Patterns in diversity, abundance, distribution and community structure of epi-pelagic copepods in the south-western Indian Ocean

By

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Submitted in fulfilment of the requirements for the Degree of Doctor of Philosophy

University of the Western Cape

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November 2016

This thesis is dedicated to my wife Rafieka and son Mueed.

To my mother, Julia, thank you for your support and encouragement through my career and my dad Cupido for introducing me to the wonderful marine life around the south and west coasts of Southern Africa. Recreational fishing with you was truly the first step into my career as a marine biologist.

Declaration

I declare that: ***Patterns in diversity, abundance, distribution and community structure of copepods in the south-western Indian Ocean*** is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Riaan Brinley Cedras November 2016

Signed ....

Table of Contents

Declaration .... **i**

List of Figures .... **iv**

List of Tables .... **vii**

General Abstract .... **ix**

Acknowledgements .... **xi**

Chapter 1: General Introduction **1**

1.1. Indian Ocean seafloor and biological oceanography 1

1.2. Biogeography and Plankton 11

1.3. Thesis Objectives 17

Chapter 2: Survey area and General Methods **18**

2.1. Study area and data collection 18

2.2. Seafloor and oceanographic structure of study area 20

2.3. Environmental variables 21

2.4. Zooplankton collection and processing 21

2.4.1. Laboratory procedures: Copepod identification and counts 23

2.5. Data Analysis 24

Chapter 3: Spatial patterns in the distribution of copepods across the South West Indian Ocean Ridge **26**

3.1. Results 27

3.1.1. Hydrography 27

3.1.2. Chlorophyll *a* concentrations 27

3.1.3. Copepod communities 32

3.1.4. Abundance 39

3.1.5. Diversity and richness 40

3.1.6. Vertical distributions 48

3.2. Discussion 63

Chapter 4: Biogeography of calanoid copepods in the Western Indian Ocean **72**

Abstract 73

4.1. Methods 74
4.1.1 Data Collection 74
4.2. Results 77
4.2.1. Distributional patterns of Western Indian Ocean copepod species 77
4.2.2. Western Indian Ocean copepod assemblages and the Longhurst provinces 79
4.3. Discussion 86
Chapter 5: General Conclusions 92
References 96
Annexure Section 110

List of Figures

Figure 1.1: Map showing the major bathymetry features and surface currents of the Western Indian Ocean (adapted from Lutjeharms & Bornman, 2010). 4

Figure 1.2: Biogeochemical provinces of the Western Indian Ocean on the basis of ocean currents, fronts, topography and recurrent features in the sea surface chlorophyll field (modified after Longhurst, 1998). 16

Figure 2.1: Map illustrating the study area of the South West Indian Ocean Ridge, showing the seven sampling stations occupied during November to December 2009. Table 2.1 list the details of each station……………………………………………………18

Figure 3.1: Map of the survey area and sampling stations (1 to 7) during November to December 2009, overlaid above are sea surface temperatures. Detailed outline of each sampling station is listed in Table 2.1, Section 2.1. The hydrography systems follow the abbreviations: ARC – Agulhas Return Current (greater than the 10 ºC isotherm; STF – Subtropical Front (between 13 ºC - 10 ºC isotherm); and the SAF – Sub-Antarctic Front (less than 10 ºC isotherm) (e.g. Orsi *et al.*, 1995; Belkin & Gordon, 1996; Read *et al.*, 2000, Lutjeharms, 2006; Pollard & Read, 2017; Read & Pollard, 2017). 29

Figure 3.2: Map illustrating the hydrography of the sampling area of vertical a. temperature (^{o}C), b. salinity (psu) and c. chlorophyll (µg l^{-1}) profiles in the upper 200 m of the water column along the South West Indian Ocean Ridge transect during November and December 2009. Station numbers are indicated on top of the Figure as summarised in Section 2.1, Table 2.1. The location of the major oceanographic zones is indicated as: ARC– Agulhas Return Current; STF – Subtropical Front; SAF - Sub-Antarctic Front. 30

Figure 3.3: Map illustrating A.) surface chlorophyll *a* concentrations (µg l^{-1}) and B.) integrated chlorophyll *a* concentrations (mg.m^{-2}) during the survey period in the upper 200 m of the water column along the South West Indian Ocean Ridge transect during November and December 2009. 31

Figure 3.4: Changes in upper mixed layer depths at each seamount along the South West Indian Ocean Ridge transect during November-December 2009. Seamounts have been defined into groups by the hierarchical cluster analysis in Figure 3.5. ARC – Agulhas Return Current; STF – Subtropical Front; SAF – Sub-Antarctic Front.. 32

Figure 3.5: Hierarchical cluster analysis of copepod communities along the South West Indian Ocean Ridge during November to December 2009. Sample data were log x + 1 transformed using the Bray-Curtis similarity index and group average linkages to define clusters. Superimposed are day (open circle) and night (closed circle). Group A = Agulhas Return Current; Group B = Subtropical Front; Group C = Sub-Antarctic Front. 33

Figure 3.6: 2-dimensional non-metric MDS ordination (nMDS) plot visualizing similarity between copepod communities across the South West Indian Ocean Ridge. Superimposed are the Groups A (▲), B (▼) and C (■) at the 55% level of similarity defined by the cluster analysis in Figure 3.5. Day and night samples were pooled... 34

Figure 3.7: dbRDA ordination performed on the copepod species composition of samples collected along the South West Indian Ocean Ridge during the study period November to December 2009. Vectors overlay shows the gradient strength and direction of the environmental predictors. Superimposed are the cluster Groups A (▲) = ARC, B (▼) = STF and C (■) = SAF derived by the cluster analysis in Figure 3.5... 36

Figure 3.8: Day (open circle) and night (closed circle) spatial variation in total abundance (ind.m^{-2}) of copepods collected at each seamount along the South West Indian Ocean Ridge during November to December 2009... 39

Figure 3.9: Species richness day (o), night (●) and number of genera day (open bar), night (close bar) of copepod samples for each seamount along the South West Indian Ocean Ridge during November – December 2009. Seamounts have been categorised into groups as derived by the cluster analysis (Figure 3.5). ARC – Agulhas Return Current; STF – Subtropical Front; SAF – Sub-Antarctic Front. Error bars SE.. 40

Figure 3.10: Vertical depth distributions of copepod species richness of samples collected along the South West Indian Ocean Ridge during November-December 2009. Groups are defined by the cluster analysis in Figure 3.5, Section 3.1.3. ARC - Agulhas Return Current; STF - Subtropical Front; SAF - Sub-Antarctic Front. Data summarised by day (○) and night (●). Total Day: Night samples: ARC = 45:44; STF = 10:9; SAF = 10:10. Total number of species Day: Night: ARC = 51:67; STF = 38:29; SAF = 33:45... 41

Figure 3.11: The relationship between species and genera richness of copepod samples collected across the South West Indian Ocean Ridge during November to December 2009. Linear function for the relationship between Species richness and Genera richness: Species richness and Genera richness: Species richness = 1.412x +7.486, R^2 = 0.277.................... 46

Figure 3.12: Species spatial changes of copepod community Shannon-Wiener's diversity index (H') day (○), night (●) at seamounts sampled along the South West Indian Ocean Ridge during period of November to December 2009. Seamounts have been classified into groups as determined by the cluster analysis (Figure 3.5). ARC – Agulhas Return Current; STF – Subtropical Front; SAF – Sub-Antarctic Front. 47

Figure 3.13: Vertical day (○) and night (●) of copepods (densities.m^{-3}) depth distribution of: top panel total copepods, middle panel total non-calanoids, bottom panel total calanoids collected along the South West Indian Ocean Ridge during November and December 2009. Groups

were defined by the cluster analysis in Section 3.1.3, Figure 3.5. ARC - Agulhas Return Current; STF - Subtropical Front; SAF - Sub-Antarctic Front. 49

Figure 3.14: Vertical day (open bar) and night (filled bar) distributions (%) of dominant copepod taxa sampled along the South West Indian Ocean Ridge (SWIOR) over the study period November to December 2009 for each major oceanographic zone. November to December 2009 for each major oceanographic zone. Numbers at bottom of plots indicates densities.m^{-3}. Day is designated as “D” and night as “N”. Groups are defined by the cluster analysis in Section 3.1.3, Figure 3.5. ARC – Agulhas Return Current; STF– Subtropical Front; SAF – Sub-Antarctic Front. Species depth distributions are plotted in decreasing abundances along the SWIOR: *Oithona*; *Oncaea*; *Corycaeus*; *Ctenocalanus vanus*; *Paracalanus parvus*; *Acartia danae*; *Farranula*; *Clausocalanus brevipes*; *Mecynocera clausi*; *Clausocalanus laticeps*; *Pleuromamma piseki*; *Calocalanus styliremis*; *Metridia lucens*; *Calanus simillimus*. 58

Figure 3.15: Weighted Mean Depths of the dominant top three taxa: top panel *Oithona* day (○) and night (●); *Ctenocalanus vanus* day (□) and night (■); *Oncaea* day (△) and night (▲) of samples along the South West Indian Ocean Ridge during the study period of November to December 2009. Stations have been classified into groups derived by the cluster analysis in Section 3.1.3, Figure 3.5. ARC– Agulhas Return Current; STF– Subtropical Front; SAF– Sub-Antarctic Front Group. 62

Figure 4.1: Dendrogram showing cluster analysis of 75 five-degree grid squares grouped in relation to Longhurst biogeochemical provinces (1998) (see Materials and Methods for acronyms full names). These presence and absence data were transformed using the Bray-Curtis similarity index and group average linkages to recognize clusters. A = southern latitude cluster of samples (including clusters A1 and A2), B = northern latitude cluster of samples (including clusters B1, B2 and B3). Cluster groups are sliced at the 14% level of similarity. 80

Figure 4.2: Map illustration to assist interpretation of the samples responsible for similarity in structure of cluster Groups as illustrated in Figure 3. Grid squares are plotted in order of cluster Groups. 5^{o} squares in yellow are those clustered within Group A1, in green are those clustered within Group A2, in light red are those clustered within Group B1, in light blue are those clustered within Group B2, whilst those in purple are from Group B3. 81

Figure 4.3: 3-dimensional unconstrained non-metric MDS ordination (nMDS) plot visualizing similarity matrices computed for the Western Indian Ocean Longhurst biogeochemical provinces on copepod assemblages (1998) (see Materials and Methods for acronyms full names). 85

List of Tables

Table 2.1: Zooplankton and hydrographic stations, on and off the South West Indian Ocean Ridge, sampled from the RV *Dr. Fridtjof Nansen* during November - December 2009. D, day: N, night. 19

Table 3.1: The results of the DistLM routine showing the marginal and sequential tests for the abundance of copepods sampled along the South West Indian Ocean Ridge during November and December 2009. Volume filtered (m^{-3}), Sea Surface Temperature (^oC), Difference Bottom-Surface Temp (^oC), Integrated Chlorophyll ($mg.m^{-2}$), Chlorophyll-MAX (m) and Upper mixed-layer depths (m) were used from the survey area as predictors 35

Table 3.2: Top panel showing top ten copepod species identified by SIMPER, responsible for similarity in structure of cluster Groups, and bottom panel list top ten copepod taxa identified by SIMPER, responsible for the dissimilarity in structure of cluster Groups as illustrated in Figure 3.5, performed on total abundance ($ind.m^{-2}$) data, log transformed (log x + 1). Top Panel: Contrib% contribution of species to the overall similarity between clusters and Cum.% = cumulative contribution of species to the overall similarity. Bottom Panel: Contrib% contribution of that species to the overall dissimilarity between clusters and Cum.% = cumulative contribution of species to the overall dissimilarity. 38

Table 3.3: The mean total abundance of copepods ($ind.m^{-2}$) of samples collected along the South West Indian Ocean Ridge transect conducted during November and December 2009. The groups were identified by the cluster analysis in Figure 3.5. ARC – Agulhas Return Current; STF – Subtropical Front; SAF – Sub-Antarctic Front. 42

Table 3.4: Daytime composition ($densities.m^{-3}$) of dominant copepod taxa sampled at different depth intervals in the upper 200 m of the water column across the South West Indian Ocean Ridge during the period of November to December 2009. Groups were identified by the cluster analysis in Figure 3.5, Section 3.1.3. ARC - Agulhas Return Current; STF - Subtropical Front; SAF - Sub-Antarctic Front. 54

Table 3.5: Nightime copepod composition ($densities.m^{-3}$) of dominant taxa collected at different depth intervals in the upper 200 m across the South West Indian Ocean Ridge for the duration of November to December 2009. Groups were derived by the cluster analysis (Figure 3.5, Section 3.1.3). ARC - Agulhas Return Current; STF - Subtropical Front; SAF - Sub-Antarctic Front. 56

Table 4.1: List of rare and widespread copepod species (31) that were excluded from the final data matrix for the Western Indian Ocean. 76

Table 4.2: Copepod species (149) selected for the construction of biogeographical provinces for the Western Indian Ocean. 78

Table 4.3: Top row list top ten copepod species identified by SIMPER, responsible for similarity in structure of cluster Groups, and below row list top ten copepod taxa identified by SIMPER, responsible for the dissimilarity in structure of cluster Groups as illustrated in Figure 5.1 based on presence and absence data. Contrib% contribution of that species to the overall similarity between clusters and Cum.% = cumulative contribution of species to the overall similarity. Below, Contrib% contribution of that species to the overall dissimilarity between clusters and Cum.% = cumulative contribution of species to the overall dissimilarity. 82

Table 4.4: List of copepod species identified by SIMPER, responsible for similarity (cumulative percentage: 60%) in structure of cluster Groups as illustrated in Figure 5.1 based on presence and absence data. Contrib% contribution of that species to the overall similarity between clusters and Cum.% = cumulative contribution of species to the overall similarity 83

Table 4.5: Results of the pairwise tests from ANOSIM for significant differences in copepod assemblages between Longhurst (1998) biogeochemical provinces (999 permutations). .. 84

General Abstract

The primary objective of this study was to investigate patterns in diversity, abundance, distribution and community structure of epi-pelagic copepods across the South West Indian Ocean Ridge (SWIOR). A survey was conducted across the SWIOR at two off-ridge and five seamount stations between 26.94 ^{o}S to 41.48 ^{o}S in November and December 2009. Copepod species richness and abundance was compared at vertical and horizontal scales day and night, at irregular time intervals across the Agulhas Return Current (ARC), Subtropical Front (STF) and Sub-Antarctic Front (SAF).

A total of 49 genera and 135 epi-pelagic copepod species were identified along the SWIOR transect, and the Order Calanoida had the most genera. Species richness was highest in the ARC and lowest at the stations associated with the frontal areas of the STF and the SAF. The total number of copepod species was higher during the night than day. Total copepod abundance along the transect was highest towards the frontal area of the STF, and the genus *Oithona* spp. comprised almost 50% of the total number in all copepod samples. Three distinctive copepod assemblages were identified by multivariate analysis, and communities were associated with the STF, ARC and SAF. *Clausocalanus laticeps*, *Metridia lucens* and *Calanus simillimus* were only recorded in the southern part of the survey area and their absence in the north may demonstrate the strong stratification of the STF, and more likely to be the physiological properties, adaptation to their environment and life histories.

Overall, the distribution and abundance of copepods appeared to be associated with temperature, salinity and chlorophyll across the major oceanographic regions. Given the maximum sampling depth (200 m) of the present investigation and the lack of seamount sampling stations, it was not possible to detect seamount advective processes.

The secondary objective of this study was to collate data to test Longhurst's ecological provinces using calanoid copepod assemblages in the Western Indian Ocean (WIO). Data were consolidated from the published literature from the WIO and combined with the dataset collected from the SWIOR. The study area between the coastal waters of Somalia (10^o N) to the Cape of Good Hope and eastwards to 65^o E was divided into 85 five-degree grid squares, encompassing the Longhurst (1998) biogeochemical provinces. Calanoid copepods were scored as present or absent in each 5^o grid square. Epi-pelagic biogeographic provinces in the WIO revealed that copepod assemblages were consistent with the major water masses. The WIO could be delineated into cold- and warm-temperate and subtropical and tropical groupings, within which there were generally strong subgroupings based on latitude and longitude. There was fairly strong support for Longhursts' biogeochemical provinces, but differences were noted. Differences amongst Longhursts' provinces were ascribed to variation in sampling effort across the region and to the qualitative nature of the analyses and dynamic nature of the physical oceanography.

Acknowledgements

I owe my sincere gratitude to my supervisor Prof. M.J. Gibbons. Since the start of my marine science career at the BSc Honours level, his patience and understanding have stood the test of time. There is no amount of words that can explain his support and assistance with my development as a marine scientist. I'm grateful and thank you for believing in me.

I would also like to thank him for arranging a workshop on copepod identification, and a special thanks to the workshop instructors Claire Davies and Anita Slotwinski of Commonwealth Scientific and Industrial Research Organisation (CSIRO) of Marine and Atmospheric Research group from Australia, for inspiring me with the taxonomical works of copepods. It was a challenging and tremendous learning experience. A special thanks to the Agulhas Somalia Current Large Marine Ecosystem Training Program (ASCLME) project co-ordinator Tommy Bornman, from the South African Environmental Observation Network (SAEON), Elwandle Coastal Node in Port Elizabeth, for allowing me to participate in the cruise conducted in 2009, which was a success. Special thanks are due to the captain and crew of the RV *Dr. Fridtjof Nansen* for the deployment and management of equipment at sea, and for their warm hospitality.

To my family, my mother Julia and father Cupido, my brother Shanick and sister Kaylin for believing in me, and their patience during my undergrad and postgraduate studies. To all my family inlaws, especially mother in law Soraya and father in law Rafiek for their support during this project.

To all my colleagues at UWC for their support and understanding, above all Martin Hendricks, Maryke Meerkotter-Malan, Bradley Flynn, Suzanne Short for stepping in my shoes during fieldtrips.

To my colleague and friend, Benjamin Mouers, his encouragement, support and opinions were needed during my studies.

To all my friends, in no particular order, Marcus Jass, Bradley Oppel, Randall Fortune and Fahiem Davis, thank you for being good friends for all the good laughs and the support and encouragement during the progress of this project.

Last and mostly, to my wife Rafieka and my son Mueed who warrants my gratitude for having the patience to cope with me, and encouragement throughout the project.

This project was made possible by bursary and financial support provided through funds by the National Research Foundation, Scarce Skills Masters and Doctoral Scholarship and the research facilities provided by the University of the Western Cape. I would also like to thank the ASCLME, and its sponsors (EAF/UNDP), for providing ship's time on the RV *Dr Fridtjof Nansen*.

Chapter 1: General Introduction

Zooplankton by definition drift with ocean currents and are at the mercy of the dynamics of water masses and currents (Mauchline, 1998). Planktonic animals have proscribed physiological characteristics and cannot be taken to far from the circumstances to which they are adapted, especially their energy requirements (Mauchline, 1998). Each species obviously needs continuity between the upstream and downstream of their habitat to maintain their populations and genetic integrity. Here we address the particular circumstances of the south-western part of the Indian Ocean that may influence epipelagic copepod assemblages. We consider the role that sea floor topology (especially seamounts) may have on circulation, the hydrography of the Indian Ocean and the way the physicochemical system drives productivity of the food web especially phytoplankton. Finally, zooplankton diversity and factors affecting it are discussed.

1.1. Indian Ocean seafloor and biological oceanography

The basin floor of the Indian Ocean consists of geomorphogical features such as abyssal plains, mid ocean ridges and a few seamounts and islands that sub-divide the whole into several major basins along sections of the central ocean ridge. The Ninety-East Ridge, the Mascarene Ridge and the Chagos-Laccadive Ridge, and active ridges of the Carlsberg Ridge and the Mid-, Southwest and the Southeast Indian Ridges all link with the global mid-ocean ridge (Demopoulos *et al.*, 2003; Ingole & Koslow, 2005). Mid-oceanic ridges form seamounts that can be isolated summits greater than 1000 m from the ocean's floor, or their summits can form part of over 100, 000 seamounts along an oceanic ridge (Clark, 2007).

Due to their differences in form, size, depth and location seamounts can sometimes influence ocean flow that lead to changes in surface production (e.g. Boehlert, 1988; Gille *et al.*, 2004; Rowden *et al.*, 2005), and the enhancement of ecological processes (e.g. Genin *et al.* 1994; Haury *et al.*, 2000), which in turn may result in differences between adjacent seamount communities along an oceanic ridge (Clark *et al.*, 2010). As such, seamounts provide habitat to fish, suspension and filter feeders and plankton communities that are often resident too a particular seamount (Rogers, 1993). The last decade has seen seamount research become increasingly important as subjects of biodiversity and conservation debate (Samadi *et al.*, 2006; Clark *et al.*, 2010; Morato *et al.*, 2010, Garcia *et al*., 2013; Djurhuus *et al*., 2017; Rogers *et al*., 2017). For example, the South West Indian Ocean Ridge (SWIOR) was investigated by the Russians in the 1970s, and was subsequently subjected to commercially fisheries in the early 1980s (Rogers, 1993; Rogers *et al*., 2017).

The Indian Ocean is characterized by climatic and oceanic variability which is a consequence of the seasonally reversing monsoon wind system and the closure of the Indian Ocean north of the equator, trapping the equatorial currents (Demopoulos *et al.*, 2003). The hydrography of the southern Indian Ocean is primarily influenced by the surface circulation of the Subtropical Gyre (STG), which flows east to west from the Indonesian region through the Saya de Malha and Nazareth Banks southeast of Seychelles (Figure 1.1). The western extension of the STG contributes its volume as the South Equatorial Current (SEC) to the

Western Indian Ocean (WIO) region (Schott & McCreary Jr, 2001), which includes the territorial waters of Somalia, Kenya, Tanzania, Mozambique and the south-eastern coastline of South Africa, as well as the islands of Madagascar, Seychelles and the Mascarene Islands (Sherman & Hempel, 2009).

Dynamic large-scale oceanographic features in the WIO region play an important role in productivity, biodiversity, fisheries and the physiochemical environment (Sherman & Hempel, 2009). The marine environment serves as a significant source of food and employment for the livelihoods of 10 countries, and some country's primary source of income is strongly dependant on living marine resources (Sherman & Hempel, 2009).

The WIO is characterised in the north by the shallow, monsoon-dominated Somali Current, which has complex interactions with the East African Coastal Current (EACC). During May to October, the EACC flows north in the northern Indian Ocean gyre circulation, but reverses its flow from December to April and turns east at ~2 °S, forming the Equatorial Counter Current that bathes the north of Seychelles and the Lakshadweep-Maldives-Chagos group of islands (Schott & McCreary Jr, 2001).

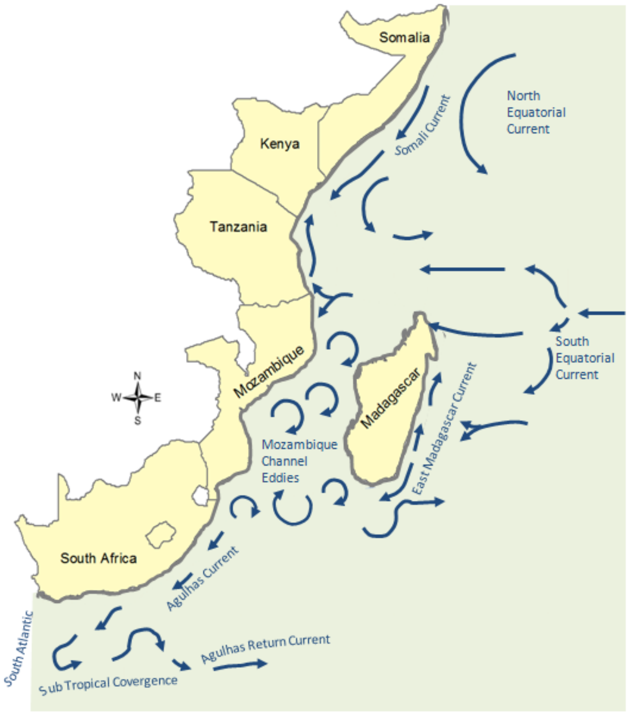

Figure 1.1: Map showing the major bathymetry features and surface currents of the Western Indian Ocean (adapted from Lutjeharms & Bornman, 2010).

In the southern part of the WIO, the SEC expands its main flow when it reaches the Madagascan coastline, and splits in the vicinity of the East African and Madagascan coast (Schott & McCreary Jr, 2001; Lutjeharms & Bornman, 2010). One branch of the SEC flows northwards as the linear EACC, as far as the Tanzanian and Kenyan coasts, whilst the other flows southward forming variably strong anti-cyclonic rings that develop in the narrows of the Mozambique Channel, and which may shift its position further poleward (Lutjeharms *et al.*, 2000; Schott & McCreary Jr, 2001; Lutjeharms & Bornman, 2010). The fast flowing and intense East Madagascar Current (EMC) flows along the edge of the narrow continental shelf off Madagascar, where one branch moves poleward and the other equatorward (Lutjeharms *et al.*, 2000). The flow of waters from the EMC and Mozambique Channel eddies contribute volume to the Agulhas Current (AC) (Lutjeharms *et al.*, 2000; Lutjeharms, 2006). The AC, which is the world's largest western boundary current (Schouten *et al.*, 2000; Lutjeharms, 2006), is associated with a strong southward transport of up to ~55 sv (Donohue *et al.*, 2000). The intense southward flow of the AC retroflects eastwards as the Agulhas Return Current (ARC) between 16 °E and 20 °E, north of the Subtropical Front, where some water of the ARC is lost to the South Atlantic; with its eastward extent limited by the SWIOR (Lutjeharms & Valentine, 1984; Lutjeharms, 1985; Sultan *et al.*, 2007). The ARC, the Subtropical Front (STF) and the Sub-Antarctic Front (SAF) form shifts between warm-saline subtropical waters and cold-less saline Sub-Antarctic waters (Read *et al.*, 2000; Sultan *et al.*, 2007; Garcia *et al.*, 2013; Pollard & Read, 2017; Read & Pollard, 2017). The meeting of these fronts further creates a marked sea surface temperature gradient of ~1 °C km^{-1} (Read & Pollard, 1993; Read *et al.*, 2000). The constant interplay between these oceanic fronts contribute to changes in biogeochemistry and phytoplankton production (Bathmann *et al.*, 1997; Llido *et al.*, 2005; Naik *et al.*, 2015) and the possible development of oceanic barriers (Orsi *et al.*, 1995; Belkin & Gordon, 1996; Lutjeharms & Ansorge, 2001, Fiala *et al.*, 2003), as well as to possible differences in faunal communities over the SWIOR (e.g. Denda & Christiansen, 2014). Ecologically distinct biogeochemical provinces are associated with the SWIOR, the Indian Subtropical Gyre Province (ISSG) in the north, and the Subtropical Convergence Province (SSTC) in the south (Longhurst, 1998).

The WIO encompasses the Agulhas Current Large Marine Ecosystem (ACLME) and the Somali Current Large Marine Ecosystem (SCLME) (Sherman & Hempel, 2009). LMEs are delimited as areas with ocean space of ≥200 000 km^2 with dynamic hydrographic systems, submarine topography, productivity and trophically dependant populations (Sherman & Alexander 1986; Sherman 1991). The region of the WIO had been noted as a moderate to high productive ecosystem (Baars *et al.*, 1995; Bakun *et al.*, 1998; Lutjeharms, 2006) and is recognised as a distinctive ecological province (Sherman & Hempel, 2009; Bensted-Smith & Kirkman, 2010), with high diversity of marine life and endemism (Sherman & Hempel, 2009). The Agulhas Somali Large Marine Ecosystem (ASCLME) region has been outlined by the Global International Waters Assessment as being severely impacted due to the overexploitation of marine resources (Payet *et al.*, 2004).

Primary productivity of the WIO is poorly known, except for water masses close to land and regions close to well established marine institutions (e.g. Conway, 2005; Richoux & Froneman, 2009; Lutjeharms & Bornman, 2010). A general overview on the region's surface chlorophyll data has been provided by Longhurst (1998) using Coastal Zone Colour Scanner (CZCS) images and published information. The Indian Subtropical Gyre Province (ISSG) is characterized by low integrated chlorophyll *a* concentrations (~0.05 mg.m^{-3}) particularly during austral winter months (July-October, 10°S) (Figures 1.1 and 1.2). Seasonal blooms occur across the shallow banks of the Mauritius-Seychelles Ridge (5 – 20 °S) and the Chagos archipelago. The advancement of nutrient-enriched surface waters on the western side of the Mauritius-Seychelles Ridge spreads as far as the islands of Seychelles (Ragoonaden *et al.*, 1987; Vethamony *et al.*, 1987). In the Eastern African Coastal Province, upwelling occurs during the Northeast monsoon south of the Madagascar Current (25 °S – 34 °S) (Lutjeharms *et al.*, 1981). The Agulhas Bank (35 °S) is characterised by seasonal succession of primary production between nano-phytoplankton and cells of >15-µM (McMurray *et al.*, 1993). The Agulhas Bank is characterized by a 60 – 95% of total production of larger diatoms throughout most of the year (Longhurst, 1998). Shelf-edge upwelling and inflow of cold water over the Agulhas Bank create a shallow thermocline (30 m) during summer months, which in turn promotes algal growth (Longhurst, 1998). Algal growth associated with the edge of shelf eddies is a common feature of the Agulhas Retroflection area (Longhurst, 1998).

The Sub-Antarctic waters of the SSTC is characterised by low nitrate concentrations <0.5 µM (Longhurst, 1998). At and near the surface, the interactions of the ARC (in the ISSG province) and Subtropical Front waters (in the SSTC province) mixes nutrient-poor and nutrient-rich water north and south across frontal zones (Longhurst, 1998; Llido *et al.*, 2005; Naik *et al.*, 2015).

Zooplankton diversity in the open Indian Ocean was comprehensively studied between the 1930's to 1960's (e.g. Pettersson *et al.*, 1957; Knudsen, 1967), along with (at that time) unprecedented scientific investigations in 1962 - 1965 during the International Indian Ocean Expedition (IIOE) (Zeitschel, 1973). The results from these cruises were published in a series of guides, some inaccessible and others in useful sources (e.g. Zeitschel, 1973). While the zooplankton of the open Indian Ocean has been fairly well documented (e.g. Timonin, 1971; Zeitschel, 1973; Madhupratap & Haridas, 1986; Rao & Griffiths, 1998) only a few detailed zooplankton biodiversity studies were carried out and published for the South Western Indian Ocean (SWIO) region, with a few off the east coast of South Africa (Huggett, 2014), Mozambique (Leal *et al.*, 2009), Tanzania (Lugomela *et al.*, 2001), and Madagascar (Gaudy, 1967; Frontier, 1973), Somalia (Smith, 1982); and between the islands of Mahé and Rodrigues (Burnett *et al.*, 2001), as well as over the Mascarene Plateau (Gallienne *et al.*, 2004; Conway, 2005).

There is a scarcity of published literature on zooplankton studies on seamounts in the south west Indian Ocean (e.g. Vereshchaka, 1995). Reports on zooplankton studies over seamounts stem mostly from the eastern Pacific Ocean (e.g. Genin *et al.*, 1988; Genin *et al.*, 1994) and the Atlantic Ocean (Nellen, 1974). Despite the large amount of data collected on seamounts in the Indian Ocean by French (e.g. Duhamel & Ozouf-Costaz, 1985) and Soviet vessels (Gubanov, 1988), only a few publications have been produced. The interactions of seamounts with surrounding waters masses might result in the displacement of zooplankton populations (Dower & Mackas, 1996; Wilson & Boehlert, 2004; Genin & Dower, 2007). For example, vertically migrating zooplankton can be advected from seamount margins into the water column above summits. At dusk, seamount summits can limit the natural range of diel migratory zooplankton, and their aggregations subsequently aid as a source of food during daylight hours for visually feeding predators (Isaacs & Schwartzlose, 1965; Genin *et al.*, 1988; Genin *et al.*, 1994; Genin, 2004; Wilson & Boehlert, 2004). However, changes in zooplankton biomass above seamounts are also related to changes in the horizontal distribution of nutrients and the interactions between ocean currents rather than localised seamount processes alone (e.g. Denda & Christiansen, 2014).

As elsewhere, the epi-pelagic layers in the open ocean and over seamounts are dominated by zooplankton (e.g. Verheye *et al.*, 1992; Rogers, 1993,), and it is likely that the mesozooplankton community of the WIO region is dominated by copepods both numerically and in terms of biomass (Zeitschel, 1973; De Decker, 1984; Jónasdóttir *et al.*, 2013). As the majority of the species are herbivorous or at least omnivorous, copepods provide an important link between the primary producers and higher trophic levels (Verheye *et al.*, 1992; Kleppel, 1993; Lugomela *et al.*, 2001). Copepods are the preferred prey of a wide variety of invertebrate and vertebrate predators including commercially exploited pelagic fish (James, 1988; Øresland, 2000; van der Lingen, 2002; Nyunja *et al.*, 2002). In complex environmental variable conditions, calanoid copepod community structure and diversity have been shown to be stable during strong environmental events (e.g. Kozak *et al.*, 2014); and their abundance and patterns in distribution may serve as good water mass indicators (e.g. Beaugrand *et al.*, 2001).

Diel vertical migration is amongst the most intriguing behaviour of copepods, which involves the vertical movement of copepods through the water column over a 24 hour cycle (Ringelberg, 2009). This behaviour has been documented for many copepods and often varies between and within species. Copepods usually migrate to deep waters during daytime to avoid being fed upon by visual predators in epipelagic layers, and at night return to the surface waters to feed on phytoplankton. The factors that influence DVM in lakes and oceanic communities have been reviewed by Ringelberg (2009) and Cohen and Forward (2009) it is widely agreed that a change in light intensity trigger this behaviour.

Diel vertical migration by deep-living copepod species above seamounts occurs at night from the mesopelagic layer, and individuals enter the euphotic zone often to feed on phytoplankton aggregations (e.g. Genin *et al.*, 1994; Haury *et al.*, 2000; Roe, 1984; Haury, 1988; Hays, 1996). The stomach contents of seamount fish have shown to be dominated by deep-living copepods, such as species of the genus *Oncaea* and *Pleuromamma* (e.g. Fock *et al.*, 2002; Christiansen *et al.*, 2009). Species that display diel vertical migration in turn transport dissolved organic carbon and nitrogen out of the euphotic zone to nourish trophic chains in deeper regions (e.g. Steinberg *et al.*, 2000; Bradford-Grieve *et al.*, 2001; Hirch & Christiansen, 2010). Otherwise, above seamounts, this production would be accessible to aggregations of visual predators when trapped in the upper water column (Genin *et al.*, 1988, 1994; Haury *et al.*, 2000; Wilson & Boehlert 2004; De Forest *et al.*, 2009).

Despite the importance of copepods in the northern Pacific and Atlantic ecosystems, a much greater understanding of zooplankton diversity, abundance and assemblage structure for the WIO region is needed. This is a crucial gap in knowledge as our understanding of species richness of the WIO lags behind that of other regional seas e.g. Pacific Ocean (Rochette & Billé, 2012), given that islands in the region are from different geological periods and experience different oceanographic conditions (Camoin *et al.*, 2004).

As we know, copepods form aggregations above seamounts (Isaacs & Schwartzlose, 1965; Genin *et al.*, 1988; Genin *et al.*, 1994; Genin, 2004; Wilson & Boehlert, 2004) and at oceanic fronts (e.g. Errhif *et al.*, 1997; Hosie *et al.*, 2014). It is likely that changes in this ecosystem are more likely to be influenced by changes in both the physical and biological environment rather than regional seamount processes (Denda & Christiansen, 2014).

This study only investigates changes in the horizontal and vertical distribution (Ch. 3) and patterns in calanoid diversity during day and night in the upper 200 m of the water column above the SWIOR. Since copepods form the bulk of zooplankton, the results can provide hypotheses regarding the distribution of other zooplankton groups.

1.2. Biogeography and Plankton

Biogeographic studies are based upon the understanding of species distributions and the relationship of distributional patterns to oceanographic features, faunal zones, and possibly a link to food web structure (e.g. Steuer, 1933; Sewell, 1948; Lawson, 1977; Dadon & Boltovskoy, 1982; Gibbons, 1997b). Zoogeographic studies for the Indian Ocean have been largely based on latitudinal gradients, and on designated recurrent zooplankton groups (e.g. Sewell, 1948; Fleminger & Hulsemann, 1973). Attempts to map the geographic distribution of copepods in the Indian Ocean have been made by Steuer (1933) and Sewell (1948). These authors noted Indo-Pacific copepods north of the subtropical front (10 ^{o}S), and subtropical cognates between 10 ^{o}S and 35 ^{o} – 45 ^{o}S. Sewell (1948) pointed out that copepod diversity decreases both longitudinally (east to west) and latitudinally (north to south) as well as with depth. Sewell (1948) was able to identify the major water masses from the Indonesian Archipelago, as well as from the Agulhas Current system.

Published results on copepods around southern Africa indicate that diversity also decreases in an east to west direction, and distinct assemblages of copepods are associated with the Agulhas Current, Agulhas Bank and Benguela upwelling region (e.g. De Decker, 1984; Huggett *et al.*, 2009). Important works on the distribution of Candaciidae in the Indian Ocean includes those of Jones (1966a, b) and Lawson (1977). These authors partitioned the Indian Ocean into distinct regions based on recurrent groups and species. In the case of Lawson (1977), morphological (mandible) clusters of candaciid species were used to separate the Indian Ocean into two distinct geographical areas: one dominated by equatorial forms, and one from the central gyre. Fleminger and Hulsemann (1973) reported that the Indian Ocean consists of different breeding habitats for epipelagic copepods. These authors suggested that the meridians 40 ^{o}N and 40 ^{o}S are a characteristic of circumglobal species, with tropical forms between the 30 ^{o}N and 30 ^{o}S.

The distribution of copepods in the Indian Ocean appears similar to that of euphausiids, as described by Brinton and Gopalakrishnan (1973). Brinton and Gopalakrishnan's (1973) accounts of the distributions of euphausiids in the Indian Ocean indicated circumglobal species (e.g. *Thysanopoda aequalis*) in the north (10 ^{o}N) and equatorial species (e.g. *T. aequalis*) at the equator (0^o). The authors noted subtropical species e.g. *Nematoscelis gracilis* extend towards 10 ^{o}S and a mixture of tropical and subtropical species e.g. *Euphausia brevis* are found between 25 - 30 ^{o}S, and tropical and temperate species (e.g. *E. recurva*) between 40 – 45 ^{o}S.

Other zooplankton groups, such as chaetognaths, have been described by Nair (1978) who recognized three major faunal zones in the Indian Ocean, which consisted of Indo-Pacific species, cosmopolitan groups, and Atlantic and Sub-Antarctic forms. Nair (1978) indicated that the hydrochemical front at 10 ^{o}S and the Sub-Tropical Front in the south were major zoogeographical zones. Zoogeographical studies during the IIOE (1960 - 1965) focused on larger zooplankton forms, due to the mesh size (greater than 200 µm) used during zooplankton collections. As such more details on macrozooplankton taxa distributions are published in Zeitschel (1973) for the Indian Ocean.

As noted, the changes of zooplankton faunal regions were both latitudinally and longitudinally for the Indian Ocean, and were to some extent consistent with the major water masses (Wyrtki, 1973; Schott & McCreary Jr, 2001). Euphausiid faunal distributions in the Indian Ocean (Brinton & Gopalakrishnan, 1973) and in the Atlantic and Pacific oceans (e.g. Gibbons, 1997b; Letessier *et al.*, 2011; Brinton, 1962) have provided information on the primary drivers of zooplankton community structure within the euphausiid assemblage. In an attempt to understand the balance between pelagic production and consumption, Longhurst (1998) delineated the Indian Ocean into eight biogeochemical provinces using satellite images in agreement with "ocean currents, fronts, topography and recurrent features in the sea surface chlorophyll field". The biogeochemical provinces suggested by Longhurst (1998), propose that groups of species within a biogeochemical province would have distinct characteristics too those from different provinces. Ekman (1953) was earlier able to identify the major marine environments from the Indonesian Archipelago using temperature regimes, allopatric vicariance of biota following evolutionary time. Ekman (1953) suggested that the epicentre for marine biodiversity for the Indian Ocean is near the Malay Archipelago and that species spread from this region to neighbouring waters via the primary pelagic drivers of ocean currents. In addition, the Malay Indonesian Archipelago consists of a dispersal of faunas from both the Indo-Polynesian and WIO regions (Briggs, 1974). Briggs (1974) divided the marine environment into large shelf biogeographic areas, by using 10% endemic biota and evolutionary events. Spalding *et al*. (2007) pointed out in their system marine ecoregions similar to those recognised by Briggs (1995), as clear evolutionary areas using temperature profiles, latitude and vicariance of populations.

Compared to the marine environment for the pelagos, assemblage changes in benthic faunal composition have been widely documented for WIO coral reef communities, where diversity patterns follow the main flow of waters from the Indo-Pacific region (Obura, 2012). The northern Mozambique Channel is characterised by a high coral diversity, with a temperature-sensitive community that appears to be susceptible to periods of intense environmental anomalies e.g. EL NIÑO (McClanahan *et al*., 2011; Obura, 2012; McClanahan *et al*., 2014). A decrease in species diversity in the Indian Ocean from east to west, and north to south, has been observed for some invertebrate taxa such as molluscs (e.g. Vermeij, 1973; Wells, 2002) and echinoderms (e.g. Clark & Rowe, 1971; Rowe & Richmond, 2004), as well as reef fishes (e.g. Allen, 2008; Cowman & Bellwood, 2013). For example, Santini and Winterbottom (2002) used coral reef endemism to divide the global marine environment into biogeographical regions and identified the WIO region into four major areas: Somali Basin, Natal Basin, Mascarene Plateau and the Chagos Ridge. Kulbicki *et al*., (2013) used a species similarity approach to cluster reef fish communities and delineated the WIO region into three biogeographic areas: Arabian Basin; the coastal regions of East Africa and the Mascarene and the Chagos-Maldives clustered together. In general, it would appear that diversity and distribution patterns of both the benthos (e.g. Obura, 2012) and pelagos (e.g. Sewell, 1948) appear to mirror the major oceanographic currents in both the tropical and subtropical regions of the Indian Ocean (Costello *et al.*, in press). And whilst the distribution patterns of the zooplankton fauna in the Indian Ocean are characterised as Indo-Pacific (e.g. Rao, 1979; Rao & Madhupratap, 1986), much less is known about the spatial distribution of species for the WIO. The secondary aim of this study therefore explores and tests Longhurst's (1998) contention by investigating copepod assemblages across the biochemical provinces (Figure 1.2) recognised by Longhurst (1998) for the WIO (Ch. 4).

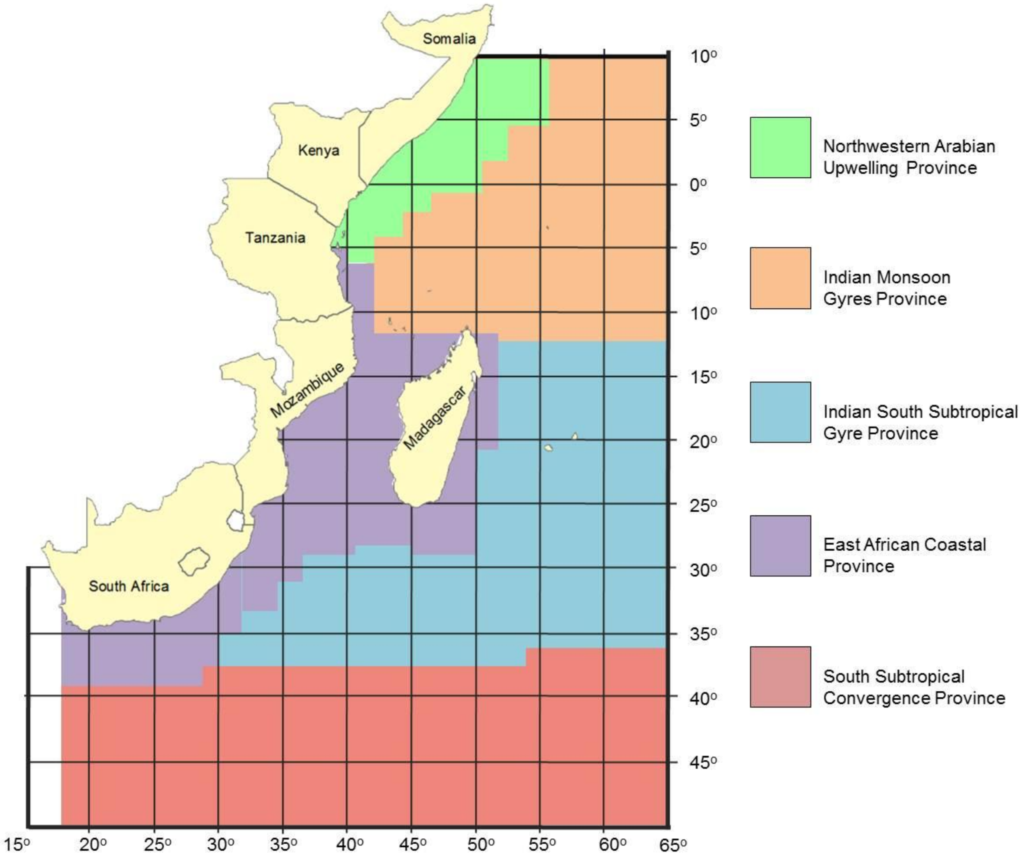

Figure 1.2: Biogeochemical provinces of the Western Indian Ocean on the basis of ocean currents, fronts, topography and recurrent features in the sea surface chlorophyll field (modified after Longhurst, 1998).

1.3. Thesis Objectives

The primary aim of this study focussed on patterns in diversity, abundance, distribution and community structure of Copepoda along the South West Indian Ocean Ridge. The secondary aim is to test the biogeography of calanoid copepods in the Western Indian Ocean. To understand the processes that may structure local assemblages and biogeographic patterns in the distribution of copepods in the WIO, this study address three questions:

1. Does coupling between the physico-chemical environment affect the density, diel vertical migration and the habitat partitioning of epi-pelagic copepods in the South West Indian Ocean Ridge (Ch. 3)?
2. How are the epi-pelagic copepod community structured at the vertical and horizontal scales day and night across the Agulhas Return Current (ARC), Subtropical Front (STF) and Sub-Antarctic Front (SAF) (Ch. 3)?
3. How does the biogeographic structure of epi-pelagic copepod assemblages change within the Western Indian Ocean among Longhurst's (1998) five provinces? Northwestern Arabian Upwelling Province (ARAB); Indian Monsoon Gyres Province (MONS); Indian Subtropical Gyre Province (ISSG); the East Africa Coastal Province (EAFR) and the Subtropical Convergence Province (SSTC) (Ch. 4).

Chapter 2: Survey area and General Methods

2.1. Study area and data collection

The materials and methods for Chapter 3 are presented here: those for Chapter 4 are provided in Chapter 4. The physical and biological data used in this study were collected across the South West Indian Ocean Ridge (SWIOR) during November and December 2009 (Figure 2.1), aboard the research vessel *Dr. Fridtjof Nansen*. The data were collected as part of a multidisciplinary cruise by NORAD's EAF-Nansen, UNDP/IUCN project funded by the Global Environment Facility and the ASCLME programme.

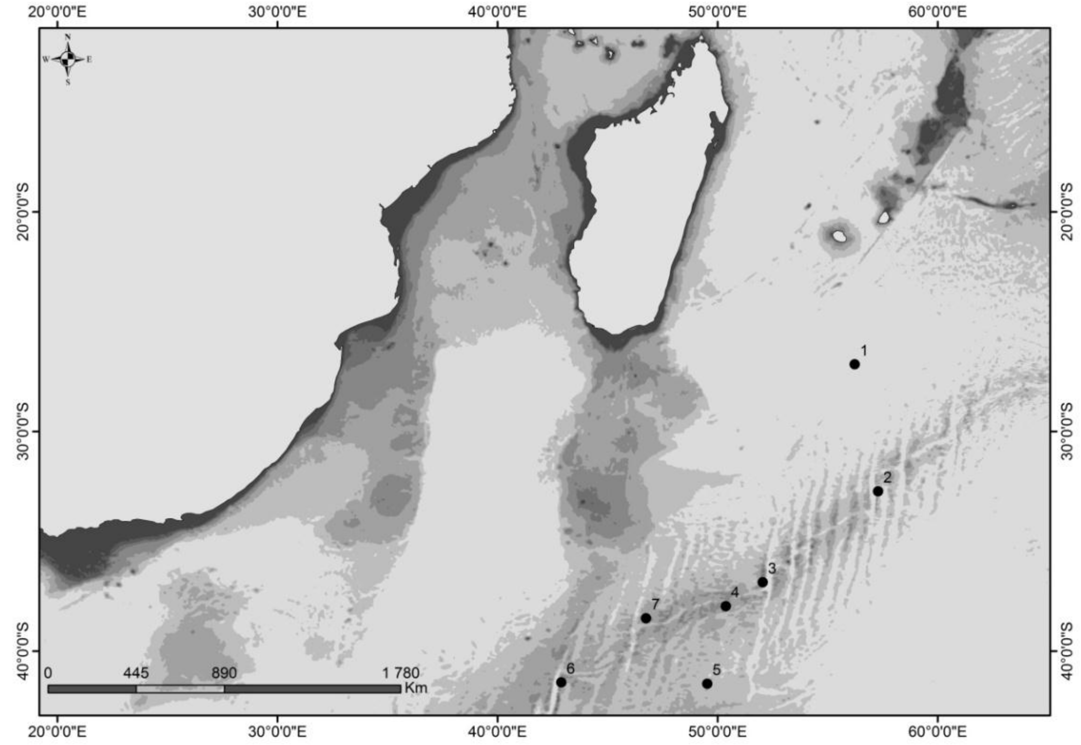

Figure 2.1: Map illustrating the study area of the South West Indian Ocean Ridge, showing the seven sampling stations occupied during November to December 2009. Table 2.1 list the details of each station.

Seven stations were occupied along a transect: including two sampling stations off the SWIOR and five seamount stations (Figure 2.1). A detailed description of sampling stations is listed in Table 2.1.

Table 2.1: Zooplankton and hydrographic stations, on and off the South West Indian Ocean Ridge, sampled from the RV *Dr. Fridtjof Nansen* during November - December 2009. D, day: N, night.

Sampling Station	**Region**	**Station number**	**Date**	**Time of Day**	**Time**	**Summit depth (m)**	**Latitude (°S)**	**Longitude (°E)**
PL4	Off-Ridge 1	1	14/11/2009	D	12:35	5055	-26.94	56.24
PL8	Off-Ridge 1		14/11/2009	N	20:42	5081	-26.94	56.24
PL18	Seamount Atlantis	2	17/11/2009	D	8:45	742	-32.72	57.29
PL26	Seamount Atlantis		18/11/2009	N	17:35	859	-32.75	57.27
PL28	Seamount Atlantis		18/11/2009	N	22:52	904	-32.75	57.27
PL30	Seamount Atlantis		18/11/2009	D	9:33	1169	-32.75	57.27
PL44	Sapmer Bank	3	21/11/2009	N	22:34	379	-36.81	52.13
PL46	Sapmer Bank		22/11/2009	D	11:42	1173	-36.87	55.39
PL54	Sapmer Bank		24/11/2009	D	9:15	4100	-36.87	52.23
PL61	Sapmer Bank		24/11/2009	N	17:19	768	-36.87	52.23
PL66	Middle of what	4	25/11/2009	D	13:31	990	-37.96	50.41
PL68	Middle of what		25/11/2009	D	14:48	1484	-37.96	50.41
PL69	Middle of what		25/11/2009	N	15:40	1136	-37.96	50.41
PL71	Middle of what		25/11/2009	N	16:55	1461	-37.96	50.41
PL95	Off-Ridge 2	5	29/11/2009	D	12:48	3640	-41.49	49.51
PL97	Off-Ridge 2		29/11/2009	D	14:04	3566	-41.49	49.51
PL102	Off-Ridge 2		29/11/2009	N	17:38	3476	-41.49	49.51
PL104	Off-Ridge 2		29/11/2009	N	18:59	3499	-41.49	49.51
PL108	Coral Seamount	7	1/12/2009	N	22:50	562	-41.45	42.86
PL110	Coral Seamount		2/12/2009	N	0:18	725	-41.45	42.86
PL111	Coral Seamount		2/12/2009	D	7:32	1458	-41.45	42.86
PL113	Coral Seamount		2/12/2009	D	9:15	1291	-41.45	42.86
PL146	Mellville Bank	6	7/12/2009	N	22:13	1016	-38.51	46.72
PL148	Mellville Bank		8/12/2009	N	23:58	1172	-38.51	46.72
PL149	Mellville Bank		8/12/2009	D	14:33	585	-38.51	46.72
PL151	Mellville Bank		8/12/2009	D	16:09	659	-38.51	46.72

2.2. Seafloor and oceanographic structure of study area

The SWIOR is in the western basin of the Indian Ocean, stretching 1,800 km from northeast to southwest and varies in width from 300 to 450 km (Romanov, 2003). The bottom basin of the north-western part ranges between 2500 to 3000 m, and the south-western part between 4000 to 3000 m (Romanov, 2003). The slopes of the SWIOR are characterised by patchy summits that are steep and rocky, and includes summits less than 1000 m from the seafloor; of which five seamounts were surveyed along the SWIOR: Atlantis Bank, Samper Bank, Middle of What Seamount, Coral Seamount and Melville Bank (Figure 2.1, Table 2.1).

Water masses above the SWIOR are characterised by three major oceanographic regions: the Agulhas Return Current (ARC), the Subtropical Front (STF) and the Sub-Antarctic Front (SAF) (Read *et al*., 2000; Lutjeharms and Ansorge, 2001; Kostianoy *et al*., 2004; Sultan *et al*., 2007; Garcia *et al*., 2013; Pollard & Read, 2017; Read & Pollard, 2017). Stations in the southern sector of the survey area are in subtropical waters and the stations in the northern sector are in Sub-Antarctic waters (Figure, 2.1, Table 2.1), and the region in between marks the formation of the Subtropical Front (Pollard & Read, 2017; Read & Pollard, 2017). The shift in the Agulhas Return Front to 41° 40’ S and its parallel flow with the SAF creates a region of complex frontal interactions across the SWIOR, with latitudinal transitions in productivity from mesotrophic in the southern part of the survey area to oligotrophic waters in the northern part (Read *et al*., 2000).

2.3. Environmental variables

The physical oceanographic data were sampled at seven stations (Figure 2.1), five of which were seamounts along the SWIOR (Table 2.1). Conductivity, temperature and depth were obtained using the Sea Bird Electronics 911+ CTD. A Sea Bird Electronics 43 dissolved oxygen sensor and Chelsea Instruments Aquatracka Mk III fluorometer were mounted on the CTD frame. The CTD was fitted with a rosette of twelve 5 L Niskin bottles and real time logging was carried out using the PC based Seabird Seasave software. The fluorescence was measured during each CTD cast by an AQUA tracka III (Chelsea Technologies Group Ltd), and sample depths were identified on the downcast, followed by the triggering of Niskin bottles on the upcast. Fluorescence recordings obtained from CTD casts showed a positive correlation (r^2=0.89) with fluorometric chlorophyll measurements (Read & Pollard, 2017; Sonnekus *et al.*, 2017), the chl *a* concentrations were measured using a Turner Designs™ 10-AU Fluorometer. The objective of this study was to investigate environmental parameters at each station that may be responsible for explaining patterns in zooplankton distribution over different spatial scales (micro- and meso-) for the different water masses above the SWIOR (Kostianoy *et al.*, 2004).

2.4. Zooplankton collection and processing

Zooplankton samples were collected (during the day and night) at irregular time intervals during the study (for reasons beyond our control) using an obliquely hauled MultiNet MiDi plankton sampler (Hydro-Bios Apparatebau GmbH). The zooplankton sampler had five nets with an opening of 0.5 x 0.5 m, fitted with 180 µm mesh. A Scanmar depth recorder was mounted onto the frame of the net and depth information was transferred acoustically to the vessel. The physical profile of each environmental station was graphically obtained through the ship's onboard computer. An immediate result of the hydrographic profile of the water column enabled nets to be triggered at identical depths: two nets below the fluorescence maximum, one net through the fluorescence maximum and two nets above the fluorescence maximum. Nets were deployed to a maximum sampling depth of 200 m and towed obliquely at a speed of 2 - 2.5 knots. The nets were retrieved at a speed of 0.5 - 1.0 m.s^{-1}. The volume of water filtered by each net was electronically calculated by the flow meters of the MultiNet.

On retrieval, the five cod ends were thoroughly washed into a sieve with a 180 µm mesh and then washed into a sample jar using filtered seawater. Labels showing full station details, net number and sampling depth range were placed into the sample jars and material was preserved with borax-buffered formalin to a 4% final concentration. The lids of all sample jars were labelled with station details – including net and station number. Any large medusa or other obstructions found in plankton samples were fixed and preserved separately (with full labels). At the end of each haul, after the samples had been processed, the cod ends were inspected for damage, repaired if necessary, and replaced on the nets.

During the survey, severe weather conditions resulted in the loss of one night-time sample at each of stations PL104 and PL148. Both samples represented the upper 25 m of the water column (Table 2.1).

2.4.1. Laboratory procedures: Copepod identification and counts

Zooplankton samples were first decanted into a graduated measuring cylinder and the volume was topped up with distilled water to 100 ml. Zooplankton were retained in suspension by bubbling air through the measuring cylinder and three 2 ml sub-samples were taken using a wide-bore Stempel pipette (Gibbons, 1997a). All copepods (including CV3 and CV4 stages) were counted and identified to major taxonomic group from sub-samples in a Bogorov sorting tray, under a dissecting stereomicroscope at varying magnifications between 10 - 40 x. Cyclopoid, harpacticoid and poecilostomatoid were grouped as non-calanoid copepods and were not identified beyond the genus level.

Following the estimation of copepod abundance, a minimum of 100 calanoid copepods were transferred onto a glass petri dish using a glass pipette or fine pointed forceps. A square permanent wax mould was made on a glass slide and small amounts of anhydrous glycerol (ethanol mixture) were placed inside. All copepods from the petri-dish were subsequently placed into the glycerol solution and placed in a desiccator for 24 hours to evaporate off the water and ethanol to leave a viscous glycerol solution. Each prepared slide was labelled according to station and sub-sample number.

Copepods were identified to species level where possible using the keys of Mauchline (1998), Bradford-Grieve *et al.* (1999); Boxshall & Halsey (2004) and the online website of Razouls (2015; http://copepodes.obs-banyuls.fr/en/). Specimens placed in glycerol solution were rotated using fine pointed needles, which allowed the successful viewing of appendages under a compound microscope between 40 - 100 x magnifications. Specimens were also dissected and mounted on glass slides for identification. Adults that were badly damaged were not included and rare copepods from the genera *Temora* and *Tortanus* were identified to the genus level only.

2.5. Data Analysis

The oceanographic data were plotted using the Ocean Data View v3.4.3 software (Schlitzer, 2012). To assess the horizontal and vertical spatial patterns in distribution of copepod communities between stations, counts of individuals per 2 ml subsample were transformed to integrated abundance individuals.m^{-2} and densities.m^{-3}, respectively. The weighted mean depth (WMD) of dominant selected taxa was calculated from abundance data (densities.m^{-3}) according to Bollens & Frost (1989). WMDs comparisons between and within taxa were tested using a one-way ANOVA. Post-hoc analyses of means were done using the Tukey-Kramer test unbalanced. Statistical analyses were performed in Statistica v. 7 (Statsoft). Variables were log$_{10}$ transformed prior to statistical analysis.

The diversity of copepod communities in each sample was calculated using the Shannon-Wiener and Pielou's evenness indices (Pielou, 1966). Both indices gave similar measures, and Shannon-Weiner index was used to compare diversity among copepod samples.

In order to determine copepod community structure, copepod abundance data from the different nets were summed as vertically integrated abundance data (ind.m^{-2}) for each station. The abundance data were (log x + 1) transformed and the similarity between the numerical composition of samples was determined using the Bray Curtis measure (Field *et al.*, 1982). The similarity matrix was graphically presented in both a 1-dimensional cluster analysis with group average linkage and a 2-dimensional unconstrained MDS ordination. The biological dataset was analysed using the Plymouth Routines In Multivariate Ecological Research package (PRIMER) version 6 software (Warwick & Clarke, 2006).

To test which copepods were responsible for the structure of each *priori* community, an *a-posteriori* similarity percentage breakdown analysis (SIMPER) routine in PRIMER was undertaken (Warwick & Clarke, 2006). In order to identify which environmental factors contributed to community structure and to explore the relationship between copepod communities and the environmental data, a Distance Based Linear Model (DISTLM) in PERMANOVA+ was employed (Anderson *et al.*, 2008). Marginal permutation tests are performed by the DISTLM, to test the proportion of the variance in copepod distribution pattern that can be explained by each predictor. DISTLM partitions the variation according to a step-wise multiple regression model. The DISTLM was then visualised using the distance-based redundancy analysis (dbRDA) routine by fitting the ordination of variables from the multivariate regression model (Anderson *et al.*, 2008). The environmental variables (temperature, salinity, chlorophyll, integrated chlorophyll) were pooled as single values per station. The environmental data were normalised using the Euclidean distance measure, and species abundance data (ind.m^{-2}) was (log x + 1) transformed using the Bray-Curtis similarity matrix, data were analysed by the DISTLM.

Chapter 3: Spatial patterns in the distribution of copepods across the South West Indian Ocean Ridge

3.1. Results

3.1.1. Hydrography

The sea surface temperature (SST) along the SWIOR ranged from 24.15 °C in the north to 5.5 °C in the south (Figures 3.1, 3.2). The stations in the north were characterised by warm saline waters (35.33 psu) and SSTs greater than 10 °C (Figure 3.1). This temperature and salinity characteristic corresponds to the ARC at the 10^{o}C isotherm (Figure 3.1) (Belkin and Gordon, 1996, Pollard & Read, 2017; Read & Pollard, 2017). To the south, and only at Coral seamount cold (5.5 °C to 10 °C), low saline waters (33.71 psu) (Figures 3.1, 3.2) identify the criteria of the SAF, in the Sub-Antarctic sector (Pollard *et al.*, 2002, Pollard & Read, 2017; Read & Pollard, 2017). In between was a region of rapid transition of temperatures (~10 °C – 12.5 °C) and salinity (~34.5 psu) (Figures 3.1, 3.2) ranges the criteria for the STF (Belkin and Gordon, 1996; Read *et al*., 2000; Pollard & Read, 2017; Read & Pollard, 2017. Overall, there was a change in temperature in the upper 200 m of the water column along the SWIOR –a latitudinal decrease in sea surface temperature southward along the transect (Figure 3.2).

3.1.2. Chlorophyll *a* concentrations

Total chlorophyll *a* (chl *a*) ranged from 0.04 µg l^{-1} to 1.15 µg l^{-1} in the upper 200 m of the water column above SWIOR (Figure 3.3A). The distribution of chl *a* ranged from 0.04 µg l^{-1} to 0.50 µg l^{-1} at stations that occupied the area of the ARC (Figure 3.3A). A deep chlorophyll maximum was observed at these stations, between 80 - 100 m (~0.23 µg l^{-1}) (Figure 3.2c), and this is partly in agreement with the chl *a* maximum results recorded by Read *et al.* (2000) in the ARC; who found in their study maximum concentration of ~1.5 mg.m^{-3} at about 80 m.

Highest surface chl *a* was found in the vicinity of the STF and in the SAF in the upper 100 m of the water column (Figure 3.2c). At stations in the SAF, the highest chl *a* occurred in subsurface layers, with concentrations of 1.24 µg l^{-1} to 0.22 µg l^{-1} between 40 – 100 m (Figure 3.2c), ranges correspondingly to Read *et al.* (2000) observations who recorded in their study chl *a* maximum between 60 and 80 m. In the STF, stations were characterised by chl *a* values ranging from 0.13 µg l^{-1} to 0.31 µg l^{-1} in the upper 100 m of water column (Figure 3.2c). Read *et al.* (2000) noted the chl *a* maximum to coincide with the convergence of the frontal area in the upper 40 m, and during this investigation, the chlorophyll maxima occurred in the upper 50 m (Figure 3.2c). These results are therefore in agreement with those obtained by Read *et al.* (2000).

Total integrated chl *a* in the upper 200 m ranged between 15.25 mg.m^{-2} and 87.15 mg.m^{-2}. Integrated chl *a* increased towards the area of the STF and SAF (Figure 3.3B). In the SAF, the highest concentration was 87.15 mg.m^{-2}, while the lowest was found in the ARC zone (15.25 mg.m^{-2}).

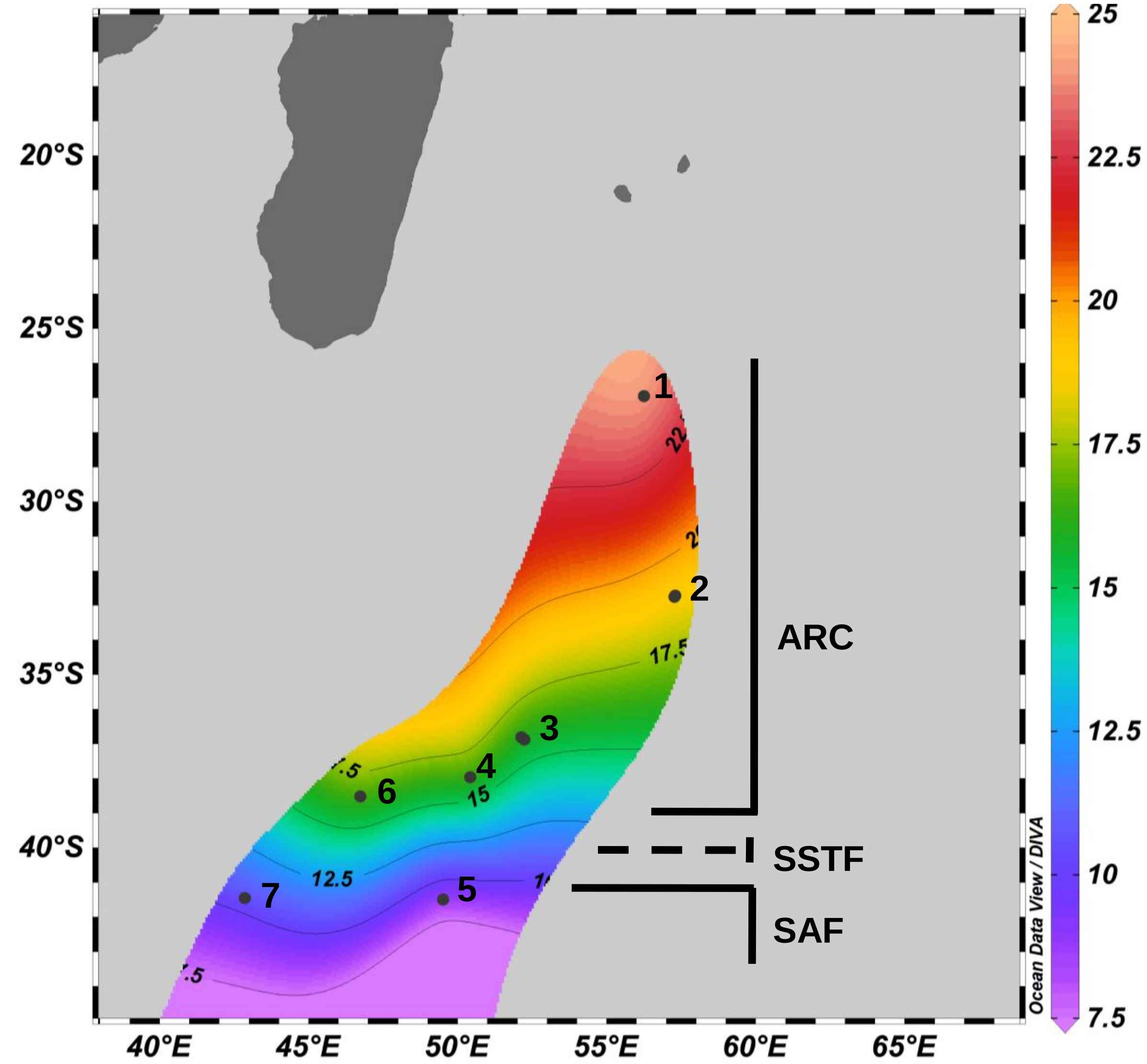

Figure 3.1: Map of the survey area and sampling stations (1 to 7) during November to December 2009, overlaid above are sea surface temperatures. Detailed outline of each sampling station is listed in Table 2.1, Section 2.1. The hydrography systems follow the abbreviations: ARC – Agulhas Return Current (greater than the 10 ºC isotherm; STF – Subtropical Front (between 13 ºC - 10 ºC isotherm); and the SAF – Sub-Antarctic Front (less than 10 ºC isotherm) (e.g. Orsi *et al.*, 1995; Belkin & Gordon, 1996; Read *et al.*, 2000, Lutjeharms, 2006; Pollard & Read, 2017; Read & Pollard, 2017).

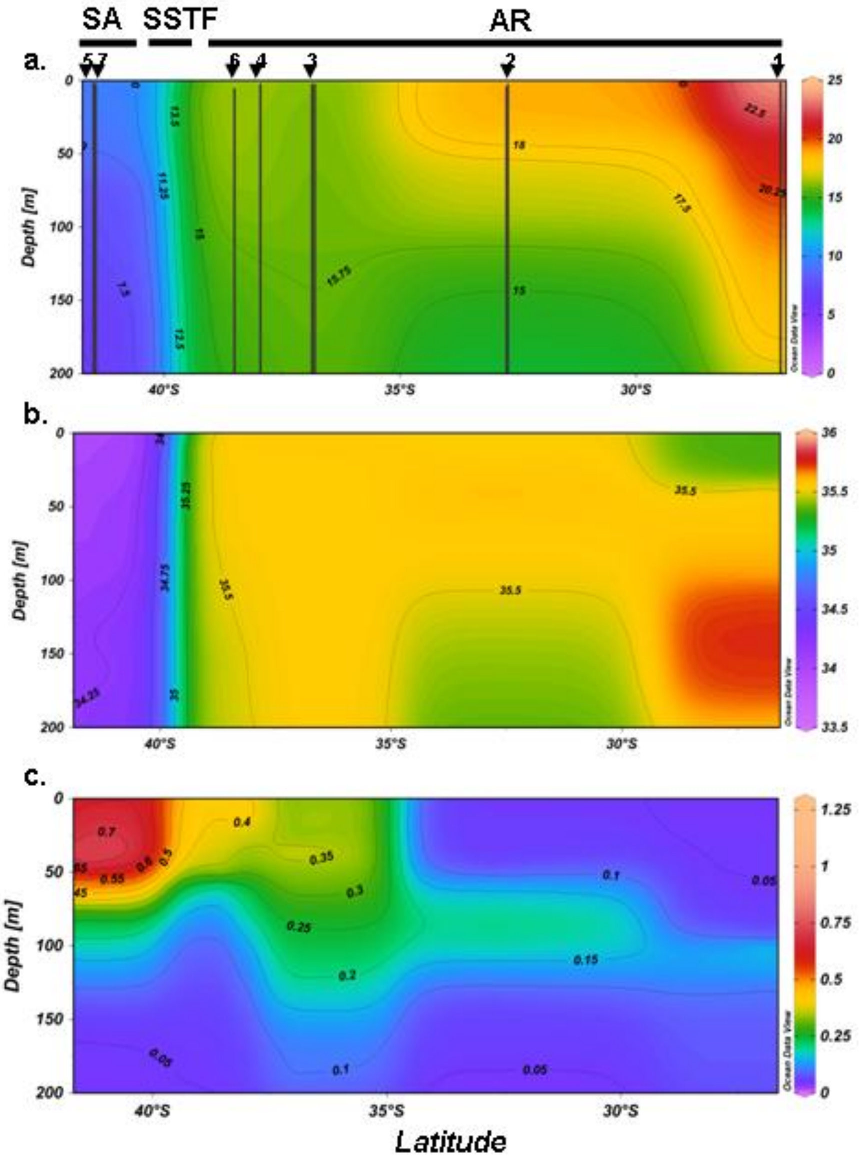

Figure 3.2: Map illustrating the hydrography of the sampling area of vertical a. temperature (°C), b. salinity (psu) and c. chlorophyll (µg l^{-1}) profiles in the upper 200 m of the water column along the South West Indian Ocean Ridge transect during November and December 2009. Station numbers are indicated on top of the Figure as summarised in Section 2.1, Table 2.1. The location of the major oceanographic zones is indicated as: ARC– Agulhas Return Current; STF – Subtropical Front; SAF - Sub-Antarctic Front.

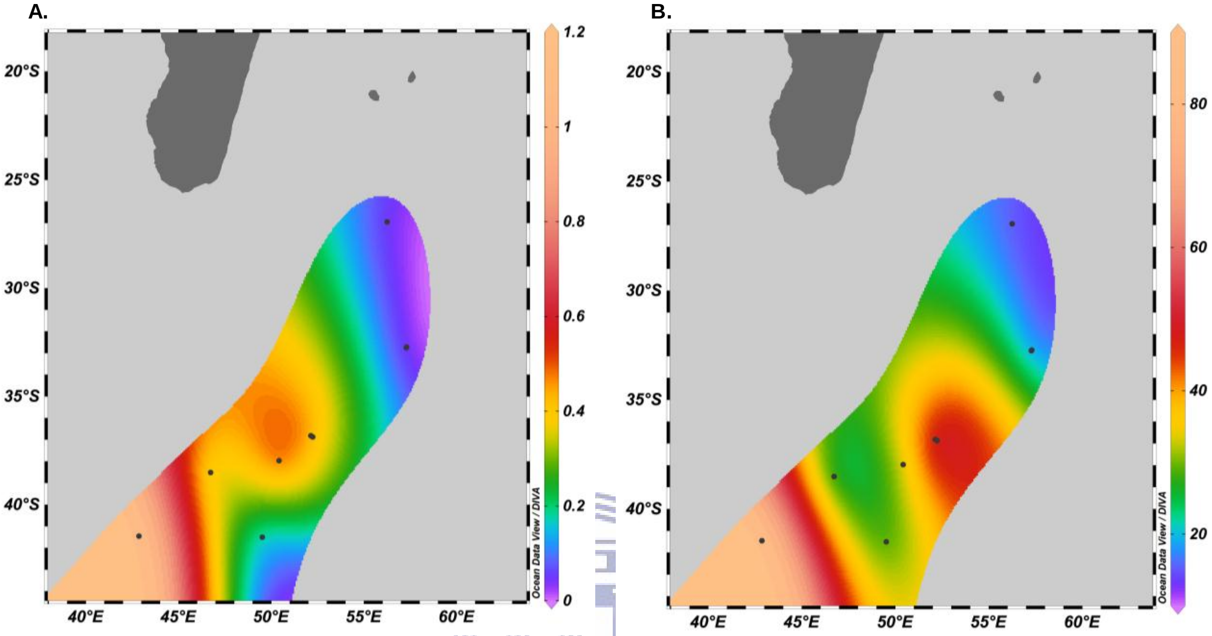

Figure 3.3: Map illustrating A.) surface chlorophyll *a* concentrations (µg l^{-1}) and B.) integrated chlorophyll *a* concentrations (mg.m^{-2}) during the survey period in the upper 200 m of the water column along the South West Indian Ocean Ridge transect during November and December 2009.

In the northern part of the SWIOR, the mixed-layer depth ranged between 20 m to 80 m. A deep mix-layered depth was observed at the "Middle of What" Seamount at 80 m (Figure 3.4), while shallower mixed-layer depths were found between 20 to 50 m at the remaining stations in the ARC. In the southern part of the survey area, shallow mixed-layer depths at 25 m and 55 m indicated stations in the area of the SAF and STF, respectively (Figure 3.4).

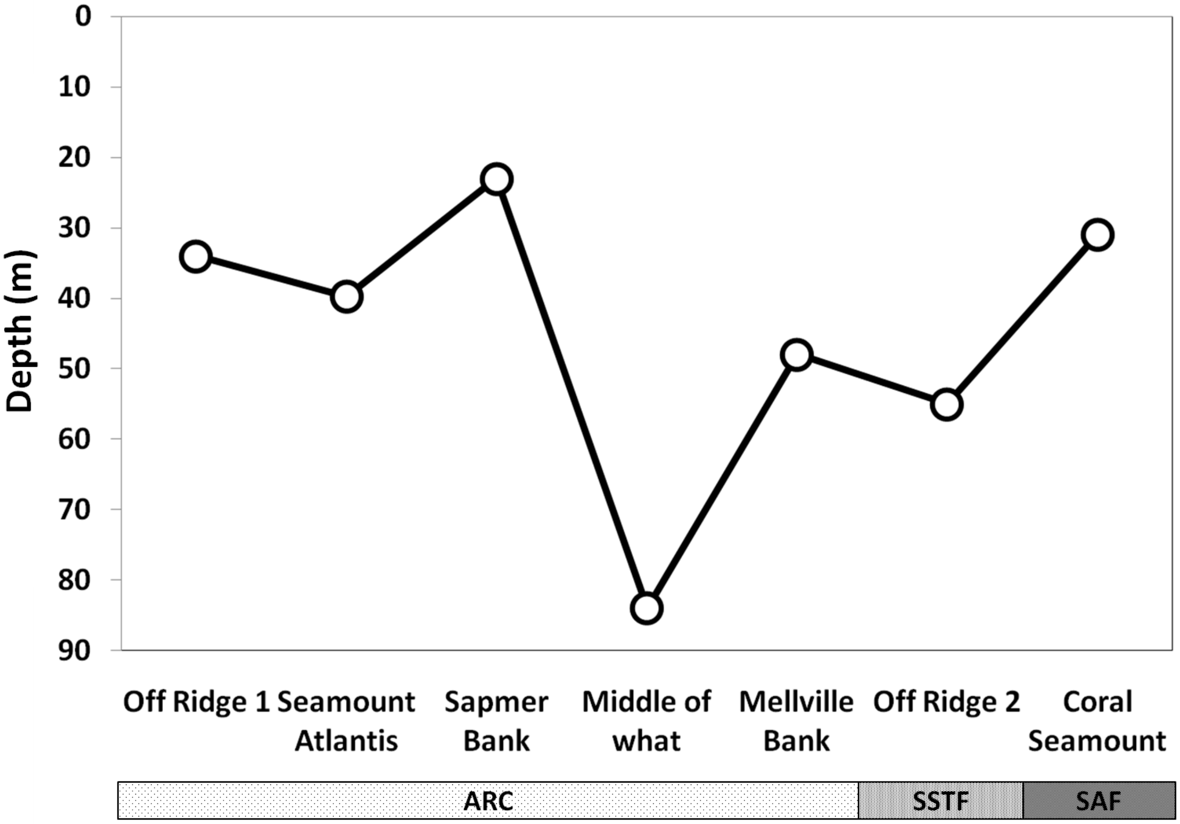

Figure 3.4: Changes in upper mixed layer depths at each seamount along the South West Indian Ocean Ridge transect during November-December 2009. Seamounts have been defined into groups by the hierarchical cluster analysis in Figure 3.5. ARC – Agulhas Return Current; STF – Subtropical Front; SAF – Sub-Antarctic Front.

3.1.3. Copepod communities

The cluster analysis categorised the stations into three groups at the 55% level of similarity (Figure 3.5). Group A consisted of eighteen stations in the northern part of the SWIOR, characterising the ARC. Group B was composed of four stations in the location of the STF (Figures 3.5 and 3.6), whilst Group C comprised of four stations that occupied the southernmost portion of the SWIOR (Figures 3.5 and 3.6), in the area of the SAF.

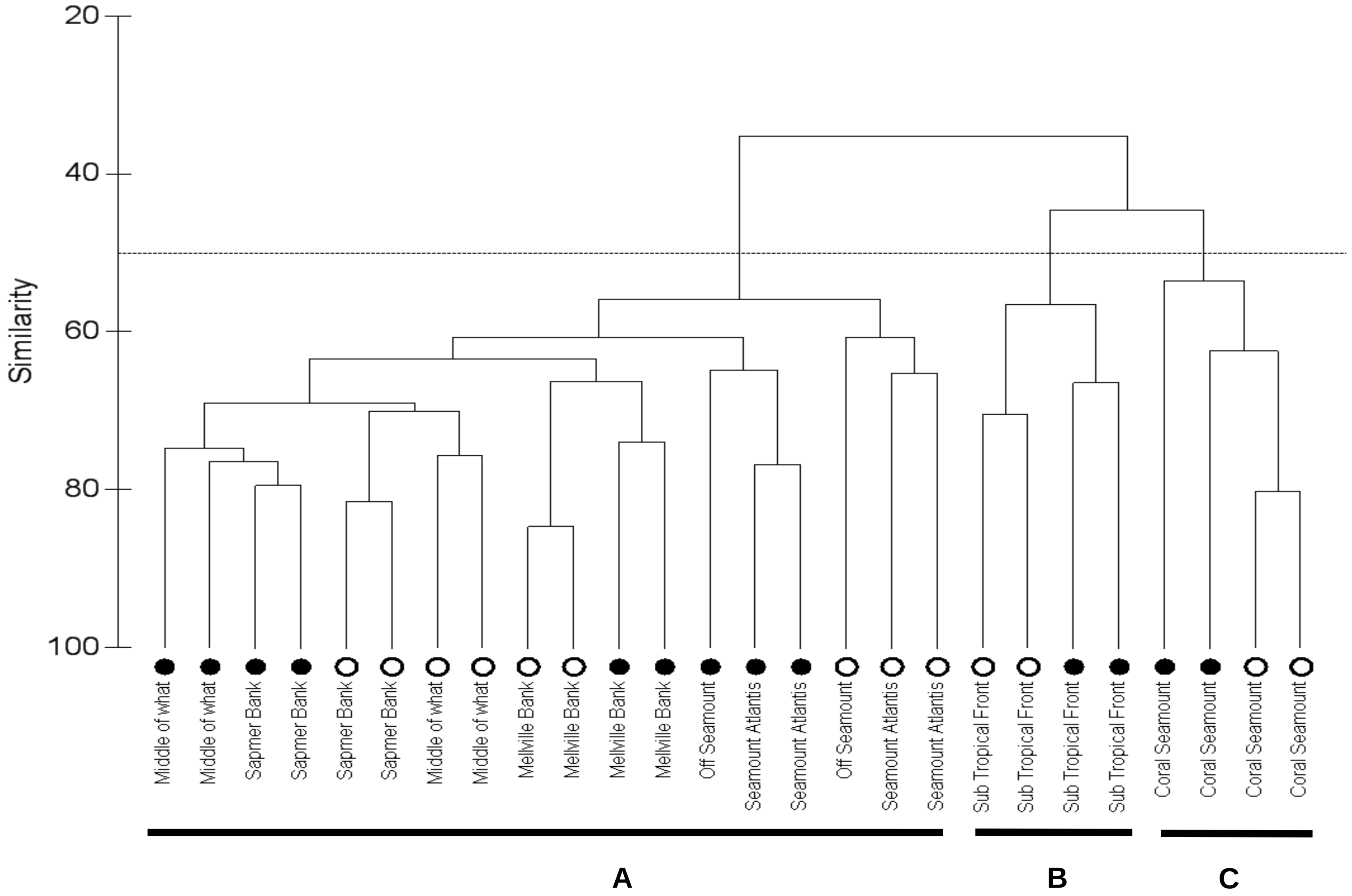

Figure 3.5: Hierarchical cluster analysis of copepod communities along the South West Indian Ocean Ridge during November to December 2009. Sample data were log x + 1 transformed using the Bray-Curtis similarity index and group average linkages to define clusters. Superimposed are day (open circle) and night (closed circle). Group A = Agulhas Return Current; Group B = Subtropical Front; Group C = Sub-Antarctic Front.

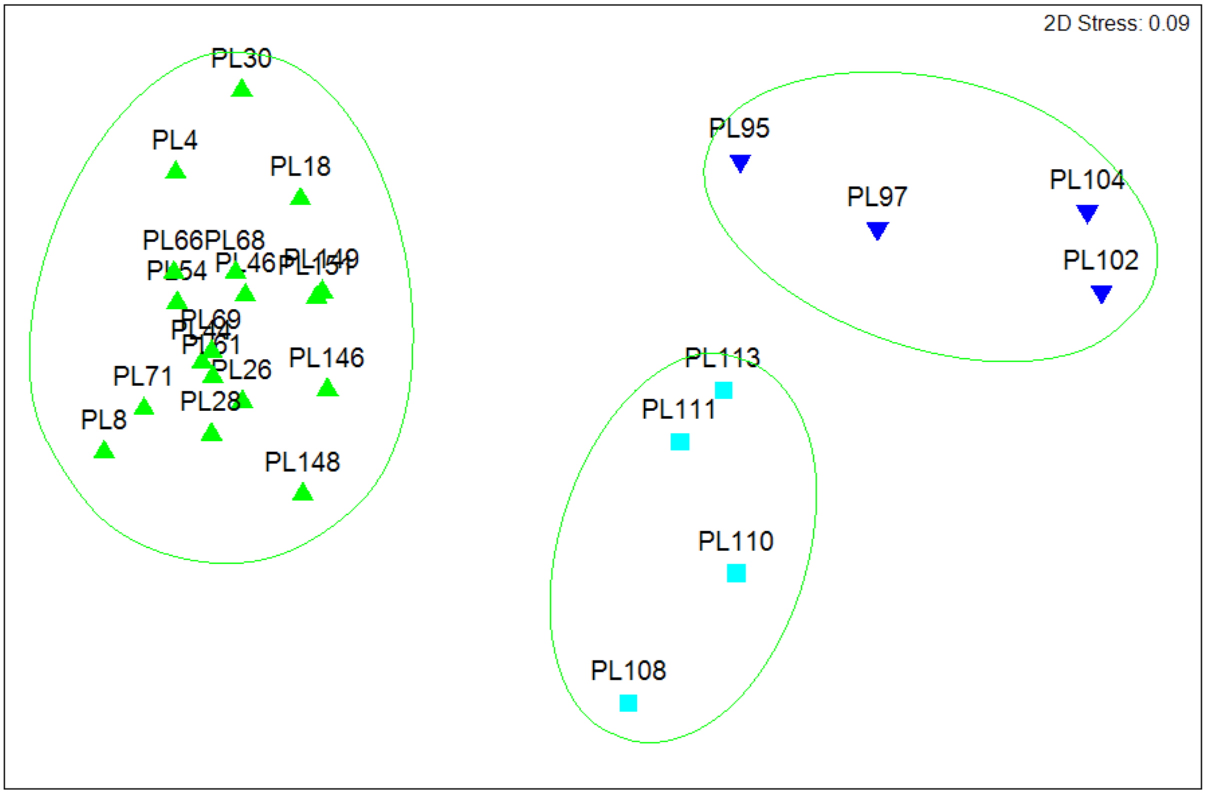

Figure 3.6: 2-dimensional non-metric MDS ordination (nMDS) plot visualizing similarity between copepod communities across the South West Indian Ocean Ridge. Superimposed are the Groups A (▲), B (▼) and C (■) at the 55% level of similarity defined by the cluster analysis in Figure 3.5. Day and night samples were pooled.

The stepwise and adjusted R^2 outputs from the DISTLM analysis are listed in Table 3.1 and the resulting dbRDA is illustrated in Figure 3.7. In Table 3.1, average sea surface temperature (^{o}C) explained 46% of the total variation, followed by integrated chlorophyll *a* (mg.m^{-2}), depth of the chlorophyll max (m), the difference between the 200 m and surface temperatures (^{o}C), as an indication of vertical stratification, and the upper mixed-layer depth explained the smallest amount (2%; Table 3.1). The final model included only five of the variables, excluding the upper mixed-layer depths (Table 3.1). 2-dimensional dbRDA representation indicated a clear separation between copepod assemblages across the SWIOR survey area

(Figure 3.7). The 2-dimensional dbRDA representation explains 84.5% of fitted variation and 54.5% of the total variation (Figure 3.7). Samples separated along the x-axis (dbRDA1), showing the influence of sea surface temperature, while along the second axis (dbRDA2), samples were separated both by integrated chlorophyll and depth of the chlorophyll max (m) (Figure 3.7).

Table 3.1: The results of the DistLM routine showing the marginal and sequential tests for the abundance of copepods sampled along the South West Indian Ocean Ridge during November and December 2009. Volume filtered (m^{-3}), Sea Surface Temperature (^{o}C), Difference Bottom-Surface Temp (^{o}C), Integrated Chlorophyll ($mg.m^{-2}$), Chlorophyll-MAX (m) and Upper mixed-layer depths (m) were used from the survey area as predictors

MARGINAL TESTS

Variable	**SS (trace)**	**Pseudo-F**	**P**	**Prop.**
Volume filtered (m^{-3})	1647.7	1.5497	0.169	6.07E-02
Sea Surface Temperature (^{o}C)	11890	18.683	0.001	0.43772
Difference Bottom-Surface Temp (^{o}C)	2126.9	2.0388	0.058	7.83E-02
Integrated Chlorophyll ($mg.m^{-2}$)	3041	3.0254	0.019	0.11195
Chlorophyll-Max (m)	2080.5	1.9906	0.096	7.66E-02
Upper mixed-layer depths (m)	740.14	0.67223	0.648	2.72E-02

SEQUENTIAL TESTS

Variable	**Adj R^2**	**SS (trace)**	**Pseudo-F**	**P**	**Prop.**
Sea Surface Temperature (^{o}C)	0.41429	11890	18.683	0.001	0.43772
Difference Bottom-Surface Temp (^{o}C)	0.47249	2090.9	3.6479	0.001	7.70E-02
Integrated Chlorophyll ($mg.m^{-2}$)	0.51476	1583.6	3.0035	0.002	5.83E-02
Volume filtered (m^{-3})	0.54604	1241	2.5158	0.010	4.57E-02
Chlorophyll-Max (m)	0.55291	642.57	1.3227	0.253	2.37E-02

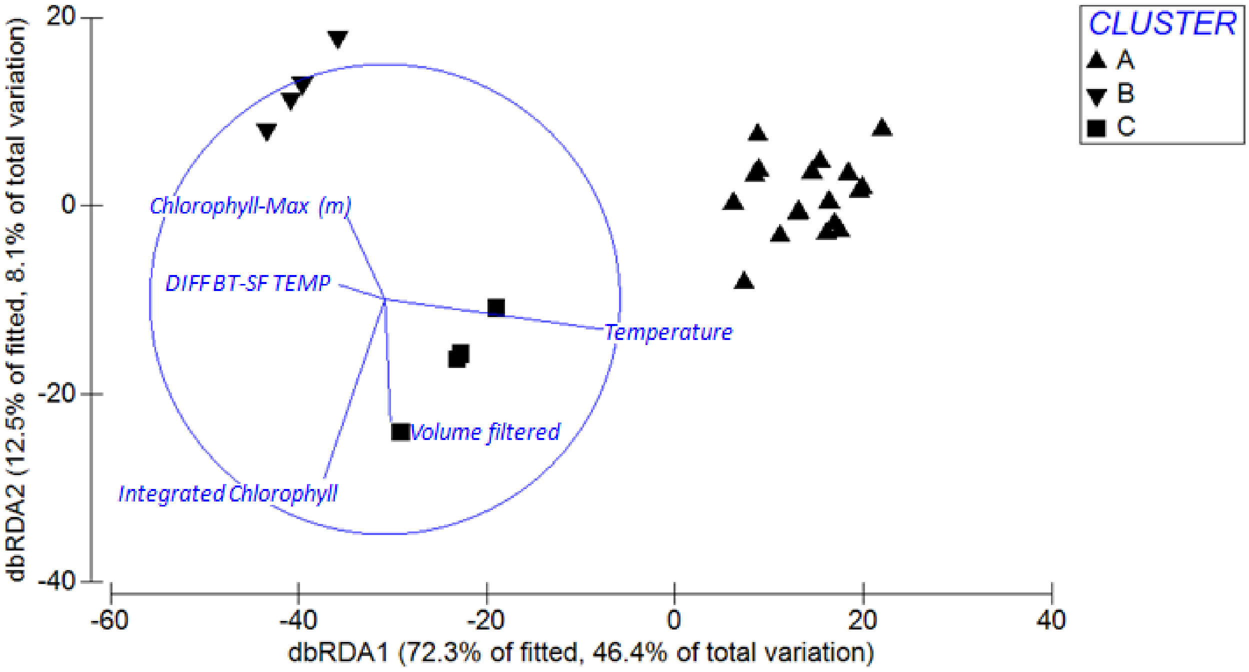

Figure 3.7: dbRDA ordination performed on the copepod species composition of samples collected along the South West Indian Ocean Ridge during the study period November to December 2009. Vectors overlay shows the gradient strength and direction of the environmental predictors. Superimposed are the cluster Groups A (▲) = ARC, B (▼) = STF and C (■) = SAF derived by the cluster analysis in Figure 3.5.

The species responsible for within-in group similarity (Figure 3.5) as identified by the SIMPER analysis are presented in Table 3.2. Given that the most abundant species will contribute towards the similarity and dissimilarity within a group (Clarke & Gorley, 2006), only the species or genera that contributed (cumulatively) to approximately 75% of the similarity of each community were selected. Species that contributed to more than (cumulatively) 75% of the dissimilarity between communities are also reported. Group A samples were heterogeneous (similarity overall: 66.8%) and ten taxa contributed ~ 45% of the similarity in Group A, with abundances of *Oithona*, *Oncaea* and *Corycaeus* contributing to the similarity within the group. Six taxa accounted for ~50% of the similarity within Group B (similarity: 65%) and here, *Oithona* spp., *Ctenocalanus vanus*, *Clausocalanus laticeps*, *Clausocalanus brevipes*, *Scolecithricella minor*, *Oncaea* spp., *Calanus simillimus*, *Rhincalanus gigas* and *Aetideus australis*, were the major contributors towards the similarity in the group samples. Group C samples were also characterised by a high abundance of *Oithona* (10%), together with six other species (*Oncaea*, *Calocalanus styliremis*, *Scolecithricella minor*, *Clausocalanus brevipes*, *C. laticeps* and *Metridia lucens*) contributed to 45% of the similarity (similarity: 64.8%) within the group.

Four taxa, *Corycaeus* spp., *Farranula* spp., *Metridia lucens* and *Acartia danae* accounted for 13% of the dissimilarity between Groups A and C. Group A and B were 67% dissimilar with *Clausocalanus laticeps*, *Corycaeus spp.*, *Nannocalanus minor*, *Acartia danae* and *Acartia negligens* contributing to ~13% of the dissimilarity (Table 3.2). The dissimilarity between Groups B and C was 50% and seven species contributed to ~24% of the dissimilarity, with *Calanus simillimus*, *Metridia lucens* and *Pleuromamma piseki* being most responsible (Table 3.2).

Table 3.2: Top panel showing top ten copepod species identified by SIMPER, responsible for similarity in structure of cluster Groups, and bottom panel list top ten copepod taxa identified by SIMPER, responsible for the dissimilarity in structure of cluster Groups as illustrated in Figure 3.5, performed on total abundance (ind.m^{-2}) data, log transformed (log x + 1). Top Panel: Contrib% contribution of species to the overall similarity between clusters and Cum.% = cumulative contribution of species to the overall similarity. Bottom Panel: Contrib% contribution of that species to the overall dissimilarity between clusters and Cum.% = cumulative contribution of species to the overall dissimilarity.

CLUSTER A (66.8%)

Species	Contrib%	Cum.%
Oithona spp.	5.48	5.48
Oncaea spp.	5.38	10.86
Corycaeus spp.	4.87	15.74
Ctenocalanus vanus	4.18	19.92
Acartia danae	4.11	24.02
Farranula spp.	4.08	28.1
Mecynocera clausi	3.97	32.07
Nannocalanus minor	3.77	35.84
Acartia negligens	3.52	39.36
Paracalanus parvus	3.51	42.87

CLUSTER B (64.8%)

Species	Contrib%	Cum.%
Oithona spp.	13.38	13.38
Ctenocalanus vanus	9.63	23.01
Clausocalanus laticeps	8.82	31.83
Clausocalanus brevipes	8.49	40.32
Scolecithricella minor	8.13	48.45
Oncaea spp.	7.81	56.25
Calanus simillimus	7.74	63.99
Rhincalanus gigas	6.65	70.64
Aetideus australis	5.55	76.19
Subeucalanus longiceps	4.68	80.87

CLUSTER C (64.8%)

Species	Contrib%	Cum.%
Oithona spp.	10.11	10.11
Oncaea spp.	6.51	16.62
Calocalanus styliremis	6.25	22.87
Scolecithricella minor	6.05	28.92
Clausocalanus brevipes	5.98	34.9
Clausocalanus laticeps	5.46	40.36
Metridia lucens	5.46	45.82
Mecynocera clausi	5.06	50.88
Aetideus australis	3.84	54.72
Eucalanus hyalinus	3.8	58.53

Dissimilarity CLUSTERS A & B (66.5%)

Species	Contrib%	Cum.%
Clausocalanus laticeps	2.88	2.88
Corycaeus spp.	2.73	5.62
Nannocalanus minor	2.68	8.3
Acartia danae	2.62	10.92
Acartia negligens	2.57	13.49
Farranula spp.	2.54	16.02
Calanus simillimus	2.5	18.52
Scolecithricella minor	2.37	20.89
Paracalanus parvus	2.34	23.23
Clausocalanus minor	2.33	25.56

Dissimilarity CLUSTERS A & C (54.2%)

Species	Contrib%	Cum.%
Corycaeus spp.	3.77	3.77
Farranula spp.	3.25	7.02
Metridia lucens	3.1	10.11
Acartia danae	2.98	13.09
Nannocalanus minor	2.75	15.85
Clausocalanus laticeps	2.52	18.37
Acartia negligens	2.51	20.87
Scolecithricella minor	2.39	23.27
Clausocalanus minor	2.34	25.61
Clausocalanus brevipes	2.01	27.62

Dissimilarity CLUSTERS B & C (49.5%)

Species	Contrib%	Cum.%
Calanus simillimus	4.75	4.75
Metridia lucens	3.76	8.51
Pleuromamma piseki	3.54	12.05
Mecynocera clausi	3.12	15.17
Paracalanus parvus	3.01	18.18
Ctenocalanus vanus	2.88	21.06
Calocalanus styliremis	2.8	23.86
Rhincalanus gigas	2.76	26.62
Clausocalanus parapergens	2.58	29.2
Clausocalanus ingens	2.48	31.68

3.1.4. Abundance

The total abundance (ind.m^{-2}) of copepods at each seamount by day and night is presented in Figure 3.8. Total copepod abundances were found to be highly variable between seamounts, and total numbers were lowest at Atlantis Seamount both during the day (12, 243 ind.m^{-2}) and night (12, 986 ind.m^{-2}), and highest at the Subtropical Front during the night (72, 992 ind.m^{-2}) (Figure 3.8).

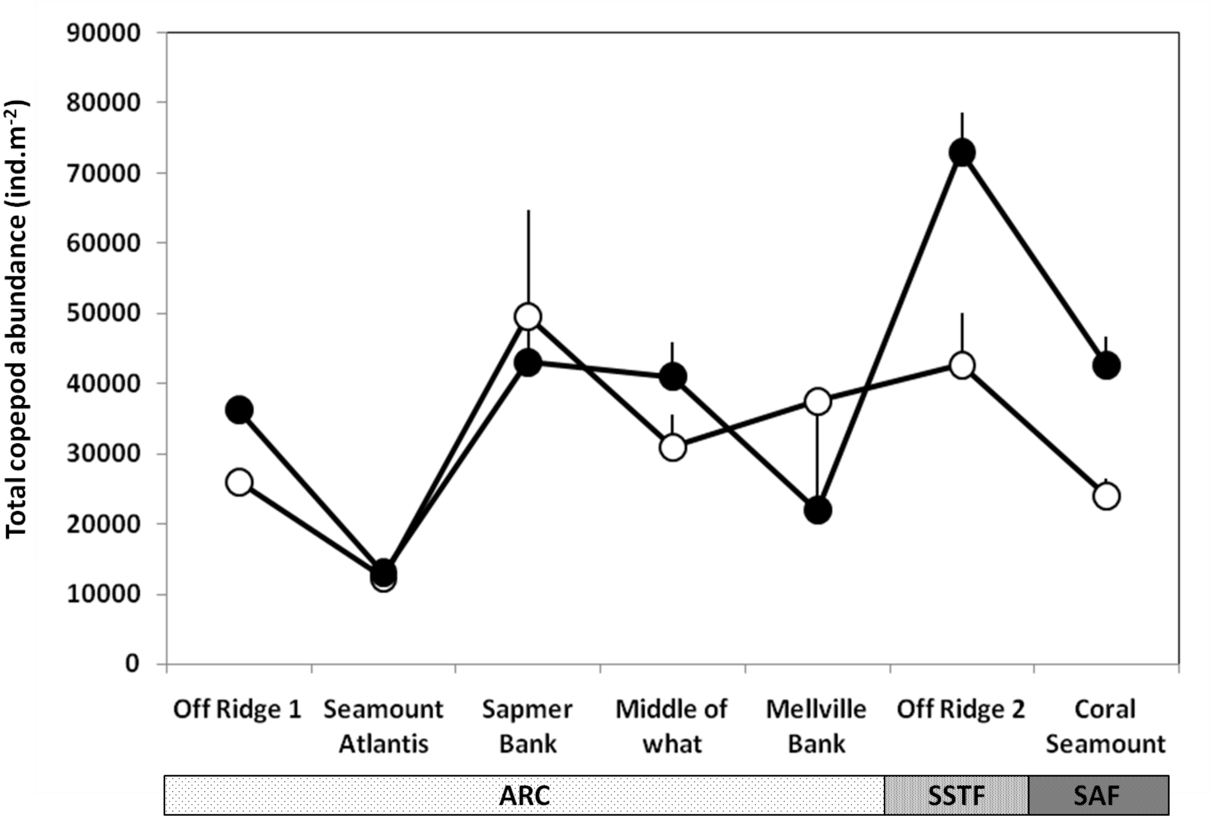

Figure 3.8: Day (open circle) and night (closed circle) spatial variation in total abundance (ind.m^{-2}) of copepods collected at each seamount along the South West Indian Ocean Ridge during November to December 2009.

3.1.5. Diversity and richness

Figure 3.9 illustrates changes in species richness and the number of genera by day and night across the sampling locations. The total number of genera and species was the highest in the ARC during the night, reaching up to 33 genera and 59 species at the "Middle of What" Seamount (Figure 3.9). At stations in the STF, the total number of genera and species was generally higher during the day than night, whereas the situation was reversed within the SAF (Figure 3.9). Vertical patterns in the diversity of copepods in the upper 200 m of the water column along the SWIOR transect are presented in Figure 3.10. To assess daytime differences in depth distributions of copepod species, the total number of copepod species found at different depth intervals at all stations (per cluster, see Section 3.1.3, and Figure 3.5, above) were pooled. Day and night changes in the vertical structure of species have been grouped similarly.

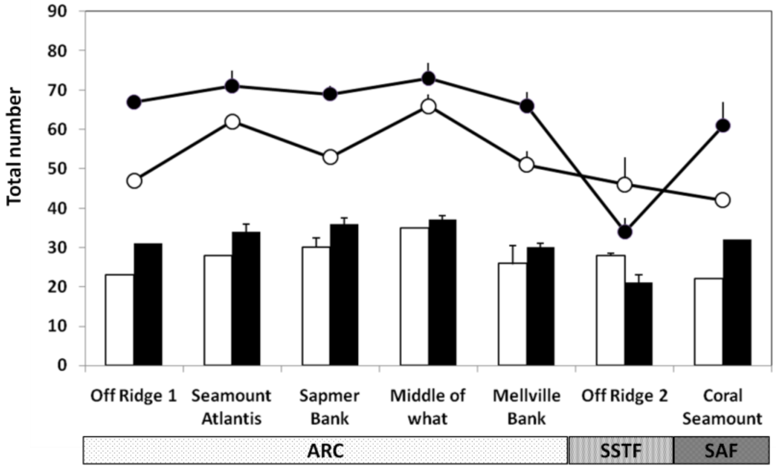

Figure 3.9: Species richness day (o), night (●) and number of genera day (open bar), night (close bar) of copepod samples for each seamount along the South West Indian Ocean Ridge during November – December 2009. Seamounts have been categorised into groups as derived by the cluster analysis (Figure 3.5). ARC – Agulhas Return Current; STF – Subtropical Front; SAF – Sub-Antarctic Front. Error bars SE.

The data summarised in Figure 3.10 show that species richness across stations increased slightly with increasing depth. This pattern in richness becomes clearer with time of day. During daylight in the ARC, highest species richness generally occurred in waters below 100 m, and at night an increase in the total number of species was observed between 100 – 200 m (Figure 3.10). In the STF, a peak in species richness occurred between 50 – 100 m during the day, while at night, species richness showed an increase at 150 – 200 m depth interval (Figure 3.10). In the SAF, a variation in species richness was observed at different depth layers, highest richness occurred between 100 – 200 m during the night (Figure 3.10).

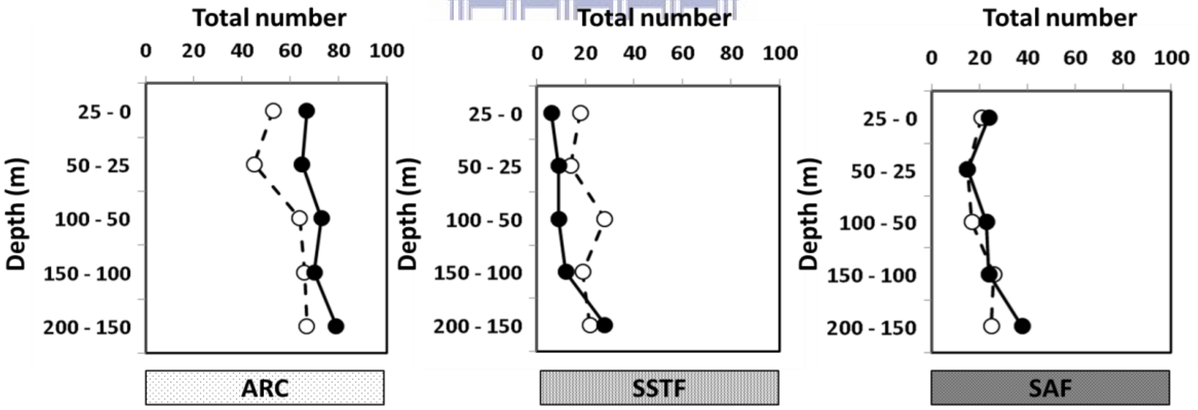

Figure 3.10: Vertical depth distributions of copepod species richness of samples collected along the South West Indian Ocean Ridge during November-December 2009. Groups are defined by the cluster analysis in Figure 3.5, Section 3.1.3. ARC - Agulhas Return Current; STF - Subtropical Front; SAF - Sub-Antarctic Front. Data summarised by day (○) and night (●). Total Day: Night samples: ARC = 45:44; STF = 10:9; SAF = 10:10. Total number of species Day: Night: ARC = 51:67; STF = 38:29; SAF = 33:45.

Table 3.3: The mean total abundance of copepods (ind.m^{-2}) of samples collected along the South West Indian Ocean Ridge transect conducted during November and December 2009. The groups were identified by the cluster analysis in Figure 3.5. ARC – Agulhas Return Current; STF – Subtropical Front; SAF – Sub-Antarctic Front.

	ARC	STF	SAF
Order Calanoida			
Family Acartiidae			
Acartia danae	972.5	4.1	2.8
Acartia negligens	546.3	0	6.3
Familiy Aetideidae			
Aetideus acutus	2.1	0	0
Aetideus armatus	3.1	16.4	0
Aetideus australis	0	132.3	51.0
Aetideus giesbrechti	8.6	0	0
Aetideus unidentified	0.5	0	0
Chiridius gracilis	2.5	0	2.8
Euchirella amoena	0.5	0	0
Euchirella pulchra	0	0	2.8
Euchirella rostrata	2.2	6.7	37.0
Euchirella truncata	6.0	0	0
Euchirella unidentified	3.3	0	0
Gaetanus minor	11.4	0	16.6
Undeuchaeta incisa	0	3.7	0
Undeuchaeta major	4.9	3.0	2.8
Undeuchaeta plumosa	0.5	0	0
Family Calanidae			
Calanoides macrocarinatus	76.4	0	87.2
Calanus simillimus	3.9	639.7	0
Cosmocalanus darwinii	21.1	0	0
Mesocalanus tenuicornis	248.3	13.4	38.6
Nannocalanus minor	640.1	0	2.8
Neocalanus gracilis	327.8	4.7	67.7
Family Candaciidae			
Candacia aethiopica	2.7	6.6	0
Candacia bispinosa	2.8	0	0
Candacia catula	1.4	0	0
Candacia cheirura	4.6	0	15.2
Candacia simplex	0.3	0	0
Candacia truncata	1.3	0	0
Candacia varicans	2.2	0	0
Candacia unidentified	0.4	0	0
Family Clausocalanidae			
Clausocalanus arcuicornis	453.8	165.5	11.6
Clausocalanus brevipes	46.0	1292.8	1331.1
Clausocalanus furcatus	34.1	30.1	8.8

Table 3.3 (continued)

	ARC	**STF**	**SAF**
Clausocalanus ingens	146.3	333.6	128.4
Clausocalanus jobei	45.4	4.1	0
Clausocalanus laticeps	3.7	1246.9	296.4
Clausocalanus lividus	84.8	181.2	21.6
Clausocalanus mastigophorus	174.6	65.5	0
Clausocalanus minor	370.5	0	2.3
Clausocalanus parapergens	278.8	83.5	209.7
Clausocalanus paululus	33.8	0	0
Clausocalanus pergens	248.8	4.4	58.3
Ctenocalanus vanus	1618.5	2749.4	67.9
Family Eucalanidae			
Eucalanus hyalinus	57.0	3.0	53.8
Pareucalanus langae	5.4	3.3	0
Rhincalanus gigas	7.5	225.2	15.5
Rhincalanus nasutus	153.7	25.5	11.4
Subeucalanus longiceps	3.4	50.6	7.2
Family Euchaetidae			
Euchaeta acuta	92.0	10.0	2.8
Euchaeta lobatus	0.8	0	0
Euchaeta media	0	3.3	0
Euchaeta spinosa	0.8	0	0
Euchaeta unidentified	0.9	6.7	0
Paraeuchaeta biloba	0	3.3	0
Pareucheata exigua	0	0	8.4
Family Heterorhabdidae			
Heterohabdus clausii	5.0	3.0	7.7
Heterohabdus lobatus	0.9	0	0
Heterorhabdus papilliger	84.5	30.6	73.2
Heterorhabdus spinifer	14.4	0	0
Heterorhabdus spinifrons	7.1	0	2.8
Heterostylites longicornis	0	0	2.8
Heterostylites major	1.4	0	8.3
Family Lucicutiidae			
Lucicutia clausii	86.3	0	0
Lucicutia flavicornis	445.9	16.8	52.3
Lucicutia gaussae	0.7	0	0
Lucicutia longicornis	19.5	0	2.8
Lucicutia longiserrata	7.2	0	0
Lucicutia magna	0.4	0	0
Family Metridinidae			
Metridia curticauda	0	0	3.8
Metridia lucens	0	5.2	1256.4

Table 3.3 (continued)

	ARC	**STF**	**SAF**
Pleuromamma abdominalis	98.2	0	74.0
Pleuromamma borealis	76.7	0	71.5
Pleuromamma gracilis	63.1	0	11.4
Pleuromamma indica	8.8	0	0
Pleuromamma piseki	301.7	0	1276.0
Pleuromamma quadrungulata	9.9	0	24.4
Pleuromamma robusta	8.7	77.3	105.0
Pleuromamma xiphias	22.2	0	5.3
Family Scolecitrichidae			
Amallothrix dentipes	0	24.9	0
Amallothrix unidentified	0.6	0	3.8
Scaphocalanus brevicornis	3.0	0	0
Scaphocalanus curtus	29.6	0	2.8
Scaphocalanus echinatus	12.2	3.0	4.4
Scaphocalanus unidentified	3.0	94.6	51.4
Scolecithricella dentata	9.4	0	0
Scolecithricella minor	8.2	798.5	423.3
Scolecithricella ovata	29.8	0	12.0
Scolecithricella tenuiserrata	0.4	0	0
Scolecithricella unidentified	1.4	3.0	0
Scolecithrix bradyi	7.0	0	0
Scolecithrix danae	0.6	0	0
Scottocalanus securifrons	0.3	3.7	7.2
Family Paracalanidae			
Calocalanus contractus	47.0	0	0
Calocalanus equalicauda	0	0	1.1
Calocalanus minor	12.2	0	0
Calocalanus pavo	82.2	0	10.9
Calocalanus plumulosus	23.0	0	5.3
Calocalanus styliremis	360.1	29.0	710.0
Calocalanus tenuicornis	4.5	0	0
Calocalanus tenuis	17.1	0	4.3
Mecynocera clausi	778.0	5.9	257.9
Paracalanus denudatus	14.0	0	0
Paracalanus indicus	118.4	3.7	0
Paracalanus nanus	69.5	3.0	0
Paracalanus parvus	899.9	6.7	270.1
Paracalanus quasimodo	38.7	0	0
Family Pontellidae			
Labidocera spp.	1.2	0	0
Family Temoridae			
Temora spp.	5.3	0	0
Family Tortanidae			
Tortanus spp.	13.2	0	0

Table 3.3 (continued)

	ARC	**STF**	**SAF**
Family Phaennidae			
Phaenna spinifera	2.0	0	0
Order Cyclopoida			
Family Oithonidae			
Oithona spp.	9279.5	48588.9	24030.0
Order Harpacticoida			
Family Ectinosomatidae			
Microsetella rosea	56.3	7.3	0
Family Clytemnestridae			
Clytemnestra spp.	8.0	0	0
Family Miraciidae			
Macrosetella gracilis	11.0	0	0
Miracia efferata	20.9	0	6.2
Miracia minor	9.5	0	0
Oculosetella gracilis	0.6	0	0
Order Poecilostomatoida			
Family Oncaeidae			
Oncaea spp.	7509.8	731.8	1986.4
Family Sapphirinidae			
Copilia hendorffi	18.6	0	0
Copilia mirabilis	0.5	0	0
Copilia vitrea	4.3	0	0
Sapphirina angusta	18.7	0	0
Sapphirina auronitens	0.5	0	0
Sapphirina intestinata	0.6	0	0
Sapphirina iris	1.2	6.1	0
Sapphirina metallina	2.5	0	0
Sapphirina nigromaculata	0.6	0	0
Sapphirina opalina	27.4	0	0
Sapphirina unidentified	5.9	0	0
Family Corycaeidae			
Corycaeus spp.	2563.3	10.7	0
Farranula spp.	971.8	9.4	0

The Order Calanoida had the most genera (40) across all samples (Table 3.3). The genera present in the southern stations were very similar to those of the northern stations (Table 3.3). Although there was no difference between the number of genera found at the frontal stations in the vicinity of the STF and SAF (Table 3.3), species of the genera *Scolecithricella*, *Ctenocalanus* and *Clausocalanus* contributed up to 10% to the total number of individuals at the frontal stations within the STF, while *Pleuromamma* and *Metridia* accounted for 10% of the total number of individuals at the stations that occupied the SAF. There was a positive relationship between species and generic richness during the entire survey (Figure 3.11).

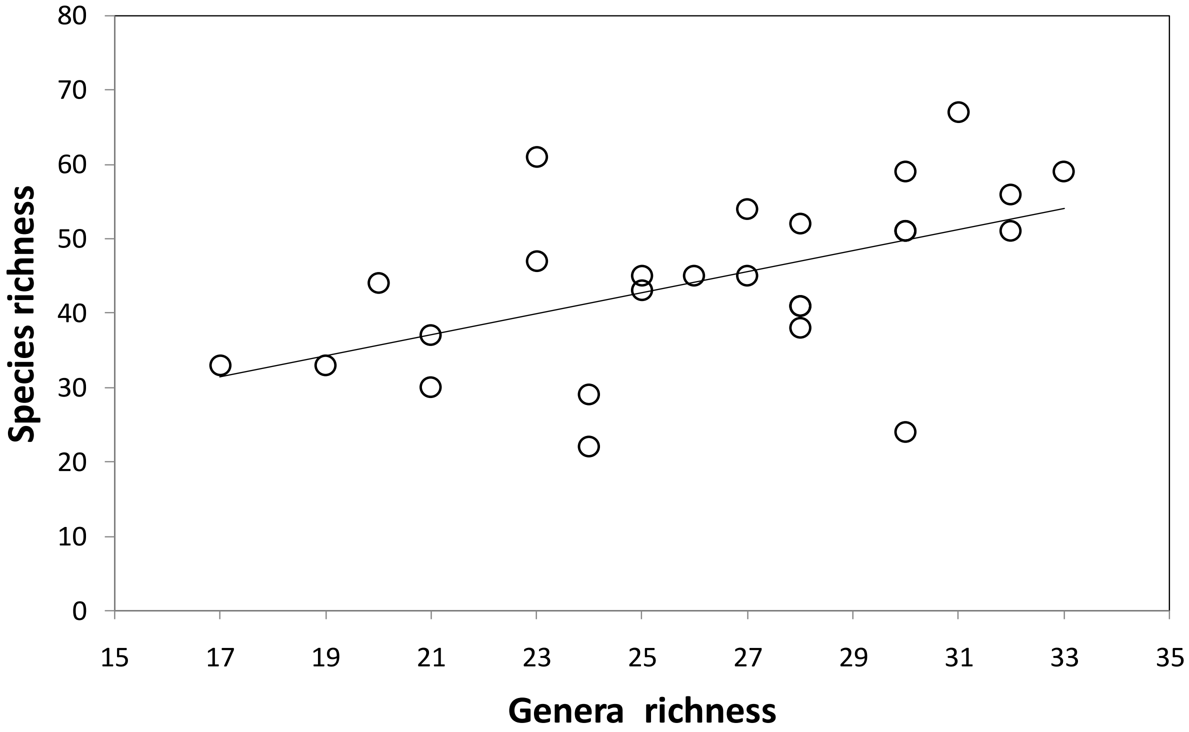

Figure 3.11: The relationship between species and genera richness of copepod samples collected across the South West Indian Ocean Ridge during November to December 2009. Linear function for the relationship between Species richness and Genera richness: Species richness and Genera richness: Species richness = 1.412x +7.486, $R^2 = 0.277$.

The spatial pattern in the diversity of copepod samples between day and night across the SWIOR is presented in Figure 3.12, and the results are similar to those observed for richness and note above. Diversity was highest at the Atlantis Seamount, both by day and night (Figure 3.12). Diversity was lowest at night in the STF, but lowest during the day at Coral Seamount in the SAF (Figure 3.12). Overall, species diversity was higher (both by day and night) at seamounts located in the ARC, while both day and night patterns showed a decrease in diversity towards the frontal area (STF), but an increase towards the SAF (Figure 3.12).

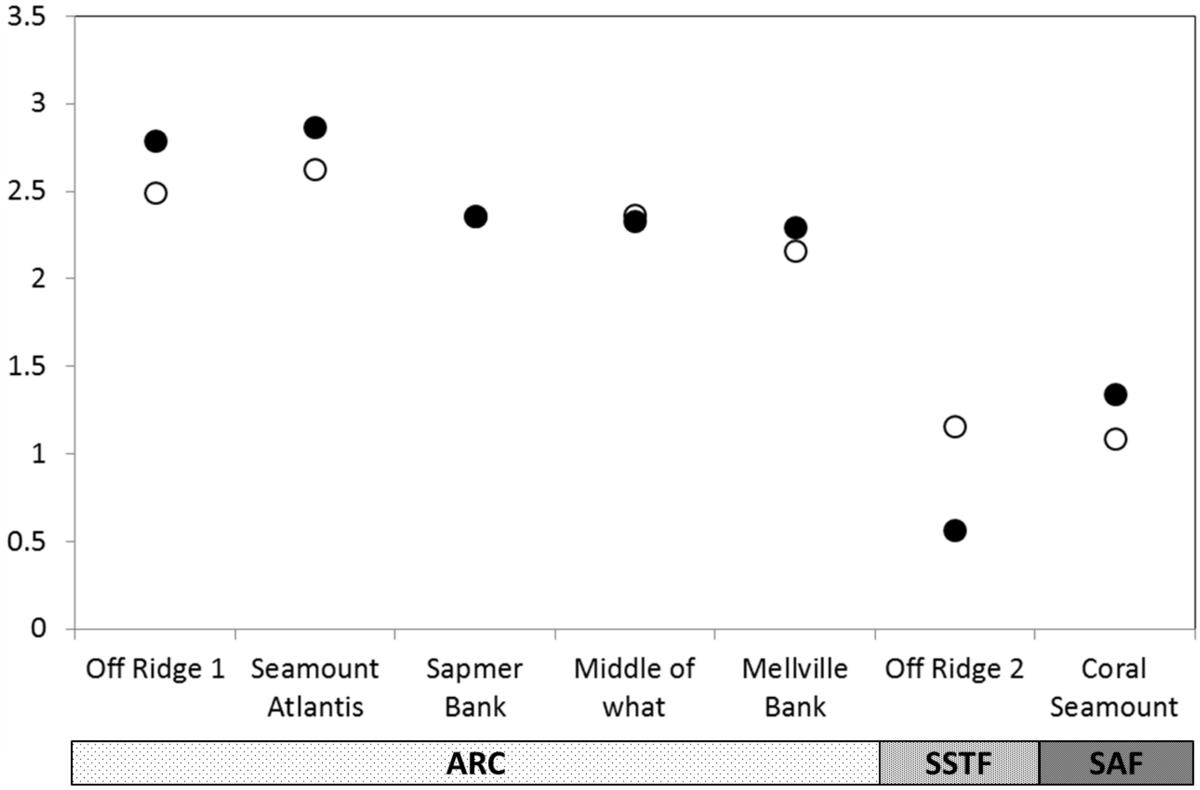

Figure 3.12: Species spatial changes of copepod community Shannon-Wiener's diversity index (H') day (○), night (●) at seamounts sampled along the South West Indian Ocean Ridge during period of November to December 2009. Seamounts have been classified into groups as determined by the cluster analysis (Figure 3.5). ARC – Agulhas Return Current; STF – Subtropical Front; SAF – Sub-Antarctic Front.

3.1.6. Vertical distributions

Total copepod densities (m^{-3}) during the day and night are shown in Figure 3.13. The highest concentrations of copepods were found during the night (1 744.m^{-3}) than by day (1 094.m^{-3}) in the upper surface waters of the SAF zone (Figure 3.13), with little changes in their depth distributions below 50 m. In the STF, copepod concentrations also showed an increase from 339 densities.m^{-3} during the day to 1 582.m^{-3} at night in the upper 50 m (Figure 3.13). Daytime copepod abundances increased from 1 338.m^{-3} to 3 612 .m^{-3} at night in surface waters of the ARC (Figure 3.13), with uniform distributions below 50 m.

The greatest abundance of calanoids occurred in the upper 50 m of the water column both by day and night: generally calanoid abundances peak at night in the upper 100 m across the three major zones (Figure 3.13). Highest abundances of non-calanoids were to be found in the upper 100 m by day and night. Generally, their depth distributions appeared to be uniform below 100 m, with peaks in abundances at night throughout the water column in all three major zones (Figure 3.13).

Overall during the day, non-calanoids accounted for more than 50% of total copepods, their diurnal depth differences varied between and within cluster groups (Figure 3.13), except in the SAF where their depth distributions appeared similar throughout the water column.

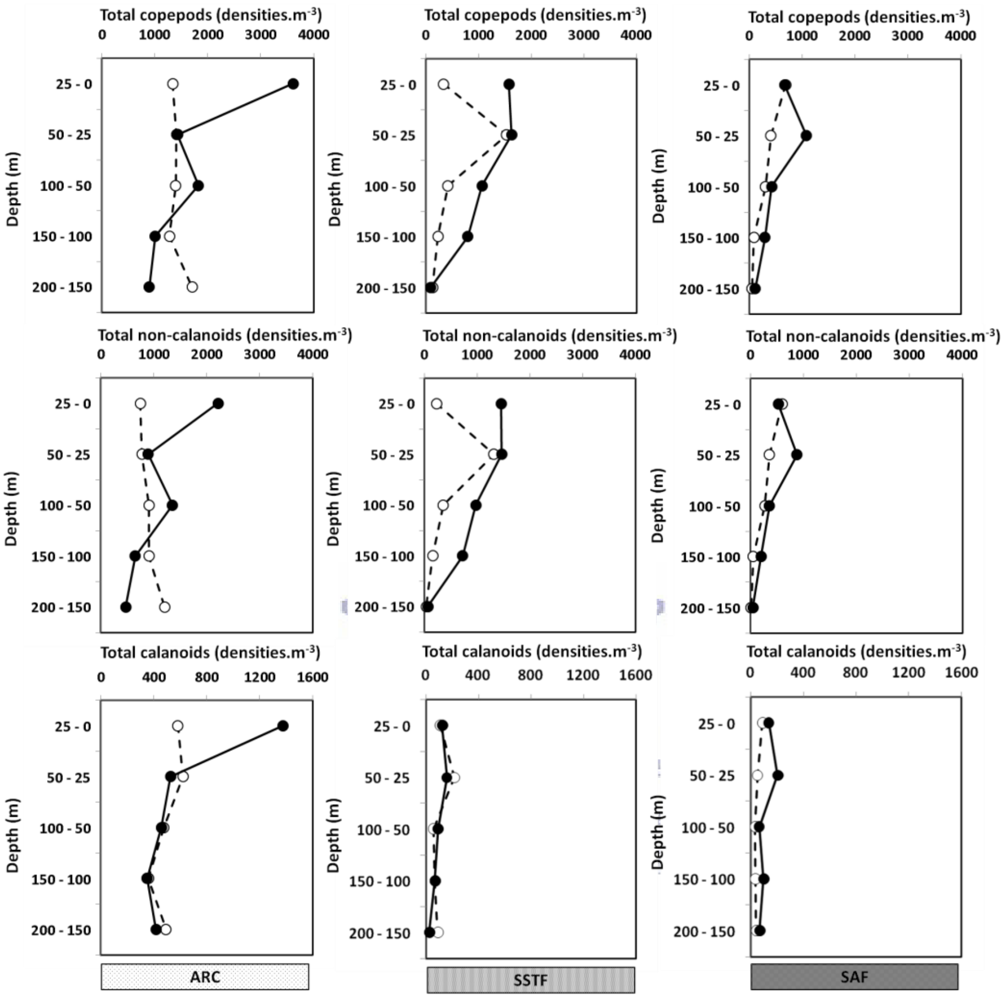

Figure 3.13: Vertical day (○) and night (●) of copepods (densities.m^{-3}) depth distribution of: top panel total copepods, middle panel total non-calanoids, bottom panel total calanoids collected along the South West Indian Ocean Ridge during November and December 2009. Groups were defined by the cluster analysis in Section 3.1.3, Figure 3.5. ARC - Agulhas Return Current; STF - Subtropical Front; SAF - Sub-Antarctic Front.

To assess the changes in depth distributions of copepod densities against time of day for the three oceanographic zones, all samples were pooled for each zone. The results of the vertical depth differences of copepod fauna between day and night along the SWIOR are summarised in Tables 3.4 and 3.5. Tables 3.4 and 4.5 shows dominant copepods contributing to more than

5 % of the total numbers for the different families, and the full dataset for day and night time sampling is represented in Annexures I and II.

During daylight, small calanoids of the families Acartiidae and Paracalanidae each accounted for more than 1% of the total calanoid abundance in the upper 100 m of the water column in the ARC (Table 3.4). Paracalanidae contributed mostly to total copepod abundance below 25 m in the SAF (Table 3.4). Clausocalanidae and Paracalanidae were mostly abundant below 100 m and their abundances accounted for more than 2 % of the total copepod number both by day and night across the major zones (Tables 3.4 and 3.5). Larger calanoids of the family Metridinidae were found to be more common at night between 100 to 200 m in the SAF (Table 3.5), whilst during the day, Lucicutiidae were commonly found at 100 – 200 m in the ARC and in the SAF (Table 3.4). Interestingly, during the day the greatest density of Calanidae was found in the surface waters of the ARC, but their abundances were found to be concentrated in deeper waters (150 - 200 m) in the SAF.

During the day and night in the upper 100 m of the water column, representatives of the families Oithonidae, Oncaeidae and Corycaeidae accounted for more than ~60 % of total non-calanoid fauna in each of the major oceanographic zones. Oithonidae strongly dominated depth distributions of copepod samples during the day and night (Table 3.4 and 3.5).

Vertical day and night depth distributions of the dominant taxa across the three major water masses are illustrated in Figure 3.14. The small numbers of individuals in some hauls (groups) should be noted.

Oithona species appeared to migrate through a lesser range by day and night in the ARC and the STF zones, but at night a peak in their upward move was observed in both areas

(Figure 3.14). By contrast in the SAF, their daytime depth distribution was concentrated at 25 - 50 m, whilst at night more individuals were found between 50 - 100 m.

Species of *Oncaea* were found generally below 50 m and appeared to remain there both during the day and night across all three major zones and an increase in their distributional depth can be seen at night (Figure 3.14).

Ctenocalanus vanus was found in high concentrations in the upper 50 m of the water column during day in the ARC and STF, with peak abundances at night in the ARC. This species did not show a change in vertical distribution in the STF. Low concentrations of this species occurred throughout the water column in the SAF (Figure 3.14).

Paracalanus parvus was absent from catches made in the STF zone, with greater concentrations of individuals found in the upper 50 m of the water column during the day than night in the SAF and ARC (Figure 3.14).

Clausocalanus brevipes showed upward movement at night in the three water zones, reaching peak abundances below the 100 m in the ARC and in the SAF, whilst their numbers were higher to some extent at night in the upper 50 m of the water column in the STF (Figure 3.14).

Mecynocera clausi in the ARC and SAF were similarly distributed through the water column by day and night (generally deeper than 100 m), however, this species was absent in the STF zone (Figure 3.14).

Clausocalanus laticeps showed an upward migration at night from below 100 m depth in the STF and SAF regions, but was very uncommon in the surface waters (50 m) during the day in the ARC (Figure 3.14).

Pleuromamma piseki showed a pronounced upward movement at night in the ARC and SAF, but this species was absent from all catches in the STF area (Figure 3.14).

The vertical distribution of *Calocalanus styliremis* varied across all three zones. The greatest concentration of individuals was found during the day in the SAF, with a peak in their concentrations at night in the upper 50 m in the ARC, and this species was found in low concentrations both by day and night in the STF (Figure 3.14).

Metridia lucens was absent from all day and night-time catches in the ARC, and day and night-time observations showed low concentrations of individuals in the upper 25 m of the water column in the STF. At night in the SAF, the species appears to show DVM (Figure 3.14).

Both day and night-time values of *Calanus simillimus* were low in the ARC, and nighttime observations showed greatest migrations of individuals below 50 m of the water column in the STF. Surprisingly this species was not recorded in the SAF (Figure 3.14).

The distribution of *Acartia danae*, and species of *Corycaeus* and *Faranula* were generally similar across all three regions (Figure 3.14). In the ARC, greatest concentrations of individuals were found during day below 100 m, with a peak of individuals (except *Faranula* species) at night in the upper 100 m. These species were found in low concentrations in the STF and SAF zones (Figure 3.14).

A plot showing diurnal changes in the WMDs of the dominant taxa, or taxa that were distributed across all three major water masses is shown in Figure 3.15. During the day, *Oithona* tended to occur deeper in the water column in the ARC, but shallow both in the STF and in the SAF (Figure 3.15). These WMD differences of *Oithona* between cluster groups by day and night are statistically significant (*F* (2, 10) = 6.671, *p* = .021 and *F* (2, 10) = 5.729, *p* = .014, respectively). *Oithona* was found closer to the surface than *Oncaea* and *Ctenocalanus vanus*, by ~100 m. *Oncaea* was generally deeper than 140 m during the day in the ARC, but this genus did not show a change in WMD during the day in the STF and in the SAF (Figure 3.15). These daytime WMD differences of *Oncaea* between cluster groups are significant (*F* (2, 10) = 5.823, p = .021). By contrast there were no significant night-time WMD differences of *Oncaea* between cluster groups (*F* (2, 10) = 0.910, p = .433). The WMD of *C. vanus* tended to occur deeper during the day and shallow during the night across all three regions (Figure 3.15). These time of day WMD differences of *C. vanus* between cluster groups are statistically significant (day: *F* (2,10) = 6.495, *p* = .015 and night: *F* (2,10) = 6.271, *p* = .017).

Table 3.4: Daytime composition (densities.m^{-3}) of dominant copepod taxa sampled at different depth intervals in the upper 200 m of the water column across the South West Indian Ocean Ridge during the period of November to December 2009. Groups were identified by the cluster analysis in Figure 3.5, Section 3.1.3. ARC - Agulhas Return Current; STF - Subtropical Front; SAF - Sub-Antarctic Front.

	ARC					SSTF					SAF				
	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	150 - 200 m	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	150 - 200 m	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	150 - 200 m
Order Calanoida															
Family Acartiidae															
Acartia danae	51.0	119.3	46.6	30.4	5.7	0.7									
Acartia negligens	122.1	36.4	30.2	5.4	3.7										
Total	173.0	155.7	76.8	35.8	9.4	0.7									
Family Calanidae															
Calanoides macrocarinatus	4.6	6.4	3.2	5.2	9.2									1.2	0.2
Calanus simillimus			0.3	0.5		9.6	18.3	4.6	0.9	5.5					
Cosmocalanus darwinii		1.9	0.1												
Mesocalanus tenuicornis	1.6	2.1	9.4	13.1	25.2			1.1						1.2	1.0
Nannocalanus minor	48.3	80.5	41.0	24.3	32.2										
Neocalanus gracilis	22.7	51.5	17.1	6.9	4.2	0.7					1.2			0.2	3.8
Total	77.2	142.5	71.1	50.0	70.8	10.3	18.3	5.6	0.9	5.5	1.2			2.6	5.0
Family Clausocalanidae															
Clausocalanus arcuicornis	6.4	9.2	15.6	19.3	37.7	5.5	0.8		4.4	5.6				0.2	
Clausocalanus brevipes	0.3				5.6	18.3	3.9	0.7	6.5	21.9	0.7	6.7	1.8	5.2	1.3
Clausocalanus furcatus	8.7		0.3					2.4			1.5				
Clausocalanus ingens	1.6	1.2	3.8	5.3	10.5	2.8	21.5	11.7	2.4	0.5	14.6	0.7		0.2	0.6
Clausocalanus jobei		0.3	1.5	5.2	4.4	0.7									
Clausocalanus laticeps				0.1	1.1	23.8	18.9	6.3	5.4	6.1	4.2	1.3	0.6	3.8	4.0
Clausocalanus lividus	5.3	3.6	5.5	3.7	3.4	13.8	0.8	0.5	2.1	5.0		0.3			0.8
Clausocalanus mastigophorus	1.3	7.0	12.5	6.9	5.5	2.8		0.5	2.9	0.5					
Clausocalanus minor	11.6	5.3	16.4	16.7	18.6						0.4				
Clausocalanus parapergens	0.6	4.1	14.0	16.8	23.1			6.1		0.5	1.1		1.7	9.3	4.9
Clausocalanus paululus	2.3	0.6	0.2	0.4	0.3										
Clausocalanus pergens	1.4	4.3	18.2	15.6	8.6			0.3					2.6	0.5	0.4
Ctenocalanus vanus	4.8	10.9	64.7	79.8	126.0	24.8	144.0	10.5	37.3	6.1	0.8	0.3	0.1	1.8	0.8
Total	44.4	46.6	152.6	169.9	245.0	92.5	189.8	39.0	61.1	46.3	23.3	9.3	6.8	21.0	12.8
Family Eucalanidae															
Eucalanus hyalinus	4.5	2.5	9.0	3.0							1.4		1.7		0.2
Rhincalanus gigas			0.3		1.5	1.1		1.6	1.1	7.9		0.7	0.5	0.2	
Rhincalanus nasutus	6.0	3.7	13.0	10.2	7.4			1.5		0.5	0.3		0.3	0.1	0.2
Total	10.6	6.2	22.3	13.3	8.9	1.1		3.1	1.1	8.5	1.7	0.7	2.5	0.3	0.3
Family Euchaetidae															
Euchaeta acuta			0.2		2.5			0.8							
Total			0.2		2.5			0.8							
Family Heterorhabdidae															
Heterorhabdus papilliger	0.4		1.5	2.1	9.6			0.8	0.2	0.5		0.3		1.0	2.1
Total	0.4		1.5	2.1	9.6			0.8	0.2	0.5		0.3		1.0	2.1
Family Lucicutiidae															
Lucicutia clausi	0.3		0.2	1.8	17.2										
Lucicutia flavicornis		0.3	5.5	8.5	77.4					1.1	0.4		0.2	0.2	1.6
Total	0.3	0.3	5.7	10.3	94.6					1.1	0.4		0.2	0.2	1.6

Table 3.4 (continued)

Family Metridinidae															
Metridia lucens								0.2			0.4		0.1	0.4	5.2
Pleuromamma abdominalis	0.3														
Pleuromamma borealis															
Pleuromamma gracilis		1.2		0.2	0.3										
Pleuromamma indica															
Pleuromamma piseki	0.5			0.3	2.1										1.2
Total	0.8	1.2		0.5	2.4			0.2			0.4		0.1	0.4	6.4
Family Scolecitrichidae															
Scaphocalanus curtus				0.2	5.0										
Scaphocalanus spp.									0.2	5.8	0.4		0.2	1.0	1.1
Scolecithricella minor			0.1	0.1	0.4	2.4	5.1	5.7	3.7	19.8	0.8	2.0	1.0	6.6	9.8
Total			0.1	0.3	5.4	2.4	5.1	5.7	4.0	25.6	1.2	2.0	1.1	7.5	10.9
Family Paracalanidae															
Calocalanus contractus	1.9		0.2	1.4	3.2										
Calocalanus pavo	10.7	3.2	1.8	2.5	4.7						0.4		0.7		
Calocalanus styliremis	22.2	17.3	22.1	18.1	2.5		3.2				7.3	25.1	20.8	1.0	0.6
Paracalanus denudatus	0.8			0.2											
Paracalanus indicus	19.0	18.0	7.4	1.7											
Paracalanus nanus	2.6	1.6	2.1	2.9	0.2										
Paracalanus parvus	153.2	144.3	47.3	14.5	8.9			0.5			40.2	0.3			
Paracalanus quasimodo	8.5	2.5	3.7	0.9											
Mecynocera clausi	50.8	77.0	56.4	31.2	8.9				0.2		13.7	14.4	2.4	0.1	
Total	269.8	264.0	141.0	73.3	28.4		3.2	0.5	0.2		61.5	39.7	23.8	1.1	0.6
Cyclopoida															
Family Oithonidae															
Oithona spp.	469.8	550.9	422.3	488.8	238.1	228.3	1312.7	356.2	139.5	24.1	596.7	351.4	265.7	39.8	2.6
Total	469.8	550.9	422.3	488.8	238.1	228.3	1312.7	356.2	139.5	24.1	596.7	351.4	265.7	39.8	2.6
Harpacticoida															
Family Ectinosomatidae															
Microsetella rosea		0.7	0.8	1.2	5.1		0.8		0.2						
Total		0.7	0.8	1.2	5.1		0.8		0.2						
Poecilostomatoida															
Family Corycaeidae															
Corycaeus spp.	132.0	93.5	263.6	90.8	54.6	0.7		0.3		0.3					
Farranula spp.	82.4	84.8	70.6	37.9	21.9		1.5								
Total	214.4	178.4	334.2	128.6	76.5	0.7	1.5	0.3		0.3					
Family Oncaeidae															
Oncaea spp.	64.0	48.8	155.3	292.2	889.3	1.4	3.9	3.6	20.6	11.4		2.3	4.0	10.2	4.1
Total	64.0	48.8	155.3	292.2	889.3	1.4	3.9	3.6	20.6	11.4		2.3	4.0	10.2	4.1

Table 3.5: Nightime copepod composition (densities.m^{-3}) of dominant taxa collected at different depth intervals in the upper 200 m across the South West Indian Ocean Ridge for the duration of November to December 2009. Groups were derived by the cluster analysis (Figure 3.5, Section 3.1.3). ARC - Agulhas Return Current; STF - Subtropical Front; SAF - Sub-Antarctic Front.

	ARC					SSTF					SAF				
	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	150 - 200 m	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	150 - 200 m	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	150 - 200 m
Order Calanoida															
Family Acartiidae															
Acartia danae	162.7	85.1	28.1	37.6	37.3										0.2
Acartia negligens	104.7	22.7	10.8	8.2	9.1						1.1				
Total	267.4	107.8	39.0	45.8	46.4						1.1				0.2
Family Calanidae															
Calanoides macrocarinatus	3.0	1.7	0.6	1.0	1.2								0.9	4.8	
Calanus simillimus					0.6	8.6	13.4	19.3	6.7	0.2					
Cosmocalanus darwinii	0.6				6.3										
Mesocalanus tenuicornis	12.3	8.0	14.1	13.3	6.8							0.7	0.5		
Nannocalanus minor	76.3	32.9	14.6	8.9	8.9										0.2
Neocalanus gracilis	38.6	19.1	12.3	8.2	13.9						0.5			0.2	0.7
Total	130.7	61.7	41.6	31.3	37.8	8.6	13.4	19.3	6.7	0.2	0.5	0.7	1.4	4.9	0.9
Family Clausocalanidae															
Clausocalanus arcuicornis	61.9	31.0	16.7	16.1	19.2					0.1	1.1		0.3		
Clausocalanus brevipes	8.7	2.5	1.0	2.0	3.4	36.6	63.3	9.7	9.8	1.2	43.8	53.3	22.0	17.9	5.6
Clausocalanus furcatus	14.9		0.2	0.3											
Clausocalanus ingens	19.4	3.6	3.9	5.5	13.0						4.3				
Clausocalanus jobei	6.1	4.4	1.9												
Clausocalanus laticeps					0.1	41.6	29.5	29.0	11.8	1.1	11.8	6.3	2.2	0.3	1.2
Clausocalanus lividus	11.0	2.1	1.8	2.2	4.2						1.6				
Clausocalanus mastigophorus	32.3	9.3	10.0	4.8	3.6										
Clausocalanus minor	44.7	10.6	19.7	23.4	8.7										
Clausocalanus parapergens	23.6	5.8	12.1	11.2	9.3									0.3	
Clausocalanus paululus	6.9	3.0	2.4	2.4	1.6										
Clausocalanus pergens	44.7	7.3	12.4	7.7	2.7						1.6		0.3		
Ctenocalanus vanus	66.4	42.1	133.4	78.6	64.2	37.9	47.8	19.3	26.9	5.0	0.5	2.9			0.4
Total	340.5	121.7	215.6	154.2	130.1	116.1	140.5	58.0	48.6	7.5	64.7	62.5	24.7	18.6	7.3
Family Eucalanidae															
Eucalanus hyalinus	3.9	2.6	1.5	1.2	0.2					0.2	0.5		1.3	0.1	
Rhincalanus gigas	1.1	1.1		0.1	0.3				0.6	3.3			0.3		
Rhincalanus nasutus	17.9	11.6	7.1	1.9	2.2									0.1	
Total	22.8	15.2	8.6	3.2	2.7				0.6	3.4	0.5		1.5	0.3	
Family Euchaetidae															
Euchaeta acuta	6.4	4.9	5.4	5.6	16.3										0.2
Total	6.4	4.9	5.4	5.6	16.3										0.2
Family Heterorhabdidae															
Heterorhabdus papilliger	2.1	2.1	2.6	5.5	7.6					0.4			0.4	0.3	2.0
Total	2.1	2.1	2.6	5.5	7.6					0.4			0.4	0.3	2.0
Family Lucicutiidae															
Lucicutia clausi	7.2	3.5	3.1	4.2	1.3										
Lucicutia flavicornis	35.8	16.3	12.8	12.8	26.2					0.1			0.8	0.5	0.7
Total	43.0	19.8	15.9	16.9	27.5					0.1			0.8	0.5	0.7

Table 3.5 (continued)

Family Metridinidae															
Metridia lucens										0.2	28.0	37.9	16.5	26.9	18.3
Pleuromamma abdominalis	16.2	9.2	7.3	3.1	16.9								1.8	2.2	1.9
Pleuromamma borealis	28.0	8.5	4.6	2.0	7.4						1.3	5.0		2.2	0.3
Pleuromamma gracilis	21.4	14.4	1.6	3.4	6.0									0.7	0.2
Pleuromamma indica	68.2	27.0	20.0	15.2	37.7						15.8	61.6	10.2	30.8	20.9
Pleuromamma piseki					3.2		0.6	0.5	2.5	1.7		10.8	1.5	1.4	
Total	133.7	59.1	33.4	23.6	71.2		0.6	0.5	2.5	1.9	45.1	115.3	30.0	64.3	41.7
Family Scolecitrichidae															
Scaphocalanus curtus	2.8	0.8	2.0	1.7	0.3										0.2
Scaphocalanus spp.				0.6	0.4					0.9					1.8
Scolecithricella minor	0.7	0.7	0.6		1.3	0.3	5.8	14.5	10.1	7.1	1.2		4.8	6.6	3.5
Total	3.5	1.5	2.7	2.4	2.0	0.3	5.8	14.5	10.1	7.9	1.2		4.8	6.6	5.5
Family Paracalanidae															
Calocalanus contractus	3.1	0.4	0.8	6.5	2.4										
Calocalanus pavo	9.6	1.9	1.3	2.0	5.7										
Calocalanus styliremis	61.8	23.4	22.5	5.8	8.6		1.0		0.3		15.4	18.3	1.0	0.5	
Paracalanus denudatus	8.7	0.4			0.3										
Paracalanus indicus	23.2	2.2	1.8	2.1	0.3					0.1					
Paracalanus nanus	17.1	5.1	4.7	1.0	3.8					0.2					
Paracalanus parvus	173.9	38.0	10.3	3.9	6.8						3.7				
Paracalanus quasimodo	7.4	2.5	0.2												
Mecynocera clausi	96.1	47.7	39.5	24.2	9.0					0.2	4.6	2.6	0.5		0.7
Total	400.8	121.5	81.0	45.5	36.9		1.0		0.3	0.4	23.8	21.0	1.5	0.5	0.7
Cyclopoida															
Family Oithonidae															
Oithona spp.	1140.1	451.4	688.6	305.1	149.4	1456.7	1467.7	971.8	720.1	61.0	517.1	869.6	320.7	131.2	9.1
Total	1140.1	451.4	688.6	305.1	149.4	1456.7	1467.7	971.8	720.1	61.0	517.1	869.6	320.7	131.2	9.1
Harpacticoida															
Family Ectinosomatidae															
Microsetella rosea	12.6	3.0	4.5	1.8	0.3										
Total	12.6	3.0	4.5	1.8	0.3										
Poecilostomatoida															
Family Corycaeidae															
Corycaeus spp.	286.5	121.9	155.3	50.4	58.7										
Farranula spp.	121.8	44.9	55.0	18.0	6.0										
Total	408.3	166.8	210.2	68.4	64.7										
Family Oncaeidae															
Oncaea spp.	660.0	275.6	452.9	280.0	259.0		0.2	4.8	8.8	5.9	7.7	5.8	34.6	64.2	34.3
Total	660.0	275.6	452.9	280.0	259.0		0.2	4.8	8.8	5.9	7.7	5.8	34.6	64.2	34.3

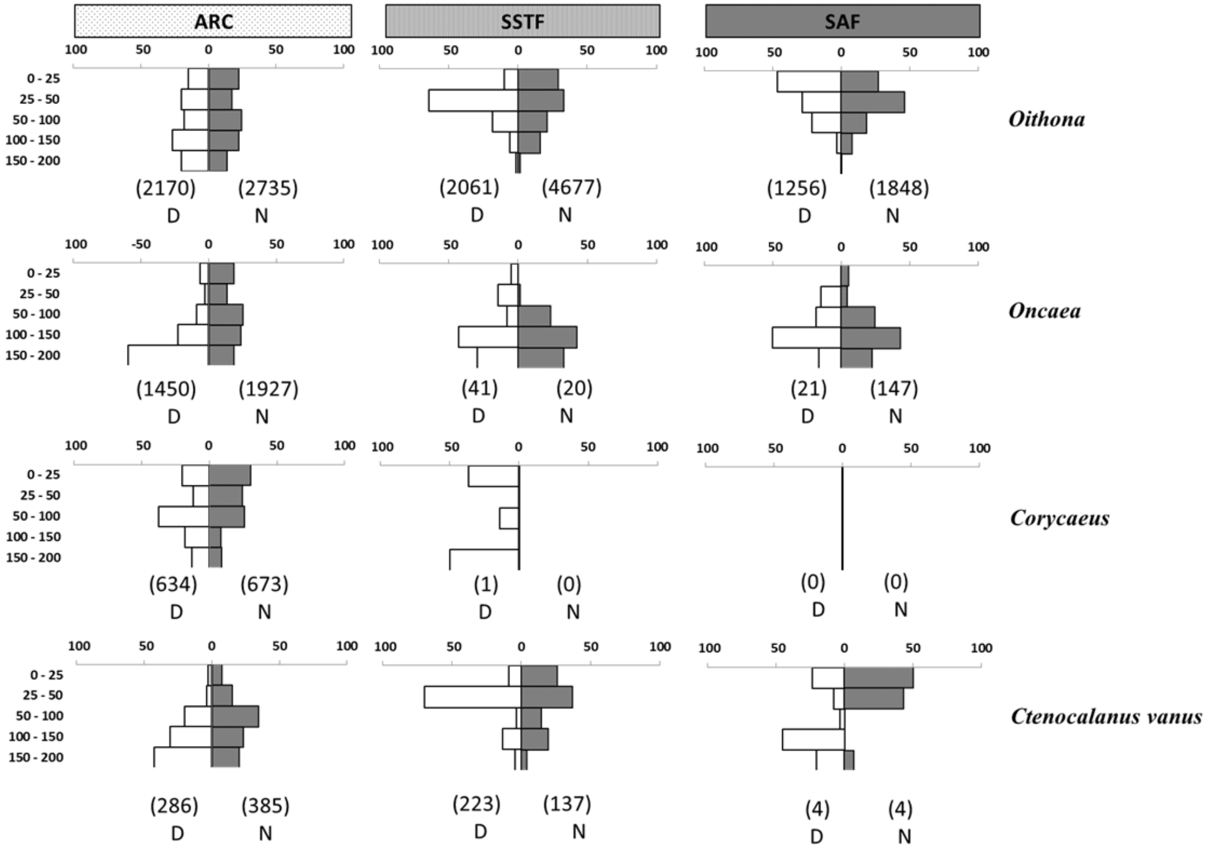

Figure 3.14: Vertical day (open bar) and night (filled bar) distributions (%) of dominant copepod taxa sampled along the South West Indian Ocean Ridge (SWIOR) over the study period November to December 2009 for each major oceanographic zone. November to December 2009 for each major oceanographic zone. Numbers at bottom of plots indicates densities.m^{-3}. Day is designated as “D” and night as “N”. Groups are defined by the cluster analysis in Section 3.1.3, Figure 3.5. ARC – Agulhas Return Current; STF– Subtropical Front; SAF – Sub-Antarctic Front. Species depth distributions are plotted in decreasing abundances along the SWIOR: *Oithona*; *Oncaea*; *Corycaeus*; *Ctenocalanus vanus*; *Paracalanus parvus*; *Acartia danae*; *Farranula*; *Clausocalanus brevipes*; *Mecynocera clausi*; *Clausocalanus laticeps*; *Pleuromamma piseki*; *Calocalanus styliremis*; *Metridia lucens*; *Calanus simillimus*.

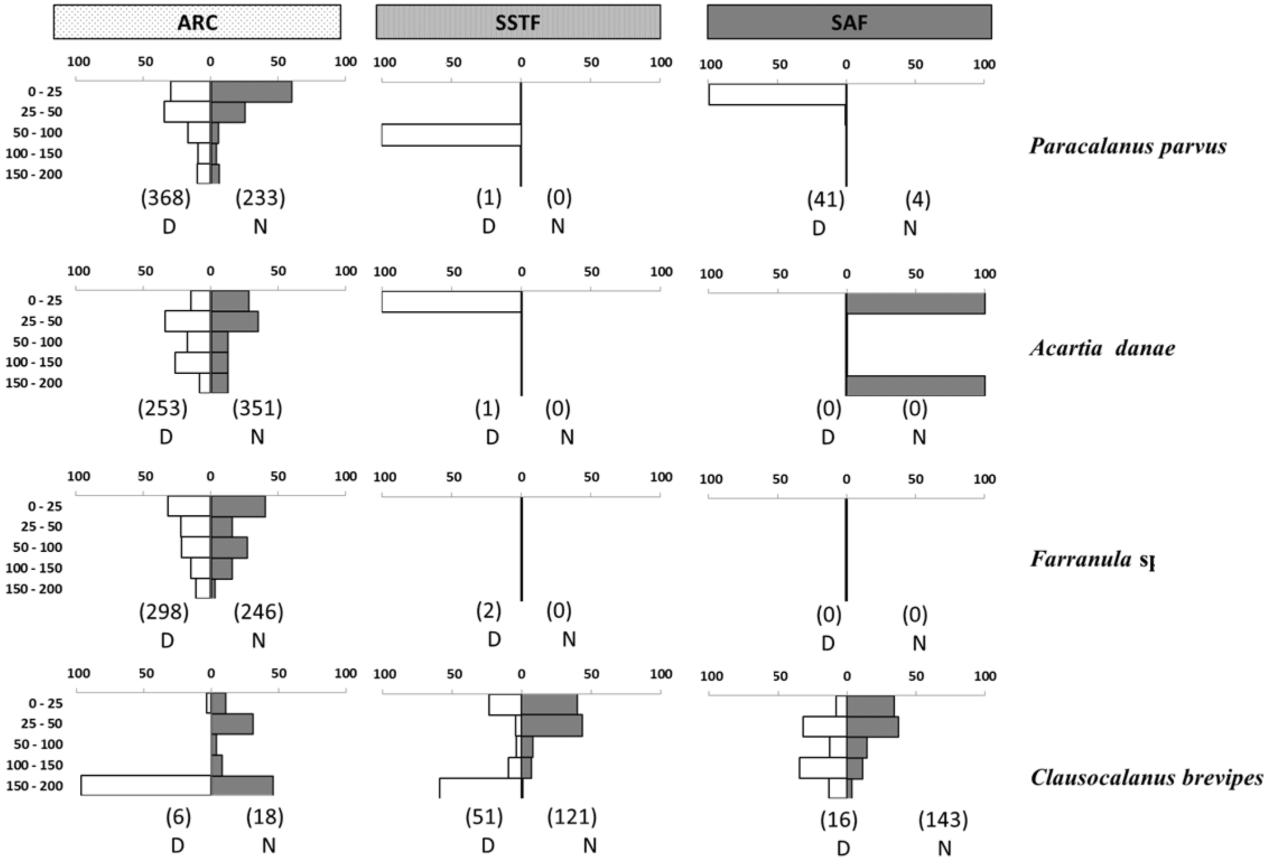

Figure 3.14: Continued: *Paracalanus parvus*; *Acartia danae*; *Farranula*; *Clausocalanus brevipes*

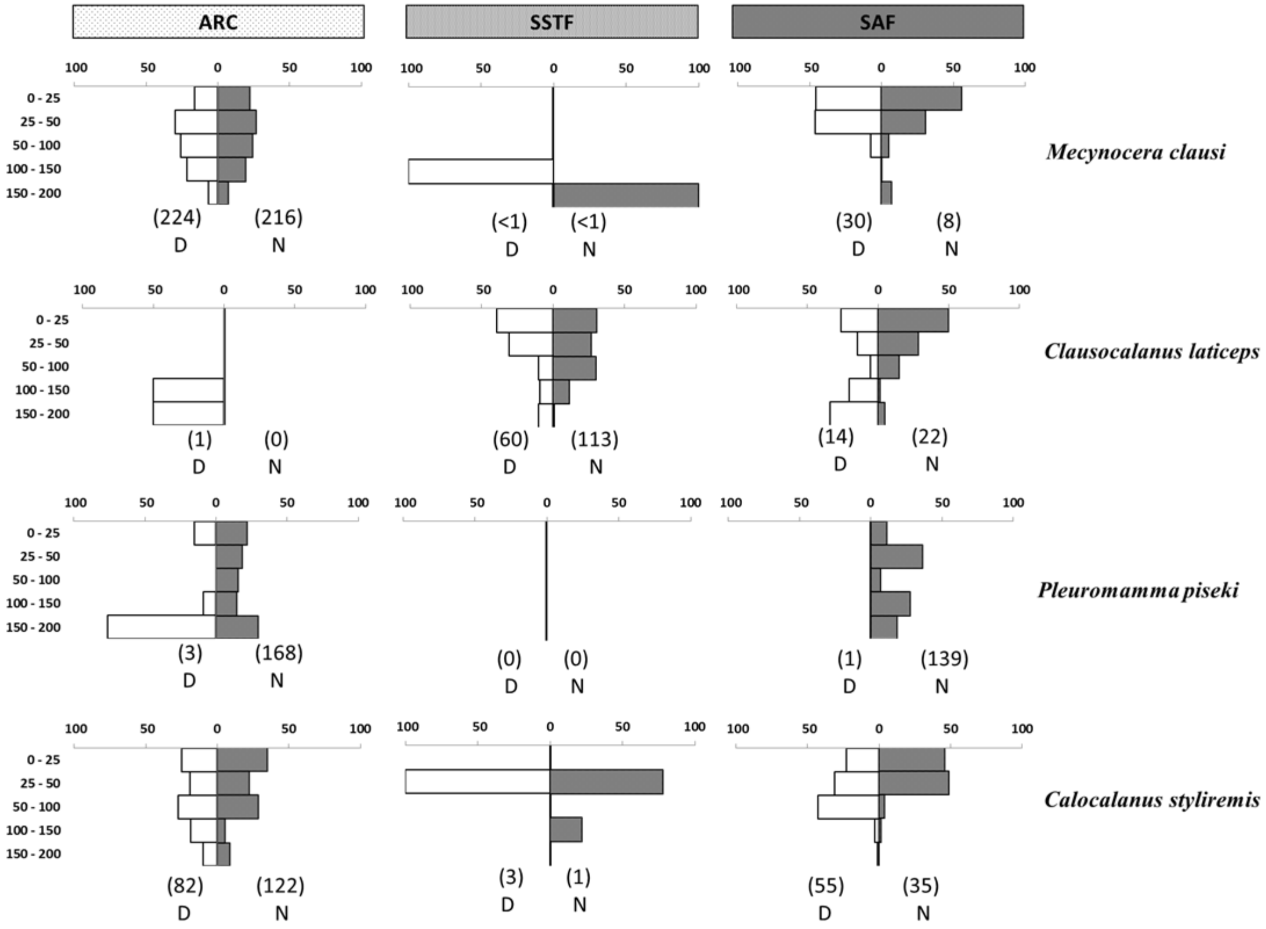

Figure 3.14: Continued: *Mecynocera clausi*; *Clausocalanus laticeps*; *Pleuromamma piseki*; *Calocalanus styliremis.*

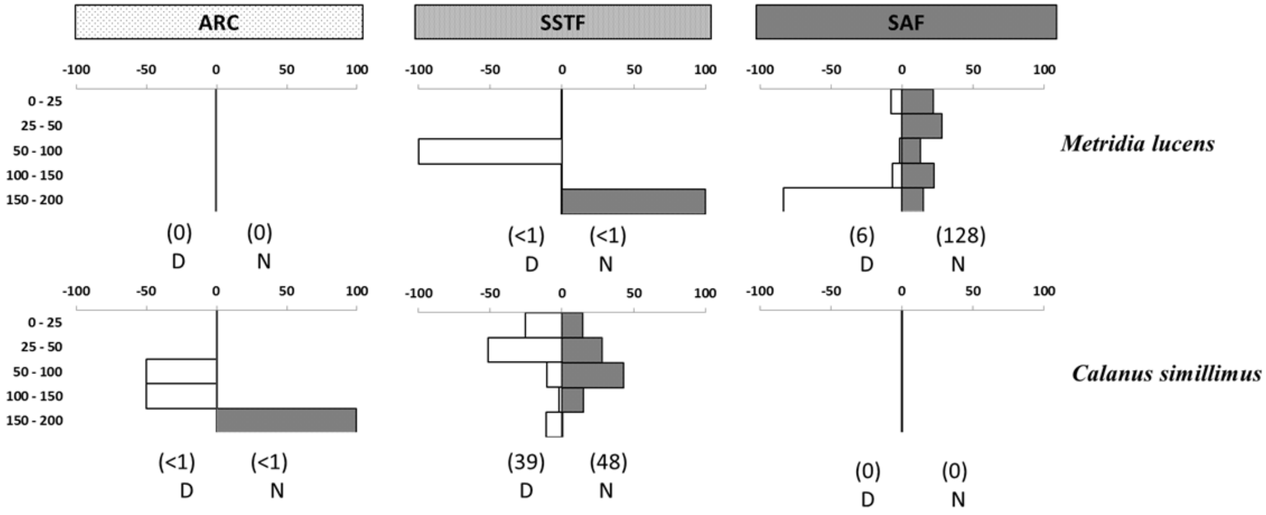

Figure 3.14: Continued: *Metridia lucens*; *Calanus simillimus.*

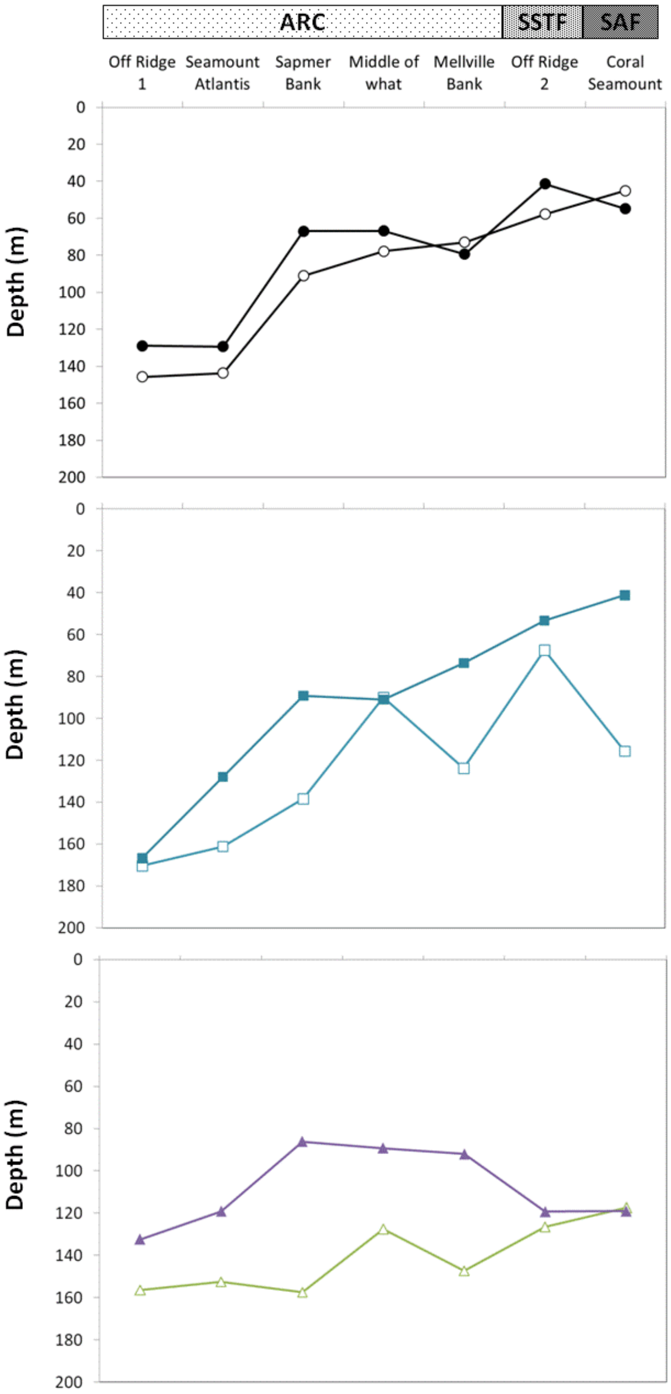

Figure 3.15: Weighted Mean Depths of the dominant top three taxa: top panel *Oithona* day (○) and night (●); *Ctenocalanus vanus* day (☐) and night (■); *Oncaea* day (△) and night (▲) of samples along the South West Indian Ocean Ridge during the study period of November to December 2009. Stations have been classified into groups derived by the cluster analysis in Section 3.1.3, Figure 3.5. ARC– Agulhas Return Current; STF– Subtropical Front; SAF– Sub-Antarctic Front Group.

3.2. Discussion

Total surface chlorophyll-*a* during the survey was low in the northern part of the SWIOR (<0.04 µg l^{-1}), and increased to about 1-2 µg l^{-1} towards the frontal regions of the STF and SAF. This result reflects the enhancement of chl *a* concentrations boundary between the ARC and the SAF (Weeks & Shillington, 1994, 1996; Read *et al.*, 2000). Read *et al.* (2000) have shown that the front between the ARC and SAF leads to the development of steep horizontal temperature and nutrient gradients (STF), a zone characterised by strong current velocities and shallow pycnoclines, which will in turn promote primary production, as result of transitions between the ARC and the SAF (Bathmann *et al*., 1997; Laubscher *et al*., 1993; Read *et al*., 2000; Fiala *et al*., 2003, Pollard & Read, 2017; Read & Pollard, 2017, Sonnekus *et al*., 2017). The results of the dbRDA plot (Figure 3.7) indicated that integrated chlorophyll (mg.m^{-2}) and depth of the chlorophyll max (m) partly explain the variation in copepod community structure between stations. Other studies have documented that integrated chlorophyll *a* (mg.m^{-2}) is one of the most important factors structuring mesozooplankton communities, particularly near oceanic fronts (e.g. Bernard & Froneman, 2003; Carlotti *et al.*, 2015).

Three copepod assemblages were identified by the cluster analysis (Figure 3.5), and each was associated with a different water mass along the SWIOR transect (Figures 3.1 and 3.2). The stations of Group A were within the ARC region, whereas the stations of Group B occupied waters of the STF, while the stations of Group C occupied the vicinity of the SAF. The results from the SIMPER analysis indicate that the differences between the communities in these different areas reflect changes in the relative abundances of the dominant species, and the presence or absence of indicator species. Group B had the most abundant copepod species, *Oithona* spp. and these dominated the total abundance near surface waters of the STF. The analysis of similarity showed that dominant *Clausocalanus laticeps*, *Calanus simillimus* and *Metridia lucens* south of the STF are associates of Sub-Antarctic waters, and characteristically indicates region of transition zones between warm-temperate and Sub-Antarctic waters (De Decker, 1984).

The total abundance of copepods was greatest towards the frontal stations, and this was attributed to elevated chlorophyll concentrations. These results are similar to those obtained by (Allanson *et al.*, 1981; Laubscher *et al.*, 1993; Pakhomov & McQuaid, 1996; Barange *et al.*, 1998; Pakhomov *et al.*, 1999; Bernard & Froneman, 2003; Richoux & Froneman, 2009), and have been observed for other zooplankton groups (Graham *et al.*, 2001; Hosie *et al.*, 2014; Stevens *et al.*, 2014; Meilland *et al.*, 2016). Read *et al*. (2000) suggested that high primary production with stable and shallow upper mixed-layer depth in the STF and SAF sector would influence the growth and abundance of phytoplankton (diatoms, nano- and picoplankton). These conditions will in turn provide food resources for different micro- and mesozooplankton species (Perissinotto, 1992; Froneman & Perissinotto, 1996; Pakhomov & Froneman, 2004). This may explain the development and the increase in the relative abundance of species (e.g. *Paracalanus parvus*) near the frontal areas during the present investigation, their life history-strategy are typically associated with highly productive areas (e.g. Ianora, 1998; Peterson, 1998; Jang *et al.*, 2013).

Copepod densities also decreased with increasing depth (Figure 3.13). The maximum copepod abundance was found in the upper 100 m (Figure 3.13), and this is in agreement with other observational studies for the ARC (De Decker & Mombeck, 1964; Heinrich, 1992, 1995). Total copepod densities were higher in the upper 100 m of the water column in the Sub-Antarctic area too, but Errhiff *et al.* (1997) found 60% of their copepod abundance at between 100 – 200 m (42 ^{o}S to 62 ^{o}S). Errhif *et al.* (1997) noted a poor relationship between total copepod abundance and chlorophyll concentrations. Subsequent studies have suggested zooplankton to exert strong grazing pressure on phytoplankton along the Indian Ocean sector of the Southern Ocean (Mayzuad *et al.*, 2002a and citations therein). Mayzaud *et al.* (2002a) indicated that the grazing pressure of numerically dominant small copepods, and larger copepodite stages rather than adults, had the greatest impact on chlorophyll concentrations. In this study, higher concentrations of copepods occurred near or above the chlorophyll maximum, suggesting displacement in copepod densities with chlorophyll maxima, and so their related feeding strategies (Morales *et al.*, 1991; Perissinotto 1992; Atkinson, 1996; Mayzaud *et al.*, 2002a, b).

The total copepod abundances increased at night (Figure 3.13). Greatest abundances were observed at night in the upper 25 m of the water column in the ARC (Figure 3.13), and non-calanoids contributed largely to these abundances, an observation noted previously by De Decker & Mombeck (1964) and Heinrich (1992; 1995). Highest calanoid abundance also occurred at night in the upper 25 m of the water column in the ARC; perhaps suggesting diurnal migration of deeper living copepods (Yamaguchi *et al.*, 2015). This was especially evident amongst larger copepods (*Paraeuchaeta biloba*, *Undeuchaeta plumosa* and *Euchaeta media*, found between 50 to 100 m layers) which were otherwise absent from daylight catches (Annexure I). The daytime abundances of copepods were higher during the day in the SAF region; perhaps copepods rarely changed their depth distribution during time of day in Antarctic waters.

Total copepod abundance varied with taxonomic groups, and while abundance of copepods was strongly dominated by species of the genera *Oithona*, *Oncaea* and *Coryceaus*, generally most calanoid genera (e.g. *Ctenocalanus*, *Clausocalanus*) showed high abundances across the survey area (Tables 3.4 and 3.5). The high numbers of *Oithona* across the survey area (Table 3.2) is in agreement with other studies on non-calanoids in upper water layers (Atkinson, 1998; Froneman *et al.*, 1999; Froneman *et al.*, 2007), and across oceanic ridges (Kosobokova & Hirche, 2000; Gaard *et al.*, 2008). Small calanoids of the family Acartiidae, Clausocalanidae and Paracalanidae were most common in the upper 100 m, whereas larger calanoids of the family Metridinidae and Lucicutidae were least common in the upper 100 m, which is in agreement with the findings from previous studies (De Decker & Mombeck, 1964; De Decker, 1973, 1984; Heinrich, 1992, 1995; Huggett, 2014).

It is worth noting that the total abundance of copepods may be strongly influenced by mesh sizes and sampling gear, which includes the collection methods (oblique or vertical hauls) used in investigations. During this study, oblique hauls were conducted for the duration of the survey period and nets were fitted with 180 µm mesh. Mesh sizes between 150 µm and

180 μm are likely to be dominated by small size copepods, in particular by species of the genera *Oithona* and *Oncaea* (Kosobokova & Hirche, 2000; Gaard *et al.*, 2008; Stevens *et al.*, 2014); results observed in the present study (Table 3.2).

The results of the present study showed that differences in WMD between day and night for the most abundant copepods was small (8 m) in all three major zones. In this study, average WMDs between dominant copepods varied between stations across the SWIOR, and WMDs appeared to be deeper in the ARC and shallower in the STF and SAF regions. Overall WMDs corresponded near or within chlorophyll-*a* maximum (Figure 3.2c). These depth changes of copepods suggest that chlorophyll might be affecting species vertical distributions, as they did too the horizontal distribution of communities. Studies have shown that phytoplankton concentrations cause a change in copepod vertical distribution patterns (e.g. Frost, 1987; Michels *et al.*, 2012; Hampton *et al.*, 2014). Such a result might be the reason why copepods tended to occur in different depths and into upper waters, which was shallow in STF and SAF. Other factors influencing vertical migration changes in copepods include light intensity; competition and predation (see Ringelberg, 2009).

The WMDs of *Oncaea* tended to be near or below the chlorophyll-*a* maxima, as has been previously noted in the Red Sea by Weikert (1982) and Böttger-Schnack *et al.*, (1989). WMDs of *Ctenocalanus vanus* varied with latitude and they appeared to scarcely migrate, for example in the ARC, their depth distributions were deep during the day and appeared shallow at night (Figure 3.15). This result might suggest feeding by *Ctenocalanus vanus* (Cornilis *et al.*, 2007), due to the oligotrophic environment of the ARC (e.g. Thomalla *et al.*, 2011);

further observations are needed. *Oithona* was found at or near the chlorophyll maximum, their depth distributions have been found to be similar under different productivity regimes (e.g. Atkinson & Sinclair 2000; Paffenhöfer & Mazzocchi, 2003). The dominance of species of the genus *Oithona* in the upper surface waters were replaced in deeper waters by *Oncaea* spp. during the study period, observations in line with other studies (Errhif *et al.*, 1997).

The sampling strategy of the present study allowed for small observations of vertical changes and depth distributions of dominant copepods. Consequently, copepods displayed what appeared to be diurnal vertical migrations as species were found in greatest concentrations at night, which support vertical distribution reports of a number of species from published literature (see review of Mauchline (1998) and Ringelberg (2009), such as found for some members in other regions: *Metridia lucens* in the Benguela Current (Pillar, 1984) and Sub-Antarctic (Atkinson *et al.*, 1996); *Pleuromamma piseki* in the northeast Atlantic (Roe, 1984); and *Clausocalanus brevipes* off New Zealand (Bradford, 1970) and *Scolecithricella minor* in the Straits of Magellan (Guglielmo *et al.*, 2011).

Among these species are members of the family Metridinidae, *Pleuromamma piseki* and *Metridia lucens* that increased in abundance at night into surface waters (Figure 3.14). These deep water species have been observed to perform diel vertical migration, for example, *Metridia lucens* migrate at night to feed on phytoplankton in other regions (e.g. Roe, 1984; Pillar, 1984; Hays, 1996; Hays *et al.*, 1997; Hays *et al.*, 2001; Timonin, 1997). The small change observed in their depth distribution during the survey period, might suggest diurnal migration above the SWIOR. Hattori (1989) found that the vertical range of Metridinidae to be 1000 m, suggesting mesopelagic coupling of these copepods with resident seamount fauna (Vereshchaka, 1995). This clearly needs further support given the sampling depth of the present study (200 m). A 24 hr diel cycle on copepods above the SWIOR could not be determined, and the present investigation consequently could not detect any probable endemism of meso- or bathypelagic copepods. A much greater research effort is clearly needed for the fauna of the SWIOR (e.g. 72 hour diel cycle).

The changes in richness across the major oceanographic zones appeared to be influence by environmental factors associated with subtropical and Sub-Antarctic waters, and more likely to be the physiological properties, adaptation to their environment and life histories. It is known that zooplankton diversity is higher in subtropical than in Sub-Antarctic regions (Rutherford *et al.*, 1999; Beaugrand *et al.*, 2001; Piontkovski & Landry, 2003; Rombouts *et al.*, 2009). However, it is possible for diversity to be higher in regions with low SSTs, as these are typically associated with higher concentrations of nutrients, which in turn provide more food resources (Woodd-Walker *et al.*, 2002). Patterns in diversity are also linked with the suspension of nutrients from deeper waters in subtropical areas (Figure 3.2 B) (Polovina *et al.*, 1995). It is likely for species with distinct temperature tolerances to have similarly constrained distributions (e.g. McGowan & Walker, 1979, 1985). Temperature and food concentration with depth have been shown to influence species diversity and so copepod community composition (Rutherford *et al.*, 1999). However, most copepod species have wide depth distributions that are relatively independent of temperature, with depth distribution effects being limited to food concentration (Ringelberg, 2009). The effect of sea surface temperature was observed in the separation of the warm-saline water from the cold-fresh water and stratified region in the dbRDA plot (Figure 3.7). This would explain the restriction of subtropical members of the genus *Clausocalanus* to the ARC zone, and their absence in the SAF. This may explain the high diversity at night during the study period, and the relationship between ecological processes on copepod fauna (Figure 3.2). The occurrence of deep water species in night-time samples may however reduce the possibility of predation while retaining feeding on the phytoplankton above the SWIOR (e.g. Frost, 1987; Dubischar & Bathmann, 1997; Mendonça *et al.*, 2015).

In the present study, the STF area represented a faunal barrier between the ARC and the SAF communities. As in other studies, oceanic fronts are subjected to large-scale hydrographic gradients and so act as limits in pelagic diversity for oceanic communities (Fager & McGowan, 1963; Hayward & McGowan, 1979; McGowan & Walker, 1979; Haury *et al.*, 1978; Beaugrand *et al.*, 2001). In the mid-Atlantic Ocean south of South Africa, a similar physical barrier appears to be weak between the ARC and the STC. Seasonal shifts of this frontal region may allow cross frontal species exchange (Lutjeharms & Valentine, 1984; Belkin & Gordon, 1996; Weeks *et al.*, 1998), and the latitudinal displacement of species could be expected into subtropical waters (e.g. Barange *et al.*, 1998; Froneman *et al.*, 2007). Generally, in the south-west Indian Ocean sector, the STF at ~41.5 °S is strong and its stratification clearly separates the Agulhas Front from the SAF at ~40 °S (Read & Pollard, 1993; Pollard & Read, 2001; Dencausse *et al.*, 2011, Pollard & Read, 2017; Read & Pollard, 2017). It could be argued here that this zone limits the northern distribution of Sub-Antarctic species, a region characterised by 8.5 - 10.7 °C surface isotherms (Figure 3.1). Similar observations have been made for copepod communities of the ARC and SAF by De Decker (1984) in the south-western Indian Ocean. More data (seasonally) are needed, however, to improve our understanding about the effects of this boundary between copepod communities of the ARC and SAF.

One hundred and thirty five copepod species were recorded during this study, and this is in agreement with the general patterns in distribution of copepod species reported from previous surveys (De Decker, 1984; Carter, 1977). De Decker (1984) too identified distinct copepod communities corresponding to water masses in the region of the Subtropical and Sub-Antarctic waters. In this study, the species list from Sub-Antarctic waters, with its main distribution in the SAF, is to some extent similar to the total number of copepod species reported by De Decker (1984). However, the subtropical community (ARC) of the present investigation is quite different. Most of the species recovered here from the region of the ARC are also found in the neritic subtropical waters of the east coast of South Africa (Carter, 1977), although some (*C. macrocarinatus*, *C. jobei*, *C. parapergens*, *H. spinifer* and *H. lobatus*) were not previously recorded by De Decker and Mombeck (1964). Carter (1977) noted similar results, and suggested that the lack of identification keys used by De Decker and Mombeck (1964) might account for the differences in species identification. Or the difference observed in the present study could be attributed to differences in the sampling depths.

Chapter 4: Biogeography of calanoid copepods in the Western Indian Ocean

Abstract

Published information on the distribution of calanoid copepods from the Western Indian Ocean (WIO) are consolidated and combined with new data collected from the South West Indian Ocean Ridge, to generate an updated biogeography for this order of copepods in the region. Eighty-five 5^{o} grid squares were mapped for the WIO. Calanoid biogeographic provinces were identified using the Bray-Curtis similarity indices. Calanoid copepod assemblages followed the major flow of water masses from adjacent provinces. The WIO was delineated into cold- and warm-temperate and subtropical and tropical groupings, within which there were strong subgroupings based on latitude and longitude. There was fairly strong support for Longhursts' biogeochemical provinces. It is speculated that the differences between groupings in the analysis and Longhursts' provinces might reflect large-scale mixing, limited sampling efforts and a wide distribution of cosmopolitan species amongst neighbouring provinces; however, more data are needed. Differences with Longhursts' provinces are ascribed to the qualitative nature of the analyses. This pattern is compared with those generated from other taxa.

4.1. Methods

4.1.1 Data Collection

The data for this study were compiled from the literature for the WIO, and were combined with new and unpublished data collected from the South West Indian Ocean Ridge (see Chapters 3). The study area encompasses coastal waters from Somalia (10^{o} N), southwards to the Cape of Good Hope (~34 ^{o}S) and 50 ^{o}S; and eastwards to 65^{o} E. The region was divided into 85 five-degree grid squares, and encloses the Longhurst (1998) Provinces: North-western Arabian Upwelling Province (ARAB); Indian Monsoon Gyres Province (MONS); Indian Subtropical Gyre Province (ISSG); the East Africa Coastal Province (EAFR) and the Subtropical Convergence Province (SSTC).

The distribution records of all copepod species from the literature were considered and were used to compile the dataset (Annexure III). Copepods were scored as present or absent in each 5 ^{o} grid square. Where authors have repeatedly found the same species through time in any one grid, it has only been scored once. Surveys devoted to the study of individual species have not been included, as have records from generalised texts such as van der Spoel & Pierrot-Bults (1986).

Due to the limited areal coverage, gaps were filled using an interpolative technique (Gibbons, 1997b). The procedure assumes that if a species was absent from an intensively sampled area, its absence was presumed genuine, and interpolation from neighbouring positive areas was not applied. If a species was recorded as absent from an area which had either not been sampled or had been only poorly sampled, interpolation from adjoining positive squares was carried out. Interpolation was limited to grid squares adjoining presence records. Many copepod species were widespread in the original dataset (Table 4.1), as a result common and widespread species were excluded from the matrix. This technique has the potential to underestimate the general patterns of distributions of more common species but is relatively unambiguous in practice.

A similarity matrix which compares copepod assemblages of all grid square samples was then constructed using the Bray-Curtis index. This was visualised as a 1-dimensional dendrogram. To characterise the species responsible for the identity of each cluster a similarity percentage analysis (SIMPER; Warwick & Clarke, 2006) was employed. A one-way analysis of similarity (ANOSIM) procedure in PRIMER was used to test whether the similarity matrix was consistent with the provinces recognised by Longhurst (1998) (Field *et al.*, 1982). The clusters were superimposed 3–dimensionally using a nMMDS (non-metric Multi-Dimensional Scaling) analysis (Warwick & Clarke, 2006). All analyses were performed using PRIMER version 6 software (Plymouth Routines In Multivariate Ecological Research; Warwick & Clarke, 2006).

Table 4.1: List of rare and widespread copepod species (31) that were excluded from the final data matrix for the Western Indian Ocean.

Acartia bispinosa
Acartia danae
Acartia erythraea
Acartia fossae
Acartia longisetosa
Acartia nana
Acartia negligens
Acrocalanus andersoni
Acrocalanus gibber
Acrocalanus gracilis
Acrocalanus longicornis
Acrocalanus monachus
Aetideopsis retusa
Aetideopsis rostrata
Aetideus armatus
Aetideus australis
Aetideus giesbrechti
Amallothrix dentipes
Amallothrix obtusifrons
Amallothrix robustripes
Amallothrix valida
Aphelura typica
Arietellus giesbrechti
Arietellus setosus
Augaptilus glacialis
Augaptilus longicaudatus
Augaptilus spinifrons
Batheuchaeta lamellata
Bathycalanus princeps
Bathycalanus richardi
Bathycalanus sverdrupi
Temorites (Bathypontia) elongata
Temorites (Bathypontia) major
Temorites (Bathypontia) minor
Temorites (Bathypontia) regalis
Temorites (Bathypontia) sarsi
Temorites (Bathypontia) similis
Temorites (Bathypontia) spinifera
Bradycalanus gigas
Bradycalanus typicus
Bradyetes florens
Bradyidius bradyi
Calanoides carinatus
Calanoides natalis
Calanopia minor
Calanus brevicornis
Calocalanus contractus
Calocalanus gracilis
Calocalanus minor
Calocalanus pavo
Calocalanus plumulosus
Calocalanus styliremis
Calocalanus tenuis
Candacia aethiopica
Candacia armata
Candacia bispinnata
Candacia bispinosa
Candacia catula
Candacia curta
Candacia inermis
Candacia longimana
Candacia magna
Candacia pachydactyla
Candacia simplex
Candacia truncata
Canthocalanus pauper
Centraugaptilus cucullatus
Centropages calaninus
Centropages elongatus
Centropages furcatus
Centropages gracilis
Centropages longicornis
Centropages orsinii
Centropages tenuicornis
Centropages violaceus
Chiridiella macrodactyla
Chiridius pacificus
Chiridius poppei
Chiridius tenuispinus
Chirundina indica
Chirundinella cara
Clausocalanus arcuicornis
Clausocalanus brevipes
Clausocalanus farrani
Clausocalanus furcatus
Clausocalanus ingens
Clausocalanus paululus
Clytemnestra rostrata
Cornucalanus chelifer
Cornucalanus indicus
Cornucalanus simplex
Cosmocalanus darwinii
Ctenocalanus vanus
Disco longus
Disco minutus
Euaugaptilus bullifer
Euaugaptilus gibbus
Euaugaptilus magnus
Euaugaptilus nodifrons
Euaugaptilus oblongus
Eucalanus attenuatus s.l.
Eucalanus crassus
Eucalanus elongatus
Eucalanus hyalinus
Eucalanus longiceps
Eucalanus monachus
Eucalanus mucronatus
Eucalanus pileatus
Eucalanus sewelli
Eucalanus subcrassus
Eucalanus subtenius
Euchaeta acuta
Euchaeta affinis
Euchaeta biloba
Euchaeta concinna
Euchaeta farrani
Euchaeta gracilis
Euchaeta lobatus
Euchaeta longicornis
Euchaeta malayensis
Euchaeta marina
Euchaeta media
Euchaeta paraacuta
Euchaeta prestandreae
Euchaeta scotti
Euchaeta spinosa
Euchaeta tonsa
Euchaeta weberi
Euchaeta wolfendeni
Euchirella bella
Euchirella bitumida
Euchirella curticauda
Euchirella formosa
Euchirella gateata
Euchirella maxima
Euchirella truncata
Euchirella venusta
Eugaugaptilus brodskyi
Eugaugaptilus elongatus
Eugaugaptilus farrani
Eugaugaptilus filigerus
Eugaugaptilus gracilis
Eugaugaptilus grandicornis
Eugaugaptilus humilis
Eugaugaptilus indicus
Eugaugaptilus longiseta
Eugaugaptilus oblongus
Eugaugaptilus quaesitus
Eugaugaptilus rectus
Eugaugaptilus rigidus
Euterpe gracilis
Farania frigida
Gaetanus armiger
Gaetanus brachyurus
Gaetanus curvirostris
Gaetanus kruppi
Gaetanus latifrons
Gaetanus minor
Gaidius brevicaudatus
Haloptilus angusticeps
Haloptilus longicornis
Haloptilus mucronatus
Haloptilus ornatus
Haloptilus spiniceps
Haloptilus tenuis
Haloptilus validus
Hemirhabdus latus
Heteramalla dubia
Heterocalanus serricaudatus
Heterohabdus clausi
Heterohabdus norvegicus
Heterorhabdus clausi
Heterorhabdus norvegicus
Heterorhabdus papilliger
Heterorhabdus spinifrons
Heterorhabdus tanneri
Heterostylites major
Isocope propinqua
Labidocera chubbi
Labidocera inermis
Labidocera kroyeri
Labidocera laevidentata
Labidocera trispinosa
Lophothrix angusta
Lophothrix insignis
Lophothrix varicans
Lucicutia bicornuta
Lucicutia bradyana
Lucicutia clausi
Lucicutia curta
Lucicutia flavicornis
Lucicutia formosa
Lucicutia gaussae
Lucicutia longispina
Lucicutia magna
Lucicutia major
Lucicutia ovalis
Lucicutia pallida
Lucicutia polaris
Lucicutia sewelli
Lucicutia simulans
Macrosetella gracilis
Mecynocera clausi
Mentranura typica
Mesocalanus tenuicornis
Metridia brevicauda
Metridia effusa
Metridia lucens
Metridia princeps
Metridia venusta
Microsetella novegica
Microsetella rosea
Mimocalanus inflatus
Mimocalanus nudus
Mormonilla minor
Nannocalanus minor
Neocalanus gracilis
Neocalanus robustior
Neocalanus tonsus
Pachyptilus abbreviatus
Pachyptilus pacificus
Paracalanus aculeatus
Paracalanus nanus
Paracalanus parvus
Paracalanus pygmaeus
Paraeuchaeta norvegica
Pareuchaeta acuta
Pareucheata biloba
Phaenna spinifera
Nullosetigera (Phyllopus) aequalis
Nullosetigera (Phyllopus) bidentatus
Nullosetigera (Phyllopus) impar
Nullosetigera (Phyllopus) muticus
Pleuromamma abdominalis
Pleuromamma borealis
Pleuromamma gracilis
Pleuromamma indica
Pleuromamma piseki
Pleuromamma xiphias
Pontella diagonalis
Pontella natalis
Pontella securifer
Pontellina plumata s.l.
Pontellina plumifera
Pontellopsis herdmani
Pontellopsis macronyx
Pontellopsis scotti
Pontellopsis speciosus
Pontoeciella abyssicola
Pontoptilus lacertosus
Pontoptilus mucronatus
Pontoptilus robustus
Pseudaugaptilus longiremis
Pseudochirella divaricata
Pseudochirella dubia
Pseudochirella magna
Pseudochirella obtusa
Pseudochirella polyspina
Pseudochirella semispina
Pseudochirella squalida
Pseudochirella tuberculata
Pseudodiaptomus sericaudatus
Racovitzanus porrectus
Ratania atlantica
Ratania flava
Rhincalanus nasutus
Rhincalanus rostifrons cornutus
Scaphocalanus affinis
Scaphocalanus bogorovi
Scaphocalanus brevicornis
Scaphocalanus curtus
Scaphocalanus echinatus
Scaphocalanus major
Scaphocalanus medius
Scolecithricella abyssalis
Scolecithricella auropecten
Scolecithricella dentata
Scolecithricella dubia
Scolecithricella maritima
Scolecithricella minor
Scolecithricella tenuiserrata
Scolecithricella timida
Scolecithricella unispinosa
Scolecithricella vittata
Scolecithrix bradyi
Scolecithrix danae
Scolecithrix fowleri
Scolecithrix nicobarica
Scotocalanus helenae
Scottocalanus longispinus
Scottocalanus securifrons
Scottula ambariakae
Spinocalanus ovalis
Spinocalanus validus
Temora discaudata
Temora turbinata
Temoria dubia
Temorites brevis
Temorites discoveryae
Temoropia mayumbaensis
Teneriforma naso
Tortanus barbatus
Undeuchaeta minor
Undeuchaeta plumosa
Undinella brevipes
Undinula vulgaris
Uneachaeta intermedia
Valdiviella insignis
Valdiviella oligarthra
Xanthocalanus fragilis
Xanthocalanus greeni
Xanthocalanus hispidus
Xanthocalanus obtusus
Zenkevitchiella atlantica
Zenkevitchiella crassa

4.2. Results

4.2.1. Distributional patterns of Western Indian Ocean copepod species

Four hundred and sixty six calanoid copepod species have been recorded in the Western Indian Ocean (Annexure III). Of these, 149 species were common enough to be included in the analysis (Table 4.2), but not so common that they were found everywhere. The cluster analysis identifies two clear and broad clusters at the 10% level of similarity (Figure 4.1), separating grid squares associated with the southern (Group A), from the northern latitudes (Group B). At the 14% level Group A1 (comprising 18 grid squares from the coastal waters of South Africa), and Group A2 (associated with 19 grid squares stretching south-eastwards from the coast of South Africa and the southern portion of the Mozambique Channel) could be identified (Figures 4.1 and 4.2). Group B was divided into Group B1, Group B2 and Group B3 at the 14% level of similarity. Group B1 comprised 13 five-degree grid squares associated with the territorial waters of Somalia, Tanzania, Kenya and the northern portion of the Mozambique Channel, Group B2 comprised five five-degree grid squares stretching north-westwards from the middle of the Mozambique Channel towards northern of Madagascar, whilst Group B3 comprised all the east oceanic five-degree grid squares (Figures 4.1 and 4.2).

Table 4.2: Copepod species (149) selected for the construction of biogeographical provinces for the Western Indian Ocean.

Acartia amboinensis
Aetideus acutus
Amallothrix emarginata
Amallothrix indica
Amallothrix paravalida
Arietellus simplex
Augaptilus palumboi
Bathycalanus bradyi
Bradycalanus sarsi
Calanoides macrocarinatus
Calanopia elliptica
Calanus algulhensis
Calanus propinquus
Calanus simillimus
Calocalanus tenuicornis
Candacia bradyi
Candacia cheirura
Candacia discaudata
Candacia guggenheimi
Candacia tenuimana
Candacia varicans
Centraugaptilus horridus
Centropages brachiatus
Centropages bradyi
Centropages chierchiae
Centropages typicus-pacificus
Chirundina streetsii
Clausocalanus jobei
Clausocalanus laticeps
Clausocalanus lividus
Clausocalanus mastigophorus
Clausocalanus minor
Clausocalanus parapergens
Clausocalanus pergens
Clytemnestra scutellata
Disco inflatus
Disetta palumboi
Disseta minuta
Drepanopus pectinatus
Euchaeta barbata
Euchaeta bisinuata
Euchaeta calva
Euchaeta dubia
Euchaeta hanseni
Euchaeta indica
Euchaeta pubera
Euchaeta rimana
Euchaeta sarsi
Euchaeta tenius
Euchirella amoena
Euchirella messinensis
Euchirella pulchra
Euchirella rostrata
Eugaugaptilus bullifer
Eugaugaptilus laticeps
Eugaugaptilus longimanus
Eugaugaptilus magnus
Eugaugaptilus nodifrons
Euterpina acutifrons
Foxtonia barthybia
Gaetanus antarcticus
Gaetanus miles
Gaetanus pileatus
Gaidius minutus
Gaidius robustus
Gaidius tenuispinus
Gaussia princeps
Haloptilus acutifrons
Haloptilus oxycephalus
Hemirhabdus grimaldi
Heterorhabdus abyssalis
Heterorhabdus austrinus
Heterorhabdus compactus
Heterorhabdus spinifer
Heterostylites longicornis
Labidocera acuta
Labidocera acutifrons
Labidocera detruncata
Labidocera minuta
Lophothrix frontalis
Lophothrix humilifrons
Lophothrix latipes
Lucicutia aurita
Lucicutia bella
Lucicutia grandis
Lucicutia intermedia
Lucicutia longicornis
Lucicutia longiserrata
Lucicutia maxima
Lucicutia parva
Lucicutia rara
Lucicutia wolfendeni
Megacalanus princeps
Metridia bicormuta
Metridia boecki
Metridia discreta
Metridia longa
Metridia macrura
Microcalanus pygmaeus
Mimocalanus cultrifer
Monacilla tenera
Monacilla typica
Oculosetella gracilis
Onchocalanus magnus
Pachyptilus eurygnathus
Paracalanus crassirostris
Paracalanus denudatus
Paracalanus indicus
Paraeuchaeta barbata
Pareucalanus attenuatus
Pareucalanus langae
Nullosetigera (*Phyllopus*) *helgae*
Pleuromamma quadrungulata
Pleuromamma robusta
Pontella fera
Pontellopsis armata
Pontellopsis regalis
Pseudeuchaeta brevicauda
Pseudochirella gibbera
Pseudochirella hirsuta
Pseudochirella pustulifera
Pseudodiapomous nudus
Rhincalanus gigas
Scaphocalanus elongatus
Scaphocalanus longifurca
Scaphocalanus magnus
Scaphocalanus subbrevicornis
Scolecithricella ctenopus
Scolecithricella glacialis
Scolecithricella laminata
Scolecithricella ovata
Scotocalanus dauglishi
Scottocalanus persecans
Spinocalanus abruptus
Spinocalanus abyssalis
Spinocalanus abyssalis var pygmaeus
Spinocalanus angusliceps
Spinocalanus magnus
Spinocalanus spinosus
Spinocalanus ventriosus
Subeucalanus longiceps
Subeucalanus mucronatus
Subeucalanus pileatus
Subeucalanus subcrassus
Temora stylifera
Tortanus gracilis
Undeuchaeta intermedia
Undeuchaeta major
Valdiviella brevicornis

Table 4.3 summarizes the contributions made by individual species towards the structure of the dendrogramme (Figure 5.1), as identified by the SIMPER analysis. Three species *Clausocalanus laticeps*, *Calanus simillimus* and *Scolecithricella* (*glacialis*) *minor* contributed to ~50% of the similarity within Group A1. Cluster A2 was also characterised by *Clausocalanus* (*C. jobei*, *C. lividus*, *C. mastigophorus*, *C. parapergens*, and *C. pergens*) (Tables 4.3 and 4.4). Four species accounted for over 50% of the similarity (*Scolecithricella ovata*, *Candacia guggenheimi*, *Paracalanus denudatus* and *Candacia varicans*) within the Group B1 (similarity index: 64.3%). *Pareucalanus attenuatus* and *Euchaeta indica* were the major contributors (55.5%) to Group B2. Group B3 samples was characterised by six species (25%), with *Eugaugaptilus magnus* (5.5%) being most responsible (Tables 4.3 and 4.4).

The copepods responsible for the greatest dissimilarity between assemblages as identified by the SIMPER routine are summarized in Table 4.3. From this *Clausocalanus laticeps*, *Calanus simillimus* and *Scolecithricella* (*glacialis*) *minor* accounted ~10% of the dissimilarity between the major Groups A and B (Table 4.4).

4.2.2. Western Indian Ocean copepod assemblages and the Longhurst provinces

The results of an *a priori*, one-way ANOSIM (Table 4.5) revealed that all groups identified were well separated with a global statistic of R = 0.484 at the 0.1 % level of significance. Pair-wise comparisons between cluster groups showed that the ARAB group was well separated from all other groups (R = 0.71). Likewise, MONS and SSTC were equally well separated from one another (R = 0.62), with a little overlap between the middle areas, separation was evident between the major groups (Figure 5.3).

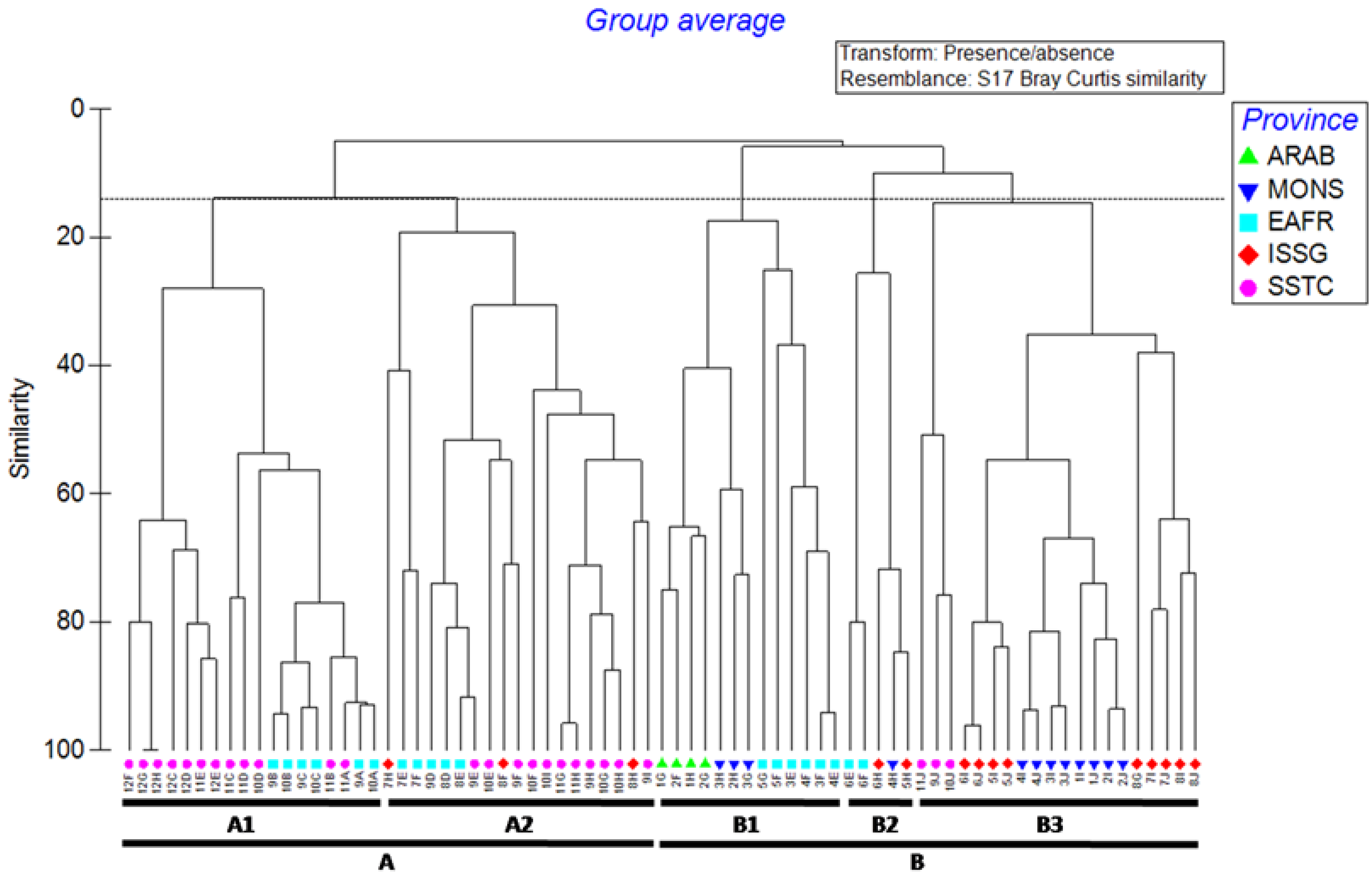

Figure 4.1: Dendrogram showing cluster analysis of 75 five-degree grid squares grouped in relation to Longhurst biogeochemical provinces (1998) (see Materials and Methods for acronyms full names). These presence and absence data were transformed using the Bray-Curtis similarity index and group average linkages to recognize clusters. A = southern latitude cluster of samples (including clusters A1 and A2), B = northern latitude cluster of samples (including clusters B1, B2 and B3). Cluster groups are sliced at the 14% level of similarity.

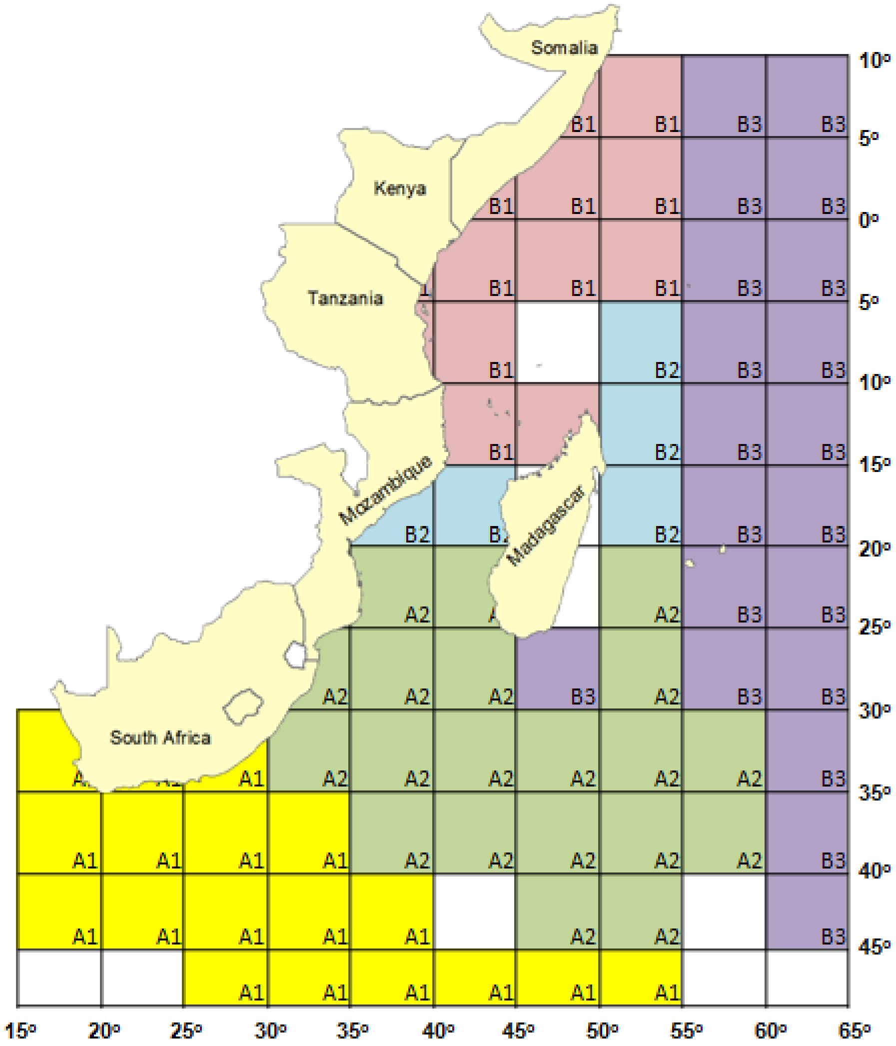

Figure 4.2: Map illustration to assist interpretation of the samples responsible for similarity in structure of cluster Groups as illustrated in Figure 3. Grid squares are plotted in order of cluster Groups. 5^{o} squares in yellow are those clustered within Group A1, in green are those clustered within Group A2, in light red are those clustered within Group B1, in light blue are those clustered within Group B2, whilst those in purple are from Group B3.

Table 4.3: Top row list top ten copepod species identified by SIMPER, responsible for similarity in structure of cluster Groups, and below row list top ten copepod taxa identified by SIMPER, responsible for the dissimilarity in structure of cluster Groups as illustrated in Figure 5.1 based on presence and absence data. Contrib% contribution of that species to the overall similarity between clusters and Cum.% = cumulative contribution of species to the overall similarity. Below, Contrib% contribution of that species to the overall dissimilarity between clusters and Cum.% = cumulative contribution of species to the overall dissimilarity.

GROUP A (27.3%)
Total number of species (33)
Total number of grids (37)

Species	Contrib%	Cum.%
Clausocalanus laticeps	11.34	11.34
Calanus simillimus	11.19	22.53
Scolecithricella (*glacialis*) *minor*	5.05	27.58
Euchirella rostrata	4.93	32.52
Gaetanus miles	4.81	37.33
Centropages chierchiae	4.8	42.12
Calanus algulhensis	4.69	46.82
Labidocera acutifrons	3.52	50.34
Clytemnestra scutellata	3.42	53.76
Clausocalanus pergens	3.26	57.02

GROUP B (19.6%)
Total number of species (59)
Total number of grids (38)

Species	Contrib%	Cum.%
Candacia guggenheimi	6.51	6.51
Scolecithricella ovata	5.32	11.83
Labidocera detruncata	3.67	15.51
Candacia varicans	3.55	19.05
Paracalanus denudatus	3.33	22.38
Eugaugaptilus magnus	3.19	25.57
Pareucalanus attenuatus	2.6	28.17
Bathycalanus bradyi	2.49	30.66
Disetta palumboi	2.35	33.01
Spinocalanus abyssalis var pygmaeus	2.28	35.29

Dissimilarity GROUPS A & B (94.95%)

Species	Contrib%	Cum.%
Clausocalanus laticeps	2.46	2.46
Calanus simillimus	2.44	4.9
Scolecithricella (*glacialis*) *minor*	1.65	6.55
Candacia guggenheimi	1.63	8.18
Centropages chierchiae	1.58	9.77
Euchirella rostrata	1.52	11.29
Gaetanus miles	1.52	12.81
Calanus algulhensis	1.52	14.33
Scolecithricella ovata	1.5	15.83
Candacia varicans	1.39	17.22

Table 4.4: List of copepod species identified by SIMPER, responsible for similarity (cumulative percentage: 60%) in structure of cluster Groups as illustrated in Figure 5.1 based on presence and absence data. Contrib% contribution of that species to the overall similarity between clusters and Cum.% = cumulative contribution of species to the overall similarity

GROUP A1 (49.2%)
Total number of species (14)
Total number of grids (18)

Species	Contrib %	Cum. %
Clausocalanus laticeps	20.48	20.48
Calanus simillimus	18.23	38.71
Scolecithricella (*glacialis*) *minor*	10.33	49.04
Centropages chierchiae	8.11	57.15
Centropages bradyi	6.27	63.42

GROUP A2 (36.4%)
Total number of species (35)
Total number of grids (19)

Species	Contrib %	Cum. %
Gaetanus miles	12.5	12.5
Clausocalanus pergens	9.51	22.01
Euchirella rostrata	5	27.01
Phyllopus helgae	4.83	31.84
Augaptilus palumboi	4.83	36.68
Clausocalanus mastigophorus	4.54	41.22
Clausocalanus parapergens	4.54	45.76
Heterorhabdus spinifer	3.71	49.47
Clausocalanus minor	3.71	53.18
Aetideus acutus	2.75	55.94
Clausocalanus lividus	2.17	58.11
Metridia bicormuta	2.14	60.25

GROUP B3 (41.6%)
Total number of species (60)
Total number of grids (20)

Species	Contrib %	Cum. %
Eugaugaptilus magnus	5.56	5.56
Bathycalanus bradyi	4.34	9.9
Spinocalanus abyssalis var pygmaeus	3.97	13.87
Spinocalanus spinosus	3.97	17.83
Eugaugaptilus nodifrons	3.72	21.56
Spinocalanus abyssalis	3.48	25.03
Disetta palumboi	3.45	28.48
Mimocalanus cultrifer	3.45	31.94
Pseudeuchaeta brevicauda	2.97	34.91
Megacalanus princeps	2.97	37.88
Lucicutia wolfendeni	2.63	40.51
Lucicutia parva	2.47	42.98
Gaetanus antarcticus	2.23	45.21
Scaphocalanus subbrevicornis	2.07	47.28
Heterorhabdus abyssalis	2.07	49.35
Disco inflatus	2.07	51.42
Lucicutia grandis	1.78	53.2
Heterorhabdus compactus	1.74	54.95
Euchaeta rimana	1.72	56.67
Scaphocalanus elongates	1.42	58.09
Metridia discrete	1.41	59.5
Amallothrix indica	1.4	60.91

GROUP B1 (32.2%)
Total number of species (11)
Total number of grids (13)

Species	Contrib %	Cum. %
Scolecithricella ovata	22.18	22.18
Candacia guggenheimi	19.63	41.81
Paracalanus denudatus	11.83	53.64
Candacia varicans	10.74	64.37

GROUP B2 (46.2%)
Total number of species (8)
Total number of grids (5)

Species	Contrib %	Cum. %
Pareucalanus attenuates	33.95	33.95
Euchaeta indica	21.55	55.51
Euchirella pulchra	5.8	61.3

Table 4.5: Results of the pairwise tests from ANOSIM for significant differences in copepod assemblages between Longhurst (1998) biogeochemical provinces (999 permutations).

	ARAB	MONS	EAFR	ISSG	SSTC
ARAB					
MONS	0.62				
EAFR	0.56	0.56			
ISSG	0.72	0.19	0.52		
SSTC	0.62	0.63	0.33	0.43	

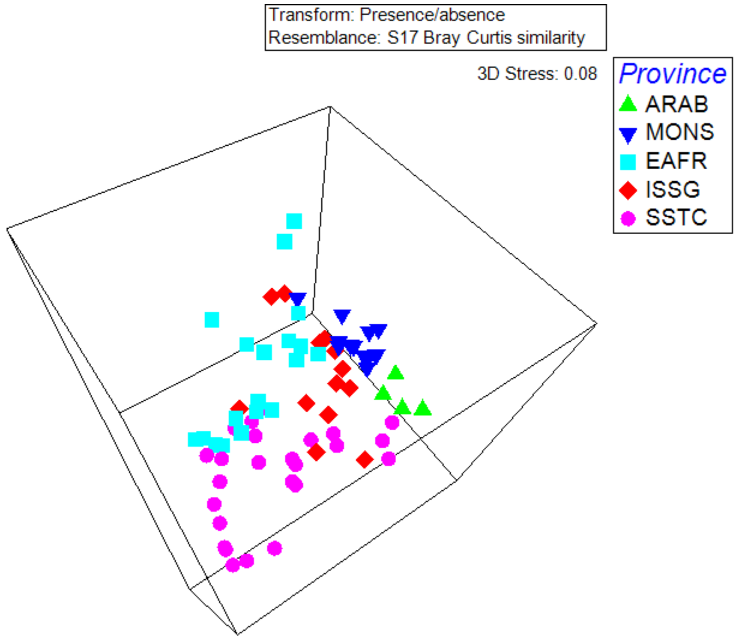

Figure 4.3: 3-dimensional unconstrained non-metric MDS ordination (nMDS) plot visualizing similarity matrices computed for the Western Indian Ocean Longhurst biogeochemical provinces on copepod assemblages (1998) (see Materials and Methods for acronyms full names).

4.3. Discussion

Five distinct assemblages of copepods for the WIO (Figure 4.2) are in broad agreement with the biogeochemical provinces recognised by Longhurst (1998) (Figure 1.2). However there were differences. Some provinces were found to extend beyond those identified by Longhurst (1998), which may indicate those regions with subdivisions and different productivity regimes, as noticed for the “missing” ISSG Province for the WIO during the study period.

The difference between the two broad marine provinces (Figures 4.1 and 4.2) could be ascribed to differences in community composition and differences in the variability between biogeographic regions (Figure 1.2). Such would explain the western boundary currents recognized by Longhurst’s (1998) biogeochemical system to comprise of four distinct bioregions. Within the EAFR province, the equatorial East African coastline, the subtropical Madagascan region, the temperate Agulhas region, and the Agulhas Return Current are all ecologically dissimilar but were grouped for convenience by Longhurst (1998).

The difference between the results of the present investigation and those provinces identified by Longhurst (1998) probably reflect the fact that in his analysis, Longhurst included sea surface temperature, productivity and ocean currents in delineating a province. The dataset used here, for the WIO are based on a limited dataset of records and the incomplete sampling records of copepods are largely nonquantitative. Therefore, the copepod presence/absence datasets alone may not substantiate a coastal province, rather a need for an inclusion of a larger class of taxa or species specific distribution data (e.g. Gibbons, 1997b); which is unfortunately beyond the scope of the present study. In addition, more data are needed to explore this zone.

The analysis of similarity revealed that copepod species distributions in the WIO seem strongly latitudinal: tropical, subtropical and temperate water communities (Figure 4.2 and Tables 4.3 and 4.4). The assemblages largely reflect the surface circulation features identified for the WIO (Wyrtki, 1973; Schott & McCreary Jr, 2001).

In the northern part of the WIO, an inshore group (Group B1) of the present study consisted of the ARAB province in the Longhurst (1998) system, and was characterised by the long extension of the coastal upwelling Somalia Current to ~15 ^{o}S (Figure 4.2). This group extends to the southern portion of East African Current System (EAFR) that occurs parallel to the east African continent from the coast of Somalia to the northern portion of the Mozambique Channel. This region is characterised by tropical and subtropical waters and oceanic eddies that might extend the ranges of many warm water species southward to about 15 ºS, and is associated with some upwelling species (e.g. Lawson, 1977; Smith 1982) *Candacia guggenheimi*, *Candacia varicans*, *Scolecithricella ovata*, *Paracalanus denudatus* and *Clausocalanus minor* (Table 4.1).

Group B3 (Figure 4.2), clustered with the western extension of the offshore Monsoon Gyre (MONS province) at 10 ^{o}N – 35 ^{o}S along the 40 – 65 ^{o}E and is associated with seasonal reversing water masses, where zooplankton distribution could be influenced by monsoon period (Schalk, 1987). This province seems to overlap the remainder of the ISSG Province of the Longhurst (1998) system (to date little knowledge exists for the ISSG province; Longhurst 1998). Circulation associated with the Monsoon gyre may feed the introduction and wide dispersion of Indo-Pacific indicators into the WIO (Annexure III), distributing e.g. *Candacia discaudata* (part of the Indo-Pacific tropical populations e.g. Mulyadi, 2004) and *Labidocera detruncata* (e.g. Dur, 2007) into the WIO through the Indonesian Through-Flow (Schott &

McCreary Jr, 2001); these species are found in high numbers in the Taiwan Strait (e.g. Lan *et al.*, 2004; Hwang *et al.*, 2006). Other studies have found species to be present in both the Indo-Pacific and Agulhas Current (e.g. Sewell 1948; De Decker, 1984 and others in van der Spoel & Pierrot-Bults, 1986). It could be argued that the large extension of the monsoon gyre onto the subtropical gyre are in connection with the widespread of species distribution into central cores' or merely a reflection of under sampling of biology. This biogeographic region seen in Figure 4.2 reflects the wide dispersal of copepods and supports the patterns of the proposed pelagic Offshore Indian Ocean realm shown by Costello *et al*. (in press).

Group B2, clustered with the central Mozambique Channel, a region that was not obvious in the EAFR province (Longhurst, 1998) but has been recognized as a distinctive region for WIO coral reef communities (Obura, 2012). The subtropical intermediate region (~15 °S) in the Mozambique Channel is associated with the advection of migrating eddies through the channel (Lutjeharms *et al.*, 1981; Lutjeharms, 1988; Stramma & Lutjeharms, 1997; Schouten *et al.*, 2000; Backeberg & Reason, 2010; Halo, 2014), and it harbours shelf and eddy species (e.g. *Pareucalanus attenuatus* and *Euchaeta indica*) and is probably a vehicle for the southward transport of copepod species to approximately 15 ºS, either to the Agulhas Current System or East Madagascar Current (e.g. *Euchirella rostrata*) (e.g. Lebourges-Dhaussy *et al.*, 2014; Huggett, 2014).

During this study, the least well defined province in the Longhurst (1998) system was the East Africa Coastal Province (EAFR), which is associated with the East African Current Systems (the East African Current harbours the Somalia Current, Mozambique Channel and Madagascar Current, Agulhas Current and Agulhas Retroflection). The Agulhas Current within the EAFR Province (Longhurst, 1998) subdivides as water masses associated with the subtropical waters of the eastward flowing Subtropical Gyre (Group A2). Group A1 clusters with the SSTC Province and the Agulhas Retroflection in the Longhurst (1998) system, which is somewhat surprising as this region is characterised by a mixture of temperate and cold water species associated with frontal eddies and intermittent waves on the Agulhas Return Current and the Subtropical Convergence (Lutjeharms, 1981a). Group A1 was recognised as biogeographic province by De Decker (1984) using copepods and later by Gibbons (1997b) on the basis of euphausiid distributions.

In the present study, the Agulhas Retroflection branches off at the 18% level of similarity (Figure 4.1). Costello *et al*. (in press) have identified a southern African realm from the Agulhas Current to the Benguela Current region. The results of the present analysis closely match the biogeographic region proposed by Costello *et al*. (in press) and demonstrates the shift in EAFR province ecosystems (Figures 4.1 and 4.2) toward a warm-temperate and dynamic region, which tends to be more related to the influence of the Subtropical Gyre on copepod fauna. The Agulhas Current affected the distribution of many warm-temperate copepods (Figure 4.2). South of Africa, the southward dispersal of warm-temperate species was associated with the Agulhas Return Current into the Subtropical Convergence. Several warm-temperate copepods (e.g. *Echirella rostrata*) appeared to be associated with the dispersion of cyclonic eddies away from the core of the Agulhas Current (De Decker, 1984). Gibbons *et al.,* (1995) and Gibbons & Hutchings (1996) observe both subtropical and warm-temperate zooplankton in the core of the Agulhas Current. The southeast distribution of subtropical species between 20 – 25 ^{o}S; appeared to be associated with the extension of the

South Equatorial Current (SEC) and is probably due to closing of its eastward flow, forming the Southern Indian Ocean Current (Stramma & Lutjeharms, 1997).

The analysis of similarity further show that warm water epi-pelagic copepods have wide patterns of distributions that occupy subtropical waters towards the Subtropical convergence, frequently carried into temperate waters forming transition zones (Fleminger & Hulsemann, 1973). This is seen for indicator congeners in Mediterranean Sea, eight cognates of species in the genus *Clausocalanus*: *C. arcuicornis, C. furcatus, C. jobei, C. lividus, C. mastigophorus, C. parapergens, C. paululus, and C. pergens* have been reported to coexist (Razouls & Durand, 1991; Mazzocchi & d'Alcala`, 1995) due to differences between species abundances and species having isolated niches (Peralba & Mazzocchi, 2004). Peralba and Mazzocchi (2004) noticed size differences between the "big" *C. mastigophorus* and the smaller *C. lividus*, as size differences permitted the two species to overlap in seasonal and vertical dispersions, perhaps results that could attribute to the present understanding of dispersion of *Clausocalanus* distribution in WIO (Annexure III).

The dissimilarity between the two broad cluster Groups A and B was high (94.9 %) (Figure 4.1, Table 4.4), and primarily reflects the presence (or absence) of cold-water species. The copepod *Clausocalanus laticeps* was the most distinguishing species identified by De Decker (1984) in his analysis of copepod distributions in the south-western Indian Ocean, but *Calanus simillimus* and *Scolecithricella* (*glacialis*) *minor* were also important.

Several studies have reported on the position of epi-pelagic boundaries for the Indian Ocean; tropical and subtropical groups are noted between 10 ^{o}N – 25 ^{o}S, transitional groups between the tropics and subtropics (25 – 30 ^{o}S); and a shift from subtropical and temperate species between 40 ^{o}S – 45 ^{o}S (e.g. Brinton & Gopalakrishnan, 1973; Nair, 1978, Navas-Pereira & Vannucci, 1991). The hydrochemical front at 10 ^{o}S, with steep subsurface salinities, has been previously pointed out to be the northern and southern limits of communities from both the Monsoon gyre and South Equatorial Counter Current (Wyrtki, 1973). This study could not detect the influence of the hydrochemical front, but a boundary for foraminifera assemblages has been noted at ~18 ^{o}S by Bé & Hutson (1977). As a result latitudinal shift of species could be possible with seasonal shifts of the front (Wyrtki, 1973). However, more data are needed, especially from the Monsoon gyre and Subtropical gyre, which have been historically under sampled.

Chapter 5: General Conclusions

Despite the efforts of the scientific investigations conducted between 1962 - 1965 (IIOE) (Zeitschel, 1973), comparatively little is still known about many planktonic populations in the Indian Ocean. Though our understanding of the oceanography of the Indian Ocean has improved since that time, only a few detailed zooplankton studies have been carried out and published, for the South Western Indian Ocean region (e.g. Gaudy, 1967; Frontier, 1973; Lawson, 1977; Smith, 1982; Burnett *et al*., 2001; Lugomela *et al.*, 2001, Gallienne *et al.*, 2004; Conway, 2005; Leal *et al.*, 2009; Huggett, 2014).

This lack of data prompted the present study, which represents a detailed examination of the epipelagic copepod fauna from along the SWIOR. Using oblique net hauls, 400 depth stratified zooplankton samples were collected, resulting in a good spatial resolution of the abundance, distribution and the biodiversity patterns of copepod faunal structure and related biogeographic patterns in the southwest vicinity of the Indian Ocean. However, the dataset could not assess the spatial changes of copepods directly associated with summit and slope regions of the seamounts sampled, and so the findings cannot contribute to understanding the influences of local seamount processes such as Taylor columns (see Rogers, 1993). Such ecological mechanisms are testable on ridges that extend well into the mesopelagic layers (1000 m depth), where active DVM is acted out by zooplankton and other mesopelagic fauna (Angel & Pugh, 2000). This thesis therefore provides a view and understanding of the variation in vertical and horizontal distribution of copepod species in the upper 200 m above the SWIOR, which was to date poorly understood.

The dataset collected here has revealed the presence of 135 copepod species, with the Order Calanoida having 40 of the 49 recorded genera. This thesis highlights the calanoid copepod community in the southwest Indian Ocean sector. The research has demonstrated that copepod community structure is related to chlorophyll, and indicated the relationship between species richness and environmental factors, and reflects association with water masses.

The present study has showed that total copepod abundances ranged between 8 377 ind.m^{-2} and 78 547 ind.m^{-2} in the study area, which are similar to the results of other studies (Pakhomov & Perissinotto 1997; Barange *et al.* 1998; Froneman *et al.* 2000). The copepod community in the survey area was numerically dominated by small copepods of the genera *Oithona*, *Oncaea*, *Ctenocalanus* and *Clausocalanus*, and their abundances were mainly characteristic of the mesh size (180 µm) adopted in the present investigation (e.g. Voronina *et al.*, 1994). Future research is clearly needed to improve calanoid catches and taxonomic diversity – especially given the rich calanoid copepod community in the study area.

At the microscale, the present study showed intra- and inter-site variability in species composition and diversity patterns. The highest total number of copepod species and abundance was observed during the night than by day. This demonstrated the importance of vertical changes of copepod species that may be a response to phytoplankton productivity, which have been shown to affect species vertical distributions (Errhif *et al.*, 1997; Pakhomov *et al.*, 2000; Mayzaud *et al.*, 2002a, b; Pakhomov & Froneman, 2004; Mayzaud & Pakhomov, 2014). Such evidence was revealed in the diurnal distribution performed by mesopelagic taxa at night (e.g. *Pleuromamma* spp and *Metridia lucens*), and possibly represented partly their diel vertical migratory behaviour, elucidate future research along the SWIOR and an ecosystem management programme to identify direct biophysical coupling carried out by mesopelagic taxa. There is a need to improve our sampling efforts on seamounts (summit and slope sampling) as well as diel cycles (e.g. 72 hour stations), which will provide and develop understanding between surface production and mesopelagic communities, in terms of energy flow (Genin, 2004).

At the mesoscale, the analysis provided an understanding of the coupling between the physico-chemical environment and community structure. The taxonomic diversity and high abundance of copepod species allowed the determination of biogeographic barriers, and so the forces responsible for structuring local assemblages above the SWIOR. The STF played a key role in influencing the northern and southern limits of both the ARC and SAF communities, thus associates of subtropical and Antarctic waters served as important water mass indicators. These results could assist with the identification of seasonal shifts in the distribution of these oceanic fronts, or the absence of Antarctic species in the SAF area could serve as warming of the ocean waters (e.g. Atkinson *et al.*, 2004; Richardson, 2008). This is interesting, and highlights the need for long term observational studies of zooplankton communities in the southwest Indian Ocean region, with a focus on seasonal studies that will allow understanding of species composition across the biogeographic regions.

The thesis addressed the wide spread copepod community at the macroscale. The qualitative data matrix of the present study generated an updated biogeography for this order of copepods. Five epi-pelagic copepod provinces were recognised, which provided an understanding of patterns in distribution of epi-pelagic copepod fauna of the WIO. Some differences were apparent between the provinces identified by Longhurst (1998) biogeochemical system and the present investigation. These are likely due to the quantitative dataset used by Longhurst (1998) to delineate biogeochemical provinces (e.g. sea surface temperature, productivity, seasonality and ocean currents). The results of the present study are based on an analysis of relatively qualitative data (absence or presence), yet they demonstrate the complex circulation features of the WIO; and so emphasize the need to include more data to delineate biogeographic patterns. This was particularly noticed for the “missing” ISSG Province of Longhurst (1998), and may reflect incomplete and inconsistent sampling efforts and a wide distribution of cosmopolitan species amongst neighbouring provinces.

A total of 466 species of calanoid copepod are recognised from the bigger WIO region, and there is a clear need for a species identification guide to the region. This guide will sharpen and enhance taxonomic skills and improve the consistency of accurate species identification. Given that the copepod communities in the WIO are largely considered as Indo-Pacific, voucher specimen collections in South Africa are needed to confirm species identifications. Both the guide and voucher collection can assist with the training of local and foreign researchers through workshops and the like, and will serve to enhance our knowledge about copepod species diversity in the WIO.

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Annexure Section

Annexure I: Daytime composition (densities.m^{-3}) of all copepod taxa sampled at different depth intervals in the upper 200 m of the water column across the South West Indian Ocean Ridge during the period of November to December 2009. Groups were identified by the cluster analysis in Figure 3.5, Section 3.1.3. ARC - Agulhas Return Current; STF - Subtropical Front; SAF - Sub-Antarctic Front.

	ARC					SSTF					SAF				
	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	150 - 200 m	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	150 - 200 m	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	150 - 200 m
Order Calanoida															
Family Acartiidae															
Acartia danae	51.0	119.3	46.6	30.4	5.7	0.7									
Acartia negligens	122.1	36.4	30.2	5.4	3.7										
Family Aetideidae															
Aetideus acutus															
Aetideus armatus					0.2			0.3	0.5						
Aetideus australis						1.4			0.9	1.9		0.3		0.2	1.4
Aetideus giesbrechti					0.7										
Aetideus unidentified															
Chiridius gracilis															
Euchirella amoena															
Euchirella pulchra															
Euchirella rostrata								0.5							0.2
Euchirella truncata					0.6										
Euchirella unidentified				0.2											
Gaetanus minor															
Undeuchaeta incisa															
Undeuchaeta major															
Undeuchaeta plumosa															
Family Calanidae															
Calanoides macrocarinatus	4.6	6.4	3.2	5.2	9.2									1.2	0.2
Calanus simillimus			0.3	0.5		9.6	18.3	4.6	0.9	5.5					
Cosmocalanus darwinii		1.9	0.1												
Mesocalanus tenuicornis	1.6	2.1	9.4	13.1	25.2			1.1						1.2	1.0
Nannocalanus minor	48.3	80.5	41.0	24.3	32.2										
Neocalanus gracilis	22.7	51.5	17.1	6.9	4.2	0.7					1.2			0.2	3.8
Family Candaciidae															
Candacia aethiopica			0.2		0.3					0.5					
Candacia bispinosa			0.2		0.4										
Candacia catula			0.2	0.1											
Candacia cheirura	0.3			0.3											
Candacia simplex															
Candacia truncata		0.3													
Candacia varicans															
Candacia unidentified				0.1											

Family Clausocalanidae															
Clausocalanus arcuicornis	6.4	9.2	15.6	19.3	37.7	5.5	0.8		4.4	5.6				0.2	
Clausocalanus brevipes	0.3				5.6	18.3	3.9	0.7	6.5	21.9	0.7	6.7	1.8	5.2	1.3
Clausocalanus furcatus	8.7		0.3					2.4			1.5				
Clausocalanus ingens	1.6	1.2	3.8	5.3	10.5	2.8	21.5	11.7	2.4	0.5	14.6	0.7		0.2	0.6
Clausocalanus jobei		0.3	1.5	5.2	4.4	0.7									
Clausocalanus laticeps				0.1	1.1	23.8	18.9	6.3	5.4	6.1	4.2	1.3	0.6	3.8	4.0
Clausocalanus lividus	5.3	3.6	5.5	3.7	3.4	13.8	0.8	0.5	2.1	5.0		0.3			0.8
Clausocalanus mastigophorus	1.3	7.0	12.5	6.9	5.5	2.8		0.5	2.9	0.5					
Clausocalanus minor	11.6	5.3	16.4	16.7	18.6						0.4				
Clausocalanus parapergens	0.6	4.1	14.0	16.8	23.1			6.1		0.5	1.1		1.7	9.3	4.9
Clausocalanus paululus	2.3	0.6	0.2	0.4	0.3										
Clausocalanus pergens	1.4	4.3	18.2	15.6	8.6			0.3					2.6	0.5	0.4
Ctenocalanus vanus	4.8	10.9	64.7	79.8	126.0	24.8	144.0	10.5	37.3	6.1	0.8	0.3	0.1	1.8	0.8
Family Eucalanidae															
Eucalanus hyalinus	4.5	2.5	9.0	3.0							1.4		1.7		0.2
Pareucalanus langae	0.4	0.4	0.3	0.2	0.5			0.3							
Rhincalanus gigas			0.3		1.5	1.1		1.6	1.1	7.9		0.7	0.5	0.2	
Rhincalanus nasutus	6.0	3.7	13.0	10.2	7.4			1.5		0.5	0.3		0.3	0.1	0.2
Subeucalanus longiceps		0.3	0.3	0.3		0.7	0.4	1.0		0.5					0.3
Family Euchaetidae															
Euchaeta acuta			0.2		2.5			0.8							
Euchaeta lobatus															
Euchaeta media								0.3							
Euchaeta spinosa															
Euchaeta spp.								0.5							
Pareucheata biloba								0.3							
Pareucheata exigua															
Family Heterorhabdidae															
Heterohabdus clausi			0.3	0.4	0.3									0.2	
Heterohabdus lobatus															
Heterorhabdus papilliger	0.4		1.5	2.1	9.6			0.8	0.2	0.5		0.3		1.0	2.1
Heterorhabdus spinifer				0.5	2.2										
Heterorhabdus spinifrons			0.2	0.1	1.1										
Heterostylites longicornis															
Heterostylites major															
Family Lucicutiidae															
Lucicutia clausi	0.3		0.2	1.8	17.2										
Lucicutia flavicornis		0.3	5.5	8.5	77.4					1.1	0.4		0.2	0.2	1.6
Lucicutia gaussae					0.3										
Lucicutia longicornis	0.5														
Lucicutia longiserrata			0.3	0.1	1.5										
Lucicutia magna				0.1											

Family Metridinidae															
Metridia curticauda															
Metridia lucens								0.2			0.4		0.1	0.4	5.2
Pleuromamma abdominalis	0.3														
Pleuromamma borealis															
Pleuromamma gracilis		1.2		0.2	0.3										
Pleuromamma indica															
Pleuromamma piseki	0.5			0.3	2.1										1.2
Pleuromamma quadrungulata	0.3		0.3	0.3	0.3										0.2
Pleuromamma robusta															
Pleuromamma xiphias					0.5										
Family Scolecitrichidae															
Amallothrix dentipes									0.7	1.3					
Amallothrix unidentified															
Scaphocalanus brevicornis			0.2												
Scaphocalanus curtus				0.2	5.0										
Scaphocalanus echinatus															
Scaphocalanus unidentified									0.2	5.8	0.4		0.2	1.0	1.1
Scolecithricella dentata				0.1											
Scolecithricella minor			0.1	0.1	0.4	2.4	5.1	5.7	3.7	19.8	0.8	2.0	1.0	6.6	9.8
Scolecithricella ovata					0.4										
Scolecithricella tenuiserrata															
Scolecithricella unidentified					0.5										
Scolecithrix bradyi			0.2												
Scolecithrix danae															
Scottocalanus securifrons												0.7		0.3	
Family Paracalanidae															
Calocalanus contractus	1.9		0.2	1.4	3.2										
Calocalanus equalicauda															
Calocalanus minor				0.5	2.6										
Calocalanus pavo	10.7	3.2	1.8	2.5	4.7						0.4		0.7		
Calocalanus plumulosus	0.8	0.6	0.6	1.2	0.7						0.3				
Calocalanus styliremis	22.2	17.3	22.1	18.1	2.5		3.2				7.3	25.1	20.8	1.0	0.6
Calocalanus tenuicornis	0.5	0.4	0.2		0.4										
Calocalanus tenuis	0.4		0.4	0.6	0.5						0.3			0.2	
Mecynocera clausi	50.8	77.0	56.4	31.2	8.9				0.2		13.7	14.4	2.4	0.1	
Paracalanus denudatus	0.8			0.2											
Paracalanus indicus	19.0	18.0	7.4	1.7											
Paracalanus nanus	2.6	1.6	2.1	2.9	0.2										
Paracalanus parvus	153.2	144.3	47.3	14.5	8.9			0.5			40.2	0.3			
Paracalanus quasimodo	8.5	2.5	3.7	0.9											
Family Pontellidae															
Labidocera spp.			0.2												

Family Temoridae															
Temora spp.		0.8	0.3		0.7										
Family Tortanidae															
Tortanus spp.	2.5	1.7	0.4	0.5	0.5										
Family Phaennidae															
Phaenna spinifera					0.2										
Order Cyclopoida															
Family Oithonidae															
Oithona spp.	469.8	550.9	422.3	488.8	238.1	228.3	1312.7	356.2	139.5	24.1	596.7	351.4	265.7	39.8	2.6
Order Harpacticoida															
Family Ectinosomatidae															
Microsetella rosea		0.7	0.8	1.2	5.1		0.8		0.2						
Family Clytemnestridae															
Clytemnestra spp.				0.1	2.8										
Family Miraciidae															
Macrosetella gracilis			0.4												
Miracia efferata	1.9	1.9	0.6	1.1	0.2										
Miracia minor	0.5	0.3	0.6	0.4											
Oculosetella gracilis															
Order Poecilostomatoida															
Family Oncaeidae															
Oncaea spp.	64.0	48.8	155.3	292.2	889.3	1.4	3.9	3.6	20.6	11.4		2.3	4.0	10.2	4.1
Family Sapphirinidae															
Copilia hendorffi	0.4	2.9	1.8	1.2	1.9										
Copilia mirabilis	0.4														
Copilia vitrea				0.2											
Sapphirina angusta	0.8		0.2	0.3	0.5										
Sapphirina auronitens		0.4													
Sapphirina intestinata	0.4														
Sapphirina iris															
Sapphirina metallina				0.3											
Sapphirina nigromaculata	0.4														
Sapphirina opalina	2.5	5.0	1.4	1.3	2.4										
Sapphirina unidentified	0.4		0.2		0.2										
Family Corycaeidae															
Corycaeus spp.	132.0	93.5	263.6	90.8	54.6	0.7		0.3		0.3					
Farranula spp.	82.4	84.8	70.6	37.9	21.9		1.5								

Annexure II: Nighttime composition (densities.m^{-3}) of all copepod taxa sampled at different depth intervals in the upper 200 m of the water column across the South West Indian Ocean Ridge during the period of November to December 2009. Groups were identified by the cluster analysis in Figure 3.5, Section 3.1.3. ARC - Agulhas Return Current; STF - Subtropical Front; SAF - Sub-Antarctic Front.

	ARC					SSTF					SAF				
	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	150 - 200 m	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	150 - 200 m	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	150 - 200 m
Order Calanoida															
Family Acartiidae															
Acartia danae	162.7	85.1	28.1	37.6	37.3										0.2
Acartia negligens	104.7	22.7	10.8	8.2	9.1						1.1				
Family Aetideidae															
Aetideus acutus					0.7										
Aetideus armatus					0.9					0.2					
Aetideus australis									1.1	3.6	0.7			1.2	0.9
Aetideus giesbrechti					2.4										
Aetideus unidentified				0.2											
Chiridius gracilis					0.9										0.2
Euchirella amoena				0.2											
Euchirella pulchra															0.2
Euchirella rostrata	0.4	0.4		0.2	0.4						0.7	2.9	0.3	0.5	0.2
Euchirella truncata					1.6										
Euchirella unidentified				1.0											
Gaetanus minor					4.1										1.3
Undeuchaeta incisa										0.1					
Undeuchaeta major			0.1		1.7					0.2					0.2
Undeuchaeta plumosa			0.2												
Family Calanidae															
Calanoides macrocarinatus	3.0	1.7	0.6	1.0	1.2								0.9	4.8	
Calanus simillimus					0.6	8.6	13.4	19.3	6.7	0.2					
Cosmocalanus darwinii	0.6				6.3										
Mesocalanus tenuicornis	12.3	8.0	14.1	13.3	6.8							0.7	0.5		
Nannocalanus minor	76.3	32.9	14.6	8.9	8.9										0.2
Neocalanus gracilis	38.6	19.1	12.3	8.2	13.9						0.5			0.2	0.7
Family Candaciidae															
Candacia aethiopica	1.0														
Candacia bispinosa	0.6		0.1												
Candacia catula	0.4														
Candacia cheirura	0.8	0.4	0.3	0.3	0.2							0.7	0.3		0.6
Candacia simplex			0.1												
Candacia truncata	0.6														
Candacia varicans	0.6			0.5											
Candacia unidentified															

Family Clausocalanidae															
Clausocalanus arcuicornis	61.9	31.0	16.7	16.1	19.2					0.1	1.1		0.3		
Clausocalanus brevipes	8.7	2.5	1.0	2.0	3.4	36.6	63.3	9.7	9.8	1.2	43.8	53.3	22.0	17.9	5.6
Clausocalanus furcatus	14.9		0.2	0.3											
Clausocalanus ingens	19.4	3.6	3.9	5.5	13.0						4.3				
Clausocalanus jobei	6.1	4.4	1.9												
Clausocalanus laticeps					0.1	41.6	29.5	29.0	11.8	1.1	11.8	6.3	2.2	0.3	1.2
Clausocalanus lividus	11.0	2.1	1.8	2.2	4.2						1.6				
Clausocalanus mastigophorus	32.3	9.3	10.0	4.8	3.6										
Clausocalanus minor	44.7	10.6	19.7	23.4	8.7										
Clausocalanus parapergens	23.6	5.8	12.1	11.2	9.3									0.3	
Clausocalanus paululus	6.9	3.0	2.4	2.4	1.6										
Clausocalanus pergens	44.7	7.3	12.4	7.7	2.7						1.6		0.3		
Ctenocalanus vanus	66.4	42.1	133.4	78.6	64.2	37.9	47.8	19.3	26.9	5.0	0.5	2.9			0.4
Family Eucalanidae															
Eucalanus hyalinus	3.9	2.6	1.5	1.2	0.2					0.2	0.5		1.3	0.1	
Pareucalanus langae	0.4	0.4		0.4											
Rhincalanus gigas	1.1	1.1		0.1	0.3				0.6	3.3			0.3		
Rhincalanus nasutus	17.9	11.6	7.1	1.9	2.2									0.1	
Subeucalanus longiceps			0.5					0.3	0.3	0.8	0.5				
Family Euchaetidae															
Euchaeta acuta	6.4	4.9	5.4	5.6	16.3										0.2
Euchaeta lobatus					0.3										
Euchaeta media															
Euchaeta spinosa					0.3										
Euchaeta spp.	0.4		0.1												
Pareucheata biloba															
Pareucheata exigua												0.7			0.3
Family Heterorhabdidae															
Heterohabdus clausi	0.4	0.4	0.2	0.5						0.2					0.4
Heterohabdus lobatus					0.3										
Heterorhabdus papilliger	2.1	2.1	2.6	5.5	7.6					0.4			0.4	0.3	2.0
Heterorhabdus spinifer	0.4		0.8	1.3	0.3										
Heterorhabdus spinifrons	0.3	0.3	0.4		0.5										0.2
Heterostylites longicornis															0.2
Heterostylites major					0.5										0.7
Family Lucicutiidae															
Lucicutia clausi	7.2	3.5	3.1	4.2	1.3										
Lucicutia flavicornis	35.8	16.3	12.8	12.8	26.2					0.1			0.8	0.5	0.7
Lucicutia gaussae															
Lucicutia longicornis	3.5	3.0	1.7	1.1	2.3										0.2
Lucicutia longiserrata	0.5	0.5			0.5										
Lucicutia magna															

Family Metridinidae															
Metridia curticauda															0.3
Metridia lucens										0.2	28.0	37.9	16.5	26.9	18.3
Pleuromamma abdominalis	16.2	9.2	7.3	3.1	16.9								1.8	2.2	1.9
Pleuromamma borealis	28.0	8.5	4.6	2.0	7.4						1.3	5.0		2.2	0.3
Pleuromamma gracilis	21.4	14.4	1.6	3.4	6.0									0.7	0.2
Pleuromamma indica	3.2	2.7	1.3	0.3											
Pleuromamma piseki	68.2	27.0	20.0	15.2	37.7						15.8	61.6	10.2	30.8	20.9
Pleuromamma quadrungulata	0.4	0.4		1.3	1.1										1.8
Pleuromamma robusta					3.2		0.6	0.5	2.5	1.7		10.8	1.5	1.4	
Pleuromamma xiphias	1.4		1.0	0.9	4.9								0.3	0.2	
Family Scolecitrichidae															
Amallothrix dentipes															
Amallothrix unidentified					0.2										0.3
Scaphocalanus brevicornis			0.9												
Scaphocalanus curtus	2.8	0.8	2.0	1.7	0.3										0.2
Scaphocalanus echinatus	0.4	0.4	0.7	0.7	2.9					0.2			0.1		0.2
Scaphocalanus unidentified				0.6	0.4					0.9					1.8
Scolecithricella dentata	1.6		0.2	0.8	1.6										
Scolecithricella minor	0.7	0.7	0.6		1.3	0.3	5.8	14.5	10.1	7.1	1.2		4.8	6.6	3.5
Scolecithricella ovata	1.8	1.8	2.0	2.9	4.5									0.5	0.4
Scolecithricella tenuiserrata					0.1										
Scolecithricella unidentified										0.2					
Scolecithrix bradyi	0.6		0.2		1.9										
Scolecithrix danae	0.4	0.4													
Scottocalanus securifrons			0.1							0.1					
Family Paracalanidae															
Calocalanus contractus	3.1	0.4	0.8	6.5	2.4										
Calocalanus equalicauda															
Calocalanus minor	0.9			1.0											
Calocalanus pavo	9.6	1.9	1.3	2.0	5.7										
Calocalanus plumulosus	2.2	0.8	0.4	1.0	2.7						0.5				
Calocalanus styliremis	61.8	23.4	22.5	5.8	8.6		1.0		0.3		15.4	18.3	1.0	0.5	
Calocalanus tenuicornis	0.9		0.1												
Calocalanus tenuis	1.8	0.3	0.5	2.0	1.0										
Mecynocera clausi	96.1	47.7	39.5	24.2	9.0					0.2	4.6	2.6	0.5		0.7
Paracalanus denudatus	8.7	0.4			0.3										
Paracalanus indicus	23.2	2.2	1.8	2.1	0.3					0.1					
Paracalanus nanus	17.1	5.1	4.7	1.0	3.8					0.2					
Paracalanus parvus	173.9	38.0	10.3	3.9	6.8						3.7				
Paracalanus quasimodo	7.4	2.5	0.2												
Family Pontellidae															
Labidocera spp.				0.3											

Family Temoridae															
Temora spp.			0.5												
Family Tortanidae															
Tortanus spp.	1.6	0.4	0.2	0.3											
Family Phaennidae															
Phaenna spinifera				0.3	0.3										
Order Cyclopoida															
Family Oithonidae															
Oithona spp.	1140.1	451.4	688.6	305.1	149.4	1456.7	1467.7	971.8	720.1	61.0	517.1	869.6	320.7	131.2	9.1
Order Harpacticoida															
Family Ectinosomatidae															
Microsetella rosea	12.6	3.0	4.5	1.8	0.3										
Family Clytemnestridae															
Clytemnestra spp.															
Family Miraciidae															
Macrosetella gracilis	2.3	0.7	2.4												
Miracia efferata	3.2	3.2	2.0	0.3							0.7			0.2	
Miracia minor	1.4	1.2	1.3												
Oculosetella gracilis	0.4														
Order Poecilostomatoida															
Family Oncaeidae															
Oncaea spp.	660.0	275.6	452.9	280.0	259.0		0.2	4.8	8.8	5.9	7.7	5.8	34.6	64.2	34.3
Family Sapphirinidae															
Copilia hendorffi	0.3	0.3													
Copilia mirabilis															
Copilia vitrea	1.2		0.5	0.4											
Sapphirina angusta	3.0	0.3	1.5	1.0	1.5										
Sapphirina auronitens															
Sapphirina intestinata															
Sapphirina iris	0.9									0.3					
Sapphirina metallina			0.1	0.3	0.2										
Sapphirina nigromaculata															
Sapphirina opalina	0.4	0.4		0.6	0.2										
Sapphirina unidentified					1.6										
Family Corycaeidae															
Corycaeus spp.	286.5	121.9	155.3	50.4	58.7										
Farranula spp.	121.8	44.9	55.0	18.0	6.0										

Annexure III: Distribution of copepod fauna consolidated from published literature of the WIO amongst the Longhurst (1998) biogeographic provinces in Figure 1.2. Sources of data: **1)** Binet & Dessier, 1968; **2)** Brady, 1914a; **3)** Brady, 1914b; **4)** Brady, 1915; **5)** Carter, 1977; **6)** Cedras, unpublished; **7)** Cleve 1904; **8)** De Decker, 1964; **9)** De Decker & Mombeck, 1964; **10)** De Decker, 1973; **11)** De Decker, 1984; **12)** Gallienne *et al.*, 2004, **13)** Gopalakrishnan & Balachandran, 1992; **14)** Grice & Hulsemann, 1967; **15)** Heinrich, 1992a; **16)** Heinrich, 1992b; **17)** Heinrich, 1995; **18)** Huggett, 2014; **19)** Lawson, 1977; **20)** Lugomela *et al.*, 2001; **21)** Madhupratap & Haridas, 1986; **22)** Mwaluma *et al.*, 2003; **23)** Okemwa & Revis, 1986; **24)** Okera, 1974; **25)** Osore *et al*, 1997; **26)** Osore *et al*, 2003; **27)** Osore et al, 2004a; **28)** Osore *et al*, 2004b; **29)** Ram & Goswami, 1993; **30)** Revis & Okemwa, 1988; **31)** Revis, 1988; **32)** SenÓ *et al* (1963); **33)** Smith, 1982; **34)** Tanaka, 1964; **35)** Tanaka, 1973.

Species	**Provinces**					**Sources**
	ARAB	**EAFR**	**ISSG**	**MONS**	**SSTC**	
Family Megacalanidae						
Megacalanus princeps			●	●	●	9, 14
Bathycalanus bradyi			●	●	●	14
Bathycalanus princeps					●	14
Bathycalanus richardi				●		14
Bathycalanus sverdrupi			●	●		14
Bradycalanus gigas			●	●		14
Bradycalanus sarsi			●	●		14
Bradycalanus typicus				●		14
Family Calanidae						
Calanoides carinatus	●	●	●	●	●	5, 6, 8, 9, 10, 11, 17, 33, 34
Calanoides macrocarinatus		●			●	11, 17
Calanoides natalis		●				2
Calanus algulhensis		●	●		●	11, 34, 32, 8, 5, 7, 6, 8
Calanus brevicornis		●				7
Calanus propinquus		●			●	4, 11, 2, 6
Calanus simillimus		●	●		●	11, 29, 34, 6
Canthocalanus pauper		●	●	●	●	14, 9, 3, 8, 11, 1, 23, 12, 14, 21, 5, 8, 30, 31
Cosmocalanus darwinii		●	●	●	●	4, 8, 9, 2, 11, 1, 14, 12, 21, 6, 5, 30
Mesocalanus tenuicornis		●	●		●	8, 11, 6, 7, 14, 5, 9
Nannocalanus minor		●	●	●	●	26, 10, 9, 5, 11, 6, 7, 1, 12, 14, 18, 17, 8, 34, 30
Neocalanus gracilis		●	●	●	●	9, 11, 1, 12, 14, 21, 6, 17
Neocalanus robustior		●	●	●	●	11, 12, 9
Neocalanus tonsus		●	●		●	9, 11, 6, 34
Undinula vulgaris		●	●	●	●	2, 4, 8, 11, 5, 7, 1, 23, 12, 21, 9, 26, 30, 31

Annexure III (continued)

Family Paracalanidae

Acrocalanus andersoni		●				5
Acrocalanus gibber		●	●	●	●	20, 9, 11, 7, 12, 21, 5, 30, 31, 3
Acrocalanus gracilis		●	●	●	●	9, 11, 5, 7, 21, 8, 30
Acrocalanus longicornis		●	●	●	●	2, 4, 9, 2, 23, 14, 21, , 30
Acrocalanus monachus		●	●	●	●	9, 11, 12, 14, 21, 8, 30
Calocalanus contractus		●	●		●	9, 11, , 14, 5, 8
Calocalanus gracilis		●				9
Calocalanus minor			●		●	6, 8
Calocalanus pavo		●	●	●	●	9, 11, 7, 5, 14, 21, 6, 8, 34
Calocalanus plumulosus		●	●	●	●	11, 9, 14, 6, 5, 8, 34
Calocalanus styliremis		●	●	●	●	11, 9, 14, 6, 5, 8, 34
Calocalanus tenuicornis					●	6
Calocalanus tenuis		●	●		●	11, 9, 6, 8, 10
Mecynocera clausi		●	●	●	●	9, 11, 6, 14, 21, 5, 17, 8
Paracalanus aculeatus	●	●	●	●	●	30, 8, 9, 11, 7, 33, 1, 23, 14, 21, 5, 31
Paracalanus crassirostris		●				30, 11, 8
Paracalanus denudatus	●	●	●	●		33, 8, 14
Paracalanus indicus			●		●	6
Paracalanus nanus		●	●	●	●	9, 14, 6
Paracalanus parvus	●	●	●	●	●	3, 9, 5, 33, 7, 21, 6, 8, 34
Paracalanus pygmaeus		●			●	5

Family Eucalanidae

Eucalanus attenuatus s.l.		●	●	●	●	4, 9, 11, 2, 7, 1, 14, 21, 8, 26
Eucalanus crassus		●	●	●	●	26, 9, 11, , 7, 14, 21, 5
Eucalanus elongatus		●	●		●	9, 7, 14, 8
Eucalanus hyalinus		●	●		●	11, 5, 14, 6, 15, 17
Eucalanus longiceps		●	●		●	9
Eucalanus monachus		●				7, 8
Eucalanus mucronatus		●	●	●	●	26, 11, 5, 7, 1, 21, 9, 8
Eucalanus pileatus		●	●	●	●	11, 7, 21, 5, 8
Eucalanus sewelli		●			●	5
Eucalanus subcrassus		●	●	●	●	11, 5, 7, 1, 21, 9, 8
Eucalanus subtenius		●	●	●	●	11, 5, 7, 21, 9
Pareucalanus attenuatus		●	●	●		18, 12
Pareucalanus langae			●		●	6
Rhincalanus gigas			●		●	11, 14, 29, 6

Annexure III (continued)

Rhincalanus nasutus		●	●	●	●	10, 8, 9, 5, 11, 7, 6, 1, 17, 14, 21, 15, 16
Rhincalanus rostifrons cornutus		●	●	●	●	4, 10, 9, 18, 12, 21, 15, 2, 11, 5, 7, 1, 23, 14, 8, 24, 30
Subeucalanus longiceps					●	6
Subeucalanus mucronatus			●	●		12
Subeucalanus pileatus			●	●		12
Subeucalanus subcrassus			●	●		12

Family Spinocalanidae

Mimocalanus cultrifer			●	●		14
Mimocalanus inflatus			●	●		14
Mimocalanus nudus			●	●		14
Monacilla tenera			●	●		14
Monacilla typica				●		14
Spinocalanus abruptus			●	●		14
Spinocalanus abyssalis			●	●		14
Spinocalanus abyssalis var pygmaeus			●	●		14
Spinocalanus angusliceps			●	●		14
Spinocalanus magnus			●	●	●	14, 9
Spinocalanus ovalis				●		14
Spinocalanus spinosus			●	●	●	14, 9
Spinocalanus validus			●			14
Spinocalanus ventriosus			●	●		14

Family Clausocalanidae

Clausocalanus arcuicornis		●	●	●	●	8, 9, 5, 7, 14, 21, 6, 34
Clausocalanus brevipes					●	6
Clausocalanus farrani	●	●	●	●	●	30, 5, 23, 14, 21, 33
Clausocalanus furcatus	●	●	●	●	●	2, 4, 9, 2, 11, 5, 7, 14, 6, 33, 8
Clausocalanus ingens		●	●		●	11, 6
Clausocalanus jobei					●	6
Clausocalanus laticeps		●	●		●	11, 34, 6
Clausocalanus lividus			●		●	6
Clausocalanus mastigophorus		●	●		●	6, 5
Clausocalanus minor	●	●	●		●	33, 6, 5
Clausocalanus parapergens		●	●		●	6, 5
Clausocalanus paululus		●	●		●	9, 14, 6, 8, 5
Clausocalanus pergens		●	●		●	9, 6, 5
Ctenocalanus vanus		●	●	●	●	10, 11, 9, 14, 6, 5, 8

Annexure III (continued)

Drepanopus pectinatus					●	11
Farrania frigida				●		14

Family Discoidae

Disco inflatus			●	●		14
Disco longus				●		14
Disco minutus				●		14

Family Aetideidae

Aetideopsis retusa			●			14
Aetideopsis rostrata					●	9
Aetideus acutus		●	●	●	●	9, 11, , 5, 14, 21
Aetideus armatus		●	●	●	●	9, 11, 7, 14, 21, 6
Aetideus australis					●	6
Aetideus giesbrechti		●	●	●	●	9, 7, 1, 12, 21, 6
Batheuchaeta lamellata			●			14
Bradyidius bradyi				●		14
Chiridiella macrodactyla				●	●	14, 9
Chiridius pacificus					●	16
Chiridius poppei		●			●	7, 14
Chiridius tenuispinus		●				1
Chirundina indica				●		14
Chirundina streetsii		●	●	●	●	9, 7, 1, 14
Chirundinella cara				●		14
Euchirella amoena				●	●	14, 6
Euchirella bella			●	●		14
Euchirella bitumida			●			14
Euchirella curticauda				●		14
Euchirella formosa			●			14
Euchirella gateata				●		14
Euchirella maxima				●		14
Euchirella messinensis		●	●			7, 14, 9
Euchirella pulchra		●	●	●		1, 12, 14
Euchirella rostrata		●	●		●	11, 6, 9
Euchirella truncata			●		●	6
Euchirella venusta		●		●		7, 9
Gaidius brevicaudatus				●		14
Gaidius minutus		●		●		1, 14
Gaidius robustus			●		●	14

Annexure III (continued)

Gaidius tenuispinus				●	●	14, 9
Gaetanus antarcticus			●	●	●	14
Gaetanus armiger		●				7, 14
Gaetanus brachyurus			●			14
Gaetanus curvirostris			●			14
Gaetanus kruppi		●	●			1, 14, 9
Gaetanus latifrons			●		●	14, 9
Gaetanus miles		●	●		●	7, 9
Gaetanus minor		●	●		●	11, 1, 14, 9
Gaetanus pileatus		●	●	●	●	14, 21, 9
Pseudochirella divaricata			●			14
Pseudochirella dubia			●	●		14
Pseudochirella gibbera				●	●	14
Pseudochirella hirsuta					●	14
Pseudochirella magna					●	14
Pseudochirella obtusa				●	●	14
Pseudochirella polyspina					●	14
Pseudochirella pustulifera			●		●	14
Pseudochirella semispina				●		14
Pseudochirella squalida			●			14
Pseudochirella tuberculata				●		14
Undeuchaeta intermedia			●	●	●	9, 12
Undeuchaeta major		●	●	●	●	9, 2, 6, 7, 1, 14, 21
Undeuchaeta minor		●				7
Undeuchaeta plumosa		●	●	●	●	9, 11, 6, 1, 12, , 14
Family Euchaetidae						
Euchaeta acuta		●	●		●	11, 9, 6, 7
Euchaeta affinis		●				7
Euchaeta barbata			●		●	14
Euchaeta biloba					●	11, 14
Euchaeta bisinuata			●	●		14
Euchaeta calva				●	●	14
Euchaeta concinna		●			●	9, 35
Euchaeta dubia					●	14
Euchaeta farrani					●	14
Euchaeta gracilis			●		●	14
Euchaeta hanseni				●		14

Annexure III (continued)

Euchaeta indica		●	●	●		12, 18
Euchaeta lobatus					●	6
Euchaeta longicornis	●	●	●	●	●	35, 7, 9
Euchaeta malayensis			●		●	14
Euchaeta marina	●	●	●	●	●	30, 11, 9, 7, 1, 23, 14, 35
Euchaeta media	●	●	●	●	●	35, 11, 9, 7, 6
Euchaeta paraacuta					●	35
Euchaeta prestandreae		●				2
Euchaeta pubera		●	●			30, 23, 35
Euchaeta rimana			●	●		11, 12, 21
Euchaeta sarsi			●	●	●	14
Euchaeta scotti			●	●		14
Euchaeta spinosa		●			●	9, 7, 6
Euchaeta tenius	●	●	●	●		30, 23, 35
Euchaeta tonsa		●	●	●	●	7, 14
Euchaeta weberi				●		14
Euchaeta wolfendeni	●	●	●	●	●	35, 11, , 9, 14, 8
Paraeuchaeta barbata			●		●	9
Paraeuchaeta norvegica					●	9
Pareuchaeta acuta					●	17
Pareucheata biloba					●	6
Valdiviella brevicornis			●	●		14
Valdiviella insignis			●	●	●	14
Valdiviella oligarthra				●		14

Family Phaennidae

Cornucalanus chelifer					●	14
Cornucalanus indicus			●			14
Cornucalanus simplex				●		14
Onchocalanus magnus			●		●	14
Phaenna spinifera		●	●	●	●	9, 11, 7, 12, 21, 6
Xanthocalanus fragilis		●				7
Xanthocalanus greeni				●		14
Xanthocalanus hispidus			●			14
Xanthocalanus obtusus			●			14

Family Scolecitrichidae

Amallothrix dentipes					●	6
Amallothrix emarginata			●		●	14, 9

Annexure III (continued)

Amallothrix gracilis						14
Amallothrix indica	●		●	●		14, 13
Amallothrix obtusifrons			●	●		14
Amallothrix paravalida			●	●		14
Amallothrix robustripes				●		14
Amallothrix valida				●		14
Lophothrix angusta	●	●		●	●	13
Lophothrix frontalis			●		●	14, 9
Lophothrix humilifrons		●	●	●		1, 14
Lophothrix insignis				●		14
Lophothrix latipes		●	●		●	9, 1
Lophothrix varicans					●	9
Scaphocalanus affinis			●			14
Scaphocalanus bogorovi			●			14
Scaphocalanus brevicornis			●	●	●	14, 6
Scaphocalanus curtus	●	●	●	●	●	5, 14, 6, 13
Scaphocalanus echinatus	●	●	●	●	●	11, 1, 13, 14, 6
Scaphocalanus elongatus			●	●		14
Scaphocalanus longifurca			●	●		14
Scaphocalanus magnus				●		14
Scaphocalanus major				●		14
Scaphocalanus medius			●		●	9
Scaphocalanus subbrevicornis			●	●		14
Scolecithricella abyssalis	●	●	●	●	●	6, 13
Scolecithricella auropecten				●		14
Scolecithricella ctenopus		●		●	●	5, 13
Scolecithricella dentata	●	●	●	●	●	14, 6, 13
Scolecithricella dubia					●	9
Scolecithricella glacialis					●	11
Scolecithricella laminata			●	●		14
Scolecithricella maritima				●		14
Scolecithricella minor					●	6
Scolecithricella ovata	●	●		●	●	14, 6, 13
Scolecithricella tenuiserrata	●	●	●	●		13
Scolecithricella timida				●		14
Scolecithricella unispinosa			●			14
Scolecithricella vittata	●	●	●	●	●	9, 13

Annexure III (continued)

Scolecithrix bradyi	●	●	●	●	●	9, 11, 1, 6, 12, 5, 14, 21, 13
Scolecithrix danae	●	●	●	●	●	4, 8, 9, 11, 5, 7, 2, 1, 23, 12, 14, 21, 30, 13
Scolecithrix fowleri			●			14
Scolecithrix nicobarica	●					14, 13
Scotocalanus dauglishi	●			●		14, 13
Scotocalanus helenae					●	14
Scottocalanus longispinus					●	9
Scottocalanus persecans		●			●	9, 7, 1
Scottocalanus securifrons	●	●	●	●	●	13, 9, 6, 7, 1

Family Arietellidae

Arietellus giesbrechti			●			9
Arietellus setosus					●	9
Arietellus simplex			●		●	14

Family Augaptilidae

Augaptilus glacialis					●	14, 9
Augaptilus longicaudatus					●	9
Augaptilus palumboi		●	●		●	9, 7
Augaptilus spinifrons					●	9
Centraugaptilus cucullatus			●			14
Centraugaptilus horridus			●			14
Euaugaptilus bullifer			●			9, 14
Euaugaptilus gibbus					●	9
Euaugaptilus magnus					●	9, 14
Euaugaptilus nodifrons					●	9, 14
Euaugaptilus oblongus					●	9, 14
Euaugaptilus brodskyi				●		14
Euaugaptilus bullifer			●	●		
Euaugaptilus elongatus			●	●		14
Euaugaptilus farrani				●		14
Euaugaptilus filigerus				●		14
Euaugaptilus gracilis				●		14
Euaugaptilus grandicornis				●		14
Euaugaptilus humilis				●		14
Euaugaptilus indicus				●		14
Euaugaptilus laticeps			●	●		14
Euaugaptilus longimanus			●	●		14
Euaugaptilus longiseta				●		14

Annexure III (continued)

Euaugaptilus magnus			●	●	●	
Euaugaptilus nodifrons			●	●	●	
Euaugaptilus oblongus				●		
Euaugaptilus quaesitus				●		14
Euaugaptilus rectus				●		14
Euaugaptilus rigidus				●		14
Haloptilus acutifrons		●	●	●	●	14, 9
Haloptilus angusticeps					●	9
Haloptilus longicornis		●	●	●	●	9, 11, 15, 17, 1, 14, 21, 5
Haloptilus mucronatus		●				9
Haloptilus ornatus		●	●			9
Haloptilus oxycephalus		●	●		●	9
Haloptilus spiniceps					●	9
Haloptilus tenuis				●		14
Haloptilus validus				●		14
Pachyptilus abbreviatus				●		14
Pachyptilus eurygnathus			●			14
Pachyptilus pacificus				●	●	14
Pontoptilus lacertosus			●			14
Pontoptilus mucronatus			●	●		14
Pontoptilus robustus				●		14

Family Heterorhabdidae

Disetta palumboi		●	●	●	●	9, 1, 14
Disseta minuta			●	●		14
Heterohabdus clausi				●		14
Heterohabdus norvegicus				●		14
Heterorhabdus abyssalis		●	●	●	●	9, 7, 1, 14
Heterorhabdus austrinus		●			●	9, 7
Heterorhabdus clausi		●	●			9
Heterorhabdus compactus		●	●	●	●	9, 1, 14
Heterorhabdus norvegicus			●		●	9
Heterorhabdus papilliger		●	●	●	●	11, 5, 7, 14, 21, 6, 9
Heterorhabdus spinifer		●	●		●	5, 6
Heterorhabdus spinifrons		●	●		●	9, 7, 14, 6
Heterorhabdus tanneri		●				7
Heterostylites longicornis					●	14, 9
Heterostylites major				●		14

Annexure III (continued)

Family Lucicutiidae

Lucicutia aurita		●	●	●		7, 14
Lucicutia bella			●			14
Lucicutia bicornuta			●			14
Lucicutia bradyana		●				7
Lucicutia clausi		●	●	●	●	9, 11, 7, 21, 6
Lucicutia curta		●	●	●	●	14, 9
Lucicutia flavicornis		●	●	●	●	4, 9, 2, 18, 5, 11, 6, 7, 1, 23, 12, 14, 21, 15, 17, 30,
Lucicutia formosa			●			14
Lucicutia gaussae		●	●			11, 14
Lucicutia grandis			●	●	●	14
Lucicutia intermedia			●	●		14
Lucicutia longicornis				●	●	14, 6
Lucicutia longiserrata			●	●	●	14, 6
Lucicutia longispina				●		14
Lucicutia magna			●		●	14, 9, 6
Lucicutia major				●		14
Lucicutia maxima		●	●	●	●	9, 1, 14
Lucicutia ovalis		●	●	●	●	14, 9
Lucicutia pallida			●			14
Lucicutia parva			●	●		14
Lucicutia polaris				●		14
Lucicutia rara			●		●	14
Lucicutia sewelli				●		14
Lucicutia simulans					●	9
Lucicutia wolfendeni			●	●	●	14

Family Metridinidae

Gaussia princeps			●	●	●	14
Metridia bicormuta			●		●	9
Metridia boecki			●	●	●	14, 9
Metridia brevicauda		●	●	●	●	7, 14, 9
Metridia discreta			●	●		14
Metridia effusa					●	14, 16
Metridia longa			●		●	9
Metridia lucens		●	●		●	9, 11, 10, 7, 14, 8
Metridia macrura			●	●		14

Annexure III (continued)

Metridia princeps		●	●	●	●	11, 14
Metridia venusta		●	●		●	7, 9, 14
Pleuromamma abdominalis		●	●	●	●	2, 8, 9, 2, 11, 6, 7, 1, 12, 14, 21, 29, 15, 16
Pleuromamma borealis		●	●		●	11, 6, 9
Pleuromamma gracilis		●	●	●	●	8, 9, 11, 7, 12, 14, 29, 6, 5, 17, 15, 16
Pleuromamma indica		●	●	●	●	30, 15, 23, 12, 14, 21, 29, 6, 18
Pleuromamma piseki		●	●	●	●	30, 9, 11, 5, 23, 12, 14, 6
Pleuromamma quadrungulata		●		●	●	11, , 14, 6
Pleuromamma robusta		●			●	11, 7, 8
Pleuromamma xiphias		●	●	●	●	9, 11, 6, 7, 12, 14, 21, 15, 17

Family Phyllopodidae

Phyllopus aequalis					●	14, 9
Phyllopus bidentatus			●			14
Phyllopus helgae		●	●		●	9
Phyllopus helgae			●			14
Phyllopus impar				●		14
Phyllopus muticus			●			14

Family Centropagidae

Centropages brachiatus		●			●	30, 11, , 23, 8, 10
Centropages bradyi		●			●	11
Centropages calaninus		●	●	●	●	30, 11, 9, 21, 8, 10
Centropages chierchiae		●			●	2, 4, 11, 7, 5, 2, 10, 34
Centropages elongatus		●	●	●	●	30, 9, 11, , 12, 8
Centropages furcatus		●	●	●	●	20, 10, 8, 2, 11, 5, 7, 1, 23, 12, 21, 9, 30, 31, 25, 3, 4, 26
Centropages gracilis		●	●	●	●	24, 10, 8, 11, 9, 1, 23, 12, 14, 21, 30
Centropages longicornis		●				11
Centropages orsinii		●				4, 11, 1, 23, 2, 9, 28, 26, 30, 31
Centropages tenuicornis		●				3
Centropages typicus-pacificus		●			●	7, 8
Centropages violaceus		●				2, 4

Family Pseudodiaptomidae

Pseudodiapomous nudus		●			●	8, 11, 34
Pseudodiaptomus sericaudatus		●				7

Family Temoridae

Temora discaudata		●	●	●	●	24, 8, 9, 11, 5, 7, 1, 23, 12, 14, 21, 26, 30
Temora stylifera		●	●		●	24, 11, 9, 7, 23, 20, 30

Annexure III (continued)

Temora turbinata		●		●	●	2, 4, 9, 2, 11, 5, 1, 23, 21, 8, 20, 22, 26, 30, 31, 25

Family Candaciidae

Candacia aethiopica	●	●	●	●	●	19, 11, 34, 1, 12, 14, 21, 6, 27
Candacia armata		●				8
Candacia bispinnata	●	●	●	●	●	19, 11, 7, 1, 9, 8, 27,
Candacia bispinosa	●	●	●	●	●	19, 9, 11, 1, 23, 12, 14, 6, 27, 30
Candacia bradyi		●				24, 1, 27
Candacia catula	●	●	●	●	●	19, 10, 8, 9, 11, 7, 1, 23, 12, 14, 21, 6, 27, 30
Candacia cheirura	●	●			●	19
Candacia curta	●	●	●	●	●	4, 8, 9, 11, 7, 1, 12, 2, 21, 19, 27
Candacia discaudata		●	●	●		19
Candacia guggenheimi	●	●		●		19, 27
Candacia inermis		●				7
Candacia longimana		●	●	●	●	19, 9, 1, 23, 14, 27, 30
Candacia magna		●		●		23, 27, 30
Candacia pachydactyla	●	●	●	●	●	4, 9, 11, 7, 1, 23, 12, 2, 21, 19, 27, 30
Candacia simplex	●	●	●	●	●	19, 11, 23, 9, 6, 27, 30
Candacia tenuimana	●	●		●	●	19, 7, 27, 30
Candacia truncata	●	●	●	●	●	4, 10, 8, 9, 11, 2, 7, 1, 12, 14, 21, 19, 27
Candacia varicans		●	●	●	●	19, 11, 9, 7, 6, 27,

Family Pontellidae

Calanopia elliptica		●	●		●	26, 11, 1, 23, 30
Calanopia minor		●	●	●	●	26, 11, 1, 21, 9, 8, 30
Labidocera acuta		●			●	4, 8, 11, 2, 7, 1, 23, 24, 26, 30
Labidocera acutifrons		●			●	11, 1
Labidocera chubbi		●				2, 4
Labidocera detruncata		●	●	●		14, 1, 12, 14, 21, 4, 2, 23
Labidocera inermis		●				2, 4
Labidocera kroyeri		●				4, 23, 2, 30
Labidocera laevidentata		●				1
Labidocera minuta		●			●	26, 8, 11, 1, 23, 21, 30
Labidocera trispinosa		●				2, 4
Pontella diagonalis			●			9
Pontella fera		●	●	●		4, 2, 12, 21
Pontella natalis (Aphelura typica)		●				2, 3, 4
Aphelura typica		●				3, 4

Annexure III (continued)

Pontella securifer		●				7
Pontellina plumata s.l.		●	●	●	●	4, 10, 9, 2, 11, 1, 23, 12, 21, 8, 26
Pontellina plumifera		●				7
Pontellopsis armata			●	●		12
Pontellopsis herdmani		●				24, 23, 30
Pontellopsis macronyx		●				24
Pontellopsis regalis		●	●		●	9
Pontellopsis scotti		●				24
Pontellopsis speciosus		●				2, 4

Family Acartiidae

Acartia amboinensis		●			●	9, 11, 8, 1, 30, 31
Acartia bispinosa		●				23, 30, 31
Acartia danae		●	●	●	●	17, 9, 11, 8, 1, 23, 5, 12, 7, 21, 6, 24, 30
Acartia erythraea		●				2, 4
Acartia fossae		●				1
Acartia longisetosa		●				3, 4
Acartia nana		●				2, 4
Acartia negligens	●	●	●	●	●	30, 10, 8, 17, 5, 9, 11, 1, 12, 14, 21, 6, 33

Family Tortanidae

Tortanus barbatus		●				23, 31, 30
Tortanus gracilis		●				24, 1, 23, 28, 30

Family Bathypontiidae

Bathypontia elongata			●			14
Bathypontia major			●			14
Bathypontia minor					●	9
Bathypontia regalis				●		14
Bathypontia sarsi				●		14
Bathypontia similis				●		14
Bathypontia spinifera			●	●		14
Bradyetes florens				●		14
Clytemnestra rostrata		●			●	11
Clytemnestra scutellata		●	●		●	11
Euterpe gracilis		●				3, 4
Euterpina acutifrons		●	●		●	11, 9, 8
Foxtonia barthybia			●	●		14
Hemirhabdus grimaldi			●	●	●	14
Hemirhabdus latus			●			14

Annexure III (continued)

Heteramalla dubia				●		14
Heterocalanus serricaudatus		●				3
Isocope propinqua		●				2, 4
Macrosetella gracilis		●	●	●	●	11
Mentranura typica		●				2
Microcalanus pygmaeus		●	●	●	●	14, 9
Microsetella novegica		●	●		●	11
Microsetella rosea		●	●		●	11
Mormonilla minor		●	●		●	9, 1
Oculosetella gracilis		●	●		●	11
Pontoeciella abyssicola		●	●			9
Pseudaugaptilus longiremis			●			14
Pseudeuchaeta brevicauda			●	●		14
Racovitzanus levis						14
Racovitzanus porrectus				●		14
Ratania atlantica			●			9
Ratania flava		●				9
Scottula ambariakae		●				1
Temoria dubia		●				3, 4
Temorites brevis			●			14
Temorites discoveryae				●		14
Temoropia mayumbaensis		●			●	5
Teneriforma naso				●		14
Undinella brevipes			●	●		14
Uneachaeta intermedia				●		14
Zenkevitchiella atlantica				●		14
Zenkevitchiella crassa				●		14