, 65, 67, 88, 121, Ku5	25
Nereis sp.	Be71, SU5,	3
Nothria	BE12	1
Onuphidae	66, BE10	9
Ophelia sp.	BM5, SU4	2
Ophelidae	1, 3, 67, 88, BE10, BE12	31
Ophelina	1	1
Orbinia sp.	BM5	1
Orbiniidae	2, 3, 4, 5, 45, 65, 67, 87, 88, 102, 106, Be71, LO4	74
Owenia fusiformis	LO4, Na5, SU5, KU6	6
Owenia sp.	3, 4, 65, 66, 71, 78, 87, 88, 101, 102, BE9, BE10, BE11, BE13, Na5, BM5, LO5, SU4, Be71, Ku4	1851
Oxydromus sp.	Na5, BM5, LO5, Be71, LU5	29

taxon	station	total number of counted individuals
Oxydromus spinosus	LO4, SU5, Na5	19
Paramphinome sp.	Be71	13
Paraonidae	1, BE9, BE11, BE12, BM5, SU5, Be71	85
Paraonis sp.	BE9, BE11, LO4, SU5, Na5	237
Paraprionospio pinnata	BM5, LO5, SU5, Be71, LU5, Na5, Ku4, Ku5, KU3	250
Pectinaria	88, 121	2
Pectinaria sp.	BM5, SU5, Na5, LO5, Be71	5
Pherusa sp.	45, 66, BE7, SU5, Ku4, Ku5, KU6	208
Pholoe sp.	Na5	1
Phyllamphicteis sp.	Na5, LO5, Be71, LU5	37
Phyllocomus sp.	LO5	1
Phyllodoce madeirensis	LO4, SU5, Na5,	9
Phyllodocidae	1, 3, 4, 67, 70, 88, 101, 121, BE10, BE12, BM5, Na5, Be71, LU5	42
Phylo foetida	BE12	1
Pilargidae	65	1
Pista brevibranchiata	SU5	1
Poecilochaetidae	3, 65, 76, BE10	8
Poecilochaetus sp.	BM5, LO5, Be71	12
Polychaeta indet. (dots)	LO5	1
Polychaeta indet. (small)	BM5, Na5	4
Polychaeta indet. (small A)	BM5	1
Polychaeta indet. (small B)	BM5	1
Polychaeta indet. (small C)	BM5	2
Polychaeta indet. (small D)	BM5	1
Polychaeta (biomass rest)	1, 3, 65, 66, 68, 72, 88, 102, 106, 121, BE10, BE11	4
Polycirrus	65	2
Polydora 7A	121	40
Polydora sp.	3, 45, 65, 101, Na5, SU4, SU5, Be71, LU5	28
Polynoidae	87	1
Praxilella	BE12	1
Prionospio	1, 5, 71, 72, 76, 78, 102, 106	31
Prionospio B	LO5, Be71, Ku5	12
Prionospio cf. *steenstrupi*	BE12	3
Prionospio ehlersi	BE11, LO4, Na5	116
Prionospio malmgreni	LO4, Na5, KU6	1823
Prionospio sexoculata	LO5, SU4	8
Prionospio sp.	BM5, Na5, SU4, Be71, LO4, LU5, Ku4, KU3	321
Prionospio steenstrupi	LO4, SU5, Na5, KU6	278
Pseudonereis B	LU5	1
Pseudonereis variegata	LO5, KU3	2

taxon	**station**	**total number of counted individuals**
Pseudopolydora antennata	Na5	12
Pygospio	1	1
Questidae	SU5	1
Rhodine sp.	BM5, LO5, SU5Be71, KU3, Ku5	9
Sabellaria eupomatoides	45, BE7, Ku4	19
Sabellidae	3, 5, 45, 65, 121, BE10, BM5, SU5, Na5	90
Scalibregma	45, 72	7
Scolelepis foliosa	SU5	3
Scoloplos cf. *johnstoni*	BE12	9
Scoloplos sp.	BE12, BE13, BM5, Na5, LO5, SU5, Be71	94
Serpulidae	4, 121, SU4	30
Sigambra?	LO5	1
Sigambra cf. *robusta*	BE7, BM5, Ku4, Ku5, KU3	6
Sigambra sp.	4, 45, 65, 78, 121, BE7, BE11, BE12, BM5, LO5, SU5, Be71, LO4, LU5, Na5, KU6	255
Sphaerodoridae	101, 102	39
Spio (black side)	1, 3, 102, BM5, LO5	75
Spio A	70	1
Spio B	70, LO5, Be71	21
Spio filicornis	SU5	2
Spio sp.	3, 101, BE13, BM5, Na5, LO5, Be71, LU5, Ku4	1121
Spio-like	LO5	1
Spiochaetopterus costarum	LU5	14
Spiochaetopterus sp.	LO4, SU5, KU6	6
Spionidae	1, 2, 3, 4, 5, 45, 65, 66, 76, 77, 87, 88, 106, 121, BE9, BE10, BE11	128
Spionidae B	65, 67	12
Spiophanes (black side)	Na5	16
Spiophanes afer	Be71	1
Spiophanes bombyx	Na5	12
Spiophanes sp.	1, 2, 3, 65, 67, 88, 102, 106, 121, BM5, SU5, Be71	59
Spirobranchus sp.	Be71	1
Spirorbinae	BE11	1
Sternaspis scutata	65, 71, 72, Be71, LU5	37
Sthenelais boa	KU6	7
Sthenelais limicola	LO4, SU5, Na5,	28
Sthenelais sp.	3, 66, 101, 102, 121, BE10, BE11, BM5, LO5, SU5, Be71, LU5	89
stalk-eye-Polychaete	45	1

taxon	station	total number of counted individuals
Syllidae	4, 45, 65, 66, 67, 88, 102, 121, BE10, BE12, BE13, Na5, Ku5, KU6	95
Syllidae 2	Na5	1
tentacle-head-Polychaete	87	3
Terebellidae	3, 4, 45, 65, 66, 76, 87, 88, 121, BE10, BE11, BM5, Na5, LO5, Be71, LU5	69
Terebellides stroemii	Na5	3
Trochochaeta ankeae	BE11	33
Trochochaeta sp.	Na5, LO5	9
Tubifex-like	BE7	1
Typosyllis sp.	SU4	1

Phylum: Arthropoda (208 taxa)

Subphylum: Chelicerata (2 taxa)

Pycnogonida (2 taxa)		**9**
Pycnogonida indet.	BM5, Na5	4
Nymphon	121, BE13	5

Subphylum: Crustacea (206 taxa)

Amphipoda (97 taxa)		**2526**
Ampelisca anisuropa	4, 65, BE12	21
Ampelisca anomala	4, 65, 70, 102, 121, BE10, BE11, BE12	61
Ampelisca brevicornis	1, 2, 3, 4, 45, 65, 66, 76, 87, 88, 121, BE10, BE12, BE13	101
Ampelisca cf. *brachyceras*	1, 3, 45, 121	62
Ampelisca palmata	3, 4, 45, 65, 71, 76, 78, 88, 101, 102, 106, 121	81
Ampelisca sp.	BE12, BM5, Na5, LO4, LO5, SU4, SU5, Be71, LU5, KU3, Ku4, KU6	581
Ampelisca spinimana	1, 3, 45, 65, 101, 102, 121, BE12	46
Amphilochus sp.	SU5	3
Amphipoda indet.	KU3	3
Amphipoda (red eyes)	Na5, SU5, Be71, LU5	5
Apherusa sp.	SU5	1
Bathyporeia sp.	2, 3	5
Caprellidae	BM5, Na5	28
Caprella sp.	Na5	1
Ceradocus sp.	66	6
cf. *Ceradocus* sp.	Na5	1

cf. *Maera* sp.	BM5, LO5, SU4	18
cf. Melitidae	LO5	1
cf. *Metopa* sp.	Na5	1
cf. *Perioculodes* sp.	Ku4	7
cf. *Phtisica* sp.	65	1
cf. Stegocephalidae	121	3
cf. Stenothoidae	Na5	4
Cheirocratus sp.	LO4	8
Dyopedos sp.	SU5, Be71	193
Ericthonius punctatus	121, BE13	9
Ericthonius sp.	Be71	1
Eriopisa B	LO5	2
Eriopisa epistomata	1, 4, 72, 88, LO4, Na5, Ku4, KU3	42
Eriopisa sp.	LO5, Be71,	9
Eriopisella sp.	LO5	3
Eupariambus fallax	1, 45, 121, BM5, Na5, Ku4	35
Gammaropsis sp.	1, 3, 45, 65, 88, 121, BE10, BM5, Na5, Be71, KU6	174
Grandidierella elongata	45, 65, 78, 121, BE12, SU5, KU6	234
Grandidierella ischienoplia	121	1
Grandidierella sp.	121, BE13	111
Harpinia sp.	Be71	7
Harpinia sp. 2	LO4	25
Heterophoxus cephalodens	121	1
Heterophoxus sp.	BE13	1
Hippomedon longimanus	4, BE10, BE12, BE13	39
Hippomedon sp.	BE12	5
Hyperia sp.	SU4	1
Isaeidae	BM5, Na5, Be71	23
Isaeidae?	LU5	1
Lemboides	BE12	11
Lembos jassopsis	BE12, BE13	12
Lembos sp.	1, 4, 45, BE10, LO4	5
Lepidepecreum cf. *longicorne*	4	2
Lepidepecreum cf. *longicornis*	BE12	6
Lepidepecreum sp.	BM5	1
Lepidepecreum twalae	106, BE13	5
Leucothoe procera	5, 65, 67, 106, BE13, LO4, Na5, Ku5, KU6	23
Leucothoe sp.	LO5, SU4, Be71	6
Listriella lindae	5, 101, KU3	10
Lysianassa cf. *ceratina*	121	2
Lysianassa sp.	BE13	2
Lysianassa variegata	5, 65, BE10	7
Lysianassidae	LO4, BM5, Na5, SU5, Ku4	30
Lysianassidae?	BM5	4
Liljeborgiidae	LO4	17
Maera grossimana	5, BE13	3
Maera sp.	LO4, SU5, Na5	17

Megaluropus sp.	BE12	9
Megamphopus sp.	SU5, Na5,	46
Melita sp.	SU5, Na5	8
Melitidae	Ku4	1
Metaphoxus sp.	BE10	2
Oeditoceridae	BM5, Na5, SU4, Be71, LU5, Ku4	19
Oeditoceridae B	Na5	1
Orchomene sp.	BM5, SU4	11
Orthoprotella mayeri	BE10	3
Othomaera cf. *othonis*	BE10, BE11	4
Othomaera cf. *schmidti*	71	1
Othomaera sp.	5	1
Pardia sp.	BE7, BE10	2
Perioculodes longimanus	2, 3, BE12, LO4, SU5, Na5,	19
Perioculodes sp.	Na5, BM5, KU3, Ku4	12
Photis longimana	121	2
Photis sp.	BE10, BE12, SU5	47
Phoxocephalidae	BM5, LO5, SU4, Be71	39
Phtisica marina	BE10, BE11, BE13, 106, 121, SU5, Na5	39
Pleustidae	BE13	35
Podocerus	45	3
Pseudomegamphopus sp.	BE12	1
Pseudoprotella phasma	BE13	12
Siphonectes	87, 88	3
Siphonoecetes sp.	BE12	1
Stenothoidae	BE12, SU5	3
Synchelidium sp.	SU5	1
Tiron australis	4, 87, 121, BE12, BE13	43
Tiron sp.	SU4	1
Tryphosites	4	2
Urothoe cf. *tumorosa*	BE12	7
Urothoe grimaldii	2, BE12	9
Urothoe serrulidactylus	67, BE13	3
Westwoodilla cf. *manta*	LO4, Na5	7
Cumacea (24 taxa)		**795**
Bodotria africana	BE12, BE13	3
Bodotria fionae	BE12	1
Bodotria glabra	45, BE7	4
Bodotria sp.	SU5, Na5, KU6	111
cf. Bodotria sp.	BM5, Ku5	13
Cumacea with melanophores	BM5	5
Cyclaspis sp.	BM5	2
Diastylis algoae	45	1
Diastylis sp.	Na5, BM5, LO4, LO5, SU5, Be71, LU5, Ku4	125
Eocuma cadenati	4, 88, BM5	4
Eocuma calmani	BE10, Be71, LO4	7
Eocuma cf. *cadenati*	BM5	15

Eocuma cochlear	45, SU5	26
Eocuma dimorphum	1, 2, 45	16
Eocuma lanatum	BM5, Na5	176
Eocuma sp.	Ku5	2
Heterocuma ambrizetensis	65, 68, 88, 106	13
Iphinoe africana	3, 45, 65, BE10, SU5, KU6	33
Iphinoe crassipes	65, BE10	5
Iphinoe nov. spez.	LO4, Na5	6
Iphinoe sp.	BM5, SU5	56
Pseudocuma longicorne longicorne	BE12	2
Upselaspis caparti	KU3, KU6	105
Upselaspis sp.	Na5	64
Decapoda (46 taxa)		**469**
Anomura	88, 101, BE7	10
Brachyura	45, 65, 101, 102, 121, BE10	29
Brachyura (triangle crab)	3, 121	8
Brachyura 5A	121	2
Brachyura A	121	1
Brachyura A2	LO5, LU5	15
Brachyura A3	LO5	26
Brachyura B	Be 71	2
Brachyura B (horn)	121	1
Brachyura B (tip)	72, 78, 121	3
Brachyura C	SU4, Be71	2
Brachyura C (heart)	121	3
Brachyura D (double tip)	121	2
Brachyura K	Be71	15
Brachyura M	Be71, LU5	2
Brachyura P	LO5	1
Calappa sp.	121	6
Callianassa cf. *kraussi*	KU3	10
Callianassa sp.	BM5, LO4, LO5, SU5, Be71	46
Callichirus kraussi	KU3	3
cf. *Dehaanius* sp.	BE13	1
Crangon sp.	Be71	1
Galathea sp.	BE13, Na5, Be71	17
Galatheidae	4, 45	5
Goneplax sp.	KU3	1
lobster larva	BM5	5
"long-neck-cancer"	121	1
Macropodia sp.	Be71	1
Majidae	BE10	1
Majidae A	121	2
Majidae B	121	13
Munidopsis sp.	SU4	13
Natantia	2, 4, 65, 66, 71, 72, 77, 78, 87, 88, 102, 121, BE10	29
Natantia A	101, Be71	6

Natantia B	LO5, LU5, Be71	19
Natantia D	LU5	1
Natantia H	Be71	1
Natantia juv.	Na5, LO5	6
Natantia Q	Be71	1
Nautlilocorystes ocellatus	SU5	1
Paguridae	2, 65, 87, 106, 121, KU6	108
Pagurus sp.	BM5, SU5, Ku4	5
Philocheras sculptus	Na5	2
Processa sp.	LO4, Na5	2
“Springkrebs”	121	27
Upogebia sp.	5, 45, 65	13
Euphausiacea (2 taxa)		**8**
Euphausiacea indet.	BM5	1
Euphausiacea juv.	LU5	7
Isopoda (22 taxa)		**281**
Apanthura sp.	4, 5, BE10, BE11	22
Apanthura sandalensis	LO4, Na5	13
Arcturellina sp.	Na5	2
Arcturidae	BM5, SU5, Na5	5
Arcturina sp.	121, BE7, BE12, BE13	31
Arcturina triangularis	45	2
Arcturinoides sexpes	87, 121	4
Astacilla mediterranea	BE13	10
Astacilla sp.	Na5	1
Cyathura sp.	65, BM5, Na5, Be71	74
Eurydice longicornis	4, 66, BE12	20
Gnathia sp.	LU5	1
Haliophasma austroafricanum	70	2
Isopoda indet.	SU5	3
Janira sp.	121	1
Malacanthura linguicauda	2, 3, 68, 88, 106, 121, BE12, BE13, Na5	19
Leptanthura urospinosa	SU5	1
Natatolana cf. *hirtipes*	5, BE10	3
Pseudione sp.	KU3	1
Sphaeroma sp.	121	1
Sphaeromatidae	BE12	39
Uromunna sheltoni	SU5, KU6	26
Leptostraca (2 taxa)		**4**
Nebalia deborahae	BE12	1
Nebalia sp.	SU5, Na5	3
Maxillopoda (2 taxa)		**48**
Balanidae	45, 121	46
common goose barnacle	45	2
Mysida (1 taxon)		**9**
Mysidacea indet.	BE11, LO5, LU5, Na5, Ku4	9
Ostracoda (1 taxon)		**2**

Philomedes sp.	LO4, SU5, Na5	2
Stomatopoda (1 taxon)		**9**
Stomatopoda indet.	1, 2, 72, SU5, Be71	9
Tanaidacea (8 taxa)		**208**
Apseudes grossimanus	BE9, Be71	5
Apseudopsis cuanzanus	LO4	14
Apseudopsis sp.	65	2
Calozodion dominiki	4, 106, 121, BE10, BE12, BE13	141
Calozodion sp.	SU4	8
Hemikalliapseudes sp.	45, 65, 102, BM5, LO5	27
Hemikalliapseudes sebastiani	Na5, LO4	9
Tanaidacea indet.	Be71	2

<u>Phylum: Brachiopoda</u> (3 taxa)

Brachiopoda indet.	Be71, LU5	21
Brachiopoda indet. B	Be71	1
Lingulata (1 taxon)	121	**1**
Linguloidea	121	1

<u>Phylum: Bryozoa</u> (2 taxa)

Bryozoa indet.	121, BE11, BE12, BE13, Na5, BM5, SU4, Be71, Ku4, Ku5; KU6	x
Bryozoa (Electra pilosa-like)	KU6	x

<u>Phylum: Cephalorhyncha</u> (2 taxa)

Priapulida (2 taxa)		**3**
Priapulida indet.	LO4	1
Priapulidae	BE12	2

<u>Phylum: Chordata</u> (4 taxa)

<u>Subphylum: Cephalochordata</u> (1 taxon)

Leptocardii (1 taxon)		**12**
Branchiostoma sp.	66, 67, 68, 87, 106, BE12	12

Subphylum: Tunicata (3 taxa)

Ascidiacea (3 taxa)		**8**
Ascidiacea indet.	BE12, Na5	4
Ciona sp.	BE12	1
Molgula sp.	BE13, Ku4	3

Phylum: Cnidaria (18 taxa)

Anthozoa (15 taxa)		**69**
Alcyonacea	121	1
Anthozoa indet.	BM5, Na5, LO5, SU4, KU3, Ku4	11
cf. Anthozoa	LU5	1
cf. Edwardsia sp.	101, BE12, BE13, BM5, Ku5	19
Edwardsia sp.	LO4	1
Funicula sp.	SU5	1
Gorgoniidae	101	X
Octocorallia	BE7	1
Octocorallia (soft)	Ku4	5
plumose anemone	BE13	1
Scleractinia A	101, 102	5
Scleractinia B	121	1
sea anemone	121	10
sea pen	BE9	2
Virgularia sp.	SU4, SU5, KU3	10
Hydrozoa (3 taxa)		**x**
Dynamena sp.	KU6	x
Hydractinia echinata	KU6	x
Hydrozoa indet.	65, 121, BE11, BE12, BE13, Na5, SU4, Be71, KU3, Ku4, Ku5	x

Phylum: Echinodermata (20 taxa)

Echinodermata indet.	Be71	1
Asteroidea (1 taxon)		**5**
Asteriidae	121	5
Echinoidea (1 taxon)		**6**
Echinoidea inet.	87, 121	6
Holothuroidea (3 taxa)		**209**
Holothuroidea indet.	BE12	1
Holothuria sp.	KU6	197
Rhopalodinaria bocherti	1, 2	11
Ophiuroidea (14 taxa)		**235**
Acrocnida semisquamata	1	1
Amphioplus aciculatus	65, BE11	4
Amphioplus sp.	Be71	4
Amphipholis nudipora	Be71, LO4	7
Amphipholis squamata	4	1

Amphiura filiformis	5, 102, BE10, Be71, LO4	35
Amphiura sp.	4, 65, LO4, SU5	8
Amphiuridae	LO4	1
Ophiactis luetkeni	121, SU4	63
Ophiactis sp.	BE13	1
Ophiura (Dictenophiura) carnea skoogi	121	12
Ophiura grubei	4, 121, BE12, Be71, Na5	57
Ophiura sp.	Na5	2
Ophiuroidea	1, 2, 3, 4, 66, 70,101, 102, 106, 121, BE11, BE12, BE13, BM5, Na5, LO4, LO5, SU5, LU5	39

Phylum: Echiura (1 taxon)

Echiuroidea (1 taxon)		**1**
Echiurus sp.	SU5	1

Phylum: Mollusca (123 taxa)

Mollusca indet.	1, 5, 45, 65, 70, 72, 76, 77, 78, 87, 88, 101, 102, 106, 121, BE7, BE10, BE11	x
Bivalvia (44 taxa)		**2092**
Abra cf. nitida	LO4, Na5, SU5, KU6	62
Abra pilsbryi	KU6	32
Abra sp.	Na5, LO5, Ku5	14
Arcidae	SU4, KU3	2
Bivalvia indet.	1, 3, 4, 5, 45, 76, 78, 88, 102, 121, BE10, BE11	174
Bivalvia A	101	2
Bivalvia D	SU5	1
Bivalvia (white, striped)	KU6	1
cf. Lucinidae	Ku5	5
cf. *Lucinoma capensis*	Be71	1
Chlamys sp.	Su5	1
cockle	66, 67, 87, 106	15
Congetia congoensis	SU5	7
Corbula sp.	LO4, LO5	4
Diplodonta diaphana	SU5	4
Dosinia lupinus	KU6	20
Dosinia orbignyi	KU6	45
Dosinia sp.	BM5	3
Felania diaphana	SU5	16
Gari sp.	BE12	1
Jolya letourneuxi	SU5	68
Macoma?	87, 106	7
Macoma sp.	SU5	2
Mactridae	SU5	7

Melliteryx sp.	SU5, KU3	2
Mytilidae	SU5, LU5, Ku5	214
Mytilus sp. juv.	KU6	236
Nucula crassicostata	LU5	1
Nucula sp.	LO4	9
Nuculana bicuspidata	BE7, SU5, KU3, Ku4, Ku5, KU6	1001
Nuculana montagui	LU5	1
Nuculana sp.	LO4	1
Pecten sp.	121, BE10	2
Pinnidae	88	1
Pitar sp.	BE7, LO5, KU3	7
Pseudopythina sp.	BE11	1
Sinupharus galatheae	SU5, KU6	51
Solemya cf. *togata*	BE10, BM5, KU6	4
Striarca lactea	BE11	1
Tellina sp.	BM5, Na5, LO4, LO5, SU5, Be71, KU6	50
Tellinidae	65, 77	7
Thyasira sp.	BM5, Na5	7
Venus chevreuxi	KU3	1
Venus sp.	65	1
Gastropoda (75 taxa)		**819**
Acteon sp.	SU5, Na5	2
Aporrhais senegalensis	BE7	1
Aspa marginata	Na5, KU3	4
Athys sp.	1	1
Bela africana	BM5, Na5	2
Bivetiella cancellata	4, 121	2
Bivetiella similis	121	1
Calyptraea sp.	121	4
Cancilla scrobiculata crosnieri	Be71	1
cf. *Coralliophila meyendorffii*	Na5	1
cf. *Neptunea* sp.	70	1
cf. *Turridae*	Ku4	1
Chauvetia sp.	2	2
Cirsotrema cochlea	87	1
Crassispira carbonaria	BE10	1
Cylichna sp.	BM5, Be71, LO4, LU5, Ku5	10
Diacavolinia longirostris	77	1
Eglisia spirata	45	1
Eulima angolosa	5	1
Eulima glabra	BE11	2
Euspira grossularia	LU5	1
Fusinus sp.	Na5	1
Fusiturris pluteata	Na5	1
Gastropoda indet.	5, 45, 71, 87, 102, BE11, BE13	13
Gastropoda indet. A (little snail)	SU5	1
Gastropoda indet. B	SU5	2
Gastropoda indet. C	SU5	1
Genota mitriformis	71	1

Genota nicklesi	4	1
Gibberula sp.	BE10, BM5	7
Gibberula?	45	1
Latirus mollis	Na5	1
Macromphalus senegalensis	LO4	1
Mangelia angolensis	4, KU3	2
Mangelia sp.	88	6
Marginella	4	1
Melanella frielei	SU5, Ku5, KU6	4
Mitrella condei	121	1
Nassarius angolensis (species inquirenda)	SU5, KU6	217
Nassarius denticulatus	121	1
Nassarius desmoulioides	BE10	4
Nassarius elatus	LO4, SU5, Be71	20
Nassarius niveus	BE10	2
Nassarius sp.	BE12	2
Nassarius vinctus	BE7, LO4, KU3, Ku4, Ku5	367
Natica acinonyx	LO4	1
Natica cf. *bouvieri*	1	2
Natica multipunctata	65, 101	1
Natica sp.	KU3	3
Naticidae	Be71, Na5	2
Neocancilla hebes	121	10
Nudibranchia	2, 3, 121, BE13, SU5, Be71, Ku5	29
Oliva sp.	BE12	1
Onoba sp.	KU3	1
Perrona spirata	45	1
Philine aperta	BM5, Ku5, KU6	10
Philine scabra	SU5	1
Philine sp.	SU5, KU6	7
Pseudotorinia architae	Be71	2
Rissoidae	SU5, LU5	4
Retusa obtusa	KU6	5
Strombina descendens	Be71	1
Tectonatica rizzae	5, 121	3
Tectonatica sagraiana	BE7, SU5, Ku4, Ku5, KU6	14
Tectonatica sp.	45	1
Terebra gaiae	121	1
Turbonilla senegalensis	KU6	2
Turridae	5, BE12, BE13, Be71	4
Turritella annulata	45	2
Turritella sp.	LO5	2
Turritella nov. spez.	1	2
Vitreolina sp.	SU5	1
Volvarina capensis	BE13	2
Volvarina sp.	4, BE12	4
Xenophora senegalensis	Be71	1
Polyplacophora (1 taxon)		**1**

Polyplacophora indet.	SU4	1
Scaphopoda (1 taxon)		**4**
Scaphopoda indet.	65, 78, 88, 121, BM5, Na5, LO4, LO5, Be71, LU5, SU5	4
Solenogastres (1 taxon)		**9**
Solenogastres indet.	LO5, LU5	29

<u>Phylum: Nemertea</u> (5 taxa)

cf. Nemertea	45, BE11, BE12, BE13, BM5, Ku5	113
Nemertea indet.	BM5, Na5, LO4, LO5, SU4, SU5, Be71, LU5, KU6	126
Anopla (1 taxon)		**10**
Lineus sp.	Be71, LU5	10
Enopla (1 taxon)		**1**
Prostoma sp.	BE11	1
Palaeonemertea (1 taxon)		**253**
Tubulanus sp.	Na5, LO4, LO5, SU5, Be71, LU5, Ku5, KU6	253

<u>Phylum: Phoronida</u> (2 taxa)

Phoronopsis sp.	LO5	1
Phoronis sp.	SU5	7

<u>Phylum: Platyhelminthes</u> (2 taxa)

Rhabditophora (1 taxon)		**5**
Prostoma sp.	BE12	5
Turbellaria (1 taxon)		**3**
Turbellaria indet.	SU5, KU6	3

<u>Phylum: Porifera</u> (2 taxa)

cf. Porifera	BE13	4
Porifera indet.	45, 121	2

<u>Phylum: Sipuncula</u> (3 taxa)

Sipuncula indet.	LO4, SU5	6
Sipunculidea (2 taxa)		**103**
Sipunculidae	1, 3, 45, 65, 71, 72, 77, 87, BE9, BE11, Na5	102
Golfingia sp.	Na5	1

In the following an alphabetical list of all determined taxa from the dredge samples is given. Their location, their taxonomic classification and the mean number of counted individuals is also stated.

Total number of taxa: 579

Phylum: Annelida (159 taxa)

taxon	station	mean number of counted individuals
Oligochaeta (2 taxa)		
Oligochaeta indet.	Ku5	93
Tubificidae	KU6	115
Polychaeta (157 taxa)		
Ampharete agulhasensis	SU5	4
Ampharete sp.	100, LO4, SU5, Na5, KU6	156
Ampharetidae	87, 88, 100, BE13, BM5, LO5, SU4, SU5, Na5, Be71, LU5, Ku5	25
Aonides sp.	100	6
Aphroditidae	66, 87, 88, BE7, BE13, LU5	16
Arabella iricolor	87	2
Aricidea	100, BE12	3
Aricidea sp.	LU5, LO4, Na5	7
Brada	107	2
Branchiomma violacea	66	1
Capitellidae	88, 100, Na5, KU6	115
Ceratonereis cf. costae	66	1
cf. *Amphictene*	Ku5	3
cf. *Chloeia* sp.	Be71	4
cf. *Heteromastus* sp.	Ku5	1
cf. *Oenonidae*	87	2
cf. *Petaloproctus* sp.	LU5	6
Chaetopteridae	66, 100	3
Chaetopterus sp.	Ku5	2
Chaetozone setosa	LO4, Na5, SU5	132
Chaetozone sp.	BM5	1
Chloeia inermis	LO4	1
Chloeia sp.	LU5	1
Chone sp.	LO4, Na5	35
Cirratulidae	66, 87, 88, 100, BE7, BM5, Be71, Ku5, KU6	7
Cirratulidae B	Ku5	9
Cirratulidae (b.-w.-eyes)	Ku5	2
Cirratulidae orange	Ku5	45
Cirriformia tentaculata	87	1
Cossura coasta	Be71, Ku5, KU6	42
Diopatra neapolitana capensis	BE13, LO4, Na5, SU5, LU5, Ku4, Ku5, KU6	198
Diopatra sp.	87, 100, BM5, LO5, Be71	30

taxon	**station**	**mean number of counted individuals**
Diplocirrus sp.	Na5, SU5	3
Dipolydora cf. *normalis*	66	4
Dorvillea sp.	66	1
Dorvilleidae	BE13	1
Drilognathus	87	1
Epidiopatra hupferiana	87	1
Epidopatra hupferiana hupferiana	87	2
Eteone sp.	87, Be71, LO4, SU5, Na5	1
Eulalia sp.	87	1
Eumida sp.	Na5	6
Eunice pennata	87	100
Eunice sp.	Be71	1
Eunice vittata	66	1
Eunicidae	66, 88, 100, 107	28
Euphrosine sp.	SU4	1
Exogone sp.	Na5	47
Fabricia sp.	LU5	1
Flabelligeridae	Na5	1
Galathowenia sp.	LO4, SU5, Ku5, KU6, Na5	343
Glycera convoluta	87	3
Glycera longipinnes	87	3
Glycera pappilosa	87	16
Glycera sp.	87, LO4, SU5, Na5	1
Glyceridae	66, 88, 100, 107, Be71	4
Glycinde sp.	Na5	33
Goniada maculata	87	2
Goniada sp.	LO4, SU5, Ku5, KU6, Na5	23
Harmothoe sp.	LO4, SU5, Ku4, KU6	3
Hermundura aberrans	SU5, KU6	1
Hesionidae	87, 100, BE13, Ku5	2
Isolda pulchella	Na5, SU5	11
Lanice conchilega	66, 87, SU5	12
Laonome sp.	66	2
Lepidasthenia	66, 88	1
Lumbrineridae	100, LO5, Be71, LU5, Ku5	9
Lumbrineris sp.	LO4, Na5, SU5, KU3, KU6	101
Lygdamis indicus	87	98
Lysidice ninetta	66	18
Lysippe sp.	87	3
Magelona	87, 100	2
Maldanidae	66, 87, 100, BE7, LO5, Be71	4
Minuspio cirrifera	Na5	1
Nephtyidae	100, LO5, Be71, LU5, Ku4, Ku5	29
Nephtys	BE7	1
Nephtys capensis	LO4	12
Nephtys cf. *macroura*	66	1

taxon	station	mean number of counted individuals
Nephtys hombergii	Na5	16
Nephtys lyrochaeta	LO4, SU5, KU6	55
Nephtys sp.	87	1
Nereididae	66, LU5	6
Nereis sp.	SU5, KU6	5
Nothria conchylega	87	849
Oenone fulgida	87	1
Onuphidae	87	3
Onuphis eremita	87	1
Ophelia agulhana	87	2
Ophelia sp.	KU6	1
Ophelidae	88	2
Orbinia bioreti	87	2
Orbinidae	100	2
Owenia cf. *fusiformis*	87	10
Owenia fusiformis	LO4, Na5, SU5, KU6	17
Owenia sp.	88, 100, BM5, LO5, SU4	10
Oxydromus spinosus	LO4, SU5	1
Paraonis sp.	Na5	39
Paraprionospio pinnata	Be71, Na5, Ku4, KU3	32
Pectinaria	100	1
Pectinaria neopolitana	87	2
Pectinaria sp.	LO5, SU4, SU5, Be71, LU5	5
Pectinaridae?	87	1
Pherusa sp.	100, SU5, KU6	9
Pholoe?	87	1
Pholoe sp.	Na5	3
Phyllamphicteis sp.	SU4, Be71, LU5	90
Phyllodoce longipes	87	26
Phyllodoce madeirensis	Na5, SU5	8
Phyllodocidae	66, 87, 88, 100, 107, LO5, Be71, LU5	8
Pista brevibranchiata	SU5	6
Pista sp.	87, LO4	3
Platyneries sp.	66	5
Polychaeta indet.	66, 87, BM5	68
Polychaeta (red abdomen)	107	1
Polychaeta (biomass rest)	87, 88, 100, BE12	x
Polydora sp.	88, 100, BE13, BM5, SU5	2
Prionospio	87, 100, BE7	4
Prionospio cf. *malmgreni*	87	1
Prionospio ehlersi	LO4, Na5	63
Prionospio malmgreni	LO4, Na5	154
Prionospio sp.	Be71, LU5	26
Prionospio steenstrupi	Na5, SU5	45
Pseudopolydora antennata	Na5	22
Sabellaria eupomatoides	66, Ku4, KU6	8

taxon	station	mean number of counted individuals
Sabellidae	66, 88, 100, BE13, SU5	12
scale-polychaeta	87	4
scale worm	Be71	2
Scoloplos sp.	Be71, Na5, SU5	3
Serpulidae	66, 88, BM5, SU4, Be71, LU5	12
Sigambra cf. *robusta*	Ku5	1
Sigambra sp.	100, Na5, KU6	5
Sphaerodoridae	100	4
Sphaerodorum gracile	Na5	1
Sphaerosyllis	87	1
Spio (black side)	88, 100	4
Spio filicornis	SU5	1
Spio sp.	87, BM5, LO4	1
Spiochaetopterus costarum	LO5, LU5	15
Spiochaetopterus sp.	66, LO4, Na5, SU5, KU6	11
Spionidae	88, 100, 107	20
Spionidae (with head lobes)	Ku5	1
Spiophanes (black side)	LO5, Be71	4
Spiophanes bombyx	Na5, SU5, KU6	17
Spiophanes sp.	66, 87, 88, 100, Be71, LO4	8
Sternaspis scutata	LO4, LO5, Be71, LU5	6
Sthenelais boa	KU6	3
Sthenelais cf. *incisa*	LO5	2
Sthenelais limicola	LO4, Na5, SU5	14
Sthenelais sp.	SU4, Be71, LU5	24
Syllidae	66, 87, BE13, BM5, SU4, SU5, Na5, KU6	49
Syllidae 2	Na5	3
Terebellidae	87, 100, BE12, BE13, Be71, LU5, Na5	7
Terebellides stroemii	LO5, Na5, SU5	9
Tharyx sp.	KU6	16
Trochochaeta ankeae	Na5	38
Trochochaeta sp.	LU5	4

Phylum: Arthropoda (210 taxa)

Subphylum: Chelicerata (2 taxa)

Pycnogonida (2 taxa)		
Tanystylum cf. *brevipes*	BE12	1
Nymphon sp.	BE13	26

Subphylum: Crustacea (208 taxa)

Amphipoda (69 taxa)		
Ampelisca anomala	87, 88, 100	6
Ampelisca brevicornis	87, 88, 100, 107	18
Ampelisca cf. *brachyceras*	88, 100	3
Ampelisca palmata	BE7, BE13, 87, 88, 100	19
Ampelisca sp.	87, Na5, LO4, LO5, SU4, SU5, Be71, LU5	60
Ampelisca spinimana	100	54
Amphipoda indet.	BE12, 66	2
Amphipoda (red eyes)	BM5	1
Amphipoda B	BM5	1
Amphipoda C	BM5	3
Bemlos cf. *leptocheiru*	88, 100	14
Caprella sp.	SU5	12
Caprellidae	SU4	1
Ceradocus sp.	BE13, 87, 88	8
cf. *Leucothoe* sp.	BM5	8
cf. *Microdeutopus* sp.	100	5
cf. *Podoceropsis*	88	1
Concholestes armatus	87	5
Dyopedos sp.	Na5, SU5	63
Ericthonius punctatus	66, 88, 107	14
Eupariambus fallax	BE12, Na5, LO4	4
Eusiridae	Be71	1
Gammaropsis sp.	66, 87, 88, BM5, Be71, Ku5, KU6	4
Grandidierella elongata	100, Na5, SU5	126
Grandidierella sp.	SU4	1
Harpinia sp.	Na5	3
Harpinia sp. *2*	LO4	53
Hippomedon	BE13	15
Hippomedon longimanus	107	1
Hyperiidae	Na5	1
Iphimedia	88	8
Iphimedia cf. *obesa*	87	1
Isaeidae	SU4, Be71	5
Laetmatophilus purus	88	18
Lemboides sp.	Na5, SU5	27
Lembos sp.	BE13, 87, Na5, LO4	51
Lepidepecreum cf. *longicornis*	BE13	1
Leucothoe procera	BE13, 66, 87, 88, LO4	13
Leucothoe sp.	SU4	3
Liljeborgiidae	LO4	23
Listriella lindae	100	1
Lysianassa variegata	88	2
Lysianassidae	Na5, LO4, KU6	2
Maera grossimana	BE13, 66	12

Maera sp.	66	2
Mallacoota subcarinata	88	1
Mandibulophoxus stimpsoni	87	2
Megaluropus sp.	87	10
Megamphopus sp.	Na5, LO4	3
Melita sp.	BE12, SU5, KU6	1
Metaphoxus sp.	Na5	4
Orchomene sp.	Na5	5
Othomaera sp.	BE13, 66, 87	2
Pardia sp.	BE7, 66	1
Perioculodes longimanus	87, 100	1
Photidae	SU5	10
Photis longimana	66, 87, 88, 100	22
Photis sp.	66, 87, Na5, BM5, SU5	42
Phoxocephalidae	66, Be71	2
Phtisica marina	BE12, 66, 88, Na5, SU5	1
Pleustidae	LO4	1
Siphonectes	100	2
Siphonoecetes dellavallei	87	66
Siphonoecetes sp.	66, 88	1
Stenothoe sp.	BE12	1
Stenothoidae	LO4, SU5	2
Tiron australis	BE13, 66, 87	129
Urothoe serrulidactylus	66, 87	1
Westwoodilla cf. *manta*	Na5, LO4	2
Cumacea (17 taxa)		
Bodotria africana	66	1
Bodotria sp.	SU5, KU6	45
Diastylis algoae	88	6
Diastylis sp.	Na5, SU5, Be71	41
Diastylis sp. 1	LO4, KU6	4
Diastylis sp. 2	LO4, KU6	1
Eocuma cadenati	88	2
Eocuma calmani	Na5, LO4	13
Eocuma cochelar	SU5, Na5	13
Eocuma ferox	66, 87, 100, Na5	1
Eocuma foveolatum	100	4
Eocuma lanatum	88,Na5, LO4	14
Heterocuma ambrizetensis	66, 87, 88	51
Iphinoe africana	100, SU5, KU6	7
Iphinoe nov. spez.	LO4, Na5	2
Leuconidae	Na5	2
Upselaspis caparti	KU6	3
Decapoda (88 taxa)		
Achaeus sp.	66	2
Anomura	66, 88, 107	13
Brachyura	BE13, 66, 88	44
Brachyura (triangle crab)	BE12, 66, 87	1
Brachyura (heart crab)	66, 87	3

Brachyura 1	LO4	1
Brachyura 1 (triangle crab)	SU5	7
Brachyura 10A	66, 87	32
Brachyura 2	LO4	2
Brachyura 2 (round, tooth)	SU5	1
Brachyura 3	SU5	6
Brachyura 4	SU5	5
Brachyura 5	SU5	1
Brachyura 5A	107	4
Brachyura 5B	107	5
Brachyura 5C	107	1
Brachyura A	87, LU5	2
Brachyura A2	LO5, LU5	10
Brachyura A3	LO5	47
Brachyura B	Be71, LU5	11
Brachyura E	LU5	40
Brachyura G	LU5	2
Brachyura H	BM5, LU5	1
Brachyura K	LO5, Be71	2
Brachyura M	BM5, Be71, LU5	4
Brachyura N	LO5	10
Brachyura O	LO5	1
Brachyura P	Be71	1
Brachyura Q	Be71	1
Brachyura-larva	88	2
Calappa pelii	Na5, SU5	2
Calappa sp.	87, LU5	1
Callianassa cf. *kraussi*	Ku4	1
Callianassa sp.	BM5, LO4	3
Caridea 1	Na5	1
Caridea 2	Na5	1
Caridea 3	Na5	1
cf. *Dehaanius* sp.	BE12	3
cf. *Galathea* sp.	BM5	17
cf. *Thaumastoplax* sp.	Ku5	1
Decapoda indet.	KU3	1
Galathea sp.	BE12, BE13, LO4, BM5, LO5, Be71, LU5	14
Galatheidae	66, 87, 88	36
"long-neck-cancer"	BE13, 87	2
Macropodia cf. *rostrata*	87	1
Macropodia sp.	BE12, LO4, SU5	2
Maja sp.	BE12, KU6	6
Majidae	BE13, 66, 88, Na5, SU5	13
Majidae B	87	5
Natantia	BE13, 66, 87, 88, 100, 107	321
Natantia 1	LO4	1
Natantia 2	LO4	1
Natantia B	LO5, Be71, LU5	8

Natantia C	SU4	1
Natantia E	Be71	25
Natantia G	Be71, LU5	54
Natantia H	BM5, LO5, Be71, LU5	11
Natantia I	LO5, Be71, LU5	5
Natantia K	LU5	1
Natantia L	Be71, LU5	1
Natantia M	LO5, Be71, LU5	22
Natantia N	BM5, LO5, Be71	1
Natantia O	BM5, Be71	8
Natantia P	LO5	1
Natantia S	Be71	3
Natantia U	Be71	1
Nautilocorystes ocellatus	SU5, KU6	1
Nautilocorystes sp.	66	1
Nikoides danae	KU3	1
Pachygrapsus sp.	Ku4	2
Paguridae	BE12, BE13, 66, 87, 100, Na5, LO4, SU5, KU6	27
Pagurus sp.	BM5, LO5, SU4, Be71, LU5, Ku5, KU3	5
Palaemon sp. *1*	SU5	1
Palaemon sp. *2*	SU5	1
Pandalina sp.	LO4	1
Penaeidae	Na5	2
Philocheras hendersoni	SU5	45
Philocheras sculptus	LO4, Na5, SU5	16
Plesionika edwardsii	KU3	2
Portunidae	66, 87, SU5	11
Processa sp.	LO4, Na5, SU5	23
Raninoides bouvieri	SU5	1
Scyllaridae	66, 87, 88	1
spider crab	107	5
“Springkrebs”	87	6
“rod-head-crab”	88	1
Stomatopoda	107	2
Upogebia sp.	LO4	1
Isopoda (19 taxa)		
Apanthura sandalensis	Na5, LO4	4
Apanthura sp.	66	1
Arcturina scutula	LO4, SU5	2
Arcturina sp.	BE12, BE13, 66, 100	2
Arcturina triangularis	100	1
Arcturinoides sexpes	87	1
Astacilla mediterranea	66	1
Astacilla sp.	LO4, SU5	1
Cirolana sp.	Na5	1
Cyathura sp.	Be71	2
Eurydice longicornis	66, 87	3

Gnathia africana	66, 87	5
Gnathia sp.	LU5	2
Gnathia sp.	BE13, 87	1
Haliophasma austroafricanum	LO4	5
Haliophasma coronicauda	Na5	1
Isopoda indet.	BM5, Ku4	1
Malacanthura linguicauda	66, 87, 100	4
Paramunna capensis	Na5	1
Leptostraca (1 taxon)		
Nebalia sp.	Na5, LO4, SU5	2
Maxillopoda (5 taxa)		
Balanidae	66, 87	4
Balanus sp.	Ku5, KU6	7
Cirripedia	107	1
Lepas sp.	66	2
Pollicipes sp.	LU5	1
Mysida (1 taxon)		
Mysidacea	BE12, SU4, KU6	1
Ostracoda (1 taxon)		
Philomedes sp.	LO4	12
Stomatopoda (1 taxon)		
Stomatopoda indet.	LO4	2
Tanaidacea (6 taxa)		
Apseudes grossimanus	Be71	1
Apseudidae nov. spez.	Na5	7
Apseudopsis cuanzanus	Na5, LO4	65
Calozodion dominiki	BE13, 66, 87, LO4, SU4	17
Hemikalliapseudes sebastiani	LO4	3
Hemikalliapseudes sp.	88, 100	7

<u>Phylum: Brachiopoda</u> (4 taxa)

Brachiopoda indet.	Be71	13
cf. Brachiopoda	BE12	1
Lingulata (2 taxa)		
Discinisca sp.	BM5, LU5	4
Lingulata indet.	66	1

<u>Phylum: Bryozoa</u> (5 taxa)

Bryozoa indet.	BE12, 66, 87, 88, BM5, SU4, LU5	x
Bryozoa indet. 1	KU6	x
Bryozoa inet. 2	KU6	x
Bryozoa indet. A	KU6	x

Gymnolaemata (1 taxon)		
Flustra sp.	KU6	x

<u>Phylum: Chordata</u> (3 taxa)

<u>Subphylum: Cephalochordata</u> (1 taxon)

Leptocardii (1 taxon)		
Branchiostoma sp.	87	26

<u>Subphylum: Tunicata</u> (2 taxa)

Tunicata indet.	BE13	5
Ascidiacea (1 taxon)		
Molgula sp.	BE12, SU5, KU6	1

<u>Phylum: Cnidaria</u> (13 taxa)

Anthozoa (11 taxa)		
Anemone	66	45
Anthozoa indet.	SU4, SU5, Be71, LU5, Ku4, KU6	2
Coralliidae	LO4, BE13, BM5, SU4, LU5	3
Edwardsia sp.	LO4, KU6	1
Funicula sp.	SU5	1
Funiculina cf. *quadrangularis*	KU3	2
Octocorallia soft	Ku4	7
plumose anemone	LU5	1
Scleractinia A	88	2
Scleractinia B	107	1
Virgularia sp.	SU5	3
Hydrozoa (2 taxa)		
Hydrozoa indet.	BE12, 66, 87, 88, LO4, BM5, SU4, SU5	3
Sertularia sp.	KU6	x

<u>Phylum: Ecinodermata</u> (30 taxa)

Asteroidea (1 taxon)		
Asteriidae	88, 107	3
Echinoidea (1 taxon)		
Echinoidea indet.	BE13, 87, 88, 107	2
Holothuroidea (7 taxa)		
cf. Cladodactyla sp.	87	2

Holothuria sp.	KU6	10
Holothuroidea indet.	87	5
Lanceophora lanceolata	88	2
Ocnus placominutus	88	3
Panningia pseudocurvata	66, 88	1
Trachythyone fallax	88	1
Ophiuroidea (21 taxa)		
Amphilimna olivacea	Be71	2
Amphiodia sp.	87	3
Amphipholis nudipora	Be71	1
Amphipholis squamata	BE13	1
Amphiura filiformis	LO4	10
Amphiura sp.	Na5, LO4	9
Ophiacantha angolensis	BE13	8
Ophiactis luetkeni	BE13, 66, 87	1
Ophiactis plana	88	1
Ophiactis sp.	66	2
Ophiolepis affinis	87	18
Ophiolepis paucispina	66	1
Ophiopsila annulosa	197	1
Ophiopsila guineensis	66	1
Ophiopteron atlanticum	66	2
Ophiothrix congensis	66	1
Ophiothrix fragilis	66	2
Ophiura (Dictenophiura) carnea skoogi	LO4, LU5	5
Ophiura grubei	88, LO4, LO5, Be71	6
Ophiura sp.	88	1
Ophiuroidea indet.	BE12, BE13, 66, 87, 88, 121, BM5, LO5, SU4, SU5,	1

Phylum: Echiura **(1 taxon)**

Echiuroidea (1 taxon)		
Echiurus sp.	SU5	1

Phylum: Mollusca **(145 taxa)**

Mollusca indet.	66, 87, 88, 100, 107	x
Bivalvia (41 taxa)		
Abra cf. *nitida*	Na5, LO4, SU5, KU6	45
Abra pilsbryi	SU5, Ku5, KU6	25
Abra sp.	LO5, Be71, LU5	13
Anomia sp.	KU6	1
Bivalvia indet.	66, 87, 88, 100, 107	30
Cardiocardita lacunosa	SU5	1
Carditella	87	1
Carditidae	87	1

cf. *Lucinoma capensis*	LU5	3
cf. *Mysella sp.*	Na5	2
cf. Ostreidae	LU5	7
Chlamys sp.	LO4, SU5	9
cockle	87	57
Congetia congoensis	SU5	2
Corbula rugifera	87	8
Corbula sp.	LO4, LO5, SU5	7
Costellipitar peliferus	Ku5	4
Crassatina paeteli	Na5	3
Cuspidaria sp.	LO4, LO5, BM5, SU5, Be71	1
Donax sp.	66, 87	13
Dosinia lupinus orbignyi	KU6	11
fan mussel	87	1
Felania diaphana	SU5	2
Glycymeris queketti	87	1
Jolya letourneuxi	LO4, SU5	120
Lucinoma capensis	Be71	1
Mactridae	SU5	46
Mytilidae	LU5, Ku5	8
Mytilus sp.	KU6	88
Nucula sp.	LO4	9
Nuculana bicuspidata	SU5, KU3, Ku4, Ku5, KU6	217
Nuculana cf. *commutata*	LU5	1
Pandora sp.	KU6	1
Pecten sp.	87	1
Pitar sp.	SU4, SU5, LU5	2
Pitar sp. *2*	Na5, SU5	4
Sinupharus galatheae	SU5, KU6	25
Tellina sp.	LO4, LO5, SU5, Be71, Ku5, KU6	5
Tellinidae	87	10
Thyasira sp.	LO4	7
Venus sp.	87	4
Cephalopoda (3 taxa)		
Octopoda	LU5	1
Octopus sp.	BE13	1
Sepia sp.	66	2
Gastropoda (96 taxa)		
Acteon sp.	LO4, SU5	2
Agaronia acuminata	66, 87	2
Agathotoma merlini	KU3	2
Aporrhais senegalensis	66, LO4	1
Aspa marginata	BE12, Na5, LO4, Ku4, KU3	9
Barleeia	BE13	1
Bela africana	SU5	6
Bivetiella cancellata	LO4, SU5	1
Bullia skoogi	KU3, Ku4, Ku5, KU6	10
Calliostoma sp.	BE13	1

Calyptraea sp.	87	9
cf. *Eulimella* sp.	87	2
cf. *Ringicula* sp.	87	1
cf. Turritellidae	100	2
Cinysca arlequin	66	1
Clavatula cf. *quinteni*	LU5	4
Clavatula sp.	87	3
commune	88	13
Conus tabidus	BE12	2
Crassispira carbonaria	BE12	8
Crassispira sp.	87	1
Crepidula cf. *porcellana*	66	1
Crepidula sp.	BE12	1
Cylichna cylindracea	87	7
Cylichna sp.	LO4, LU5	9
Cyllene desnoyersi lamarcki	87	15
Cyllene owenii	87	6
Cythara sp.	Na5, LO4, SU5, KU6	6
Dactylastele burnupi	87	28
Diaphana sp.	88	6
Euspira fusca	LU5	16
Euspira grossularia	LU5	13
Euspira notabilis	LU5	1
Fasciolariidae	BE12	2
Fusinus albinus	Na5	9
Fusiturris cf. *pluteata*	SU5	5
Fusiturris pluteata	SU5, KU6	21
Gastropoda indet.	87	11
Genota vafra	Be71	1
Gibberula gruveli	LO4	1
Hastula lepida	87	1
Hexaplex rosarium	66	1
Latirus mollis	BM5	2
Lippistes cornu	LU5	1
Lunatia grossularia	LO4	4
Macromphalus senegalensis	LO4	1
Mangelia angolensis	Be71	2
Mangelia congoensis	87	4
Mangelia sp.	Na5	9
Marshallora adversa	66	1
Melanella frielei	LO4	1
Mitrella cf. *rac*	87	1
Muricidae	BE13	1
Nassarius angolensis	Na5, KU6	135
Nassarius arcadioi	Na5	1
Nassarius elatus	100, LO4, SU5, Be71, Ku5	69
Nassarius sp.	LO5, KU3	2
Nassarius vinctus	BE7, KU3, Ku4, Ku5	260
Natica acynonyx	LU5	5

Natica canariensis	BM5	1
Natica cf. *marochiensis*	KU6	1
Natica cf. *multipunctata*	KU6	2
Natica fulminea	87	1
Natica fulminea cruentata	66, 87, 107	1
Natica marchadi	Ku5	1
Natica multipunctata	87, 107, LO5	1
Nudibranchia	BE13, 66, 87, Na5	7
Nudibranchia 1	SU5	6
Nudibranchia 2	SU5	2
Nudibranchia 3	SU5	2
Odostomia boteroi	SU5, KU6	1
Oliva flammulata	87	5
Oliva paxidus	87	2
Oliva sp.	BE13, 66	3
Opalia sp.	87	1
Orania fusulus	BE12	3
Philine aperta	BE12, SU5, LU5, Ku5	18
Philine scabra	LO4, SU5	2
Philine sp.	88, BM5, LO5, SU4, LU5, KU6	8
Pusionella vulpina	Na5	1
Pyramidellidae	87	1
Ranellidae	66	1
Retusa obtusa	Na5, KU6	2
Ringicula conformis	SU5	4
Ringicula turtoni	87	1
Tectonatica rizzae	LU5	2
Tectonatica sagraiana	LO5, SU5, Be71, Ku4, Ku5, KU6	19
Terebra sp.	66, SU5	10
Tomopleura spiralissima	SU5	1
Triphora sp.	BE12	1
Triphoridae	BE13	3
Turbonilla senegalensis	KU6	2
Turritella sp.	LO5, SU4, SU5, Ku4, KU6	13
Vitrinella bushi	SU5	1
Volvarina capensis	BE13	2
Volvulella acuminata	SU5	5
Polyplacophora (1 taxon)		
Chitonidae	66	1
Scaphopoda (2 taxa)		
Dischides politus	LU5	187
Scaphopoda indet.	87, Na5, LO4, LO5, Be71	17
Solenogastres (1 taxon)		
Solenogastres indet.	LO5, LU5	3

<u>Phylum: Nemertea</u> (4 taxa)

cf. Nemertea	Ku5	10
Nemertea indet.	LO4, SU4, SU5, KU6	6
Anopla (1 taxon)		
Lineus sp.	LO5, Be71, LU5	1
Palaeonemertea (1 taxon)		
Tubulanus sp.	Na5, BM5, SU5, Be71, LU5, KU6	7

<u>Phylum: Phoronida</u> (1 taxon)

Phoronis sp.	SU5	2

<u>Phylum: Platyhelminthes</u> (1 taxon)

Turbellaria (1 taxon)		
Turbellaria indet.	LO4, SU5, KU6	1

<u>Phylum: Porifera</u> (1 taxon)

Porifera indet.	BE13, 66	2

<u>Phylum: Sipuncula</u> (2 taxa)

Sipuncula indet.	SU5	8
Sipunculidea (1 taxon)		
Sipunculidae	BE13, 87, 88, 100	28

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A III- Declaration of Academic Honesty

I declare that this master's thesis is wholly my own work and that no part of it has been copied from any work produced by other persons.

I declare that all referenced work from other people have been properly cited and documented on the reference list.

Ribnitz-Damgarten, 20^{th} of August 2013

Gesine Lange