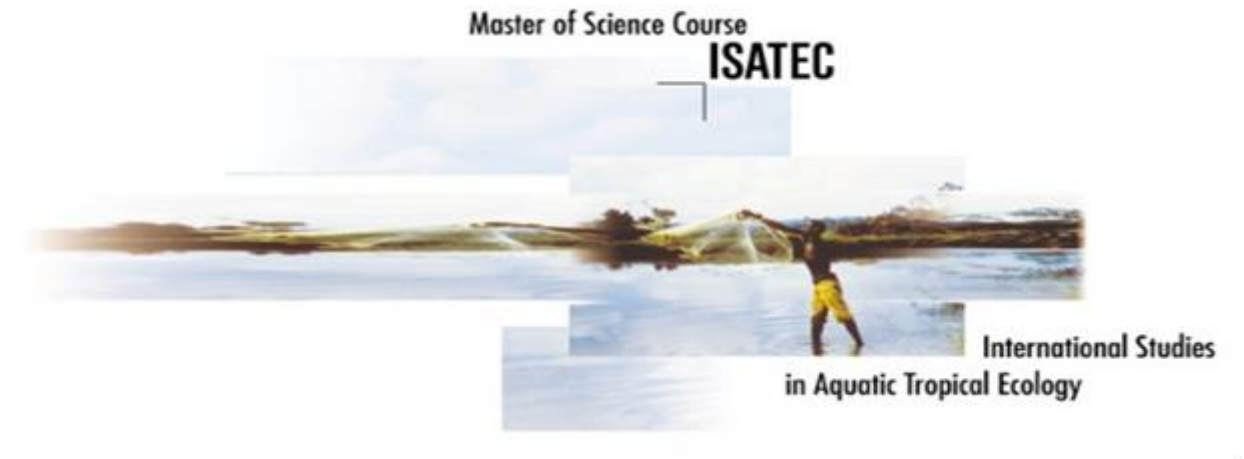

Population Dynamics of Euphausiid Species of the Benguela Current off the Namibian Coast

by

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Presented to the Faculty of Biology and Chemistry

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Statement according to

§10 (11) Allgemeiner Teil der Masterprüfungsordnungen der Universität Bremen vom 27. Oktober 2010:

I hereby declare that I have written this Master's Thesis entitled

Population Dynamics of Euphausiid Species of the Benguela Current off the Namibian Coast

on my own without any assistance from third parties. Furthermore, I confirm that no other sources and resources have been used than those indicated in the thesis itself and that all quotations are marked.

15 August 2014,L.S MLAMBO

…….

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List of Acronyms

ABF	Angola-Benguela Front
ABFZ	Angola Benguela Frontal Zone
AC	Angola Current
AWI	Alfred -Wegener - Institute for Polar and Marine Research
BC	Benguela Current
BUS	Benguela Upwelling System
DVM	Diel Vertical Migration
NBUS	Northern Benguela Upwelling System
GENUS	Geochemistry and Ecology of the Namibian Upwelling System
DVM	Diel Vertical Migration
ODV	Ocean Data View
KN	Kunene
MOCNESS	Multiple Opening and Closing Net and Environmental Sensing System
UNAM	University of Namibia
SDS	Sexual Maturity Stages
SI	Stable Isotope
TL	Trophic Level
WB	Walvis Bay

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DEDICATION

To Mainini Monie, Mai Bee & Mrs. Sue

Abstract

The abundance and population structure of euphausiids of the Northern Benguela Upwelling system were investigated during the periods of 29 August 2013 to 2 October 2013 (Upwelling season) and 27 December 2014 to 18 January 2014 (Off-peak season). A total of 16 stations were considered for this research investigation. 10 stations were selected from the Walvis Bay (23° S) and 6 Kunene (17°S) transects respectively. The abundance of euphausiids harvested by the integrative net (Net 1) of a single MOCNESS varied per Station from 6 to 188 Ind.m-2 during the Upwelling season then from 2 to 549 Ind.m-2 during the Off-peak season. Species identified and used for abundance and biomass determination were *Euphausia hanseni, Euphausia lucens, Euphausia recurva,Nematoscelis megalops* and *Nyctiphanes capensis* and their mean lengths were 19,56 ± 0,10, 14,52 ± 0,22, 11,57 ± 0,31,1,60 ± 0,26, and 13,43 ± 0,25mm respectively. The horizontal distributions patterns of these species revealed that *Nyctiphanes capensis and Euphausia lucens* are neritic species *Nematoscelis megalops* and *Euphausia hanseni* are shelf/slope related while *Euphausia recurva* is associated with oceanic waters. The euphausiid population had an overall 2:1 female to male ratio. Significant differences were found in krill abundances showing that Off-peak season had more of krill densities than the Upwelling. This contradicted the theoretical expectation that Upwelling is more productive than Off-peak seasons. Kunene transect showed a more abundance of krill than the WB probably due to intrusion of warm Angola Benguela waters. Species population structures did not show pronounced differences in terms of length frequency distributions. Trophic level differences were noted amongst species under study with *E. lucens* showing the highest trophic level and *E. recurva* showing the lowest tropic levels. This was expected as there were dietary regime shifts at two transects in two seasons. The comparison of values of the species between seasons and regions show considerable shifts both in ^{15}N – position as well as ^{13}C as a consequence, food preference (carnivory/herbivory) as well as the carbon-source changes

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1. NTRODUCTION

Euphausiids (krill) are holoplanktonic crustaceans, exclusively marine and distributed worldwide in high abundances, ranging from tropical to high latitude polar regions (Siegel 2000). They occupy the epi- and mesopelagic realms as well as the bathypelagic (Gibbons *et al*. 1999). Although euphausiids have very restricted patterns of distribution, they are frequently associated with particular water masses or environments (Dadon & Boltovskoy, 1982; Gibbons *et al*. 1995) and therefore have been useful tracers of water movement. Krill are an excellent model system for process studies of growth and maturity, for connections between theory, experiment, and observation, and for tests of evolutionary theory in the field. They are also ideal model organisms for studying the interaction between environmental and organismal variability (Mangel & Nicol 2000). Moreover their study is inherently an interdisciplinary field, crossing boundaries and using a combination of oceanography, biochemistry, physiology, evolution, and ecology to understand krill and their role in the ecosystem (Mangel & Nicol 2000).

By planktonic standards euphausiids are relatively large and they frequently dominate zooplankton communities especially over continental shelf and in regions of high environmental productivity (Boltovskoy 1999), like the Benguela Upwelling System (BUS). They are generally very successful animals which thrive even under extreme environments (Quetin & Ross 1991). They are easily recognizable and relatively mobile organisms (Pillar *et al.* 1989; Barange & Pillar 1992). Owing to their large size, high abundance and omnivorous diets, euphausiids play a vital role in functioning of ecosystems (Stuart & Pillar 1990). Their biomass, physiological plasticity and importance as a trophic link between primary production and higher trophic levels enable these animals to fill key positions in marine ecosystems (Werner *et al*. 2012). They occupy a pivotal position in the pelagic food web as they transfer the organic energy produced by unicellular algae to higher trophic levels such as pelagic fish stocks exploitable to man (Haris *et al.* 2000). Krill (especially the southern ocean krill *E. superba*) are central to pelagic marine food webs, in the sense that most organisms are either directly predators of krill or are just one trophic level removed from krill (Mangel & Nicol 2000). Many species of euphausiids display pronounced diel vertical migration (DVM) and frequently traverse distances in excess of 200m at night (Mauchline 1980). Through this, krill are capable of transferring

surface production to the sediments directly via DVM and may play and important role in the carbon flux (Noji 1991).

The quantitative food environment seems to influence the amount of time spent by euphausiids in the upper water layers which can result in asynchronous individual movement (Gibbons 1993). This determines the depth of nocturnal occupation which appears to be influenced both by the food environment and thermal stratification of water (Andersen & Nival 1991; Werner & Buchholz 2013). There is a lot of known information about euphausiids' life history (Pillar *et al*. 1989, Barange & Pillar 1992) for example that in many euphausiid species, life cycle evolution has involved adaptation to poor nutritional conditions interspersed with seasons of high productivity.

Fluctuations of euphausiids abundances and distributions are generally influenced by direct impacts of variability in the large-scale physical environment, such as changes in ocean circulation (Murphy & Reid 2001). Other factors generating variations in population structure include water temperature and chlorophyll a concentrations (Kim *et al*. 2010) which in turn result in variations in blooming of phytoplankton. In high latitude seas for example, the spring phytoplankton bloom has been documented as a key mechanism driving biological processes in marine ecosystems (Kim *et. al* 2010) with many copepod and euphausiid species known to have life cycle patterns synchronized with the spring phytoplankton bloom (Wassman *et al.* 2006; Ikeda *et al.* 2008).

1.1 The Benguela Current

The Benguela Current ecosystem is situated along the coast of south western Africa, stretching from east of the Cape of Good Hope, in the south, northwards into Angola waters and encompassing the full extent of Namibia's marine environment (Hutchings *et al*. 2009). It is one of the four major coastal eastern boundary upwelling ecosystems (EBUEs) of the world also comprising the California, Canary and the Humboldt currents (Shannon & O´Toole 2003). It is divided in two subsystems: northern Benguela ecosystem, a typical upwelling system with equator-ward winds, cool water and in contrast, the southern Benguela region is characterized by pulsed, seasonal and wind driven upwelling events at discrete centers (Hutchings *et al*. 2009).

The Benguela is an upwelling system within which biological and chemical and fluctuations are inevitable due to its seasonal upwelling and off peak seasons. Upwelling occurs when cool bottom water induced by strong south-easterly trade winds cause a strong offshore Ekman transport of surface water masses which results in a north to north-westward flow of the current along the coast (Nelson & Hutchings 1983). This boosts primary and general productivity of the whole system. Thus the magnitude of the phytoplankton bloom in turn affects the recruitment rates of the euphausiids and the subsequent growth of their young (Kim *et al*. 2010).

So far, the impacts of anthropogenic activities decreasing ocean productivity, reduced abundance of habitat-forming species, shifting species distributions, and a greater incidence of disease (Hoegh-Guldberg & Bruno 2010) has not been reported for the BUS. On the other hand, ocean warming which is generally expected to impose a negative impact on zooplankton's (krill's) role as consumers and producers according to Hünerlage *et al*. (2011) has also not been highlighted for the same system. For this cause seasonal and eventually climate mediated changes in krill abundances have to be continuously taken into account when we want to understand the dynamics of this ecosystem in a warmer future (Agersted & Nielsen 2014).

1.2 Euphausiid populations

Natural population systems seem to exhibit exponential growth and decline depending on favorability of the environment. Erratic population fluctuations may be exhibited by populations inhabiting extremely variable environments (Berryman & Kindlmann 2008) since the environment provides the system with inputs such as food and may also supply immigration into the population (Berryman & Kindlmann 2008).

In the wild, krill are able to adapt to strong seasonal and regional changes in feeding conditions (Buchholz 1991) and their populations fluctuate in response to environmental changes (Everson 2000). Among the species that dominate the euphausiid fauna of the Northern Benguela system are *Euphausia hanseni, Nematoscelis megalops* and *Nyctiphanes capensis* (Olivar & Barange 1990; Barange *et al*. 1991). These species reproduce in the Benguela more or less continuously throughout the year (Pillar & Stuart 1988; Barange & Stuart 1991) and do not depend on adult spawning habitat preference. They form one of the major prey items for commercially imported anchovy (James 1987) and are also known to be important

constituents and the diets of many other fish species of Namibia (Macpherson 1983, Macpherson & Roel 1987).

Regarding the issues of ocean warming, particularly for cold water krill, the most clear and profound influences of climate change on the world's oceans are its influences (Hoegh-Guldberg & Bruno 2010) on krill species' survival and altered marine food webs dynamics (Everson 2000). If long term climate variability is present, the question arises whether krill population dynamics will show enduring effects and how serious these effects are on the krill distributions (Everson 2000). By studying the population dynamics of krill, we could possibly find out what potential effects regional environmental changes have on stock structures and survival rates of the euphausiid species (Siegel 2000). Against this background a research on temporal and spatial abundances during upwelling and off-peak seasons would enable us to conclude on the current state of the krill populations in the NBUS.

1.3 Purpose of study

The basic physiological and behavioral properties of species and individuals making up a population are considered crucial inputs into the system as these qualities act in conjunction with the environment and govern the processes of mortality and migration which control the state of that system (Berryman & Kindlmann 2008). The study of krill can provide considerable insight into questions concerning growth and maturity. Krill show what might be considered "standard" patterns of aging, with increasing mortality rates at later ages (Mangel & Nicol 2000). Krill are also ideal model organisms for studying the interaction between environmental and organismal variability (Siegel 2000).

Krill face variation and uncertainty on a number of scales:

(i) unpredictable short-term variation

(ii) seasonal meso- and large-scale variation

(iii) interannual variability, and

(iv) regime shifts (Mangel & Nicol 2000).

The aim of the research is therefore to quantify biomass and abundances and to examine the spatial and temporal population dynamics with special consideration to

variations i) and ii), particularly to the three major NBUS euphausiid species *Euphausia hanseni, Nematoscelis megalops* and *Nyctiphanes capensis.* In general, we expect some fluctuations in abundances and patterns of krill during the upwelling and the off peak seasons due to some variations in phytoplankton biomass and distributions in the BUS. However, Barange & Stuart (1991) are of a different view and highlight that despite seasonal differences in upwelling intensities in the Benguela system krill distribution patterns remain fairly constant throughout the year. The aim of this study was to also assess differences in krill diet composition so as to determine species trophic levels and the role of krill in the coastal food web of the NBUS (Barange & Stuart 1991) by means of stable isotope analysis.

In order to understand the variability of krill population parameters which can assist in interpreting fluctuations in euphausiid populations, it is imperative to have knowledge about potential longevity of an individual as well as the age composition of populations (Siegel 2000).

Therefore the major objectives of study were to:

a) Formulate length mass relationships of species populations

Of particular importance in classifying species at both individual and population level is the knowledge of basic body components such as length, total wet mass/dry mass needed for the formulation of biomass calculations (Siegel & Nicol 2000). Length and mass form a backbone for production and energy budget determinations (Falk-Petersen & Hopkins, 1981).

b) Analyze spatial and seasonal variability in krill abundance/biomass

A population system consists of a number of interacting individuals and species which coexists in certain geographic boundaries (Berryman & Kindlmann 2008). For the sake of this study, the Walvis Bay transact located along the 23°S and the Kunene transect located on the 17° S longitudinal lines were the predetermined upwelling geographical limits. The Walvis Bay line is mainly influenced by waters originating from e.g. Agulhas current in South Africa while the Kunene lies around the Angola Benguela Front (Barange *et al*.1992) which is influenced by the Angola Current (AC).

Conferring to Agersted & Nielsen (2014), species distribution seems to depend on temperature and bathymetry (Einarsson, 1945; Mauchline & Fisher, 1969). Walvis Bay shows a broader shelf while Kunene shows a narrower shelf. These bathymetric differences may have further influence on food availability, thermal stratification and other factors influencing krill abundances, vertical migration and patchiness at the two transects.

c) Analyze length frequency distributions for each species

Age is a significant variable for krill populations because older individuals are larger and size differences affect maturity and fecundity (Siegel 2000). Therefore, since the age of krill is hard to measure directly, total body length has generally been used as the basic indicator of age (Nicol 2000). Once we obtain estimates of age and abundance, we can investigate primary demographic parameters such productivity (Siegel 2000).

d) Analyze euphausiids species stable isotopes (^{13}C & ^{15}N) in order to calculate krill trophic position in the BUS

Aim d) can be inferred based on the principle that 'you are what you eat', i.e. that the isotopic ratios in the tissues of consumers reflect the mixture of the isotopic ratios present in the different food items consumed (Ehrich 2010).

e) Analyze sexual maturity staging of the Benguela euphausiid species

According to Siegel (2000), populations are not composed of a series of identical individuals. Two major variables distinguish individuals in populations; sex and age. Therefore, sexual maturity or adult population determines the recruitment of next generation (Siegel 2000).

Research questions are:

1: Are there are significant seasonal differences in euphausiids abundances and population structure of the NBUS during the Peak (Upwelling) and Off-Peak season?

2: Are there are significant spatial differences in euphausiids abundances and population structure at the boundary transects (17°S and 23°S) of the NBUS during the Upwelling Peak) and Off-peak season?

3: Are there are significant differences in the trophic levels of the different species of the NBUS?

2. METHODOLOGY

2.1 Investigation area

The BUS extents along the southwestern coast of Africa, covering the western South African and Namibian coastline roughly from Cape Agulhas (34° S) to the Angola Benguela Frontal Zone (ABFZ) (Hutchings *et al*. 2009) which is around 14°and 16°S (Meeuwis & Lutjeharms 1990). Emerging from the south, the cold Benguela current system converges with warm tropical waters of the Angola Current (AC). Along the coast of southwestern Africa, the interaction of southerly trade winds with coastal topography forces upwelling, this is strongest at three distinct upwelling cells (Shillington *et al*. 2006; Hutchings *et al*. 2009). The Lüderitz upwelling cell (26° S) accounts for roughly 50% of physical upwelling and separates the upwelling region into a northern and a southern subsystem (Shannon1985; Duncombe Rae 2005). In the southern region (south of 26°S) the trade winds are seasonal and upwelling maximizes during austral spring and summer. The northern region (from 26° S to the ABFZ) is characterized by perennial alongshore winds and upwelling along the coast (Shannon 1985) (Fig. 1). In the NBUS lies the two transects under investigation.

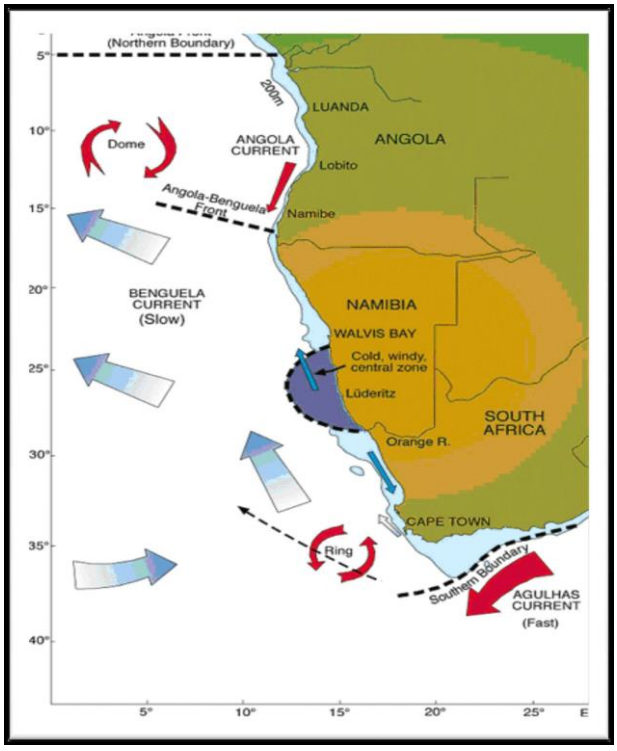

Figure 1: The external and internal boundaries of the Benguela large marine ecosystem, bathymetric features and surface currents

(Adapted from www.bclme.org)

2.2 Field sampling

During the R/V Meteor M100/1 (September 2013) and M103/1 (January 2014) cruises euphausiid sampling was conducted using a MOCNESS (Multiple Opening and Closing Net with Environmental Sensing System) at various stations during both day and night times (Table I). The stations were located on transects Kunene (KN, 17°S) and Walvis Bay (WB, 23°S) (Fig. 2). A total of 16 oblique hauls were conducted at specified transects stations (represented by a red dot on map) during both seasons. Maximum sampling depth intervals were pre-determined by considering stations' bottom depths bearing in mind the krill`s vertical migration behavior (Werner & Buchholz 2013).

Table I: Stations sampled in the NBUS

with information on locations, time of net deployment and maximum sea floor bottom depths

Station	**Gear**	**Date**	**Time (UTC)**	**Lattitude (S)**	**Longitude (E)**	**Bottom Depth (m)**
Upwelling						
WB1.1	MOC	01.09.2013	21:05	23° 2, 26'	14° 3, 83'	132
WB2.1	MOC	02.09.2013	14:18	23° 0,05'	13° 8, 41'	314
WB3.1	MOC	23.09.2013	19:41	23° 0, 38'	13° 3, 04'	410
WB4.1	MOC	24.09.2013	21:03	23° 0, 20'	12° 48,01'	896
WB5.1	MOC	24.09.2013	11:35	23° 0,24'	12° 48,01'	897
WB6.1	MOC	25.09.2013	13:46	23° 2, 31'	11° 48,17'	2891
KN1.1	MOC	18.09.2013	23:23	17° 19, 27'	11° 18, 51'	401
KN2.1	MOC	19.09.2013	09:13	17° 18,15'	11° 18, 59'	401
Off-peak						
WB1.2	MOC	08.01.2014	05:11	23° 01, 207'	13° 37, 586'	150
WB2.2	MOC	07.01.2014	01:04	23° 00, 980'	13° 01, 964'	470
WB3.2	MOC	06.01.2014	08:06	23° 04, 653'	12° 45,451'	1054
WB4.2	MOC	05.01.2014	16:18	23° 02, 506'	12° 18,686'	2098
KN1.2	MOC	12.01.2014	04:59	17° 17,645'	11°29, 116'	246
KN2.2	MOC	12.01.2014	14:30	17° 17, 113'	11° 18, 497'	417
KN3.2	MOC	13.01.2014	02:21	17° 17, 791'	11° 10, 554'	951
KN4.2	MOC	13.01.2014	15:22	17° 15, 131'	10° 59, 919'	2120

Ideally, each of the four stations on one transect had to lie within the coastal, shelf, slope and oceanic waters in order to obtain an idea of neritic/oceanic distributions of

krill species respectively. Number of oblique hauls conducted per transect per season are given in Table I.

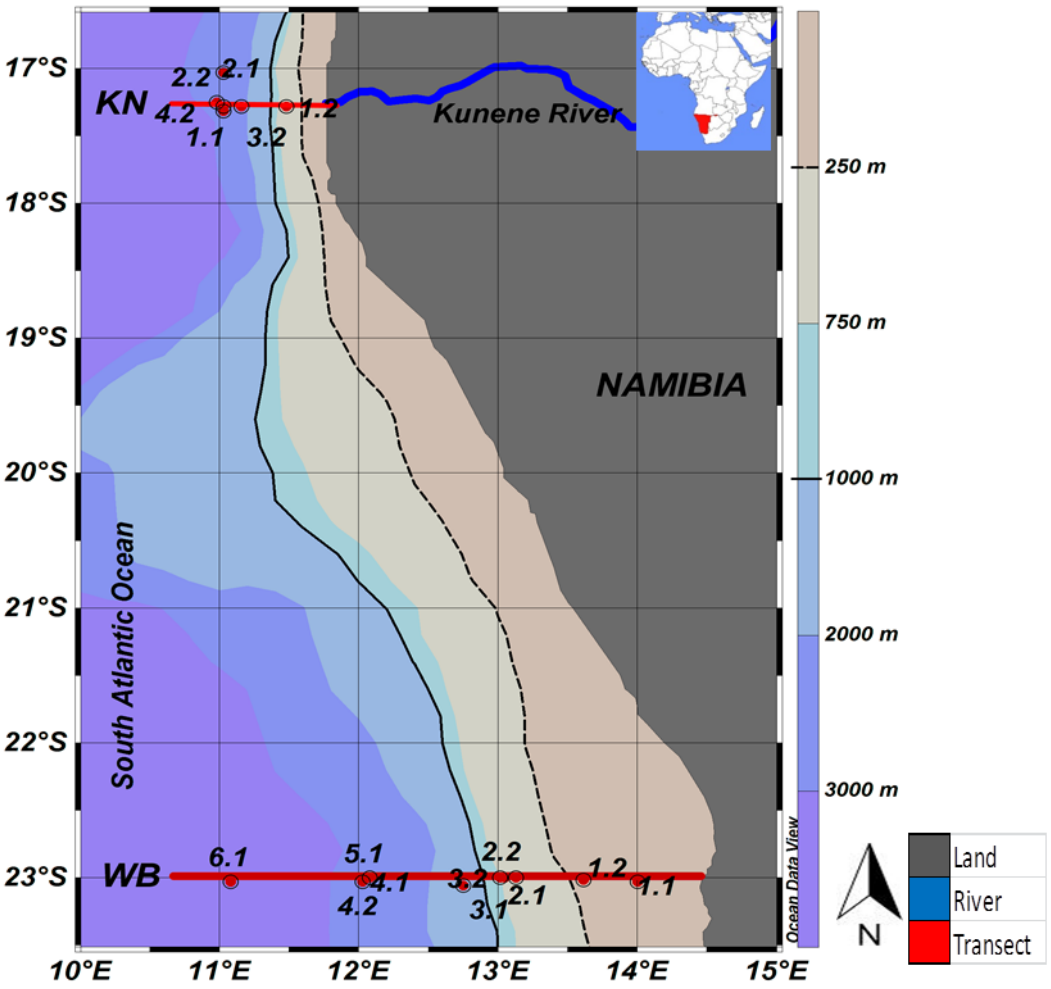

Figure 2: The BUS showing the sampled stations at the Kunene and Walvis Bay transects in both seasons.

Red lines indicate transects while red dots sampled stations

2.2.1 MOCNESS

The ultimate aim of a sampling programme is to obtain a set of results that are considered representative of the population under study (Watkins in Everson 2000). Accordingly, a reliable gear has to be used in order to reduce bias on catch. One ideal kind of a gear is the MOCNESS (Fig. 3). The MOCNESS is equipped with nine rectangular frames of nets with sensors. The nets are optimized for krill catch as they are made of soft materiel and are 2mm mesh size. Nets open and close on computer generated commands successively by commands transmitted from the surface deck unit through a single conducting cable to the underwater unit. This enables the

sampling of euphausiids to be conducted at discrete depths intervals. MOCNESS was towed obliquely (45° angle) at average ship speed of 2 knots. The volume of seawater passed through the nets was obtained from the computer reading and recorded on protocols. Environmental parameters (temperature, salinity and wind speed) were also obtained through MOCNESS computer and recorded on protocols Information was further used to calculate abundance and biomass.

Figure 3: Lateral view of the MOCNESS (http://www.soki.aq/display/StandMeth/MOCNESS)

2.2.2 Baseline sampling

A hand-net (55µm) was used to collect baseline samples from each station for further trophic level calculations. With pre-information from the oceanographers on how deep Chlorophyll could be detected, the hand net was cast (usually to about 10m deep) into the sea. Baseline was collected into an opaque bottle and in the lab filtered through sieves of different mesh sizes in order to remove any large matter that could possibly bias results. The remaining fine residues were washed with sea water and transferred into labelled Eppendorf caps and immediately frozen at -80° C. Baseline samples were not personally collected, they were obtained from our GENUS colleagues (Simon Geist, ZMT, Bremen) upon request.

After retrieval an estimate of the number of krill was recorded in a net protocol. Depending on catch at least some 10 live animals per station were dipped in Milli-Q water, briefly blotted on Kim-Wipes, individually placed in Eppendorf caps and frozen at -80°C for further analysis in the laboratories on land (e.g. stable isotope analysis).

The rest were preserved in 3-4% buffered formaldehyde in seawater in well labeled bottles and further stored at 4°C.

2.3 Laboratory analysis

2.3.1 Length-wet mass relationships

In order to determine length-mass relationships, individual krill (not gender differentiated) of all species found were analyzed (Agersted & Nielsen 2014). Length was measured from front of the eyes to tip of the telson (Hünerlage & Buchholz 2013) in (mm). Individual krill were also weighed on a fine scale in (mg). These results were used to plot regression graphs which were selected by considering highest R^2 values except in the case of *E. hanseni* where a regression resulting only positive biomass calculations was chosen.

2.3.2 Species and sex identification

Krill were sorted with respect to species using “An Introduction to the Zooplankton of the Benguela current region” (Gibbons 1990) and “Euphausiids of the Benguela current region” by Bodekke 1950/52 as identification keys. The whole sample or a quarter sub-sample (splitting factor4) containing a minimum of 150 individuals was analyzed. Their gender and stages (juvenile, sub-adults and/or adult) were classified by identifying their secondary sexual characters; petasma for males and thelycum for females according to Makarov & Denys (1980)`s Stages of Sexual Maturity of *Euphausia superba* modified for the species under study particularly adapted to *Euphausia hanseni* according to F. Buchholz (Table II). For adults males were identified as mature when they had fully developed petasma and/or spermatophores were visible in the duct otherwise were staged as sub adult. Females were identified as mature when thelycum was fully developed, had spermatophores attached to thelycum, a pouch of eggs or showed signs of spawning signs otherwise classified as sub adult. Where thelycum or petasma were not present, the specimen was identified as juveniles (Agersted & Nielsen 2014).

Table II: Krill maturity stages (acc. Makarov & Denys) adapted to Euphausia hanseni acc. to F. Buchholz

	Stages	**Description**	**Stages**	**Description**
	Males		**Females**	
Juvenile	**I**	no petasma	**I**	no thy
Subadult	**IIA**	petasmae visible but not fully developed	**IIB**	small thy present, colourless
Adult	**IIIA**	petasmae fully developed, no spp	**IIIA**	thy fully developed but empty, red/coloured
	IIIB	fully formed spp in ejaculatory duct, 2 additional forming in duct above	**IIIB**	1 or 2 spp attached to thy, sperm plug present, ovary grown from 1/3 to 3/4 of full size (cpx height)
			IIIC	ovary full size, extension 1/3 into first abdominal segment
			IIID	cpx sometimes swollen with eggs (orange/coloured)
			IIIE	batch spawned, shrunk ovary

spp: spermatophore

cpx: carapace

thy: thelycum

2.3.3 Abundance and biomass determination

In a population, abundance refers to number of individuals occupying a unit cubic meter of sea water (1) or number of individuals per unit square meter in a specified depth layer (2). Parameters that may characterize abundance include species ratios and their connection with the ecological influences while population's structure may include length frequency ratios, sex ratios and maturity stages of individuals. Due to high number of individual per catch and limited analysis time, only samples from the integrative net (Net 1) were investigated. The abundance data for each euphausiid species was calculated by applying the following formula:

Equation 1: $$Abundance\ (Ind.\,1000m^{-3}) = \frac{No.\ of\ Ind. \times (Splitting\ factor) \times 1000}{Volume\ filtered\ (m^3)}$$

"Splitting factor" was applied only for very large samples which needed to be separated into quarters then one quarter subset analyzed. These were samples from WB3.1, KN1.2, KN2.2 and KN3.2. Since the abundance per cubic meter was way too low to comprehend, the multiplication by 1000 on right side of equation (1) was applied to standardize to volume of 1000 m^3.

The standing stock abundance per area depth layer was calculated using the formula:

Equation 2: $$Abundance\ (Ind.\,m^{-2}) = \frac{No.\ of\ Ind. \times Depth\ Interval\ (m)}{Volume\ filtered\ (m^3)}$$

Using mass length relationships, biomass of each species found per station was calculated by applying the following equation:

Equation 3: $$Biomass\ (mg\ m^{-3}) = \frac{Mass\ (mg)}{Volume\ filtered\ (m^3)}$$

The standing stock biomass for each depth layer was calculated by using the formula below:

Equation 4: $$Biomass\ (mg\ m^{-2}) = \frac{Mass\ (mg) \times Depth\ Interval\ (m)}{Volume\ filtered\ (m^3)}$$

2.3.4 Stable Isotope (SI) analysis

Stable isotopes are used as integrators and tracers of ecological processes at naturally occurring levels (Robinson 2001). They provide ecological information across a range of spatio-temporal scales, i.e. from cell to ecosystems, and across a time scale of seconds to millennia (Dawson *et al*. 2002). Recently, it has been demonstrated that the measurement of the abundances of naturally occurring stable isotopes of carbon ($^{13}C/^{12}C$) and particularly nitrogen ($^{15}N/\ ^{14}N$) can provide trophic level information in marine food webs (reviewed by Fry & Sherr 1988; Owens 1988). Natural isotopic abundance is reported on a delta scale which indicates the deviation (in ‰) of the isotopic composition of a sample from an internationally accepted standard (e.g. Robinson 2001). By measuring the isotopic concentrations of tissues of a suite of consumers it may thus be possible to determine relative or absolute trophic positions within a marine community (Hobson & Welch 1992).

In the laboratories, frozen animals were dissected from second to fourth segment to separate muscle tissue from the rest of the body (Fig. 4). In order to avoid any bias to the SI results, the gut and chitin skin of each individual were separated from the rest of the muscle tissue.

For calculation of the trophic level baseline samples were thawed and centrifuged for 5mins at 4°C at 3500 rpm in an Eppendorf Centrifuge 5430R. Sea water was pipet out and replaced with 200ml milli q de-ionized water to avoid salt content in the baseline from crystalizing during the process of freeze drying the baseline samples. Together with muscle tissue samples, all Eppendorf caps were arranged and left open on a pre-cooled aluminum bock then transferred into a freeze dryer for 18.5 - 25 hours.

After drying, muscle tissues and base line samples were transferred into tin caps and weighed on fine scale. Muscle tissue masses ranged from 0.5mg to 3.5mg. They were arranged in order of ascending mass on plastic trays. Samples were sent to AgroIsoLab (TÜV-Rheinland, Germany) for determination of Carbon (^{13}C) and Nitrogen (^{15} N) fractionation. SI signature results were used to calculate the euphausiid food source and trophic levels respectively.

The trophic levels were calculated by applying the following formula:

Equation 5: $$TL = \lambda + \frac{(\delta^{15}N_{Consumer} - \delta^{15}N_{Base})}{3{,}4\ (‰)}$$

Where λ is the trophic level of the organism used to estimate $\delta^{15}N_{Base}$ (1or 2 in this case), $\delta^{15}N_{Consumer}$ is the SI mean value for krill species and 3.4 (‰) resembles according to Minagawa & Wada (1984), the average enrichment in $\delta^{15}N$ per trophic level.

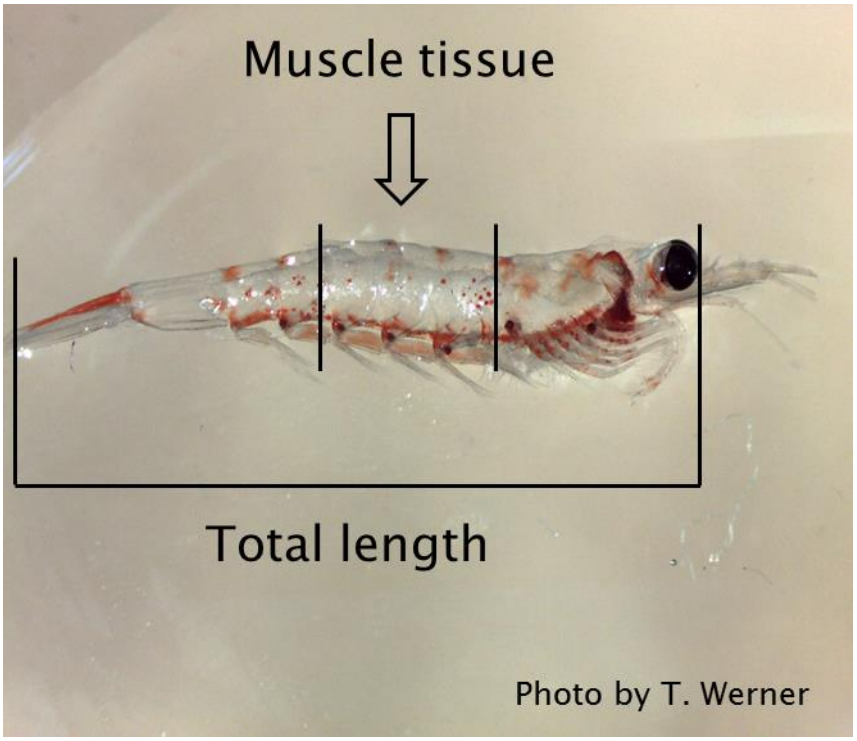

Figure 4: Krill image showing section of krill abdomen dissected for stable isotope muscle tissue and total length determination.

Individual krill hepatopancreas color was also analyzed using respective codes in order to determine individual animal food source.

2.4 Statistical Analysis

Abundances, biomass and SI contents in the different samples were given as absolute mean values or Mean (±SE) unless otherwise stated. Statistics were performed using GraphPad Prism6 (GraphPad Software, Inc., USA).

3. RESULTS

3.1 Hydrography

Time series area statistics for NBUS derived from Giovanni Modis Aqua gave temperatures and Chlorophyll a ranges the two seasons as follows (Table III):

Table III: Mean SST and Mean Chlorophyll a (± SD), mimimum and maximum during Upwelling and Off-peak seasons in the NBUS.

	SST (°C)		**Chlorophyll a (mg.m^{-3})**	
	Upwelling	Off-peak	Upwelling	Off-peak
Mean (± SD)	15,3 ± 1,0	20,8 ± 1,1	1,40 ± 2,2	1,47 ± 1,92
Minimum	12,70	16,80	0,29	0,16
Maximum	18,80	23,00	51,00	22,00

SST ranged from 12,70°C to 18,80°C during the Upwelling season and from 16,80° C to 23,00°C in the Off-peak season. Chlorophyll a values ranged from 0,29 mg.m-^{3} to 51,00 mg.m-^{3} during Upwelling season and from 0,16mg.m^{-3} to 22,00 mg.m^{-3} during the Off-peak season. Differences in the mean SST were apparent between the two seasons whereas mean Chlorophyll a values showed no significant difference (Fig.5).

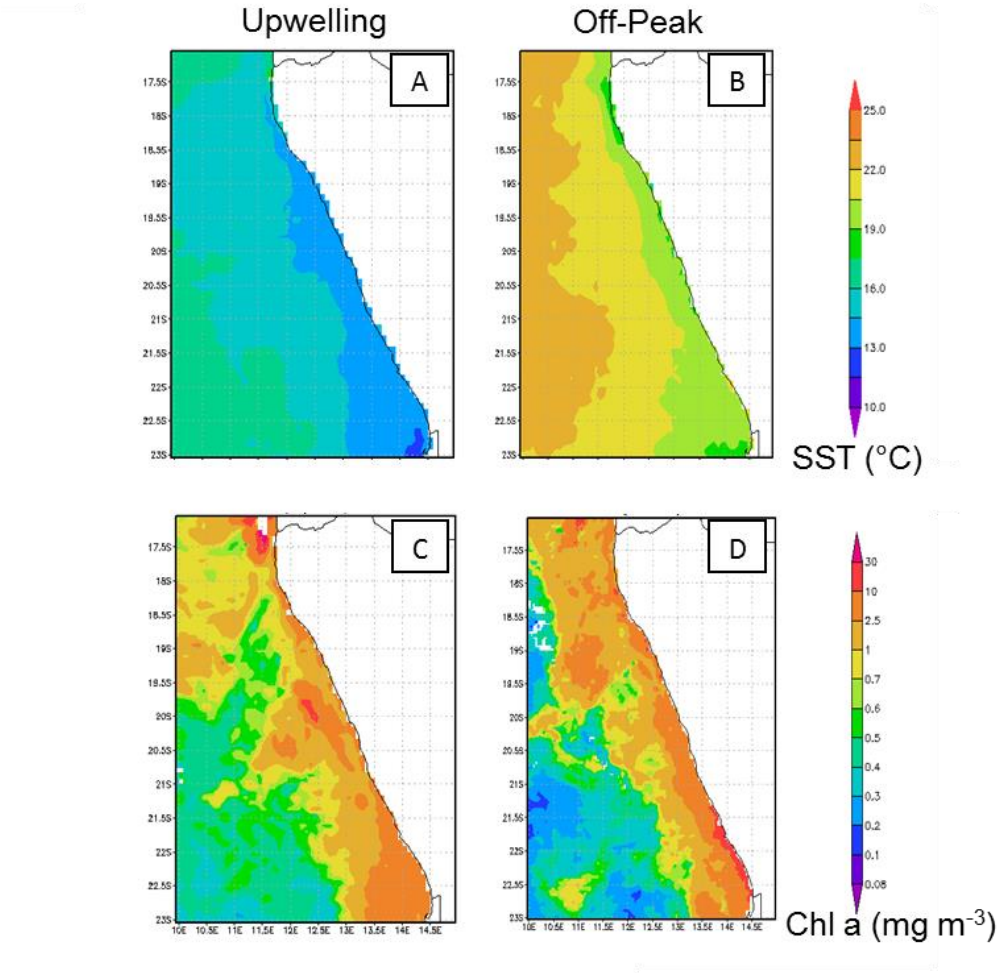

Figure 5: Satellite images of SST (in °C) during A) Upwelling and B) Off-peak season and Chlorophyll a (in mg.m$^{-3)}$ during C) Upwelling and D) during Off-peak (modified from MODIS-Aqua http://disc.sci.gsfc.nasa.gove/giovanni)

3.2 Species distributions

3.2.1 Species occurrences

Species caught and identified *Euphausia hanseni, Euphausia lucens, Euphausia recurva, Nematoscelis megalops* , *Nyctiphanes capensis* and *Thysanoessa gregaria* (Table IV). However, only the first five species were the used for abundance and biomass determination at the two transects.

Table IV: Occurrence of different species at the two transects in the two seasons.

Species	**Upwelling (WB23°S)**	**Upwelling (KN 17°S)**	**Off-peak (WB23°S)**	**Off-peak (KN 17°S)**
Euphausia hanseni	X	x	x	x
Nematoscelis megalops	X	x	x	x
Nyctiphanes capensis	X			
Euphausia recurva	X		x	
Euphausia lucens			x	
Thysanoessa gregaria			x	

E. hanseni was found during Upwelling and Off-peak seasons and at both WB and KN transects. The same was observed for *N. megalops* which also appeared in both seasons at the two transects. *N. capensis* appeared only once during the Upwelling season at the WB transect. *E. recurva* was harvested during both Upwelling and Off-peak seasons but only at the WB transect. *E. lucens* and *T. gregaria* only appeared once at the WB transect during the Off-peak season.

3.2.2 Species horizontal distributions

The horizontal distributions of species found at WB across the NBUS are believed to be the same along the whole coast of Namibia (Barange & Stuart 1991). The results from the WB transect during the Upwelling season illustrate an overall picture of the horizontal distributions of the species between the KN and WB transects (Fig. 6)

During the Upwelling season, high densities of *N. capensis* were found in shallow coastal waters of < 350m bottom depth. *Euphausia hanseni* and *Nematoscelis megalops* were found further offshore, associated mainly to the shelf slope.

Euphausia recurva appeared at deeper more westerly stations in the oceanic water mass.

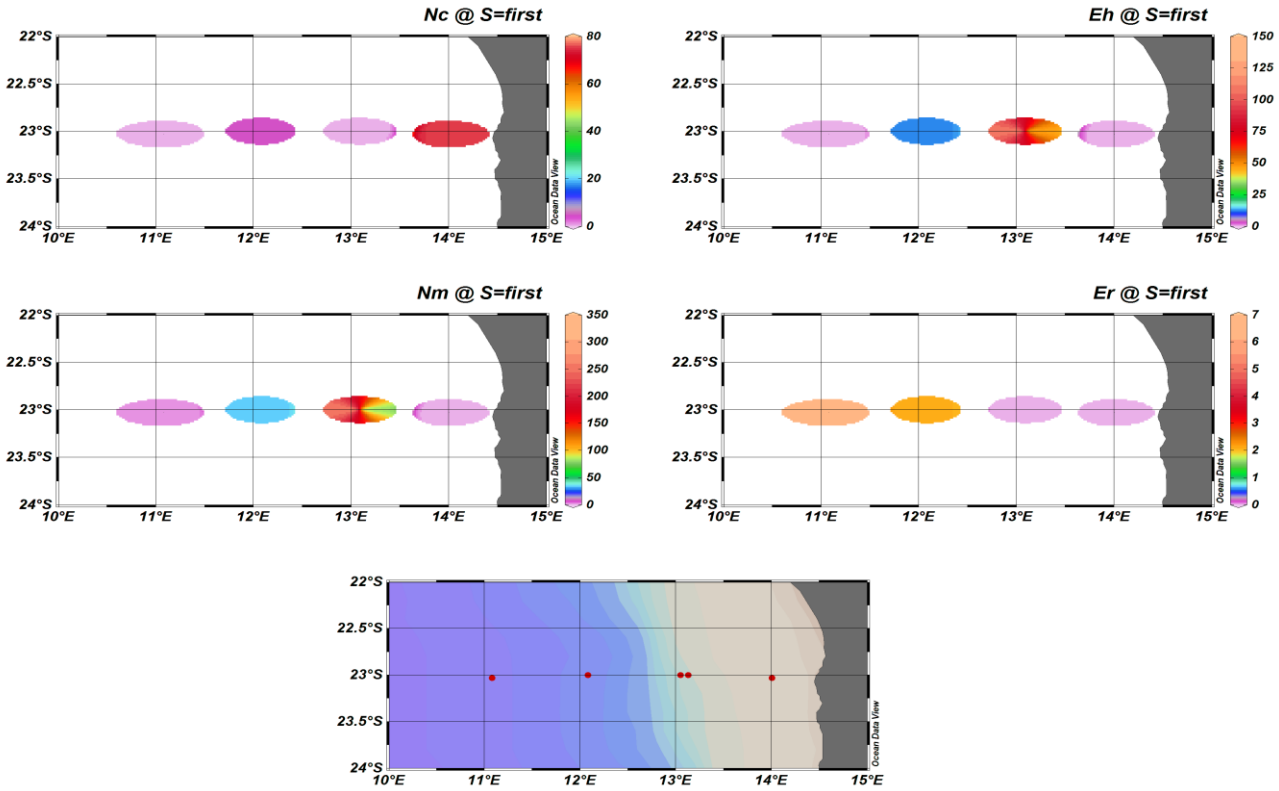

Figure 6: ODV grid function illustrating horizontal abundance distributions of euphausiid species across the WB transect during the Upwelling season. Images Nc shows the abundaces (Ind.m^{-2}) of *N. capensis*, Eh shows the abundances of *E. hanseni*, Nm shows the abundances of *N. megalops* and Er are the abundances of *E. recurva* species

3.3 Population structure and distribution patterns

3.3.1 Abundances

Overall densities of krill showed that Upwelling had lower abundance, 358 Ind.m^{-2} than Off-peak season which had a total of 1618 Ind.m^{-2}. During Upwelling, krill abundances per station varied from 6 Ind.m^{-2} (WB2.1) to 188 Ind.m^{-2} (WB3.1) and during Off-peak from 2 Ind.m^{-2} (WB3.2) to 549 Ind.m^{-2} (KN1.2) (Table V).

Table V: Station densities of different krill species given as individuals per unit area (Ind.m^{-2})

Station	**Bottom Depth (m)**	***Abundance* (Ind. m^{-2}*)***					
Upwelling		*E. hanseni*	*N. megalops*	*N. capensis*	*E. recurva*	*E. lucens*	**Total**
WB1.1	132			9			9
WB2.1	314	6	<1				6
WB3.1	410	54	134				188
WB4.1	896	9	22	3	2		36
WB5.1	897	11	32	4	1		48
WB6.1	2891		1		7		8
KN1.1	401	25	<1				25
KN2.1	401	46	1	<1			47
Total		**151**	**190**	**16**	**10**		**358**
Off-peak							
WB1.2	150		3			23	26
WB2.2	470	8	87				95
WB3.2	1054		2		<1		2
WB4.2	2098	2	<1		5		7
KN1.2	246	549					549
KN2.2	417	393	8				401
KN3.2	951	431	66				497
KN4.2	2120	32	8				41
Total		**1415**	**174**	**0**	**5**	**23**	**1618**

3.3.2 Biomass

Length-mass regressions for respective species are shown in (Fig. 7**).** The combined length-mass regression (mm-mg) from the five species later used to convert abundances into biomass (Annex 3).

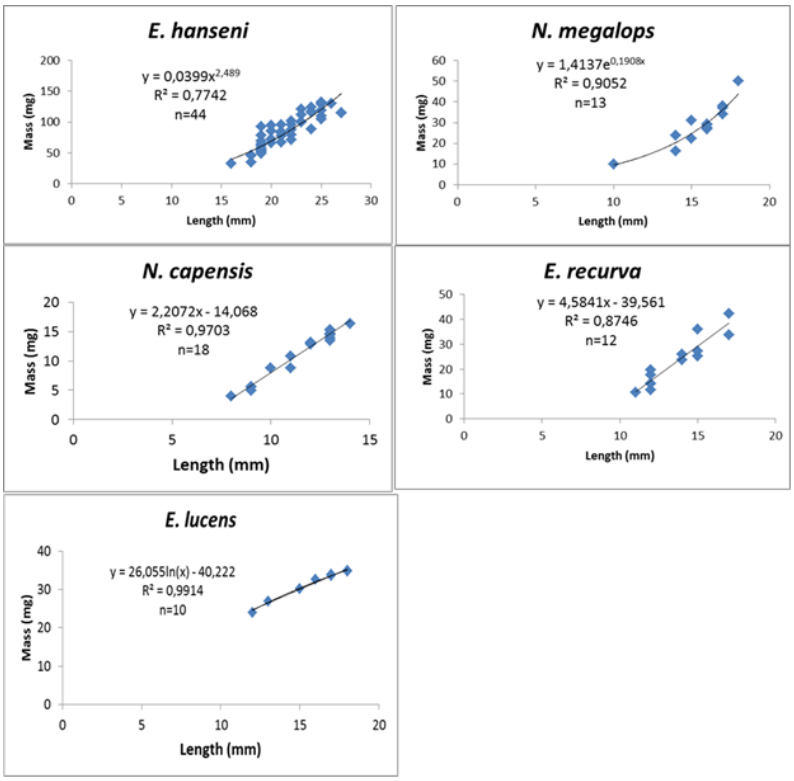

Figure 7: Length- mass relationships of different species n≥10 species individuals (Obtained from frozen samples)

Sum total of krill biomass during Upwelling (13638 mg.m^{-2}) was lower than the total during the Off-peak season (90958 mg.m^{-2}). During Upwelling, krill biomass varied from a total of 144 mg.m^{-2} (WB6.1) to 4320 mg.m^{-2} (KN2.1) and Off-peak varied from 46 mg.m^{-2} (WB4.2) to 40854 mg.m^{-2} (KN1.2) (Table VI).

Table VI: Species biomass in mg.m^2

Station	**Bottom Depth (m)**	**Biomass (mg. m^{-2})**					
Upwelling		*E. hanseni*	*N. megalops*	*N. capensis*	*E. recurva*	*E. lucens*	***Total***
WB1.1	132			145			145
WB2.1	314	572	131				703
WB3.1	410	3013	1012				4025
WB4.1	896	277	538	44	33		892
WB5.1	897	360	643	61	25		1089
WB6.1	2891		44		100		144
KN1.1	401	2312	9				2321
KN2.1	401	4290	24	6			4320
Total		**10824**	**2400**	**256**	**158**	**0**	**13638**
Off-Peak							
WB1.2	150		75			659	734
WB2.2	470	485	368				853

WB3.2	1054		69		15		84
WB4.2	2098	11	19		16		46
KN1.2	246	40854					40854
KN2.2	417	23816	157				23973
KN3.2	951	22582	269				22851
KN4.2	2120	1532	31				1563
Total		**89280**	**1131**	**0**	**31**	**659**	**90958**

3.3.3 Abundances per season/station

3.3.3a Species mean abundances (Ind.m-^{2}) - Upwelling

During Upwelling (Fig. 8), species found *were E. hanseni, E. recurva, N. capensis* and *N. megalops*. *E. hanseni* was found at all stations except at WB1.1and WB6.1. *E. recurva* was found at stations WB4.1, WB5.1 and WB6.1. *N. capensis* appeared in four stations, WB1.1, WB4.1, WB5.1 and KN2.1. The species mainly dominating during the Upwelling season was *N. megalops* which appeared first at WB2.1 then peaked in abundance at Station WB3.1. *N. megalops* then appeared at WB4.1, WB5.1 and KN1.1 though in much lower abundances compared to the Station WB3.1. *E. recurva* was only found at the WB stations. *E. lucens* was not found during the Upwelling season (Fig.8).

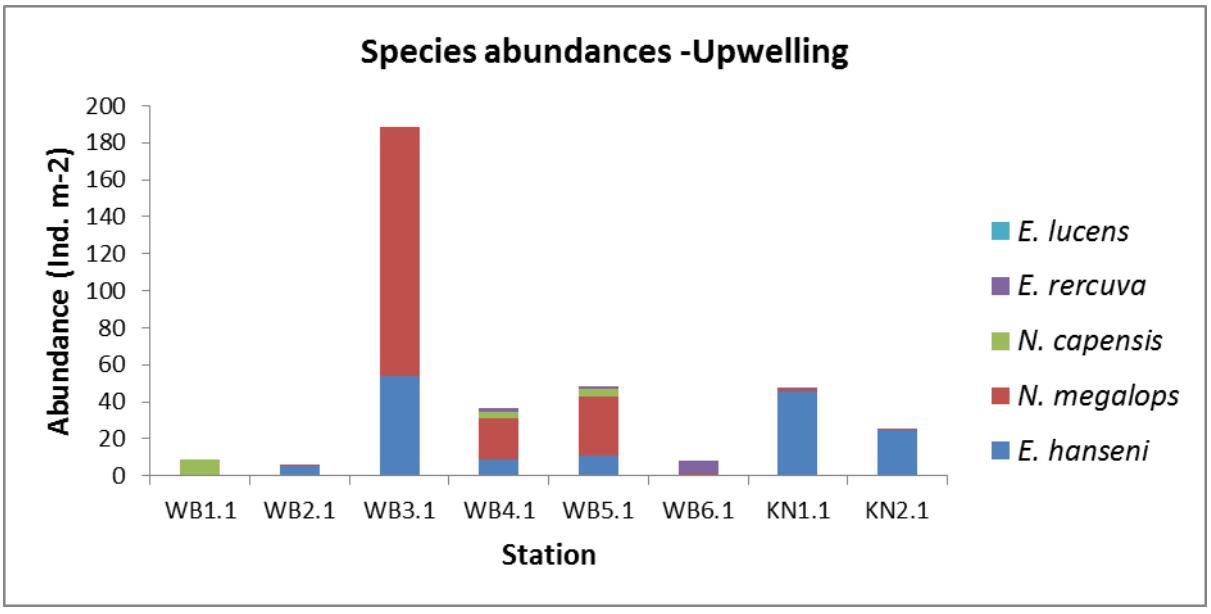

Figure 8: Individuals per unit area (Ind.m^{-2}) of species found during the Upwelling season.

3.3.3b. Species mean abundances (Ind.m-^{2}) - Off-peak

During Off-peak (Fig. 9), species found *were E. hanseni, E. lucens, E. recurva,* and *N. megalops*. *E. hanseni* was found at all stations except at WB1.2 and WB3.2. *E. lucens* only appeared at station WB1.2 at the WB transects. *E. recurva* was found at the two stations WB3.2 and WB4.2. *N. megalops* appeared at all stations except at KN1.2. Dominating species during this season was *E. hanseni* which peaked at station KN1.2 at the KN transect. *N. capensis* was not found during this season (Fig.9).

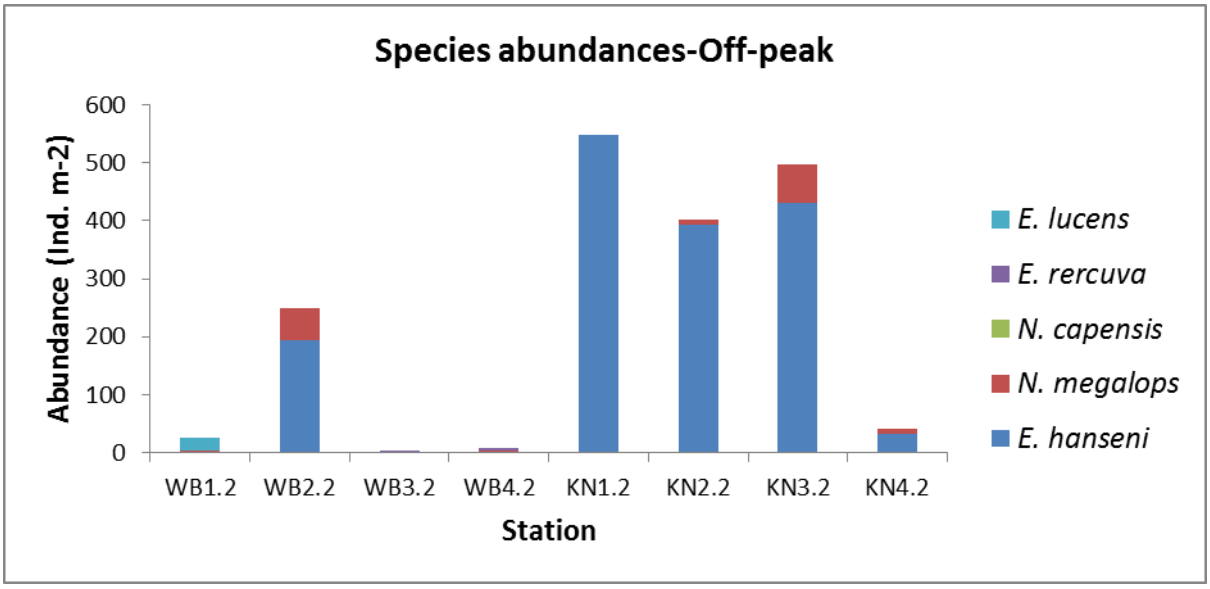

Figure 9: Individuals per unit area (Ind.m^{-2})of species found during the Off-peak season

3.3.3c Same depth stations abundance compared

Two stations were sampled at the KN transect during the Upwelling season as opposed to six at WB transect in the same season. A comparison of two stations from each transect WB2.1 & WB3.1 and KN1.1,& KN2.1 with the same depth range (314,410 & 401,401 m respectively) was done in oder to verify differences in abundances at the KN and WB transects showing that WB had a higher abundance of krill abundance than KN at (same bottom depths ranges) (Fig.10).

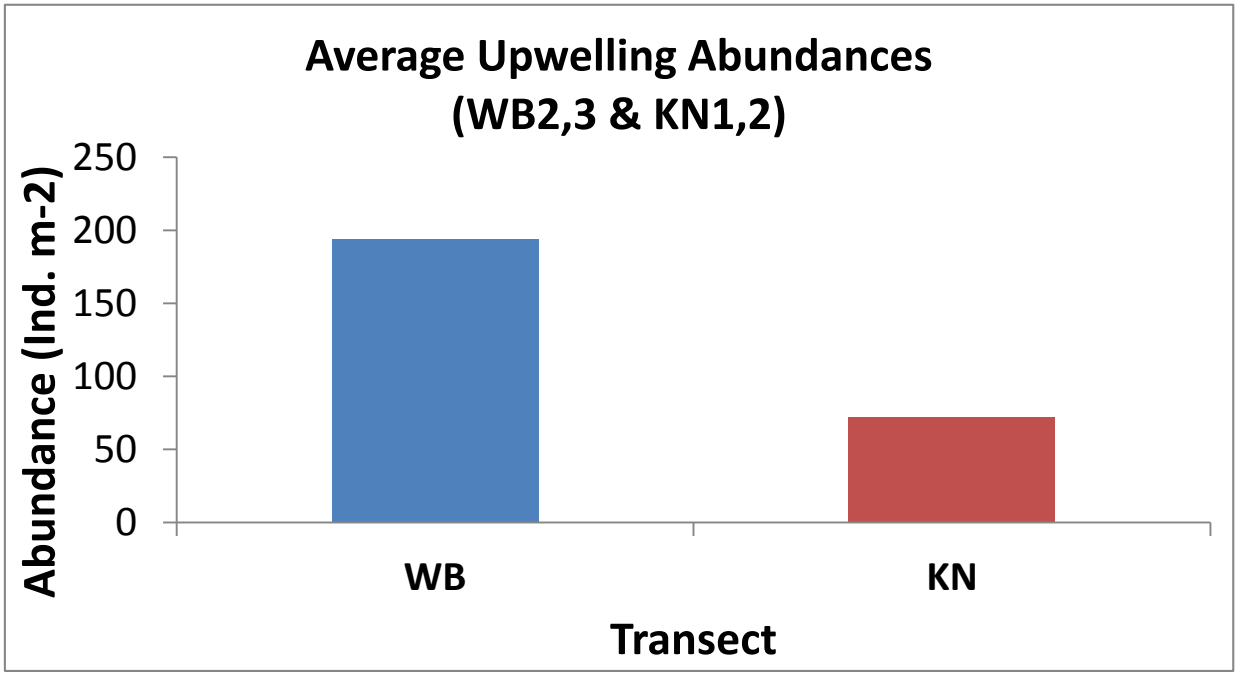

Figure 10: Stations abundances compared at transects WB and KN.

3.3.4 Overall mean abundance and biomass compared

KN transect showed lower abundance (average of 33 Ind.m^{-2}) compared to WB transect (average of 49 Ind.m^{-2}) during Upwelling (Fig10) WB transect had a lower average abundance during Off-peak (34 Ind.m^{-2}) than KN with (371 Ind.m^{-2}). Overall, Off-peak season had a higher abundance of krill than the Upwelling season with KN transect showing lowest abundance during Upwelling and highest during Off-peak season.

WB had lower mean biomass during Upwelling (1166 mg.m^{-2}) than at KN (3320 mg.m^{-2}). The same trend followed for the Off-peak season where WB average biomass was lower (429 mg.m^{-2}) compared to KN (22311 mg.m^{-2}). Biomass was lowest at WB transect during Off-peak season (429 mg.m^{-2}) compared to KN with 22311 mg.m^{-2} biomass in the same season. Overall, Off-peak season had higher biomass than the Upwelling season (Fig. 11).

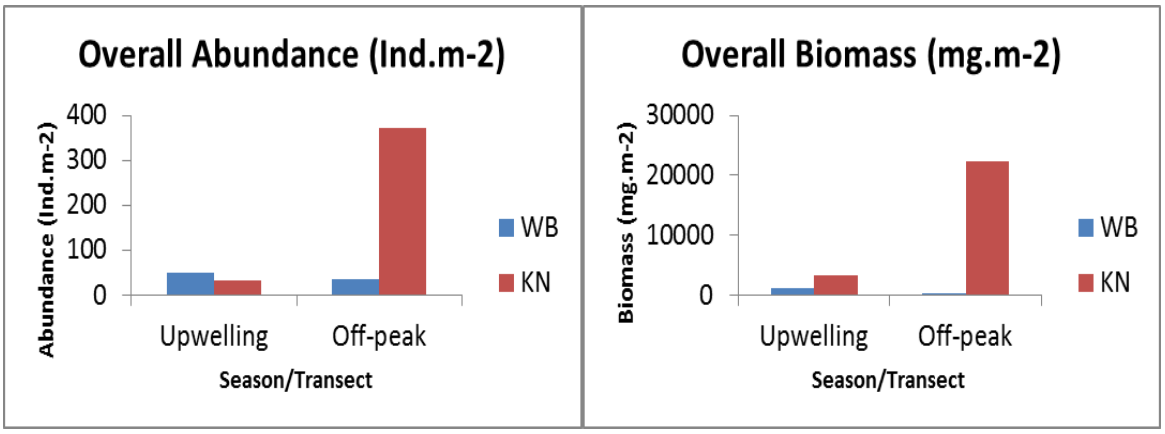

Figure 11: Comparison of mean abundances (Ind. m-2) and biomass (mg.m^{-2}) during Upwelling and Off-peak seasons at KN and WB transects

.

Overall abundance during Upwelling showed that WB transect had slightly more abundant krill (49,30 Ind.m-2) than KN (35,99 Ind.m^{-2}). Overall abundance during the Off-peak season, on the other hand indicated a demarcation in quantity of euphausiids with KN having higher number of individuals per area (371,80 Ind.m^{-2}) than at WB (71,09 Ind.m^{-2}).

3.3.4. Species total abundance and biomass compared

E. hanseni had the highest abundance hence biomass during Off-peak seasons than the Upwelling season particularly at Station KN1.2. *N. megalops* showed a higher abundance hence biomass during Upwelling season than during Off-peak season specifically at Station WB3.1. *E. recurva* had higher abundances hence biomass during Upwelling especially at Station WB6.1 (Fig. 12).

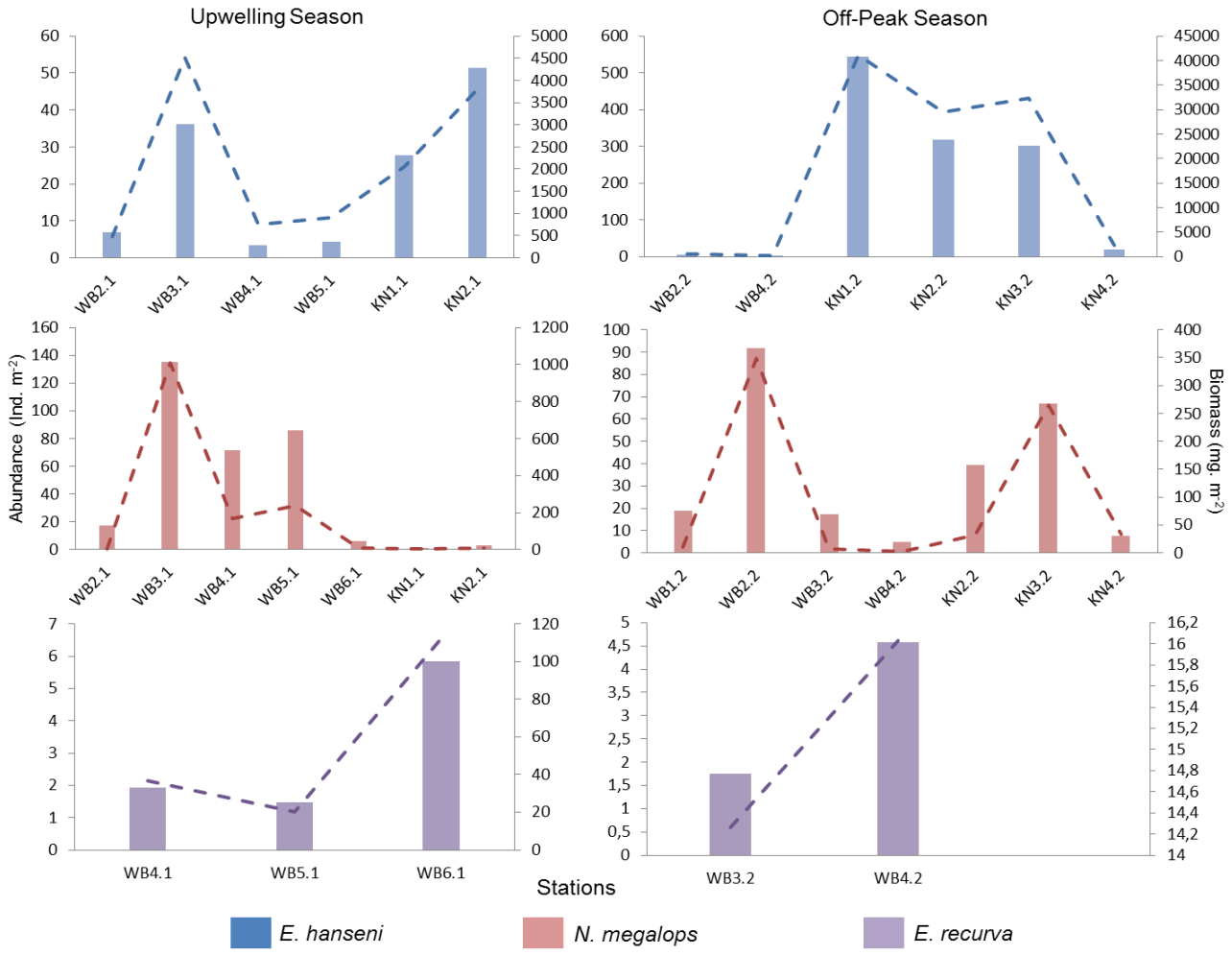

Figure 12: Abundance (left y-axis, Ind.m^{-2}) and biomass (right y-axis, mg.WMm^{-2}) plots for three species found during both seasons. Bars represent the biomass while dotted lines represent the abundance. (Note scale differences)

3.3.5 Length frequency distributions

Analyses showed that *E. hanseni* had a mean length 19,56 ± 0,10mm, *E. lucens* mean length 14,52 ± 0,22, *E. recurva* mean length 11,57 ± 0,31, *Nematoscelis megalops* mean length 14,60 ± 0,26 and *Nyctiphanes capensis* mean length was 13,43 ± 0,25mm respectively (Table VII).

Table VII: *Overall species statistical data (Length mm)*

	Species				
Length (mm)	*E. hanseni*	*N. megalops*	*N. capensis*	*E. recurva*	*E. lucens*
N	1182	322	65	45	107
Minimum	8,00	8,00	8,00	9,00	8,0
Median	20,00	15,00	13,00	12,00	14,0
Maximum	27,00	25,00	18,0	15,00	22,00

Mean	19,56	14,60	13,43	11,57	14,52
SD	3,78	2,91	2,02	1,34	2,30
SE	0,10	0,26	0,25	0,31	0,22

The overall mean length values of different species showed that *E. hanseni* had slightly higher mean sizes during Upwelling (19,69 ± 0,22mm) than Off-peak (19,44 ± 0,11mm) and an overall mean of length equal to 19, 56 ± 0,10mm (Fig. 12). *E. recurva* followed suit with mean length during Upwelling as 12,1 ± 0,25mm and Off-peak 11,07 ± 0,37 mm. *N. megalops* showed a different trend with a higher mean length at 15,99 ± 0,32 mm during Upwelling and 14,32 ± 0,20mm during Off-peak. Although *N. capensis* and *E. lucens* could not be compared in terms of seasons, results show that *N. capensis* appeared during Upwelling with a mean length of 13,43 ± 0,25mm while *E. lucens* appeared during Off-peak with mean length 14,52 ± 0,22mm (Fig.13).

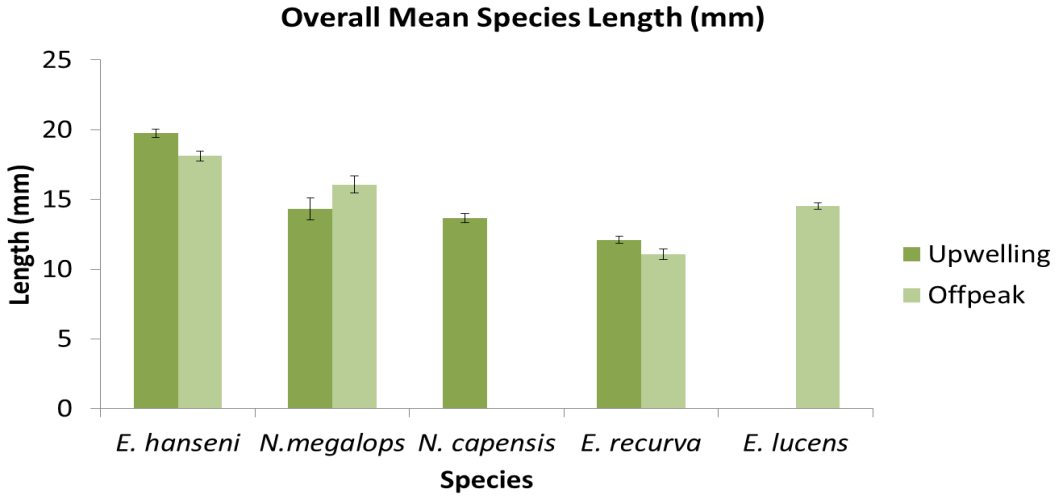

Figure 13: Species means lengths (mm) for five species found in both seasons compared.

Length frequency distributions of three species that occurred in both seasons were plotted (Fig. 14). *E. hanseni* had higher number of individuals during Off-peak season than during Upwelling. In contrast, *N. megalops* and *E. recurva* had higher numbers during Upwelling than in Off-peak season. All three species show bi-modal curves, indicating two age classes, presumably the zero-group, i.e. juveniles and the 1+ year-

group. Taking the modal values into account, growth could not be differentiated between seasons.

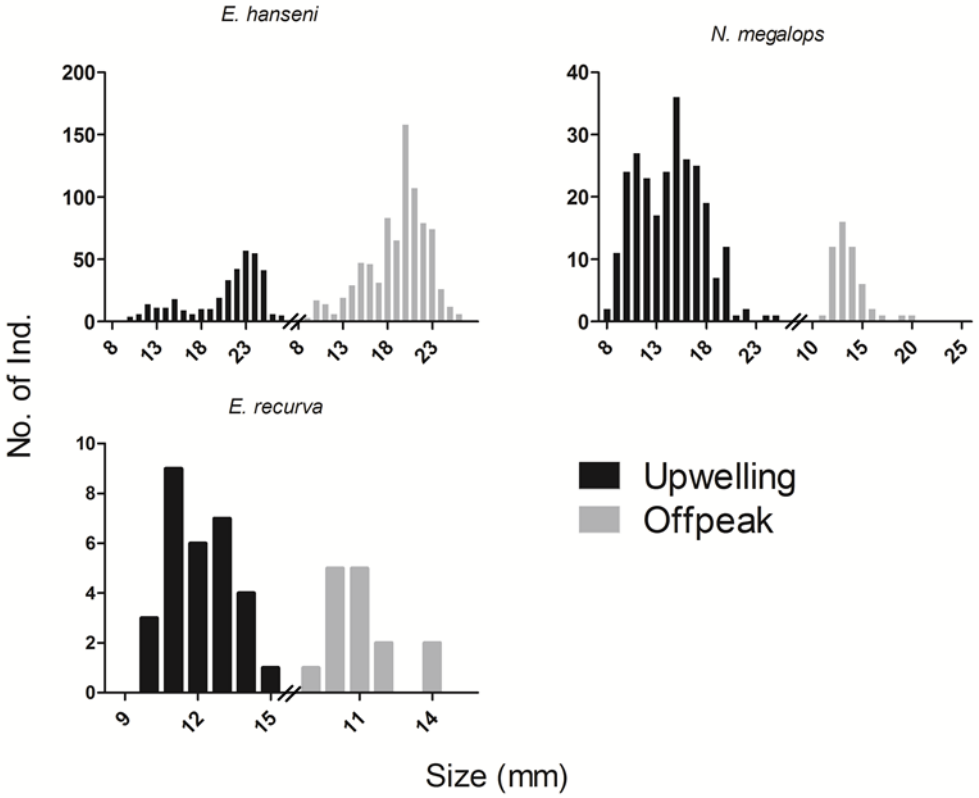

Figure 14: *E. hanseni, N. megalops and E. recurva* overall length frequency graphs during Upwelling and Off-peak seasons

3.3.6 Sexual Maturity Seasonal Comparisons

E. hanseni sexual maturity stages (according to Table II) varied from stage 2a to 3c. Juveniles were found in both seasons. The highest percentage of the population was stage 3b (males and females). Excluding the juveniles, females show a higher proportion than males for *E. hanseni* in both seasons (Fig. 15).

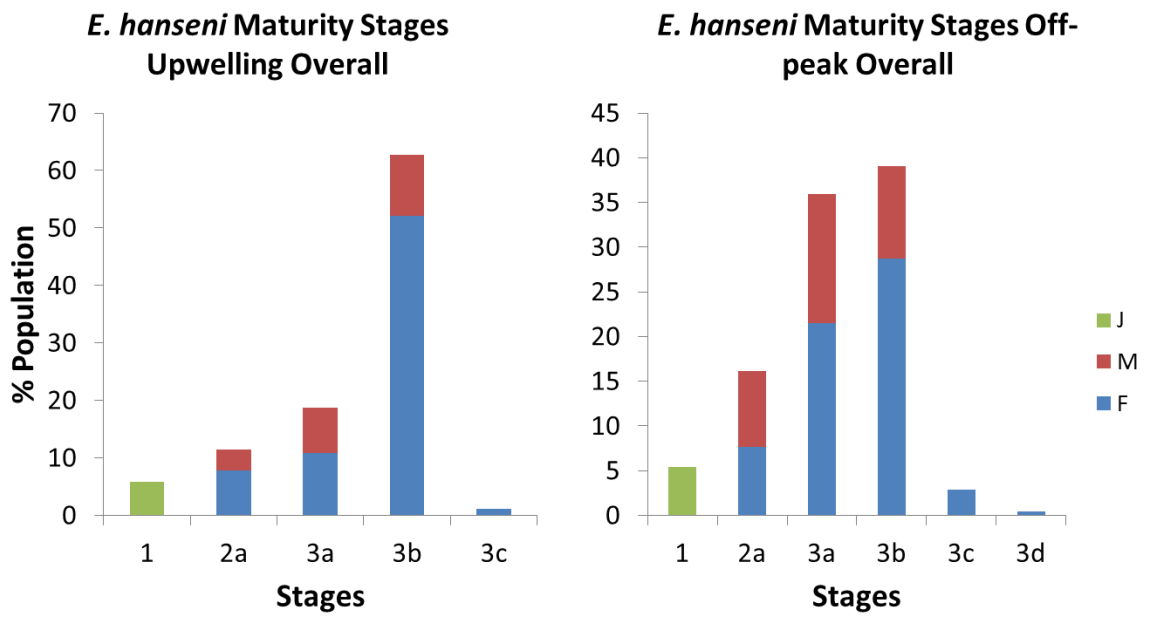

Figure 15: *E. hanseni* sexual maturity stages in both seasons.

In both Upwelling and Off-peak, *N. megalops* had juvenilles, subadults and mature individuals as part of its population. Sub adults male/female of stage 2a were dominating during Upwelling. During Off-peak season, males/female at stage 3a dominated the population (Fig.16).

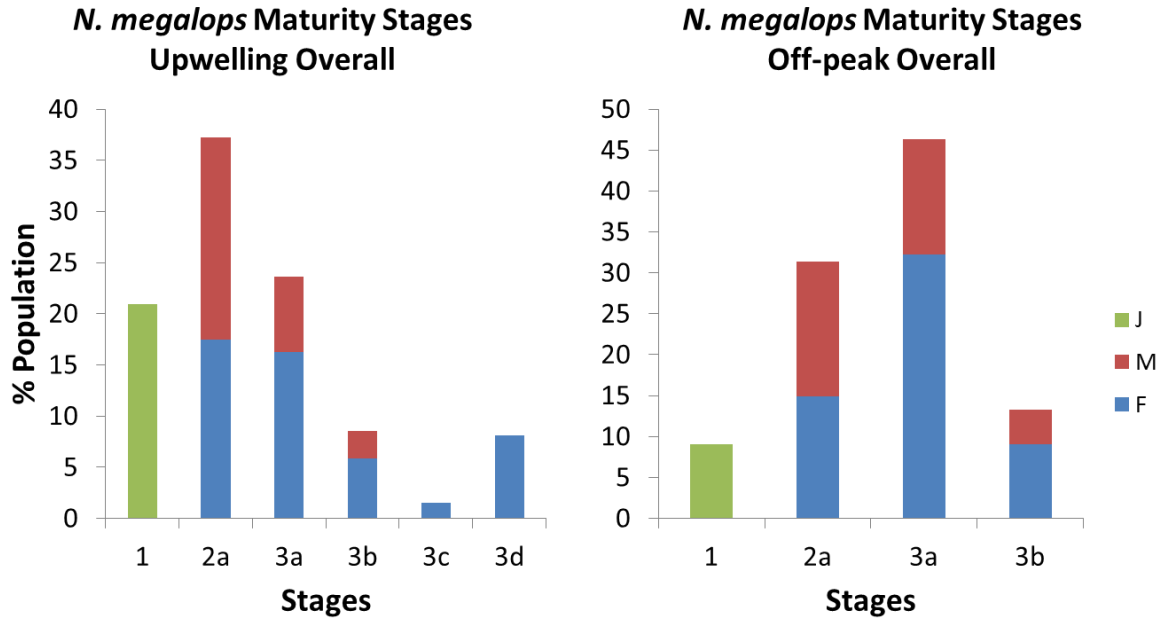

Figure 16: *N. megalops* sexual maturity stages in both seasons

E. recurva during the Upwelling season had its population dominated by mature males/females at Stage 3b. Some juveniles appeared during Off-peak season though the population is dominated by adults of Stage 3a (Fig. 17).

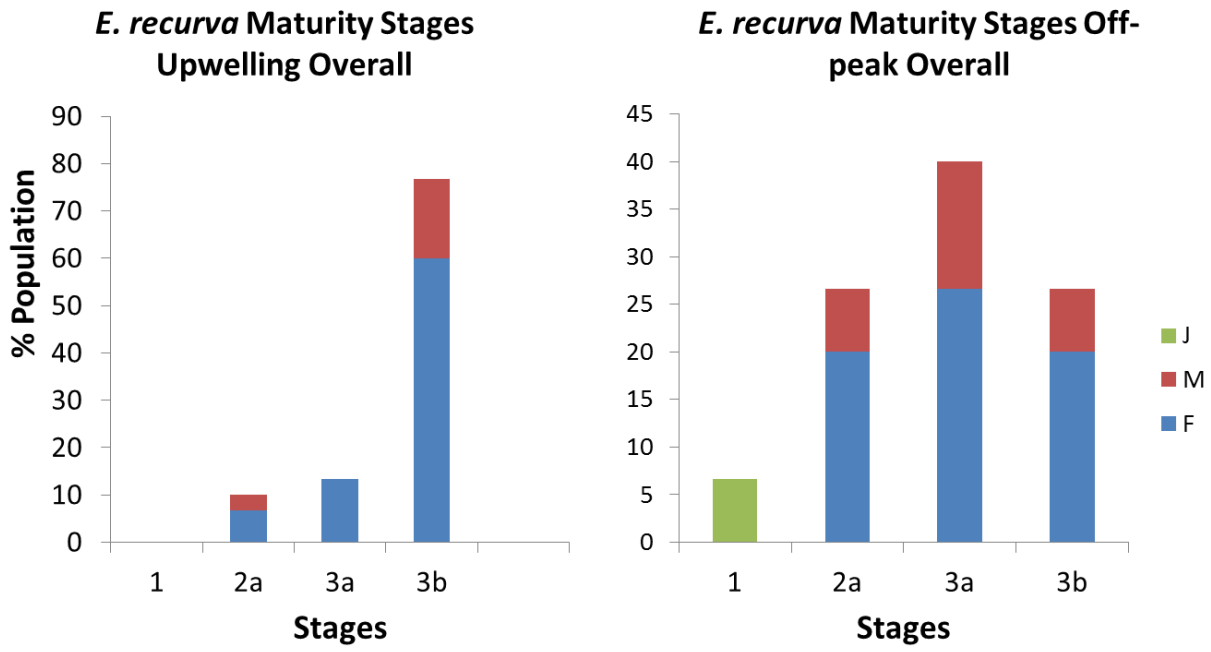

Figure 17: *E. recurva* sexual maturity stages in both seasons

3.3.7 Sex Ratios

Females generally appeared more frequently than males. All females and males were considered if they showed sub-adults characteristics or were mature. The overall for both seasons show a ratio of 2:1 female to male. However, species-specific differences were apparent with *N. capensis* showing the lowest sex ratio of 1,4 and *E. recurva* showing highest ratio of 3,4 (Table VIII).

Table VIII: *Total female to male ratios for different species in both seasons*

Species	Total Female	Total Male	Sex ratio
E. hanseni	763	354	2,2:1
N.megalops	197	121	1,6:1
N. capensis	35	25	1,4:1
E. recurva	34	10	3,4:1
E. lucens	66	39	1,7:1
Ratio	1095	545	2:1

3. 4 Stable Isotope Analyses

3.4.1 Baseline samples

In order to calculate final species trophic levels (TL) the raw information of baselines such as its color, components and station of retrieval were considered to determine which consumers its SI value would be used to calculate TL. KN1.1 baseline sample (Table IX) was a dense green mixture of phytoplankton. WB5.1 baseline was brown in color and had a thick dense consistency. WB6.1 was also brown and contained a lot of foraminifera under the microscope. KN1.2, KN2.2 and KN3.2 were brown in color and contained a lot of calanoid copepods. These baselines were used to

Table IX*: Raw baseline observations and their SI results*

Station	**Transect**	**Notes**	**$^{13}C/^{12}C$ [‰]**	**$^{15}N/^{14}N$ [‰]**	**C (%DM)**	**N (%DM)**	**Used as baseline**
Upwelling							
KN1.1	KN	Very dense green phytoplankton	-21.9	1.1	9.7	1.3	X
1920-3	WB	Calanoid copepods	-21.8	3	19.6	3.5	
1921-5	WB	A lot of calanoid copepods	-22.9	3.1	23.8	3.6	
WB5.1	WB	Brown, very dense	-21	2.6	17.2	3	X
WB6.1	WB	Brown+forami-nifera	-20.4	0.5	14.6	1.9	X
Off-peak							
WB3.2	WB	N/A	-20.5	4	5.6	<1	X
WB3.2	WB	N/A	-20.1	4	7.6	1.2	X
WB2.2	WB	N/A	-19.4	5.9	12	2	X
WB2.2	WB	N/A	-18.8	6.4	2.5	<1	X
KN1.2	KN	90% copepods, very brown	-19.2	7.9	28.2	4.7	X
KN2.2	KN	50/50% copepods, very brown	-19.3	6	16.2	2.5	X
KN3.2	KN	90% copepods	-19.5	7.2	25.5	4.1	X

3.4.2 Species SI signatures

E. hanseni, *E. recurva* and *N. megalops* all showed a higher $\delta^{15}N$ fractionation during the Off-peak season than during the Upwelling season. $\delta^{13}C$ showed little variation in the same species though a slight shift from heavier to lighter sources from Upwelling to Off-peak season. *E. lucens* showed the highest $\delta^{13}C$ and $\delta^{15}N$ during the Off-peak season while *N. capensis* showed lowest during Upwelling season (Fig.18)

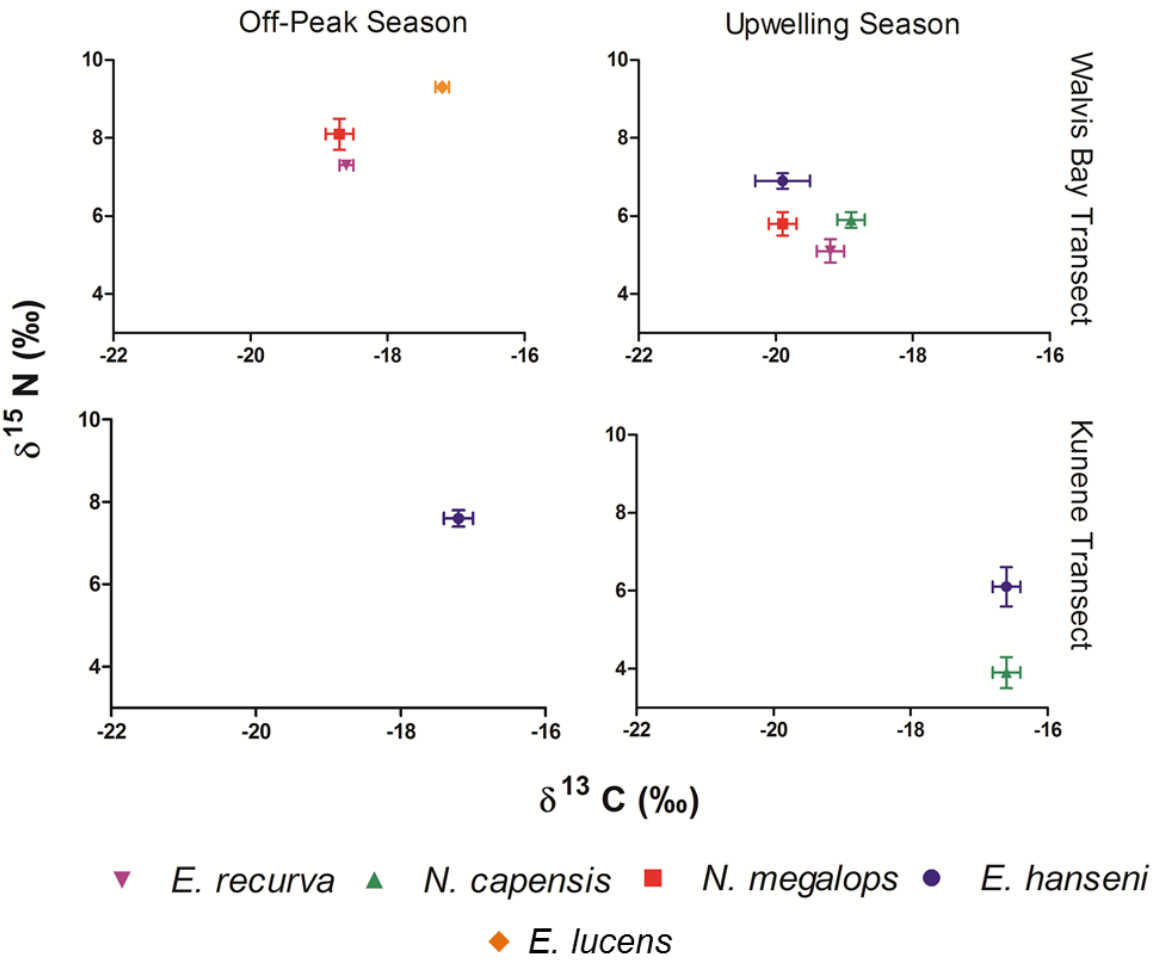

Figure 18: $\delta^{13}C$ and $\delta^{15}N$ fractionations for species found at the two transects in both seasons at both transects

During Upwelling, baseline from KN1.1 was used to calculate TL for species found at KN transect during this season. λ (Equation 5) was set to 1 for all calculations that used KN1.1 baseline as it contained mainly phytoplankton. The WB5.1 and WB6.1 averages were used to calculate average ^{15}N values for species found at the WB transect. λ values for baseline

sample KN1.2, KN2.2 and KN3.2 were set to 2 as these baseline samples mainly contained copepods. TL calculations were calculated accordingly (Table X).

Table X: *TL calculations showing different species in the two seasons and two transects*

			Upwelling			
Species	**$\delta^{15}N_{Consumer}$**	**λ**	**$\delta^{15}N_{Base}$**			**TL**
E. hanseni	6,4	1,0	1,6	3,4	1,4	**2,4**
E. recurva	5,1	1,0	1,6	3,4	1,0	**2,0**
N. megalops	5,8	1,0	1,6	3,4	1,3	**2,3**
N. capensis	5,3	1,0	1,6	3,4	1,1	**2,1**

			Off-peak			
Species	**δ15N Consumer**	**λ**	**δ 15NBase**			**TL**
E. hanseni	7,7	2	6,9	3,4	0,2	**2,2**
E. recurva	7,3	2	6,9	3,4	0,1	**2,1**
N. megalops	8,1	2	6,9	3,4	0,4	**2,4**
E.ucens	9,3	2	6,9	3,4	0,7	**2,7**

Transects							
	Species	**δ15N Consumer**	**λ**	**δ 15NBase**			**TL**
17°	*E. hanseni*	7.1	1	1.1	3.4	1.8	**2.8**
	N. megalops	3.9	1	1.1	3.4	0.8	**1.8**
23°	*E. hanseni*	7.3	1	4.6	3.4	0.8	**1.8**
	E.lucens	9.3	1	4.6	3.4	1.4	**2.4**
	E. recurva	6	1	4.6	3.4	0.4	**1.4**
	N.capensis	5.9	1	4.6	3.4	0.4	**1.4**
	N. megalops	6.9	1	4.6	3.4	0.7	**1.7**

3.5 Euphausiid seasonal diets

In order to determine the type of food a krill species fed on, hepatopancreas colour of indiduals were analyzed. A numerical code was allocated for each likely food source of the krill (Table XI).

Table XI: *Hepatopanceas classification color codes*

Color	Numerical code	Likely food source
Transparent	0	Non/empty
Yellow	1	Phytoplankton
Green	2	Phytoplankton +
Brown	3	Phytoplankton ++
Orange-Red	4	Zooplankton
White	5	Zooplankton continuous

3.5.1 Species seasonal diets compared

Differences in species diets were noted particularly for the two species, *E. hanseni* and *N. megalops. During Upwelling, E. hanseni* seemed to prefer grazing on phytoplankton as the greater fraction of these species showed a yellow hepatopancreas though some fed on zooplankton and or entirely zooplankton. During Off-peak season these opportunist euphausiid fed more on zooplankton and others or entirely on zooplankton (Fig. 19).

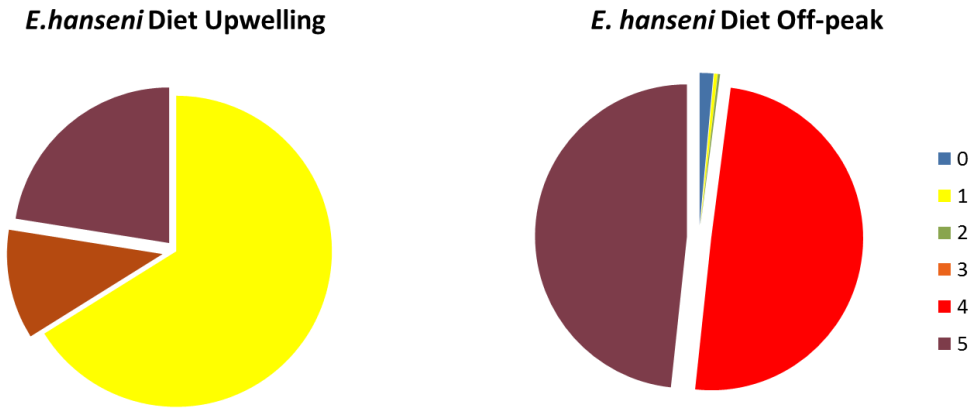

Figure 19: *E. hanseni* diet during Upwelling Off-peak seasons compared

N. megalops diet during both Upwelling and Off-peak season was mainly zooplankton though a certain proportion fed on phytoplankton. During Off-peak, greater part of the species fed on zooplankton while some fed on phytoplankton on different phytoplankton species (Fig.20).

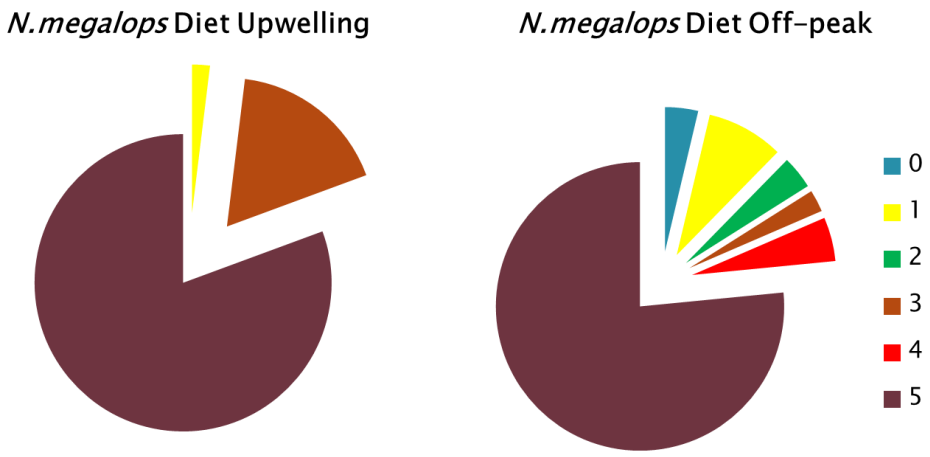

Figure 20: *N. megalops* diet during Upwelling and Off-peak seasons compared

4. DISCUSSIONS

4.1 Hydrography

SST during Upwelling was notably lower during Upwelling than Off-peak seasons. As Upwelling is a process that brings in cool nutrients rich waters to the surface, it is expected that SST becomes lower during this time than during any other season. Wind stress, advection and mixing of water disrupt the thermal stratification of the water layers hence cooling the Upwelling system during this season. During Off-peak season, waters are more stable and a defined thermocline enhances the SST to increase thus accounting for the differences in the SST during the two seasons.

Chlorophyll a showed little variation in the satellite images. This could be explained by the fact that there could have been enough nutrients in the system due to some subtle upwelling process that occur throughout the year as Stander (1964) and (Shannon 1985) highlight that upwelling is considered perennial, though there is a maximum upwelling in spring and minimum in autumn. Again as suggested by Barange & Boyd (1992) the Bus environmental conditions maintain relatively dense and constant phytoplankton populations hence a low variation in Chlorophyll a.

4.2 Species and Zonation

In this study, species caught and identified were *Euphausia hanseni, Euphausia lucens, Euphausia recurva, Nematoscelis megalops, Nyctiphanes capensis* and *Thysanoesa gregaria. Though T. gregaria* was not used for abundance and biomass determination, it was necessary to record it as part of the species community caught during the Off-peak season.

E. hanseni and *N. megalops* seem to be able to adapt to seasonal, environmental and spatial geographic conditions since they were caught in both Upwelling and Off-peak seasons at KN and WB transects. *N. capensis* appeared only once during the Upwelling season at the WB transect while *E. lucens* appeared once at WB during the Off-peak season. There is a possibility that two species could have been present during both season at the WB transect but were simply not harvested at the specified sampled stations (Table I). *E. recurva* was harvested during both Upwelling and Off-peak seasons but only at the WB transect. *T. gregaria* also appeared once at the WB transect during the Off-peak season.

From the results we can conclude that the WB transect is a habitat for the species *T. gregaria, E. hanseni, N. megalops, N. capensis* and *E. lucens* and N. capensis while the KN is a habitat for *E. hanseni* and *N. megalops* since these were the only species found there during the study. This matches Barange *et al*. (1992) statement that the inner shelf off the Namibian coast is dominated by *N. capensis* whereas *E. hanseni* dominates at the shelf break.

4.3 Horizontal distribution

A horizontal krill zonation was noticed at the WB transect. This study showed that *N. capensis* was found mainly in the coastal waters although coastal populations of krill have the possibility of being advected (Agersted & Nielsen 2014) off shore due to Ekman transport. Since the species is a small one, active swimming to maintain position in the shallow area is not feasible but retention mechanisms brought about by the complex current regime would be.

E. hanseni and *N. megalops* were found mainly over the shelf break confirming that *E. hanseni* and *N. megalops* are the most abundant euphausiid species at and just beyond the shelf break in the northern Benguela (M. Barange unpubl.). *E. recurva* was found only along the WB transect in the oceanic Atlantic waters (Barange *et al.* 1992). In Shannon & Pillar (1986) & *Pillar et al*. (1992), *E. recurva* did not extend further north than 20° S during their cruises thus they concluded that the latitude 20° S is the northern most position and the biogeographical boundary of typical Benguela fauna (Barange et al. 1992). This matches findings of my research since no *E. recurva* was recorded along the KN transect (17°S).

Water column properties and phytoplankton is reflected in the meso-zooplankton communities offshore (Agersted & Nielsen 2014) which could explain that variations in the species' horizontal distributions depends on differences in phytoplankton found in different water masses off shore.

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4.4 Abundance and Biomass

This study showed a difference in abundance and biomass during Upwelling and Off-peak season. Initially, it was expected that the Upwelling season would produce higher abundance of krill than during the Off-peak; findings contradict these theoretical expectations as there was significantly lower abundances/biomass of krill during Upwelling compared to the Off-peak season. Normally it is assumed that during Upwelling, there are more nutrients in the water enhancing primary and overall production of the system. This in turn is expected to promote higher growth rates and increases reproduction which will affect krill abundance. However the opposite was observed. This may be explained by the idea that though primary production is triggered by nutrients in the water column, it promotes phytoplankton blooming when interacting with light. Because of water mixing during upwelling brings about turbulence, suspended particles cause water to become turbid thus reducing light penetration within the photic zone of the ocean impeding primary production. This could be a reason why we observed less abundance of krill in Upwelling. Another reason could be currents and wind stress causing advection dispersing krill thus lowering their chances of reproduction. The ultimate explanation of these findings may be due to the assumption that production is uncoupled from the seasonal Upwelling regime, meaning that the physical processes which lead to high nutrients in the water column during Upwelling are not the basic principle of our actual biological observations.

In the Off-peak season on the other hand, the system still maintained high abundances of phytoplankton as shown on the Chlorophyll a satellite images. Due to lack of extensive upwelling leading to a calm and stable environment, water layer stratification is enhanced in the Off-peak season, enabling light penetration thus facilitating primary production. There were also higher SST observed at both transects. Generally as warmer environments are favorable for enzymatic and biological activities within living organisms, we expect krill to thrive in these environments. Therefore we could conclude that the interactions between water stratification, light penetration, presence of phytoplankton and warmer temperatures are a possible explanation why higher krill abundances were found during Off-peak than during the Upwelling season.

Spatial differences were observed at the two transects KN and WB. KN had a higher abundance/biomass of krill than WB. The observed dissimilarities may be accounted to the fact that the two transects show differences in the bathymetric zonation. The WB has a wide neritic zone (Fig. 2) which favors retention of plankton and maintaining high densities of species such as *N. capensis* (Barange & Boyd 1992) however not favorable for many other species which my may not be adapted to shallow waters which are prone to stress associated with wind circulation and advection. Furthermore, WB being close to the Lüderitz upwelling cell (Barange *et al.* 1992) may continuously experience some mixing which may generally not be conducive for krill reproduction and growth. Since bathymetry and temperature determine distributions of krill (Agersted & Nielsen 2014) euphausiid species exhibit diel vertical migration (Mauchline 1980) which may be more feasible in deeper and steeper waters than shallower ones. *E. hanseni* and *N. megalops* were the two species found at the KN transect and these are believed to abide in waters beyond the shelf break in the northern Benguela (M. Barange unpubl.). Since the shelf break at KN is much closer to the coast, the krill swarms are more concentrated and this could be an explanation for the higher abundances found.

Furthermore, the higher abundance of euphausiids at the KN than at WB could be due to a poleward undercurrent along the west coast of southern Africa (Hart & Currie 1960, De Decker 1970, Bailey 1979 & Nelson 1989). The strong alongshore jet-like equatorward current may be the compensation for the poleward undercurrent (Shannon 1985). These currents over the shelf and shelf break probably transport zooplankton populations north when living in the surface or mid depth layers (Barange &Pillar 1992) thus acting as a major dispersal mechanism of zooplankton components along the Benguela area.

The area North of the 20° S off Namibia is characterized by warmer water throughout the year (Boyd & Agenbag 1985), especially from January to April when warm, more saline near surface water invades the Namibian shelf from the north (Boyd et al. 1987) and is as a result of the extension of Angolan water over the shelf (Barange et al. 1992). Off-peak season was taken to be January 2014 which coincides with the period assumed by Boyd & Agenbag (1985) as warmest. The warm current from the North characteristic for the season may have transported additional krill to the KN (see also Hünerlage & Buchholz 2013).

4.5 Population structure

Averaged lengths of different species during the Upwelling and Off-peak seasons did not show substantial variation (Fig. 14). However, within the three species that were found in seasons, (*E. hanseni, N. megalops* and *E. recurva*) there were similar trends discernible in their length frequency distributions. Assuming length (size) is a function of age, different age groups were noted from respective Upwelling and Off-peak histograms. The peaks at the histograms showing modal lengths indicate andseparate the age classes of different species thus separate cohorts to some extent (Fig. 15). Different cohorts are an indicator of continuous development which agrees with Barange & Stuart (1991) for *E. hanseni*, *E. lucens* and *N.capensis* However, modal values were similar between seasons and locations indicating mixing of swarms from different origin so that a thorough statistical analysis of cohort composition and growth rates was not feasible.

4.6 Maturity stages and sex ratios

E. hanseni, maturity stages did not differ much between the two seasons. All stages were represented from juveniles to sub-adults and adults in both Upwelling and Off-peak seasons. The dominating stage in both seasons were males and females of stage 3b where adult males had spermatophores in their ejaculatory duct or females had spermatophores attached to their thelycum. Sex ratios for *E. hanseni* during upwelling were 3,3:1 females to males and 1,8:1 for Upwelling and Off-peak respectively.

N. megalops showed a higher abundance of juveniles during Upwelling than Off-peak season. More stages were represented in the Upwelling season ranging from juveniles to females of stage 3d (carapace swollen with eggs). The greater part of the *N. megalops* population during upwelling was stage 2a which means the krill were sub-adults. Continued breeding can be concluded since the Off-peak season showed more or less the same population structure, however showing more 3a staged krill meaning the population individuals were growing and maturing all year round. Sex ratios for this species were both 1,6:1 both during Upwelling and Off-peak seasons showing that females had the majority.

E. recurva sexual maturity stages showed stage 3b as the highest in population, showing that for females spawning was to take place soon. This was observed in the Off-peak season where juveniles were part of the population but the greater part of the population was mature males and females (stages 3a and 3b). Because all stages were observed in both seasons, this may indicate continuous breeding throughout the year, also in this species. Sex ratios were 4:1 and 2,5:1 during Upwelling and Off-peak seasons.

The krill population showed a census of more females than males with an overall ratio of 2:1. This is beneficial to the population as spawning success is more dependent on older female age groups as they have higher fecundity (Siegel 2000)

4.7 Stable Isotopes, Baselines and Trophic levels

Stable Isotopes (SI) signatures can be used to infer krill food so that the isotopic ratios in the tissues of consumers reflect the mixture of the isotopic ratios present in the different food items consumed (Ehrich 2010). In this case, SI fractionation was done in order to draw conclusions on what different krill species feed on in different seasons. It was also to determine the trophic levels of different species depending on prevailing environmental or geographical conditions hence seasonal and spatial comparisons. Results helped to detect alterations in food source and trophic levels of different species. Different species appeared to be feeding on different carbon sources during Upwelling and Off-peak seasons as well as at the different transects. *N. megalops* and *E. recurva* showed a higher $\delta^{15}N$ during the Off-peak season than during the Upwelling season. During Upwelling, *N. megalops* fed mainly on phytoplankton and zooplankton. However, though diet remained the same, some individuals of this species fed on different phytoplankton. *E. hanseni* fed mainly on phytoplankton but in the Off-peak season shifted to zooplankton. This points out the different seasonal shifts in terms of the $\delta^{13}C$ in the two seasons as reflected in Fig. 18. For spatial comparisons, *E. hanseni* had both higher $\delta^{13}C$ and $\delta^{15}N$ signatures at KN than at WB. This supports the hypothesis that krill from ABF partake a more carnivorous diet than those from NBC (Hünerlage & Buchholz 2013) and this is explained by the different trophic regimes e.g. shifts from diatoms to dinoflagellates in krill diet from Upwelling to Off-peak season.

4.7.1 Baselines

A raw baseline analysis was done before freeze drying samples in order to define baselines composition. This information was essential as it was later used to determine λ value during TL calculations. For TL calculations, It was important to allocate transect baselines to respective consumer species in order to avoid bias in the calculations. By using the right base line value for each TL calculation, a proper comparison was then drawn for different species from different seasons and transects.

4.7.2 Trophic levels

The Trophic Level (TL) calculations were done in order to determine the krill trophic position in the BUS under different environmental conditions. Because these calculations involve $\delta^{15}N$ for baseline samples and λ, the trophic level of the organism used to estimate $\delta^{15}N$, it was essential to consider the composition of baseline (e.g phytoplankton) so one can decide which λ value to use. If the baseline consisted mainly of phytoplankton, λ was set to 1, but if baseline consisted of mainly copepods, λ was set to 2. By so doing, no biases were introduced to species TL level hence results were comparable. Significant differences were noted in different species TL. *E. lucens* had the highest trophic level of 2,7 (during Off-peak season) lowest was *E. recurva* (TL=2,0) during the Upwelling season. At the two transects, E. hanseni showed a higher TL at KN transect while *N. capensis* and *E. recurva* each showed 1,4 TL at WB. This explains the carnivorous diet preference of krill during Off-peak season and at the KN transects.

5. CONCLUSIONS

The Off-peak season (January 2014) showed a meaningfully higher krill abundance/biomass than the Upwelling season (September 2013). This contradicts our expectation that Upwelling season should be highly productive hence produce high krill abundance. Uncoupling of physical and biological processes seems to be the best way of trying to explain this mismatch, in which the theoretical assumptions that physical upwelling favors high productivity does not tie with krill biological processes. Maximum Upwelling may not support krill production because i) Upwelling brings up cool waters to the surface thus decreasing SST which determine krill biological processes ii) The Upwelling process involves mixing of waters which may be rough and stressful factors not favoring krill productivity iii) enhanced advection and ensuing loss of krill from the area due to Ekman transport and iv) Upwelling produces thermal stratification and decreases light penetration to euphotic zones due to increased turbidity with negative effects on krill feeding. These amongst other effects may be disadvantages to promoting krill abundance during the Upwelling season.

The KN (17°S) transects showed significantly higher krill abundances than the WB (23° S) transect. This may be mainly because the KN transect is generally deeper, much warmer due to the ABF water intrusions and generally more stable in terms of currents. Zooplankton larval advection may significantly depopulate the WB transect and instead populate the KN transects.

Population structures did not differ greatly in both space and time. Length frequency distributions did not show any pronounced differences indicating that the species under study showed a continuous annual breeding trend. Sex ratios showed females to dominate in all species. The population structure showed more or less a uniform distribution amongst different sexual development stages. The only difference noticed was that more adults were found during Off-peak than upwelling season as most females found had spermatophores attached to their thelycum while males had visibly clear spermatophores in the ducts showing greater level of mature individuals in Off-peak than Upwelling season which also uncouples the expectations from the

Upwelling season. Apparently, the krill simply showed linear but slow development over the time between the two time windows investigated.

Different trophic levels of the species in space and time were observed, suggesting further investigations to determine the reasons of changes in food selection in krill with implications to seasonal food web composition. Generally, the observations and conclusions of the current work towards krill biology within the environmental frame can be further reviewed in the greater context of the on-going GENUS-project (Geochemistry and Ecology of the Namibian Upwelling System) under which the current thesis was elaborated.

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ANNEXES

Annex 1: Krill biomass (mg.1000m^3) per Equation 1

Station	Bottom Depth (m)	Abundance (Ind. m^{-3})					
Upwelling		*E. hanseni*	*N. megalops*	*N. capensis*	*E. recurva*	*E. lucens*	**Total**
WB1.1	132			75			75
WB2.1	314	19	1				20
WB3.1	410	136	336				472
WB4.1	896	11	28	4	3		46
WB5.1	897	14	40	5	2		61
WB6.1	2891		1		7		8
KN1.1	401	65	1				66
KN2.1	401	114	3	1			118
Total		**359**	**410**	**85**	**12**	**0**	**866**
Off-peak							
WB1.2	150		19			167	186
WB2.2	470	81	218				299
WB3.2	1054		4		1		5
WB4.2	2098	4	1		9		14
KN1.2	246	2385					2385
KN2.2	417	983	20				1003
KN3.2	951	861	133				994
KN4.2	2120	65	17				82
Total		**4379**	**412**	**0**	**10**	**167**	**4968**

Annex 2: per (Equation 3)

Station	Bottom Depth (m)	Biomass (mg. m^{-3})					
		E. hanseni	***N. megalops***	***N. capensis***	***E. recurva***	***E. lucens***	**Total**
WB1.1	132			1			1
WB2.1	314	2	0				2
WB3.1	410	8	11				18
WB4.1	896	0	1	0	0		1
WB5.1	897	0	1	0	0		1
WB6.1	2891		0		0		0
KN1.1	401	6	0				6
KN2.1	401	11	2	0			13

WB1.2	150		0		5	5
WB2.2	470	10	7			17
WB3.2	1054		0	0		0
WB4.2	2098	0	0	0		0
KN1.2	246	178				178
KN2.2	417	60	0			60
KN3.2	951	45	1			46
KN4.2	2120	3	1			4

Annex 3.Regression equations obtained from length-mass relationships of the different species. (Obtained from frozen samples).

Species	**Length-mass regression**	**R^2**
E. hanseni	$Y = 0{,}399x\text{^}2{,}489$	R^2 =0,77
N. megalops	$Y = 1{,}4173e\text{^}0{,}1908x$	R^2 =0,91
N. capensis	$Y = 2{,}207x - 14{,}068$	R^2 =0,97
E. recurva	$Y = 4{,}5841x - 39{,}561$	R^2 =0,88
E. lucens	$Y = 26{,}055\ln(x) - 40{,}22$	R^2=0,99