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BIODIVERSITY AND FEEDING ECOLOGY OF PELAGIC DECAPODS IN THE SOUTH-EAST ATLANTIC OCEAN

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Contents

ABSTRACT

Pelagic decapods play an important role in the food web of marine ecosystems, as predators for zooplankton and as prey for fishes. Due to their diel vertical migration, they also contribute to the vertical flux of organic matter, by transferring carbon from the surface to the deep ocean. In the Benguela upwelling system their distribution, abundance and community structure has been registered in previous studies, but no data exist on their ecology. Therefore, in this study the biodiversity of pelagic decapods has been determined and their feeding ecology has been elucidated by the use of trophic biomarker analysis.

Decapods were sampled in the northern Benguela upwelling system (17°-23°S and 10˚-12˚E) during the cruise of the FRS Africana in December 2009. Fatty acids and stable isotopes were applied as trophic biomarkers to elucidate dietary composition and trophic level.

Sergestes sp. showed to be the most common species and they all distributed along the continental rise and in oceanic waters. Total lipid content remained stable with 7-20 % of dry mass, across all species up to a body mass of 130 mg,individuals above this weight accumulated higher amounts of lipids (15-40% of DM). Eleven fatty acids contributed more than 1% of total fatty acids in almost all species, but four stood out in percentage: 16:0, 18:1(n-9), 20:5(n-3) and 22:6(n-3). *Stylopandalus* cf. *richardi, Gennadas sp.,* unidentified caridean sp3 and sp4 did not contained any fatty alcohol, while *Acanthephyra.* cf. *pelagica* and *Sergia* cf. *splendens* presented the higher percentages of wax ester in total lipid content. All species presented values higher than 1 for both fatty acid biomarker ratios, for the ratio 18:1(n-9)/18:1(n-7) *Gennadas sp.* showed the highest value and for PUFA/SFA unidentified sp4. Values for stable carbon isotope ratios ranged from -18.2 to -15.2 ‰ and for stable nitrogen isotope ratios ranged from 6.1 ‰ to 8.8‰.

All decapods in the Benguela upwelling system presented a carnivory trophic level, according to the fatty acid carnivory indices and delta ^{15}N values, with differences in the degree of carnivory. They showed a difference in the dietary composition, hence their fatty acid and alcohol composition was different between species. Some species utilized wax ester as lipid storage, which may be an adaptation to successfully cope with long periods of food shortage or highly unpredictable food supply. Ontogenetic changes were identified with regard to lipid accumulation. Decapods showed an increase in lipid content in relation to a higher body mass and an increase in their trophic level according to fatty acid ratio indices.

1. Introduction

Pelagic decapods play an important role in the food web of marine ecosystems, as predators for zooplankton and as prey for fishes. They have been reported as prey of oceanic tuna and flying fishes in the open ocean and of various fish species inhabiting shelf waters that support coastal commercial fisheries (Smale 1992, Karuppasamy et al. 2006). They also contribute to the vertical flux of organic matter, by transferring carbon from the surface to the deep ocean. Due to their diel vertical migration through the water column they accelerate the transfer of organic material to depth as gut contents to be either defecated (production of fast sinking fecal pellets), or assimilated into biomass, and then respired or consumed by predators at depth (Kikuchi and Omori 1985, Longhurst and Harrison 1988, Longhurst et al. 1990, Mincks et al. 2000, Karuppasamy and Menon 2005, Karuppasamy et al. 2006).

In the Benguela upwelling system 29 species of pelagic decapods occur (Macpherson 1991); their distribution in the area has been registered from the Kunene River as the northern limit (15-16˚S), down to the Cape of Good Hope in the south (Kensley 1981, Macpherson 1991, Bianchi et al. 1999, Kensley 2006). Most reports for the area are mainly taxonomic in nature: Kensley (1981) provided a brief discussion on the zoogeography of decapods in southern African waters; Macpherson (1991) presented data on the community structure of benthic and pelagic decapods off the coast of Namibia, and their distribution; Gibbons et al. (1994) recorded data on the distribution and abundance of one caridean species *Pasiphaea semispinosa*; and Kensley (2006) documented the species diversity and associations off South Africa. But no data exist on the decapods ecology, trophic level and role in the food web in this complex upwelling system.

Therefore, the aim of this study is to determine the biodiversity of pelagic decapods and elucidate by use of trophic biomarkers analysis their feeding ecology in the south-east Atlantic Ocean during austral spring of 2009.

In order to pursue these objectives, the following working hypotheses will be tested:

- Pelagic decapods occur in the northern part of the Benguela upwelling system, in offshore oceanic waters and present a species-specific distribution throughout the stations.
- Carideans and penaeideans shrimps occupy the same trophic level in the Benguela upwelling system.
- Decapods present different fatty acid and fatty alcohol composition, therefore the dietary composition between species is different.
- Within pelagic decapods, different lipid storage strategies have been developed to cope with variability in food supply. Some species accumulate wax esters, while others store triacylglycerols.
- Decapods suffer ontogenetic changes during their life: lipid content increases in relation to a higher body mass, resulting in a change of diet, so carnivory levels increases.

2. Materials and Methods

2.1 Study area

The Benguela Current upwelling system is located in the South East Atlantic Ocean along the coast of south western Africa, stretching from east of the Cape of Good Hope, in the south, northwards into Angolan waters about 15-16˚S (Fennel 1999) (Fig. 1), and encompassing the full extent of Namibia's marine environment. It is one of the four major coastal upwelling ecosystems of the world which lie at the eastern boundaries of the oceans. It is characterized by a predominately equatorward flow, high levels of Ekman-driven coastal upwelling, and a highly productive coastal ecosystem (Boyer et al. 2000, Shannon and OToole 2003). Its distinctive bathymetry, hydrography, chemistry and trophodynamics combine to make it one of the most productive ocean areas in the world, with a mean annual primary productivity of 1.25 kg of carbon per square meter per year—about six times higher than the North Sea ecosystem (Shannon and O'Toole 2003).

What makes the Benguela upwelling system so unique in the global context is that it is bounded on both northern and southern ends by warm water systems, the tropical warm Angola Current in the north, and the Indian Ocean western boundary Agulhas Current system in the south (Shannon and Nelson 1996, Shannon and O'Toole 2003, Shillington et al. 2006) (Fig. 1).

In the region between 15-37˚S, the surface currents are generally equatorward, with vigorous coastal upwelling cells, strong and narrow equatorward shelf edge jets (near Cape Town which is situated at 34˚S, 18˚E and off Lüderitz; 28˚S, 15˚E), and a poleward undercurrent along the shelf slope and bottom (Shillington et al. 2006).

The poleward Angola Current is a fast (40–50 cm s^{-1}), narrow and stable geostrophic flow of warm (>24 °C), saline (36.4) water that reaches 250–300 m depth and meanders laterally and vertically over both the continental shelf and slope of the Angolan coast (Lass et al. 2000); it meets the Benguela Upwelling System at the Angola-Benguela Frontal Zone (ABFZ) at ~15-17˚S (Shannon et al. 1987, Shillington et al. 2006).

The principal upwelling centre which is situated off Lüderitz in Namibia, and is the most intense found in any upwelling regime, forms a natural internal divide within the Benguela, with the domains to the north and south of it functioning rather differently (Bianchi et al. 1999, Shannon and Jarre-Teichmann 1999, Boyer et al. 2000, Shillington et al. 2006) (Fig. 1).

There are also teleconnections between the Benguela and processes in the Atlantic and Indo-Pacific Oceans. The thermohaline fluxes of the Benguela Current are an important part of the South Atlantic meridional flux, balancing to some level the poleward movement of the warmer, saltier thermocline water within the Brazil Current (Garzoli and Gordon 1996).

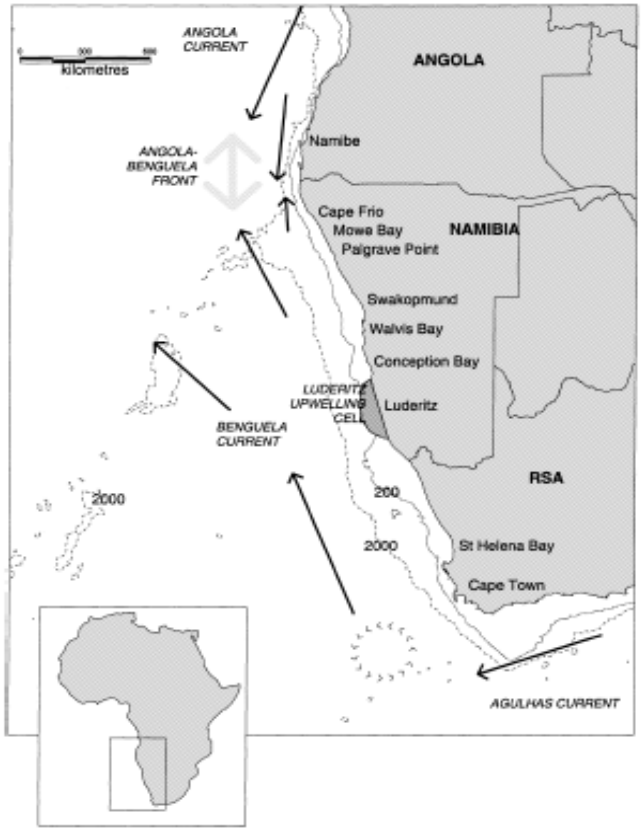

Fig 1. Map of Southwestern Africa, including main oceanographic features, bathymetry and surface circulation (Boyer et al. 2000).

Large-scale, multiyear climatic variations in the Benguela upwelling region have been observed from time to time and have been dubbed “Benguela Niños” as an analogue to the Pacific event (Shillington et al. 2006). The Benguela Niño, like its Pacific counterpart, has a strong effect on regional fisheries and this in turn has led to an effort to forecast these events. Benguela Niños have been observed or reported in 1934, 1963, 1972/3, 1984, 1995 (Shannon et al. 1987, Shillington et al. 2006).

Moreover, the southern Benguela lies at a major choke point in the “Global Climate Conveyor Belt.” Warm surface waters move from the Indo-Pacific into the Atlantic Ocean mainly in the form of rings shed from the retroflection of the Agulhas Current. The South Atlantic is the only ocean in which there is a net transport of heat towards the equator. As a consequence, not only is the Benguela at a critical location in terms of the global climate system, but it is also potentially extremely vulnerable to any future climate change or increasing variability in climate (Shannon and OToole 2003).

2.2 Sampling method

Pelagic decapods were sampled in the northern Benguela upwelling system off the coast of Namibia between 17°-23°S and 10˚-12˚E (Table 1, Fig. 2).The samples were collected during the cruise of the FRS Africana (Voyage 258) in December 2009; as part of the German Geochemistry and Ecology of the Namibian Upwelling System (GENUS) programme.

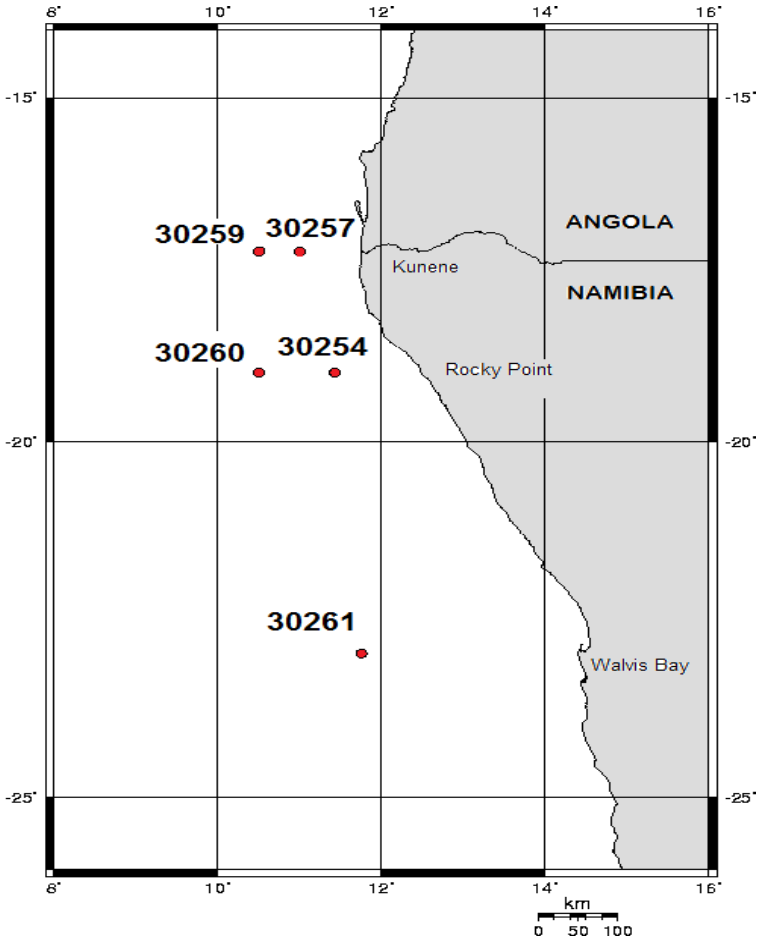

Fig. 2. Study area and position of the stations were decapods were collected in the FRS Africana cruise, December 2009.

Samples derived from stratified vertical hauls using different gears: Multinet (Hydrobios) Type Midi (0.25 m2 mouth area) with five 200 µm (vertical hauls) and 500 µm (oblique hauls) meshed nets; MOCNESS (Multiple Opening and Closing Net and Environmental Sensing System) with nine 333 µm meshed nets; and WP-2 net (300 µm, with modified, large-volume cod-end) – vertical hauls.

Table 1. Geographical position of Stations.

Station	Date	Latitude (˚S)	Longitude (˚E)	Water depth (m)
30254	09.12.2009	19˚00’	11˚26’	400
30257	10.12.2009	17˚15’	11˚00’	850
30259	10.12.2009	17˚15’	10˚30’	3000
30260	11.12.2009	19˚00’	10˚30’	3000
30261	12.12.2009	23˚00’	11˚45’	3000

Each individual was sorted out on board and individually deep-frozen at -80°C. They were transported to the Department of Marine Zoology at the University of Bremen for their subsequent analysis.

2.3 Determination of Total Lipid Content, Fatty Acids and Fatty Alcohols

The analysis of lipid composition has been applied successfully to reveal food web relationships in marine ecosystems. This trophic biomarker concept is based on observations that specific dietary lipid components, particularly fatty acids, are incorporated into the consumers’ body tissues largely unmodified (Graeve et al. 1994, Parrish et al. 2000, Stübing et al. 2003, Alfaro et al. 2006).

This approach can provide information where the classical gut content analysis fails (e.g. soft-bodied organisms, advanced digestion). Instead of a snap-shot impression, biomarkers integrate the trophic information over a longer time scale of several weeks. However, lipid signatures usually do not have the precision to identify species-specific interactions. Rather, they provide trophic information on the level of higher taxonomic groups (Stübing et al. 2003).

In this study total lipid was extracted by a method modified from Folch et al. (1957) and Bligh and Dyer (1959) and total lipid content in percent of dry mass was determined gravimetrically (Hagen 2000). Dry mass was determined after lyophilisation. Dried samples were homogenised and total lipid was extracted by organic solvent (dichloromethane/methanol 2:1 per volume) according to Folch et al. (1957) as modified by Hagen (2000) (For more details see ANNEX I).

Fatty acids were converted to methyl esters (FAME’s) by transesterification with methanol containing 3% concentrated sulphuric acid at 80˚C for 4 h. FAME and fatty alcohols were analysed in a gas chromatograph (Agilent Technologies 7890A) equipped with a KAS 4 (cold injection system) and a DB-FFAP column (30 m length, 0.25 mm inner diameter, 0.25 µm film thickness) using temperature programming (80-240°C) and helium as the carrier gas (Peters et al. 2006). Peaks were identified according to their retention times using standards of known composition for reference (For more details see ANNEX I).

2.4 Stable Isotope Analysis

Measurement of carbon ($^{13}C/^{12}C$; δ^{13} C) and nitrogen ($^{15}N/^{14}N$; δ^{15} N) stable isotope ratios has enhanced our understanding of food webs and energy flow in aquatic ecosystems (Vander Zanden and Rasmussen 2001).

In isotopic fractionation, the heavier isotopes are accumulated in the animal's body tissue, whilst the lighter isotopes are more quickly excreted (Vander Zanden and Rasmussen 1999, Bode and Alvarez-Ossorio 2004). The isotopic composition of a consumer thus reflects the isotopic composition of its prey, but it is further enriched in heavier isotopes (DeNiro and Epstein 1978, Minagawa and Wada 1984, Michener and Schell 1994). In particular, nitrogen isotope ratios become enriched at successive trophic levels, thereby allowing estimates of consumer trophic position (Vander Zanden and Rasmussen 1999, 2001). Consumers become enriched in ^{15}N relative to their food by 3-4‰ (with a mean of 3.4‰) (DeNiro and Epstein 1978, Minagawa and Wada 1984, Cabana and Rasmussen 1999).

In contrast, δ^{13} C values are more conserved "along the food chain," but vary with the source of primary production and local biogeochemical regime at the base of the food chain. Therefore, the δ^{13} C of aquatic consumers can provide information about the sources of energy to higher consumers (Vander Zanden and Rasmussen 1999).

Stable isotope ratios of carbon and nitrogen were determined by TÜV Rheinland Agroisolab GmbH (Jülich, Germany) with a mass spectrometer (Carlo Erba Instruments, EA NA1500 Series 2) using PeeDee Belemnite (PDB) limestone as a standard for carbon and atmospheric nitrogen (N_2) as a reference for nitrogen. Isotopic ratios of $\delta^{13}C$ and $\delta^{15}N$ are given in the unit ‰.

For the calculation of isotope ratios, the following formula was used:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

Where X is the element in question, ^{13}C or ^{15}N;
R is the corresponding ratio of the heavy over the light isotope, ^{13}C:^{12}C or ^{15}N:^{14}N;
and $R_{standard}$ for ^{13}C is PDB and for ^{15}N is atmospheric air (N_2).

2.5 Fatty Acid Biomarker ratios

In order to have a distinct measure for classification into feeding types, a variety of fatty-acid biomarker ratios has been proposed. Tested via feeding experiments, but mostly based on field observations, such indices have been established to allow the assignment of different species into trophic categories (Stübing and Hagen 2003).

Two fatty acid biomarker ratios were used in this study: the ratio 18:1(n-9)/18:1(n-7), which is frequently used to estimate the degree of carnivory versus herbivory (Graeve et al. 1997, Nelson et al. 2001, Stübing and Hagen 2003); and the ratio of polyunsaturated fatty acids/saturated fatty acids (PUFA/SFA), which has been proposed to be a measure of carnivory in krill, with possible extension to other crustaceans (Cripps and Atkinson 2000).

2.6 Statistical analysis

Statistical analyses were conducted with the software Prism version 5.01. All data were checked for the normality and variance homogeneity requirements for parametric analyses with the K-S normality test. Total lipid content, fatty acids and alcohols were analysed using 1way ANOVA and tukey test, to find significant differences between species.

3. Results

According to the classification of De Grave et al. (2009), all species of decapods identified in this study belong to the suborders: Dendrobranchiata and Pleocyemata.

The Caridean shrimps belong to the Infraorder Caridea, Suborder Pleocyemata. In this suborder the following species were found: *Acanthephyra* cf. *pelagica* (Risso, 1816) and *Oplophorus* cf. *novaezeelandiae* (de Man, 1931), belonging to the family Oplophoridae; *Plesionika* cf. *martia* (A. Milne Edwards, 1883) and *Stylopandalus* cf. *richardi* (Coutiere, 1905) from the family Pandalidae; and two unidentified carideans (unidentified sp1 and unidentified sp2).

The Penaeidean shrimps belong to the Infraorder Peneaeidea, in the Suborder Dendrobranchiata, where the following species were found: *Gennadas* sp. (Bates, 1881) from the Family Aristeidae; *Sergestes* cf. *armatus* (Kroyer, 1855), *Sergestes* cf. *orientalis* (Hansen, 1919), *Sergestes* sp. (Milne-Edwards, 1830), and *Sergia* cf. *splendens* (Sund, 1920) from the family Sergestidae; and two unidentified penaeideans (unidentified sp3 and unidentified sp4).

Morphological identification was made while the individuals were still frozen, to avoid the specimens to melt entirely, because they were still needed for the biochemical analysis. Therefore, the process of identifying to species level represented a challenging task and was not possible for all 13 species.

Tissue samples were extracted from all decapods for genetic species identification by DNA barcoding. Unfortunately, due to the short experimental time determined for the master program, samples could not be analysed on time to include the results in this thesis (for more details on the morphological identification see ANNEX II).

All decapods sampled during the Africana cruise 2009, occurred in five stations, having a distribution along the continental rise and in oceanic waters. There were no species found in other stations of the Africana cruise, which were located in shelf water or along the shore during the whole cruise. Both groups, Carideans and penaeideans, presented a species-specific distribution within the five stations. Unidentified sp4 was the only species found in the station 30254, the one closest to the shore of all five stations, and was the only one captured at depths between 200-330 m. *O.* cf. *novaezeelandiae*, *P.* cf. *martia,* and *S.* cf. *splendens* were found in station 30257 at depths between 0-750 m; *A.* cf. *pelagica* and *S.* cf. *armatus* in stations 30257 and 30259 and also at depths between 0-750 m; *S.* cf. *orientalis*, unidentified sp3 and unidentified sp1 in station 30259 at depths between 0-750 m; *Sergestes sp*. was found in stations 30259 and 30260 at depths between 0-750 m; *S.* cf. *richardi* and unidentified sp2 were the two species found in station 30261 at depths between 0-650m and *Gennadas* sp. was the species with the broader range occurring in all stations, except 30254. Even though there was no pattern for carideans or penaeideans shrimps, they all distributed in the northern part of the Benguela upwelling system.

Of all the species found, *Sergestes sp*. showed to be the most common in the Benguela area with 30 individuals collected of different sizes. In contrast, there were other species where only one specimen was found in all stations sampled (Table 2).

Total Lipid Content

There were big differences in the body dry mass (DM) between individuals of the different species, ranging from 4-138 mg (Table 2); but total lipid content remained stable with 7-20 % of dry mass, across all species up to a body mass of 130 mg. Individuals above this weight accumulated higher amounts of lipids, ranging from 15 up to 40 % of DM (Fig. 3).

Between both groups of decapods there were no significant differences in the total lipid content in this study. But there were significant differences ($p<0.001$) between individuals of the same species related to body mass. Individuals of *Sergestes sp*. clearly showed two separate groups, one of small size individuals and small body mass, and another one with bigger size and higher body mass individuals; and presented a growth trend with a higher accumulation of TL when increasing the body dry mass (Fig. 3).

Table 2. Dry Mass (DM), Total Lipid Content (TL) in mg and Total Lipid Content in percentage of the Dry Mass for all species, data given as mean ± Standard Deviation (SD); and number of individuals per species (n). Significant difference denoted with asterisks.

Species	DM (mg) ± SD	TL (mg) ± SD	TL % DM ± SD	(n)
Carideans				
Acanthephyra cf. *pelagica*	114.24 ± 22.03	17.86 ± 7.77	15.44 ± 4.87	3
Oplophorus cf. *novaezeelandiae*	138.03 ± 27.35	43.66 ± 19.52	30.63 ± 7.96	3
Plesionika cf. *martia*	49.65	6.93	13.96	1
Stylopandalus cf. *richardi*	110.47	11.99	10.85	1
Unidentified sp1	12.08	1.42	11.75	1
Unidentified sp2	17.52	2.98	17.01	1
Penaeideans				
Gennadas sp.	135.45 ± 38.20	25.67 ± 5.00	19.43 ± 2.82	4
Sergia cf. *splendens*	134.51 ± 32.58	26.28 ± 8.69	19.32 ± 1.78	2
Sergestes cf. *armatus*	64.13 ± 28.34	8.35 ± 4.16	12.79 ± 2.77	5
Sergestes cf. *orientalis*	34.56 ± 37.48	5.67 ± 7.31	13.19 ± 4.55	3
Sergestes sp.	47.83 ± 47.80	7.36 ± 8.80	12.47 ± 3.52	30
Unidentified sp3	3.79	0.43	11.35	1
Unidentified sp4	62.27 ± 13.11	6.91 ± 1.90	11.33 ± 3.49	8

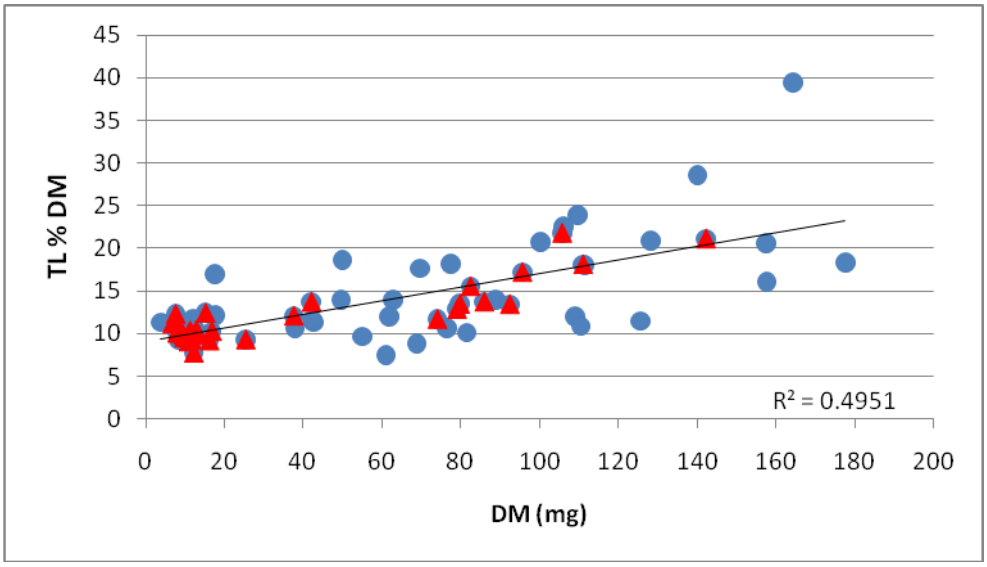

Fig. 3. Correlation between Total Lipid content % of Dry Mass and Dry mass for all decapods. In red triangles individuals of *Sergestes sp*. and in blue circles all other species. Linear trendline is shown.

Fatty Acid and Fatty Alcohol composition

Eleven fatty acids contributed more than 1% of total fatty acids in almost all species. Of this 11 there were four fatty acids, which stood out in percentage in both groups of shrimps, they comprised: long-chain polyunsaturated fatty acids (PUFA) 20:5(n-3), 22:6(n-3); monounsaturated fatty acid (MUFA) 18:1(n-9); and one shorter-chain saturated fatty acid (SFA) 16:0 (Table 3 and 4). The unidentified caridean sp2 was the exception, having the highest values among all decapods for 16:0 and 20:1(n9); very low values for 20:5(n-3), 22:6(n-3); and cero percentage for two fatty acids (Table 3). *Gennadas sp*. showed significant differences ($p<0.05$) with all other penaeideans for the MUFA 18:1(n-9) and PUFA 20:5(n-3), having the highest value of 39.03 ± 2.80 %, and the lowest of 5.76 ± 0.64 % respectively. Intraspecific variation in fatty acid composition with size was not identified for: *Sergestes sp*. There was no significant difference between the small size individuals and the big size individuals, thus there was no ontogenetic change.

Percentage of Wax ester (%WE) in total lipid content was calculated with the total percentage of fatty alcohols each species had. There was a strong difference among species, having *A.* cf. *pelagica* the highest with 36% while *S.* cf. *richardi* did not present any fatty alcohol in their tissue within the carideans. Among the penaeideans *S.* cf. *splendens* presented a high percentage of 31% and *Gennadas sp*., unidentified sp3 and unidentified sp4 did not contained any fatty alcohol (Table 3 and 4).

In the carideans that presented fatty alcohols in their body, there were no similarities observed in the percentages between species. In contrast, within penaeideans the short-chain saturated fatty alcohols

14:0 and 16:0, and the long-chain monosaturated moieties 20:1 and 22:1, dominated in percentage (Table 3 and 4).

The ratio 18:1(n-9)/18:1(n-7) ranged from 3 – 12 in the carideans, as compared with almost the same values for the penaeideans, but with the highest values by *Gennadas sp*. of 21. No clear pattern emerged with regard to the PUFA/SFA ratio between both groups of decapods, where the caridean unidentified sp2 presented the lowest value of 0.2 and the penaeidean unidentified sp4 had the highest value of 2 (Table 3 and 4).

In carideans shrimps there was a significant difference ($p<0.05$) with the ratio 18:1(n-9)/18:1(n-7) for *O*. cf. *novaezeelandiae,* which had the highest value of all species; indicating that it may show a higher degree of carnivory and even occupy a higher trophic level, in comparison with other carideans. But with the ratio PUFA/SFA, there was no significant difference for this species or any of the carideans.

Gennadas sp. was for the penaeideans the only species presenting significant difference ($p<0.05$) with the ratio 18:1(n-9)/18:1(n-7), having also the highest value among all species. In contrast unidentified sp4, with the highest value for the ratio PUFA/SFA, showed a significant difference ($p<0.01$) only with *Gennadas sp.* Also something that was not clear, since *Gennadas sp.* had the highest value for the first ratio and the lowest one for the second one.

Small individuals of *Sergestes sp*. presented significantly different ($p<0.001$) lower values (5.2 ± 0.3) for the ratio 18:1(n-9)/18:1(n-7) in comparison with the big individuals (6.2 ± 0.5) and same results for the ratio PUFA/SFA, with values of 1.7 ± 0.1 and 2 ± 0.2, for small and big individuals respectively and showed a significant difference ($p<0.01$) (data not shown in tables).

Stable Isotopes

Values for stable carbon isotope ratios ranged from -18.2 to -15.2 ‰ in *A.* cf. *pelagica* and unidentified sp3, with the lowest and highest values respectively. Stable nitrogen isotope ratios displayed values from 6.1 ‰ for *P.* cf. *martia* to 8.8‰ for *S.* cf. *splendens* (Fig. 4).

No significant differences were found between all species of carideans and all species of penaeideans in average of delta ^{15}N ratios, indicating that both group of shrimps feed on similar trophic levels; similar case occured with the average of delta ^{13}C ratios for all carideans. *Gennadas sp.* with the lowest delta ^{13}C ratio within the penaeideans, was significantly different ($p<0.05$) with *Sergestes* cf. *armatus*, species with the highest value; indicating that the carbon source might be different between both species.

For *Sergestes sp*. values of small and big size species were plotted for comparison (Fig. 4). There was a significant difference ($p<0.001$) in both isotopic ratios for *Sergestes sp*. Indicating that even though there are no ontogenetic changes in the dietary composition, there are in the trophic level for this penaeidean species.

Table 3. Caridean shrimps: Fatty acid content in percentage of total fatty acids, fatty alcohol content in percentage of total fatty alcohols, wax ester content in percentage of total lipid (WE%), fatty acid ratios used as carnivory indices, and number of individuals analysed per species; data presented as mean ± Standard Deviation (SD).

Carideans						
Fatty acids	***Acanthephyra* cf. *pelagica***	***Oplophorus* cf. *novaezeelandiae***	***Plesionika* cf. *martia***	***Stylopandalus* cf. *richardi***	**Unidentified sp1**	**Unidentified sp2**
14:0	0.90 ± 0.30	2.23 ± 0.62	3.60	2.39	1.56	3.64
16:0	11.26 ± 0.28	17.13 ± 2.82	20.17	17.99	15.74	37.06
18:0	2.03 ± 0.07	2.66 ± 0.49	6.40	4.04	2.87	4.8
16:1(n-7)	3.86 ± 0.21	4.54 ± 0.43	7.54	2.47	2.01	1.64
18:1(n-7)	4.61 ± 0.22	2.79 ± 0.45	5.15	3.28	3.74	3.32
18:1(n-9)	26.47 ± 6.71	32.44 ± 1.93	16.50	17.96	32.57	16.74
18:2(n-6)	1.03 ± 0.15	1.08 ± 0.10	0.64	1.57	1.18	0
20:1(n-9)	7.13 ± 1.09	2.99 ± 0.09	2.68	1.9	1.33	15.91
20:4(n-6)	1.29 ± 0.13	1.23 ± 0.12	0.75	2.38	0.82	0
20:5(n-3)	11.51 ± 1.02	10.79 ± 1.28	12.46	12.58	12.11	0.97
22:6(n-3)	10.33 ± 1.79	11.03 ± 1.59	11.00	22.09	14.21	4.7
Fatty alcohols						
14:0A	0	6.81 ± 2.28	11.11	0	9.65	0
16:0A	10.39 ± 9.23	0.84 ± 1.45	10.87	0	5.4	92.59
16:1A	1.71 ± 1.28	0	0	0	3.19	0
18:0A	2.26 ± 0.93	0	0	0	11.98	4.75
18:1(n-7)A	3.79 ± 4.53	0	0	0	7.10	2.67
18:1(n-9)A	3.75 ± 3.69	1.58 ± 2.73	3.09	0	52.73	0
20:1A	17.63 ± 5.59	21.16 ± 3.62	13.85	0	3.15	0
22:1A	60.48 ± 8.27	69.61 ± 7.19	61.08	0	6.81	0
WE %	35.60	7.60	6.24	0	9.42	11.98
Ratios						
18:1(n-9)/18:1(n-7)	5.73 ± 1.29	11.87 ± 2.41	3.20	5.48	8.71	5.04
PUFA/SFA	2.18 ± 0.19	1.32 ± 0.41	0.96	1.62	1.51	0.17
(n)	3	3	1	1	1	1

Table 4. Penaeideans shrimps: Fatty acid content in percentage of total fatty acids, fatty alcohol content in percentage of total fatty alcohols, wax ester content in percentage of total lipid (WE%); data presented as mean ± Standard Deviation (SD).

Penaeideans							
Fatty acids	***Gennadas sp.***	***Sergia* cf. *splendens***	***Sergestes* cf. *armatus***	***Sergestes* cf. *orientalis***	***Sergestes sp.***	**Unidentified sp3**	**Unidentified sp4**
14:0	1.28 ± 0.34	2.23 ± 0.03	1.69 ± 0.70	1.40 ± 0.90	1.43 ± 0.67	1.45	1.28 ± 0.61
16:0	17.69 ± 1.60	13.69 ± 0.40	19.31 ± 1.01	18.87 ± 1.19	18.15 ± 1.82	21.85	12.02 ± 7.44
18:0	3.25 ± 0.74	2.24 ± 0.42	2.95 ± 1.08	3.84 ± 1.26	4.17 ± 0.94	4.99	5.03 ± 0.65
16:1(n-7)	3.01 ± 0.59	9.87 ± 0.71	5.34 ± 1.15	4.49 ± 1.75	4.83 ± 2.09	4.00	3.72 ± 0.72
18:1(n-7)	1.93 ± 0.27	3.59 ± 0.09	2.84 ± 0.27	3.01 ± 0.16	2.90 ± 0.23	2.93	4.28 ± 0.40
18:1(n-9)	39.03 ± 2.80	24.27 ± 0.78	15.86 ± 2.93	16.09 ± 2.72	15.47 ± 2.78	9.81	20.37 ± 1.93
18:2(n-6)	0.65 ± 0.17	1.35 ± 0.11	1.47 ± 0.11	1.46 ± 0.14	1.55 ± 0.13	1.47	1.14 ± 0.14
20:1(n-9)	6.96 ± 0.84	3.53 ± 0.11	2.91 ± 0.76	2.95 ± 0.92	2.20 ± 0.31	1.40	2.90 ± 0.59
20:4(n-6)	0.81 ± 0.14	1.05 ± 0.15	1.31 ± 0.28	1.37 ± 0.68	1.61 ± 0.48	1.50	1.34 ± 0.31
20:5(n-3)	5.76 ± 0.64	10.53 ± 0.23	12.67 ± 1.65	14.82 ± 1.58	15.49 ± 1.68	17.79	16.36 ± 1.66
22:6(n-3)	10.13 ± 0.61	12.43 ± 0.64	14.70 ± 1.75	16.51 ± 4.31	17.77 ± 3.89	21.88	13.87 ± 1.36
Fatty alcohols							
14:0A	0	1.29 ± 0.04	42.34 ± 42.02	11.90 ± 11.99	19.50 ± 13.14	0	0
16:0A	0	63.28 ± 0.08	29.23 ± 25.12	58.96 ± 7.53	65.26 ± 9.25	0	0
16:1A	0	1.78 ± 0.81	0.22 ± 0.49	0.43 ± 0.75	1.55 ± 3.33	0	0
18:0A	0	5.62 ± 0.48	3.44 ± 4.16	2.86 ± 2.48	2.49 ± 2.92	0	0
18:1(n-7)A	0	1.85 ± 0.27	0.24 ± 0.53	0.61 ± 1.05	0.70 ± 0.95	0	0
18:1(n-9)A	0	3.13 ± 1.43	2.78 ± 3.31	4.93 ± 3.16	2.51 ± 3.16	0	0
20:1A	0	9.64 ± 0.38	4.92 ± 5.09	8.01 ± 8.58	2.85 ± 3.69	0	0
22:1A	0	13.42 ± 2.54	16.84 ± 16.83	12.30 ± 11.32	5.13 ± 6.43	0	0
WE %	0	31.11	8.11	10.77	8.44	0	0

Continuation Table 4. fatty acid ratios used as carnivory indices, and number of individuals analysed per species; data presented as mean ± Standard Deviation (SD).

	Gennadas sp.	*Sergia* cf. *splendens*	*Sergestes* cf. *armatus*	*Sergestes* cf. *orientalis*	*Sergestes sp.*	Unidentified sp3	Unidentified sp4
Ratios							
18:1(n-9)/18:1(n-7)	20.60 ± 3.92	6.77 ± 0.05	5.59 ± 0.86	5.33 ± 0.83	5.34 ± 0.81	3.35	4.78 ± 0.45
PUFA/SFA	0.88 ± 0.05	1.66 ± 0.04	1.34 ± 0.10	1.47 ± 0.02	1.60 ± 0.19	1.52	2.40 ± 1.53
(n)	4	2	5	3	30	1	8

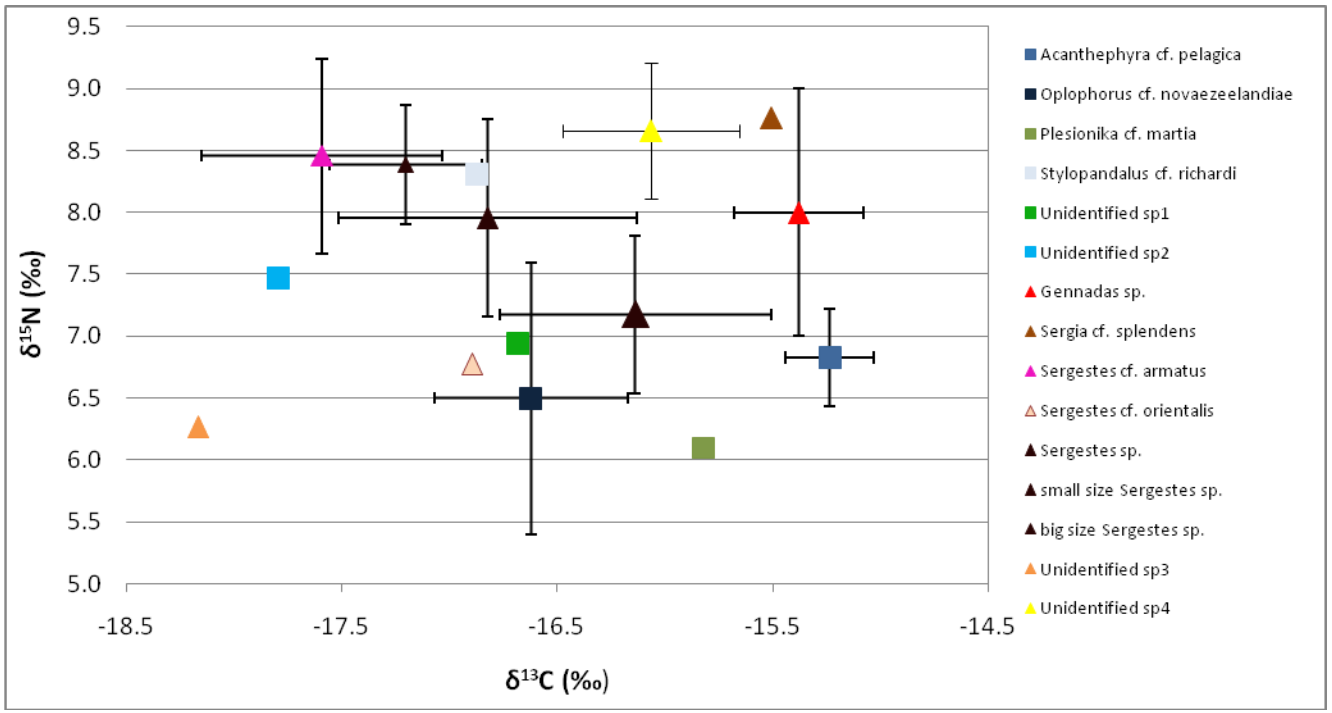

Fig. 4. Relationships between stable nitrogen (δ15N) and stable carbon (δ13C) isotopic signatures of decapod species; data shown as single values or mean values ± standard deviation (squares represent carideans and triangles penaeideans).

4. Discussion

In this study the decapods distribution was confined to the northern part of the Benguella upwelling system and they occurred only in 5 stations located above the continental rise and in oceanic waters. In contrast to Macpherson (1991), who found two distributions of pelagic decapods off Namibia: one inshore association, next to the coast; and one offshore association, with more than 70 miles off the coast. Also in the previous study the stations were located only off the coasts of Namibia from 12˚ to 14˚E, and in the present study the stations were from 10˚ to 12˚E.

Even though the information is limited, due to the low number of stations and possible sampling limitations, it can be implied that the penaeidean *Gennadas sp*. has the widest distribution in the Benguela upwelling system. Similar to Kensley (2006), with the species *Gennadas scutatus* and *Gennadas brevirostris,* that distributed throughout the whole Benguela system.

The proposed hypothesis on regional distribution can be accepted, since pelagic decapods occurred only in the northern part of the Benguela upwelling system, and they were found in offshore oceanic waters. There was also a species-specific distribution contrary to what is known in the literature, where pelagic decapods have been found from Cape of Good Hope in the south, up to the Kunene River in the north.

High delta ^{15}N ratios and high values of carnivory index ratio 18:1(n-9)/18:1(n-7) for most species of caridean and penaeidean suggest that pelagic decapods in the Benguela upwelling system are carnivorous. Moreover published data on gut content of closely related species from other parts of the world ocean also support this interpretation (Bottino et al. 1980, Clarke and Holmes 1986, Graeve 1997, Bragagnolo and Rodriguez-Amaya 2001).

In the west coast of India, *Oplophorus typus* mainly fed on detritus, crustacean remains, chaetognaths, and shrimps remains (Karuppasamy and Menon 2004); also in the north east Atlantic, it was reported that *A. pelagica* fed on mysids, euphausiids, chaetognaths, copepods and other crustaceans (Roe 1984).

Similar diet composition has been reported for penaeidean shrimps, in the Gulf of Mexico. *Gennadas sp*. was characterized as a carnivorous species, containing in the guts food items that ranged from small tintinnids and gastropods (<0.5 mm) to copepods (1-2 mm) and larger prey such as euphausiids and chaetognath (Hefferman and Hopkins 1981); similar results were found for *Gennadas elegans* in the north east Atlantic (Roe 1984) and for eleven sergestid species (between them *Sergestes armatus* and *Sergia splendens*), from the Gulf of Mexico, characterized as zooplanktivores, with crustaceans as the predominant food (Flock and Hopkins 1992). Also from the Arabian Sea results of gut content showed: detritus; crustacean remains, mainly from copepods; fish eggs, scales, and bones; and occasional radiolarians, for the species *Gennadas sordicus*. *Sergia filictum* and *Sergia creber* appeared to feed heavily on crustaceans, although euphausiids and other shrimp were more prevalent in the gut than copepods (Mincks et al. 2000).

High levels of the calanid copepod marker 20:1(n-9) were reported for various species of the genus *Penaeus* in the Gulf of Mexico, similar to the unidentified caridean sp2 suggesting that calanid copepods are an important food item for this decapod also in the Benguela System.

Base on these results, the hypotheses on trophic level and dietary composition can be accepted. All decapods occupy the same trophic level, as shown by stable isotopes biomarkers and carnivory index ratio, in the Benguela upwelling system and they present a different dietary composition, since the fatty acid percentages and the fatty alcohol composition varied between species.

The high wax ester content of *Acanthephyra* cf. *pelagica* resembles to what was found for the same species in the Southern Ocean, which uses primarily wax ester for its long term energy storage (Clark and Holmes 1986); so in the event of food scarcity, they utilise these wax ester stores (Lee et al. 2006). Similarly the penaeidean *S.* cf. *splendens* presented high values of WE. Wax ester storage is a sophisticated way of efficiently exploiting pulses of intense food availability, and it has been proposed that WE are more slowly catabolised than triacylglycerols (Sargent 1978). This means that these species are better adapted to the short and often unpredictable events of high production at the northern limit of the upwelling region. Other species with this behaviour have been found in Polar Regions with a strongly seasonal production regime, like the caridean *Pandalus borealis*, and in bathyal zones, like the penaeidean *Aristeus antennatus* (Cartes and Sarda 1989). The other decapods with low values of WE, probably use triacylglycerol as energy reserve.

The suggested hypothesis on the different lipid storage strategies within pelagic decapods can be accepted. There two groups of decapods with clearly two strategies: one group stored wax esters and the other stored triacylglyceros.

During growth *Sergestes sp*. accumulates increasing amounts of lipid. Interestingly, at the same time delta ^{15}N ratios decreased indicating an ontogentic change in dietary composition with larger specimens occupying a lower trophic level. This is not supported by the fatty acid carnivory indexes, which showed higher values for big individuals.

Several studies on the diet of decapods highlight ontogenetic changes as one of the most important biotic factor in the diet variability. For example, in the central and eastern Mediterranean Sea, comparison of the diet composition, dietary diversity and feeding activity between the small and large individuals revealed that *Parapenaeus longirostris* undergoes changes in its feeding habits with ontogeny. Larger specimens are more efficient predator than smaller ones because of their greater swimming ability. It was found however, that almost the same prey occurred in the stomachs of small and large specimens, but in different proportions (Kapiris 2004). Also Burukovsy (1969) in samples from the Gulf of Cadiz and off the northwest African coast indicate different diets according to age.

Even though the results for delta ^{15}N ratios regarding trophic level, contradicts the results on fatty acid biomarker ratios, the hypothesis on ontogenetic changes can be accepted, since decapods showed an increase in lipid content in relation to a higher body mass, which resulted in a change of diet, and according to values on the biomarker ratios, carnivory levels also increase.

5. Conclusions

Based on the data in this study, decapods occurred offshore in oceanic waters and in the northern part of the Benguela upwelling system. But published data showed that pelagic decapods occurred in the whole area of the Benguela system, from Cape of Good Hope in the south, northwards into Angolan waters (Macpherson 1991, Bianchi et al. 1999, Kensley 2006). Other authors like Macpherson (1991) described a clear zonation in the area, one with species next to the coast or inshore and another zone offshore, being the latter the community with larger number of pelagic decapods.

All decapods in the Benguela upwelling system were carnivores, according to the fatty acid carnivory indices and delta ^{15}N values. But there were differences in the degree of carnivory based on both approaches. Some species presented higher values of carnivory index than others and some showed higher values of delta ^{15}N. Between both approaches the degree of carnivory was assigned differently.

They also presented a difference in the dietary composition, since their fatty acid and alcohol composition was different. Most species presented high levels of the fatty acid 18:1(n-9), which is a biomarker indicating a carnivore diet. Some species with high levels of 20:1(n-9) may feed on calanid copepods, e.g. *Calanoides carinatus*, because *C. carinatus* produces high levels of this MUFA. Or species with high levels of 22:6(n-3) rely more on a dinoflagellate-based food chain, since this PUFA is found in dinoflagellate.

Decapods have developed different lipid storage strategies. It was found that some species utilized wax ester as lipid storage, which may be an adaptation to successfully cope with long periods of food shortage or highly unpredictable food supply. Species that presented low wax ester percentage of total lipid content used triacylglycerol as energy reserve.

Ontogenetic changes were identified with regard to lipid accumulation. Decapods showed an increase in lipid content in relation to a higher body mass. And they also increased in their trophic level according to fatty acid ratio indices.

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Materials and Methods

Determination of Total Lipids

The total lipid content is the fraction of lipid that can be extracted from entire specimens or tissues, expressed as percent of wet mass (WM) or dry mass (DM). The extraction of total lipids is based on the rapid and efficient methods of Folch et al. (1957) and Bligh and Dyer (1959), which have been modified in various details depending on the respective requirements. The total lipid content can be obtained by different methods; in this case gravimetric determinations, modified after Hagen (2000) were used.

The samples kept frozen at -80 °C. were lyophilised for about 48 h in a freeze-dryer (Christ®, Alpha 1-4 LD plus). They were left for 30 min in evacuated desiccators and then dry mass of each sample was determined, as well as the weight of the lipid glasses and reference glasses, on a micro-balance (Sartorius R200D, precision ± 10 µg). Reference glasses were weighed emptied before and after the lipid has been extracted to overcome the influence of temperature and air pressure on the weight, so a correction on the values of the dry mass could be made. The readings were taken constant in each case after 30 seconds, due to settling time on the scale of 15 seconds (Hagen 1988).

To determine the total lipid content, the samples were transferred to homogenizer vials (Potter S, B. Braun Biotech International) and 4 ml of dichloromethane and methanol solution 2:1 per volume (DCM/MeOH) were added. They were homogenised first for 2 minutes under 1200 rpm on ice and then were sonicated for 30 seconds under an ultrasonic homogeniser (Bandelin UW2070). The supernatant was poured into a test tube and, the homogenisation step was repeated but this time the samples were homogenised for 90 sec. The supernant was added to the first one in the test tube and was stored on ice.

For the extraction, 2 ml 0.88% KCl were added to the supernatant extract and it was shaken well for about 30 sec, and centrifuged for 10 min with 1495 g at 2 °C (Sigma 6K15), so that the aqueous phase settled on top of the organic phase. The aqueous phase was removed with a short pipette and discarded, while the organic phase with all extracted lipids was removed carefully with a long pipette and transferred into the previous weighted lipid glasses. The solvent was evaporated with Nitrogen and the lipid glasses were transferred into evacuated desiccators and kept for 30 min drying and then weighted again. The total lipid content was obtained after deducting the weight of the lipid glasses and a correction based on the before and after weighted reference glasses. The lipids were dissolved again in 1 ml of DCM/MeOH (2:1 per volume), the air in the glasses was replaced by nitrogen to prevent oxidation processes and samples were stored at -80 °C (Folch et al. 1957, Hagen 1988).

Determination of Fatty Acids and Fatty alcohols

The total lipid extract was analysed in greater detail by gas-liquid chromatography (GC), which determines the quantitative fatty acid and fatty alcohol compositions of the lipids.

Subsamples were taken from the frozen samples and dried under nitrogen. The lipids were hydrolysed and the fatty acids were converted to their methyl ester derivatives (FAME) and fatty alcohols by adding 1 ml of 3% sulphuric acid in methanol and 0.25 ml of hexane and heating them for 4 h at 80 °C. After cooling, 4 ml of Aqua bidest. plus 1.5 ml of hexane were added; they were shaken vigorously for 30 sec and centrifuged for 10 min at 1495 g. The lipid phase remained on the top and was transferred to a vial and put under nitrogen to evaporate the solvent; this procedure was repeated twice. Hexane was added and the FAMEs and fatty alcohols were stored at -80 °C. after replacing the air in the vials by nitrogen (Kattner and Fricke 1986).

The extracted FAMEs and fatty alcohols were analysed in a gas chromatograph (Agilent Technologies 7890A) equipped with a KAS 4 (could injection system) and a DB-FFAP column (30 m length, 0.25 mm inner diameter, 0.25 µm film thickness) using temperature programming (80-240°C) and helium as the carrier gas (Peters et al. 2006). FAMEs and fatty alcohols were detected by flame ionization and identified by comparing retention time data with those obtained from standard mixtures (fish oil for fatty acids; copepod-standard for fatty acids and fatty alcohols).

Stable Isotope Analysis

For the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope analysis different species of decapods were utilised. Frozen samples were lyophilised for about 48 h in a freeze-dryer (Christ®, Alpha 1-4 LD plus) and then transferred for 30 more min into evacuated desiccators. Only the telson and/or part of the uropods were transferred into little tin capsules. The final weight of each sample had to be between 1 mg and 8 mg in order to be properly analysed.

Stable isotope ratios of carbon and nitrogen were determined by TÜV Rheinland Agroisolab GmbH (Jülich, Germany) with a mass spectrometer (Carlo Erba Instruments, EA NA1500 Series 2) using PeeDee Belemnite (PDB) limestone as a standard for carbon and atmospheric nitrogen (N_2) as a reference for nitrogen. Isotopic ratios of $\delta^{13}C$ and $\delta^{15}N$ are given in the unit ‰.

Classification of decapods (resume of annotations, special characteristics and pictures)

Caridean shrimps (Suborder Pleocyemata, Infraorder Caridea):

Acanthephyra* cf. *pelagica (Photos 1,2 and 3)

Colour is strong red; has a long rostrum with dorsal and ventral spines; there are 2 post-rostrum spines; it has a tooth on posterior margin on the 3rd, 4th, 5th and 6th abdominal somite, the one on the 3rd somite very pronounced; size: 64mm.

The difference between *A. quadrispinosa* and *A. pelagica* is that the first have only 4 pairs of lateral spines in the telson, and the latter hast between 7-11 lateral telsonic spines. In this specimen, the telson seems to have more than 4 pairs of spines, but they were broken.

Photo 1. Whole individual

Photo 2. Zoom on the carapace and rostrum

Photo 3. Zoom on the telsonic spines

Oplophorus* cf. *novaezeelandiae (Photos 4 and 5)

Colour is reddish with white stripes; has very big spines in the dorsal margin on the 3rd, 4th and 5th abdominal somites; presents a short rostrum (probably around 5 spines, which were broken); telson with 3-4 pairs of lateral spines; outer margin of scaphocerite smooth, no barb on inner margin; size: 35 mm.

Photo 4. Whole individual

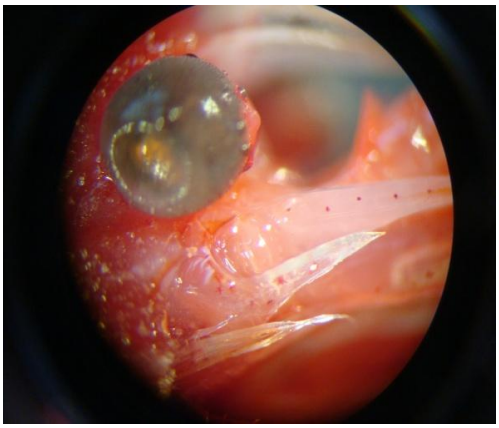

Photo 5. Zoom on the scaphocerite

Plesionika* cf. *martia (Photos 6 and 7)

Colour is orange; rostrum is very long, but less than twice length of carapace and has 7 visible dorsal teeth only on the base (others along the rostrum might have been broken); dorsal ridge extends from rostrum until the whole carapace; telson has two apical spines at the end; size: 29 mm.

Photo 6. Whole individual

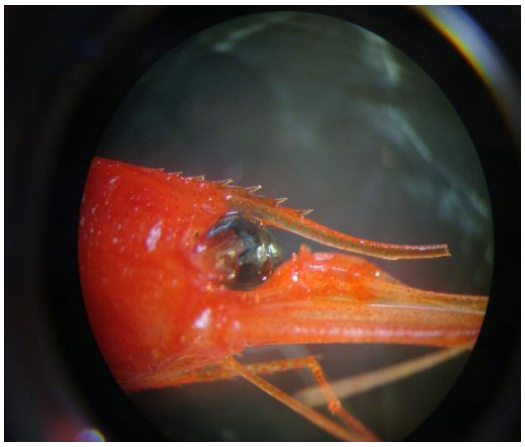

Photo 7. Zoom on the rostrum

Stylopandalus* cf. *richardi (Photos 8 and 9)

Colour is red on the head and dorsal part of the body until the 3rd abdominal somite, then becomes white; has a very long rostrum with 2 post-spines and continues with spines dorsally and ventrally (probably broken); 5th, 4th, 3rd and 2nd pereopods are white; 1st pereopod and 3rd maxilliped are orange; size: 39 mm.

Photo 8. Whole individual

Photo 9. Zoom on the rostrum

Unidentified sp1 (Photos 10, 11 and 12)

Colour is red on the carapace but rest of the body is white with red/orange spots; has very long rostrum, probably with 10 spines (broken) dorsally and ventrally; the 3rd abdominal somite with a marginally dorsal spine (probably big spine but broken), 4th abdominal somite has the same; telson with 5 lateral pairs of lateral spines; 2 first pereiopods chelates; size: 19 mm.

Photo 10. Whole individual

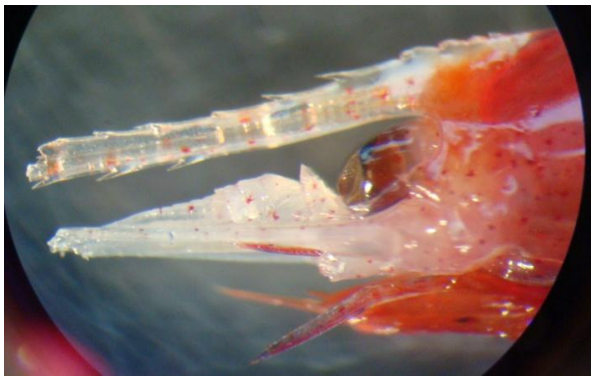

Photo 11. Zoom on the rostrum

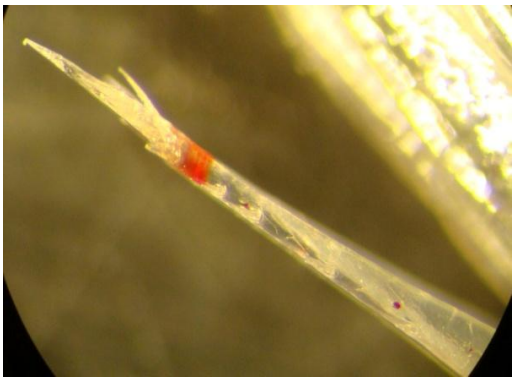

Photo 12. Zoom on the telson

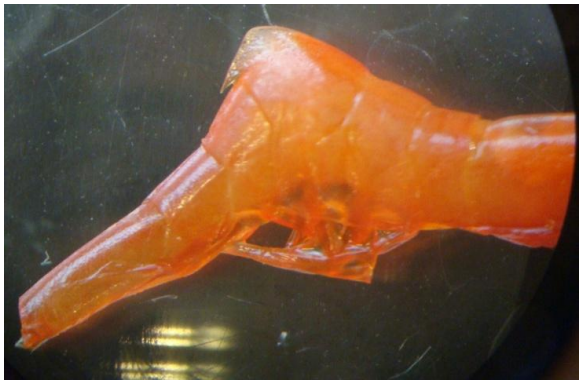

Photo 13. Zoom on the dorsal hump (3rd abd. Somite)

Unidentified sp2 (Photos 13, 14 and 15)

Colour is orange; has a long rostrum with dorsal and ventral spines (around 10) and ventral spines (around 5); presents a characteristic hump ending on a big spine on the 3rd abdominal somite; the 4th, 5th, and 6th abdominal somite end in a small spine; the telson has 6 pairs of lateral spines; size: 21 mm.

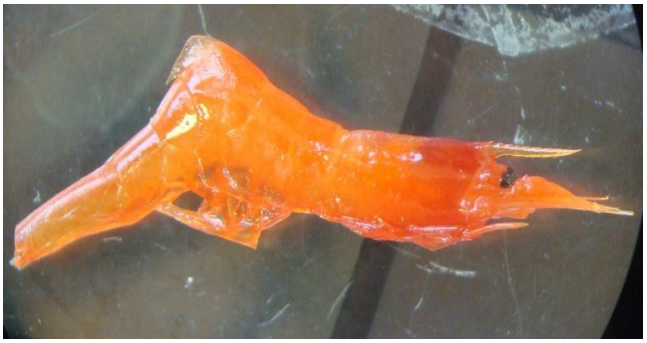

Photo 14. Whole individual

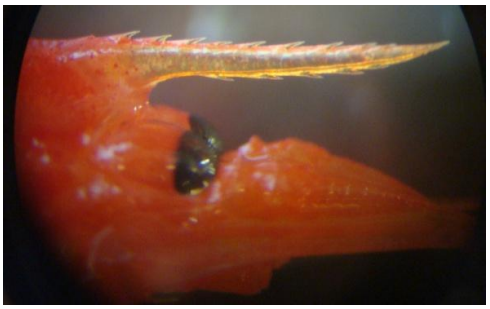

Photo 15. Zoom on the rostrum

Penaeidean shrimps (Suborder Dendrobranchiata, Infraorder Peneaeidea):

Gennadas sp. (Photos 16 and 17)

Colour is dark red with black spots between the pleuropods; does not have a rostrum but a single dorsal tooth with lots of bristles (hairs); the carapace looks like an armour with cervical and postcervical sulci reaching the midline; has very long rounded antennal flagellum; telson has 1 spine or appendage at the end; size: 42 mm.

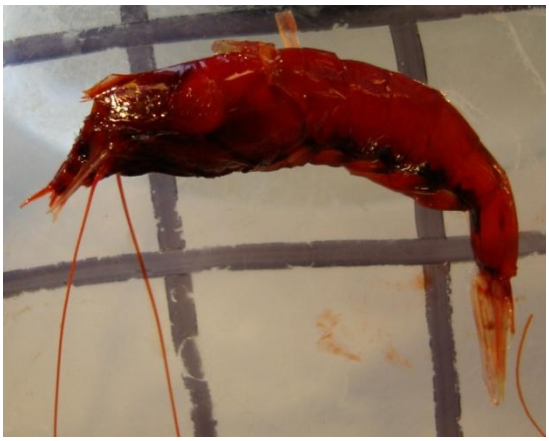

Photo 16. Whole individual

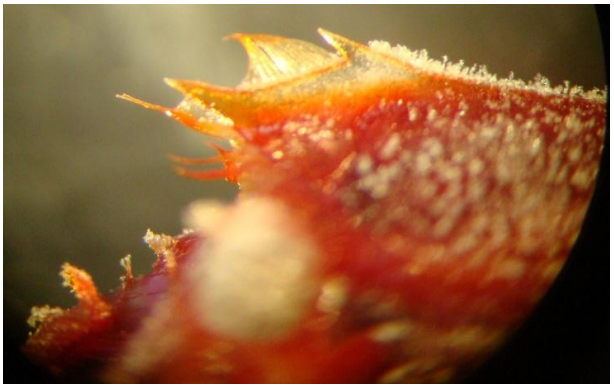

Photo 17. Zoom on the dorsal tooth

Sergia cf. ***splendens*** (Photos 18 and 19)

Colour is orange/red; does not have a proper rostrum but just one tooth, not broadly rounded, but with hint of ventral denticle; 4th and 5th pereiopods smaller than first 3 and with a paddle shape; 5th abdominal somite with a little spine; telson with 4 pairs of lateral spines; size: 42 mm.

Photo 18. Whole individual

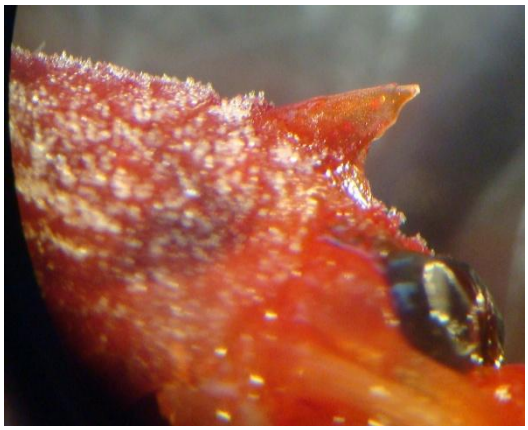

Photo 19. Zoom on the dorsal tooth

Sergestes sp. (Photos 20 and 21)

Colour is orange; with a tooth and not a rostrum; the 3rd maxillipeds are longer than the 3rd pereiopods; 4th and 5th pereiopods have a paddle shape and are smaller than first 3 pairs; size: 55 mm.

Photo 20. Whole individual

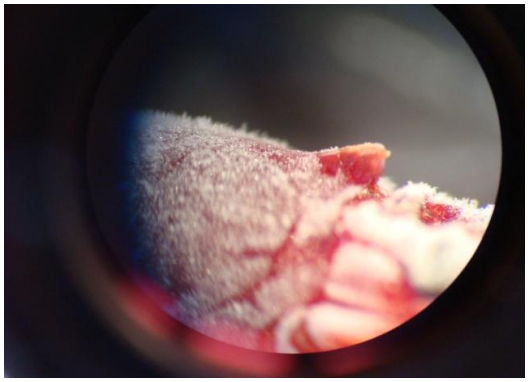

Photo 21. Zoom on the dorsal tooth

Sergestes* cf. *armatus (Photos 22, 23 and 24)

Colour is from the head until the 3rd abdominal somite with red and orange dots, the rest of the body is white/translucid; 4th and 5th pereiopods are smaller than 3 first; not real rostrum but just a dorsal tooth; 6th abdominal somite with a little dorsal ending spine; 3rd maxillipeds very well developed; dactylus and distal half of propodus of 3rd maxilliped armed with spines but not forming comb-like structure and consisting of 4 segments; size: 34 mm.

Photo 22. Whole individual

Photo 23. Zoom on carapace

Photo 24. Zoom on the dactylus of 3rd maxilliped

Sergestes* cf. *orientalis (Photos 25 and 26)

Colour is orange in carapace but white the rest of the body; has no real rostrum but a dorsal tooth (broken); 3rd maxillipeds very well developed; dactylus and distal half of propodus of 3rd maxilliped armed with spines but not forming comb-like structure and consisting of 6 segments; size: 40 mm.

Photo 25. Whole individual

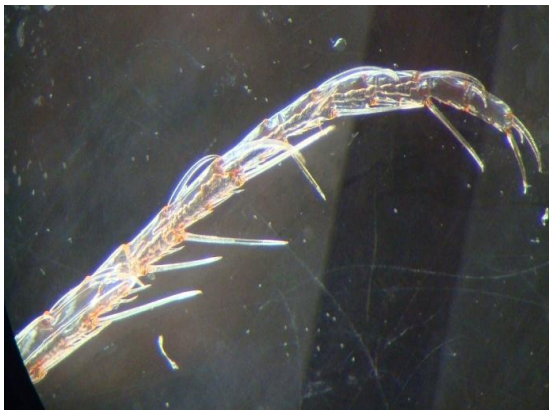

Photo 26. Zoom on the dactylus of 3rd maxilliped

Unidentified sp3 (Photos 27 and 28)

Colour is orange in carapace but white the rest of the body; has no real rostrum but dorsal spine with a very small post-dorsal apical spine; the 4th and 5th pereiopods are smaller than first three; has dorsal spines on the 5th and 6th abdominal somites; size: 11mm.

Photo 27. Whole individual

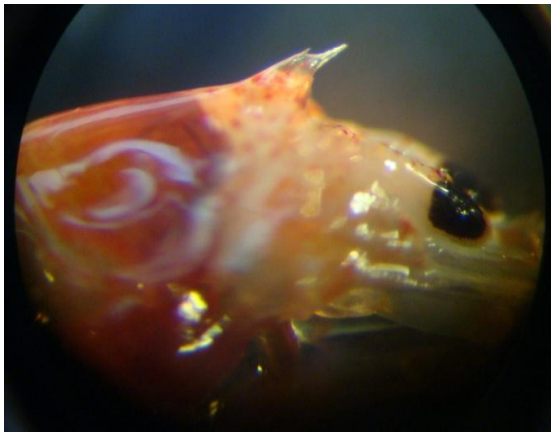

Photo 28. Zoom on the rostrum (tooth)

Unidentified sp4 (Photos 29 and 30)

Colour is white/translucid with orange dots below the pereiopods and pleopods; not real rostrum but dorsal spine; the 4th and 5th pereiopods are smaller than first three; 1st and 2nd pereipods with chelae; has very big antenulla flagellum; 4th and 5th abdominal somites with dorsal marginal spines; telson ends in a spine; size: 53 mm.

Photo 29. Whole individual

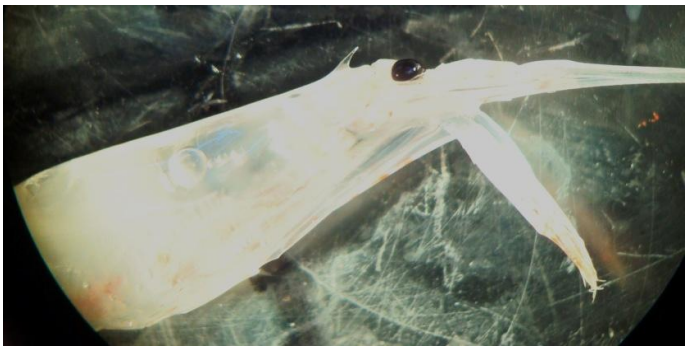

Photo 30. Zoom on the dorsal tooth (spine)

DECLARATION

☼ No data can be taken out of this work without prior approval of the thesis-promoter'

☼ I hereby confirm that I have independently composed this Master thesis and that no other than the indicated aid and sources have been used. This work has not been presented to any other examination board.

June 7, 2010