Changes in communities of Hydrozoa (Siphonophorae and Hydromedusae) across the Atlantic sector of the Southern Ocean

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I declare that

“Changes in communities of Hydrozoa (Siphonophorae and Hydromedusae) across the Atlantic sector of the Southern Ocean.” is my own work, that it has not been submitted for any degree or examination at any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

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Acknowledgements

I would like to state to the reader that I am an Afrikaans mother-tongue language speaker and ask that he/she would please forgive my errors in grammar and spelling, accordingly. A sincere and special thanks to my family and friends who have always encouraged and supported me throughout the completion of this degree. To Dr. Delphine Thibault for her continuous supervision and advice concerning species identification and writing. To Professor William Froneman from Rhodes University for providing the samples used during this study. I am also grateful for his comments and those of Dr Gillian Mapstone which greatly improved this thesis. The Biodiversity and Conservation Biology department (BCB) for the research opportunity and the National Research Foundation for their financial support. To all the colleagues within the BCB department for their friendship, support, and guidance, ensuring that the duration of this study was an unforgettable experience. Lastly, but most important, to Professor Mark J. Gibbons for his continuous supervision, advice, support and guidance, without whom this project would not have been a success.

Abstract:

The species composition, abundance and distribution of siphonophores and hydromedusae was investigated from some archived zooplankton samples that were collected along a transect between South Africa and Antarctica conducted in January and February 1993. This is the first study that has investigated siphonophore assemblages across the whole Atlantic sector of the Southern Ocean. In total 21 species of siphonophore were collected, and five different hydromedusae. *Dimophyes arctica* was the most abundant and widely distributed siphonophore collected (avg. abundance: 137 ± 152 ind. 1000 m^{-3}, max. density 519 ind. 1000 m^{-3}): all other species had narrower distribution ranges and were mostly confined to specific frontal locations. The distribution of siphonophore communities was similar to that of documented mesozooplankton and carnivorous communities. There were noticeable differences in communities across the region. There was a clear separation in Antarctic and temperate siphonophore species at the Subantarctic Front, separating the communities within the Atlantic sector of the Southern Ocean into two distinct assemblages. Chlorophyll-*a*, mesozooplankton biomass, mixed layer depth, sea surface salinity (SSS) and sea surface temperature were all responsible for the observed assemblages along the transect, of which SSS was the most important contributor.

Keywords: Antarctic, Atlantic Sector, Community structure, Pelagic cnidaria, Southern Ocean, Zooplankton

1 INTRODUCTION

1.1 Southern Ocean

The Southern Ocean extends southward from approximately 40˚S to the Antarctic continent. It is a large body of water, with a total area of 20.327 million km^2 (Bineesh et al. 2011; Joyner 2011). It contributes to the global oceanic circulation as a component of the Meridional Overturning Circulation (MOC) and plays a vital role in the global transport of heat and water (Ansorge et al. 2005). The Antarctic Circumpolar Current (ACC) is the largest contributor to this transport and it extends all the way around Antarctica, being driven by strong westerly surface winds (Nowlin et al. 1986; Orsi et al. 1995, Ansorge et al. 2005). This eastward flowing current is associated with four fronts, which divide four zones of relatively uniform water masses (Whitworth 1980; Orsi et al. 1995; Ansorge et al. 2005). These fronts and zones from south to north, respectively, are the Antarctic Divergence (AD), the Marginal Ice Zone (MIZ), the Permanently Open Ocean Zone (POOZ), the Antarctic Polar Front (APF), the Polar Frontal Zone (PFZ), the Subantarctic Front (SAF), the Subantarctic Zone (SAZ), and Subtropical Convergence (STC) (Figures 1 & 2).

The AD encompasses the southern branch of the ACC and is the region where there is a change between easterly and westerly wind forcing (Deacon 1982; Orsi et al. 1995). It is located at approximately 65°S, where the subsurface temperature minimum weakens significantly due to warmer water being upwelled from the deep (Deacon 1982; Lutjeharms 1985), though this minimum could in fact just indicate the edge of the Weddell Sea (Figure 2) (Lutjeharms 1985). The AD is associated with the MIZ, which can cover up to 60 % of the area south of the PFZ by the end of winter, and up to 12 % at the end of summer (Deacon 1982). The currents associated with the Weddell Sea are known to transport ice across the Atlantic sector (Ackley 1981; Deacon

1982), while upwelling and Ekman drift occur around the AD playing a vital role in the reduction of ice cover (Deacon

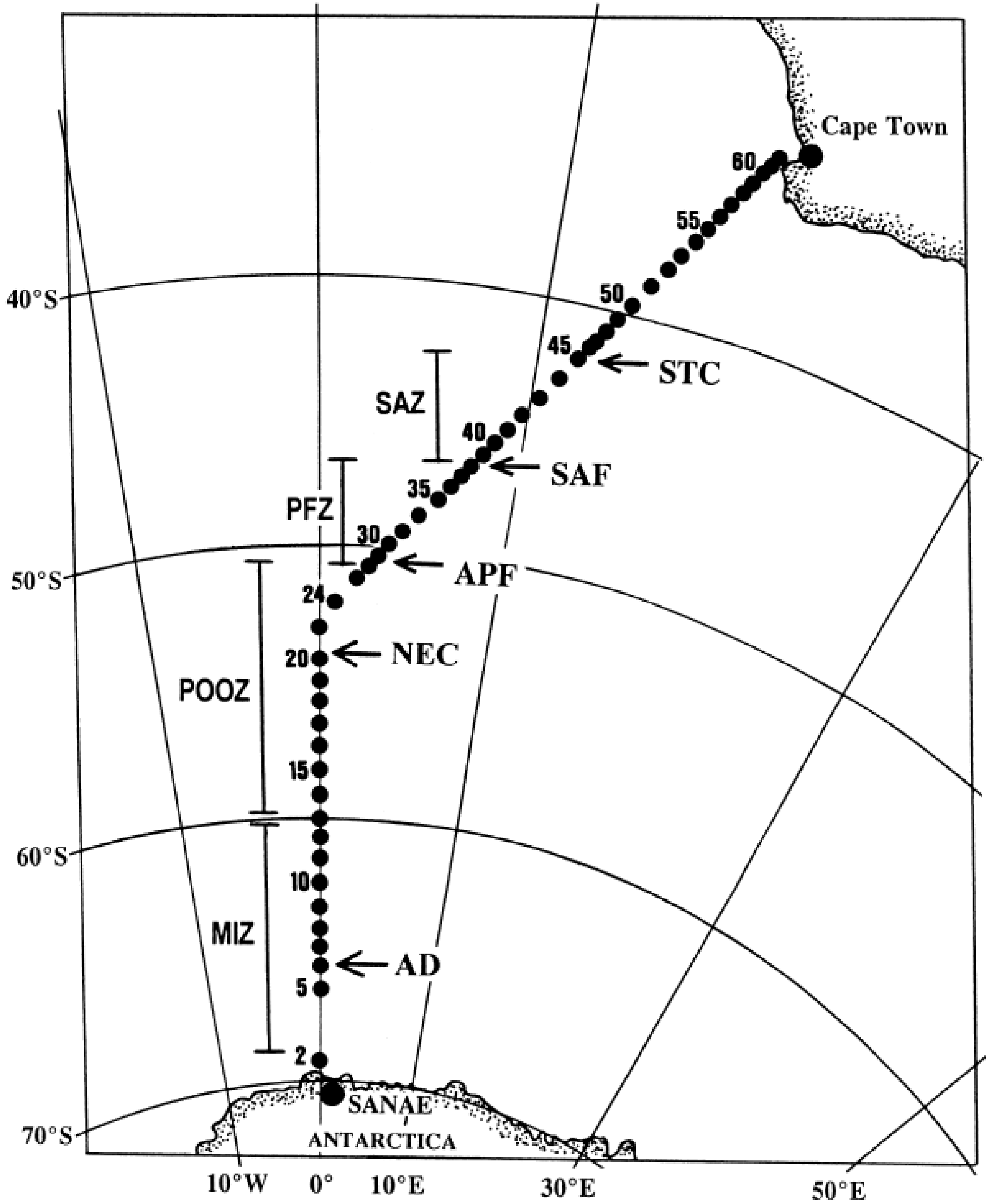

Figure 1: Cruise track of the SAAMES II voyage between South Africa and Antarctica, including the station positions from Pakhomov et al. (2000), STC: Subtropical Convergeance, SAF: Subantarctic Front, APF: Antarctic

Polar Front, NEC: northern expansion of the zero isotherm, AD: Antarctic Divergence, SAZ: Subantarctic Zone, PFZ: Polar Frontal Zone, POOZ: Permanently Open Ocean Zone, MIZ: Marginal Ice Zone.

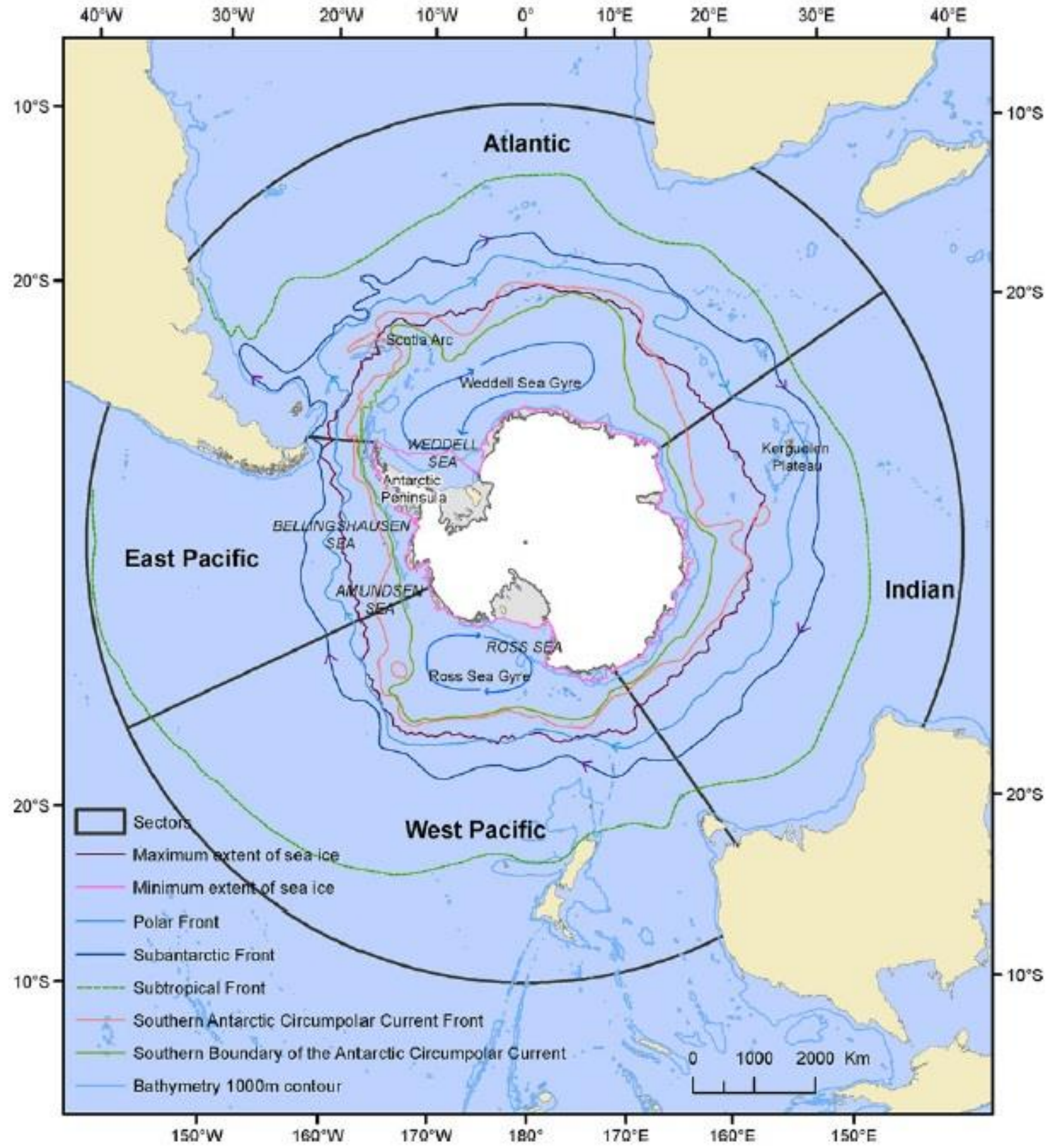

Figure 2: The four major sectors of the Southern Ocean and its physical features which differentiates the ecosystems. These features are the extend of the sea ice, the Subtropical Converceance (STC), the Subantarctic Front (SAF), the Antarctic Polar Front (APF), the Southern Boundary of the Antarctic Circumpolar Current, and the 1000 m depth contour (Constable et al. (2014).

1982). North of the MIZ lies the Permanently Open Ocean Zone (POOZ) which extends to 50 °S (Arrigo et al. 1999). This zone covers a large area of 23.8 x 10^6 km^2 and remains permanently open and ice-free throughout the year (Arrigo et al. 1999).

The PFZ extends from approximately 52.5°S to 48.5°S and is associated with the APF and the SAF (Tremblay et al. 2002). Pollard et al. (2002) and Tremblay et al. (2002) have described the PFZ as two separate zones; the Northern Polar Frontal Zone (NPFZ) and the Southern Polar Frontal Zone (SPFZ). Within the SPFZ lies the APF, which marks the northern boundary of the Antarctic zone (Lutjeharms 1985). The northern limit of the APF is characterized by a temperature limit of 2˚C at 200 m depth (Lutjeharms 1985; Ansorge et al. 2005). In this area the Antarctic surface water sinks below the Sub-Antarctic water and surface temperature exhibits a sharp change associated with the strongest mean west wind stress and the greatest northward Ekman drift (Deacon 1982; Lutjeharms & Valentine 1984). The mixed layer depth here undergoes seasonal variation, deepening from between 50 m to 150 m during summer to 250 m deep during winter (Ansorge et al. 2005). Ansorge et al. (2005) described the subsurface expression of the APF to be situated at 50°22’S with temperatures ranging from -1.8°C to 6°C and salinity from 33.4 to 34.2, while the surface expression positioned the APF between 50°14’S and 52°51’S. The surface expression has temperatures ranging between 1.46°C to 4.7°C and salinities between 33.796 – 33.894 (Ansorge et al. 2005). This coincides with observations from Luthjeharms & Valentine (1984), who described its surface temperature regime to range between 2°C and 6°C.

The SAF represents the northern boundary of the PFZ and is positioned at 46°23’S (Lutjeharms & Valentine 1984), spreading around 2.5° of latitude north and south (Lutjeharms 1985). This front is located at the most vertically orientated isotherm which is essentially a vertical line with a subsurface temperature gradient between 3˚C and 5˚C, while at the surface a gradient between 4˚C and 8˚C is noted (Lutjeharms 1985; Ansorge et al. 2005). Its mixed layer depth extends from the surface to ~50 m deep (Le Moigne et al. 2013). The SAZ extends from the SAF to the STC and is characterized by a slightly negative salinity gradient, ranging from depths of a 100 m to more than 400 m (Gordon et al. 1977). It also acts as a boundary, separating the colder, nutrient-rich Southern Ocean waters from the warmer oligotrophic Subtropical Zone Waters (Bowie et al. 2011).

The Subtropical Convergence (STC) marks the northern border of the separation between the above-mentioned water masses (Ansorge et al. 2005; Bowie et al. 2011). There is a considerable latitudinal variation in the position of the front south of South Africa and its average position is at around 41˚40'S (Lutjeharms 1985; Ansorge et al. 2005) with an average temperature of 14.2˚C (SE ±1.7˚C) (Lutjeharms & Valentine 1984; Lutjeharms 1985; Ansorge et al. 2005) and salinities ranging from 35.17 to 34.63 across the surface of the front (Lutjeharms & Ansorge 2001).It marks the boundary between the Southern Ocean and the Atlantic, Indian and Pacific Oceans (de Blij 1978), with a mixed layer depth up to 50 m deep (Le Moigne et al. 2013). The STC experiences high variability in currents and meridional heat transport due to the warm-core eddies that occasionally cross this zone generated by the Agulhas Return Current (Biastoch & Krauss 1999; Ansorge et al. 2005).

The Agulhas Return Current (ARC) lies between 40˚40'S and 39˚20'S (Lutjeharms & Ansorge 2001) and extends to around 15˚E (Lutjeharms & Ballegooyen 1988; Biastoch & Krauss 1999). The Agulhas Current retroflects into the Indian Ocean at 15 ˚E, and within this region warm core saline rings are formed and shed westward (Gordon 1985; Biastoch & Krauss 1999) into the eastern South Atlantic Ocean (Olson & Evans 1986). Approximately 20% of the Agulhas Current is thus injected into the South Atlantic (Gordon 1985). Each year, four to six of these rings each varying in size (up to 320 km in diameter) (Lutjeharms 1981) and temperature (up to more than 21°C) (Lutjeharms 1988) can leave the retroflection at around and travel to around 15˚W and 30˚S (Biastoch & Krauss 1999). These eddies have a significant effect on the overall kinetic energy balance of the South Atlantic Ocean (Lutjeharms & Ballegooyen 1988).

The Southern Ocean plays a major role in the uptake of carbon dioxide (Caldeira & Duffy 2000; Le Moigne et al. 2013). Water masses, such as those of the Antarctic Bottom Water (AABW) contribute to the uptake and transport of anthropogenic carbon dioxide (Caldeira & Duffy 2000; Le Moigne et al. 2013). Nutrients are transported within the thermocline of the Antarctic Intermediate Water (AAIW) and Subantarctic Mode Water (SAMW), which by means of vertical mixing and advection, help to sustain primary production at low latitudes (Le Moigne et al. 2013). The Southern Ocean is considered as a high nutrient, low chlorophyll (HNLC) region due to iron deficiency resulting in low phytoplankton biomass distributions across the region (Laubscher et al. 1993; Bathmann 1998; Pollard et al. 2002). The absence of significant land masses, weak resuspension of sediments in the coastal and off-shore areas as well as the paucity of iron-rich dust explain the lack of iron in the region (Martin 1990; Martin et al. 1990a; Martin et al. 1990b; Laubscher et al. 1993).

Elevated productivity is generally recorded at the fronts can be attributed to accumulations of phytoplankton through the convergence/divergence of different waters masses (Olson and Backus 1985; Heywood and Priddle 1987; Franks 1992; Laubscher 1993). Laubscher et al. (1993) and Le Moigne et al (2013) described the biochemical features of the Atlantic sector of the Southern Ocean. Chl-*a* concentrations appear not to exceed 0.5 mg m^{-3} within the surface waters across the Southern Ocean (Le Moigne et al. 2013). The STC is an oligotrophic region, which is associated with low concentrations of nutrients (ammonium, silicate, nitrate and phosphate) (Le

Moigne et al. 2013), where max Chl-*a* reach 3.12 mg m^{-3} and primary production 2.93 mg C m^{-3} ·h^{-1} (Laubscher et al 1993). During the austral summer (1990–1991), Chl-*a* concentrations in the SAF are ~ 2.74 mg m^{-3} and its primary productivity in the northern and southern edges are the highest (0.92 mg C m^{-3}· h^{-1} and 0.81 mg C m^{-3} · h^{-1} ,respectively) (Laubscher et al 1993). Highest surface Chl-*a* and primary productivity was reported in the APF (3.5 mg m^{-3} and 2.78 mg C m^{-3} ·h^{-1}) respectively at its southern edge (Laubscher et al 1993). Chl-*a* concentrations in the POOZ (0.1 – 0.2 mg m^{-3}) are lower than that of the APF but then increases to 3 mg m^{-3} towards the Weddell Sea (Le Moigne et al. 2013).

1.2 Southern Ocean Zooplankton

Zooplankton community structure, zooplankton grazing, and the predation impact of carnivorous and gelatinous zooplankton have been investigated in the Atlantic Sector of the Southern Ocean (Pakhomov & McQuaid 1996; Perissinoto et al. 1997; Pakhomov et al. 1999; Pakhomov et al. 2000; Froneman et al. 2000; Pakhomov & Froneman 2004a; Pakhomov & Froneman 2004b). Mesozooplankton (> 300 μm) abundance and biomass vary remarkably across the Atlantic sector of the Southern Ocean, ranging from 2.1 ind m^{-3} to 211.5 ind m^{-3} and 1.2 mg dry weight m^{-3} to 91.5 mg dry weight m^{-3} respectively; as described by Pakhomov et al. (2000). High mesozooplankton abundances and biomass were found in the MIZ, POOZ, APF, and the northern region of the STC (Pakhomov et al. 2000; Pakhomov & Froneman 2004a).

Copepods, ostracods and pteropods dominate the standing stock of zooplankton within the Southern Ocean (Foxton 1956; Pakhomov et al. 2000; Pakhomov & Froneman 2004a), where between the region of the APF to the MIZ copepods alone account for 68 – 97% of the zooplankton (Pakhomov & Froneman 2004a). Carnivorous zooplankton biomass was small in proportion to the total zooplankton biomass (between 10% and 30 %) and had the highest densities in the MIZ (11.2

g DW 1000m^{-3}) and between the APF and STC (6.5 g DW 1000 m^{-3}) (Pakhomov et al. 1999). The STC and POOZ were characterized by the lowest densities of carnivorous zooplankton (<1 g dry weight 1000 m^{-3}) (Pakhomov et al. 1999). On average, only 10% to 30% of the zooplankton stock consisted of carnivorous zooplankton, but around the APF and STC carnivores did not exceed 6% (Pakhomov et al. 1999). However, in the SAZ carnivorous zooplankton dominated the total biomass making up between 42% to 96% of the total biomass within the area (Pakhomov et al. 1999).

Within the Southern Ocean, most species have a circumpolar distribution and total biomass appears to be mostly similar between the different sectors (Foxton 1956; Atkinson et al. 2012). Zooplankton abundance, biomass and diversity tends to increase from high latitudes towards the APF, which often has the highest abundances and biomasses (Foxton 1956; Rudjakov 1996; Fransz & Gonzalez 1997; Atkinson & Sinclair 2000; Pakhomov and McQuaid 1966; Pakhomov et al. 2000; Woodd-Walker et al. 2002; Pollard et al. 2002; Atkinson et al. 2012).

It is known that within the Atlantic and Indian sectors of the Southern Ocean the STC, SAF, APF and the AD acts as boundaries separating distinct zooplankton communities (Tarling et al. 1995; Pakhomov & McQuaid 1996; Errhif et al. 1997; Gibbons 1997; Pakhomov et al. 1999; Pakhomov et al. 2000; Atkinson & Sinclair 2000; Hunt & Hosie 2005). Pakhomov et al. (2000) described four macroscale zooplankton assemblages within the Atlantic sector. These were all separated by the major frontal systems; the APF, the SAF and the STC (Pakhomov et al. 2000). The zooplankton community south of the APF were 66% similar, of which *Calanus propinquus*, *Calanoides acutus, Rhincalanus gigas, Metridia gerlachei* and *Oithona* spp., contributed to more than 65% of the similarity within this group (Pakhomov et al. 2000). Within the PFZ three taxa namely; *Calanus simillimus, R. gigas* and *Euchaeta* spp., accounted for more than 60% similarity amongst the stations in the group (Pakhomov et al. 2000). The group within the SAZ had a lower similarity of 57%, while *Sagitta gazellae* and *Eukrohnia hamata* contributed to more than half of the average similarity (Pakhomov et al. 2000). The stations in the South Atlantic Ocean had the lowest similarity (54%), within which *Pleuromamma abdominalis, Salpa fusiformis, Pyrosoma* sp., *Calanus tonsus, C. australis* and ostracods accounted for more than 70% of the similarity in the group (Pakhomov et al. 2000).

Although Pakhomov et al. (2000) described four (macroscale) mesozooplankton assemblages within the Atlantic sector of the Southern Ocean, on a finer resolution they described seven significantly different assemblages (Table 1). The different assemblages mostly coincided with the physical zones identified by the oceanography (Table 1) (Pakhomov et al. 2000). These groups are: the MIZ, the northern proximity of the MIZ, the southern proximity of the APF, the PFZ, the SAZ, the STC, and north of the STC (nSTC; Table 1) (Pakhomov et al. 2000).

The SAF may act as a major barrier for zooplankton communities (Pakhomov et al. 2000). South of the SAF, communities were dominated by copepods such as *Calanus propinquus, C. simillimus, Rhincalanus gigas, C. acutus*, and *Metridia gerlachei* (Table 1) (Pakhomov et al. 2000). The two groups within the MIZ and one within the POOZ had significantly lower densities than that within the APF although the three groups did not have any significant difference in densities between them (Pakhomov et al. 2000). Euphausiids were less prevalent along the transect but *Euphausia superba* and *Thysanoessa macrura* accounted for up to 80% of the total zooplankton biomass in the region of the POOZ (Pakhomov et al. 2000). The APF however, acted as the major barrier for copepod species, while *C. propinquus* was collected south of the APF and *C. simillimus* was collected north of the front (Pakhomov et al. 2000). In addition, other taxa such as *E. superba* and *T. macrura* were in general collected south of the APF, but were replaced by

Table 1: The physical zones and different mesozooplankton assemblages (including average abundances and major contributing species) within the Atlantic sector of the Southern Ocean during January to February 1993. Table modified from Pakhomov et al. (2000).

Physical Zones	**Mesozooplankton Assemblages**	**Average abundances ± SD ind. 1000 m^{-3}**	**Major Contributors**
Marginal Ice Zone (MIZ)	MIZ (Group 1)	32200 ± 33200	*Calanus propinquus*, *Metridia gerlachei*, *Rhincalanus gigas*, *Tomopteris* spp., *Oncaea* spp., Ostracoda, Chaetognatha, *Euchaeta* spp.
Permanently Open Ocean Zone (POOZ)	Northern Proximity of the MIZ (Group 2)	45000 ± 22000	*Calanus propinquus*, *Tomopteris* spp., *Calanoides acutus*, *Metridia gerlachei*, *Euchaeta* spp., *Rhincalanus gigas,* Siphonophora, Ostracoda, *Eukrohnia hamata*, Chaetognatha
	Southern Proximity of the APF (Group 3)	14600 ± 10200	Chetognatha, *Metridia gerlachei*, *Euchaeta* spp., *Oithona* spp., *Rhincalanus gigas*, Ostracoda, *Calanoides acutus*, *Calanus propinquus*, *Tomopteris* spp., *Calanus simillimus*, *Euphausia superba*
Antarctic Polar Front (APF)			

(Continued on next page)

Table 1 (continued)

Physical Zones	Mesozooplankton Assemblages	Average Abundances ± SD ind. 1000 m^{-3}	Major Contributors
Polar Frontal Zone (PFZ) **Subantarctic Front (SAF)**	PFZ (Group 4)	84200 ± 21900	*Calanus simillimus, Rhincalanus gigas*, Chaetognatha, *Euchaeta* spp., Ostracoda, Euphausiid furcilia, *Lucicutia* spp., *Eukrohnia hamata, Metridia* spp., *Scolecithryx* spp.
Subantarctic Zone (SAZ)	SAZ (Group 5)	13400 ± 17400	*Eukrohnia hamata, Sagitta* sp., *Euchaeta* spp., Ostracoda, Chaetognatha, *Calanus simillimus, Nematoscelis megalops, Scolecithryx* spp., *Aetideus* sp., *Lucicutia* spp.
Subtropical Convergence (STC)	STC (Group 6)	69200 ± 80100	*Pleuromamma abdominalis, Euchaeta* sp., *Salpa fusiformis*, Ostracoda, Euphausiid furcilia, Siphonophora, *Euphausia recurva, Aetideus* spp., *Lucicutia* spp., *Metridia lucens*
North of the STC (nSTC)	nSTC (Group 7)	19300 ± 11900	*Pyrosoma* sp., *Pleuromamma* spp., *Calanus australis, Calanus tonsus*, Ostracoda, *Euchaeta* spp., Chaetognatha, Euphausiid furcilia, Siphonophora, *Scolecithryx* spp.

Euphausia triacantha, *Euphausia frigida* and *T. macrura* north of the front (Pakhomov et al. 2000). Within the PFZ, *C. simillimus* accounted for more than 80% of the total mesozooplankton abundance and biomass, which alone contributed to 25% of the dissimilarity between the communities at the zone and to those to the south and north of it (Pakhomov et al. 2000).

The SAZ consisted of low densities of mesozooplankton, which were numerically dominated by carnivorous taxa, while a separate group at the STC had higher densities and only a few species of copepods and tunicates dominating the community (Table 1) (Pakhomov et al. 2000). The community within the South Atlantic stations mostly consisted of large pyrosomes and subtropical copepods (*Pleuromamma* spp., *C. australis* and *C. tonsus*) and together with chaetognaths these taxa contributed to more than 60% of the average dissimilarity between the communities separated by the STC (Table 1) (Pakhomov et al. 2000).

The communities of carnivorous zooplankton along the Atlantic sector of the Southern Ocean comprised mainly euphausiids, amphipods, decapods, siphonophores, hydromedusae, ctenophores, chaetognaths and fish (Pakhomov et al. 1999). Chaetognaths and euphausiids made the highest contribution to carnivore biomass along a transect between South Africa to Antarctica (Pakhomov et al. 1999). Pakhomov et al. (1999) indicated the presence of three significantly different assemblages of carnivorous zooplankton within these waters (Table 2). Like that of mesozooplankton, carnivorous communities were also separated by major frontal systems (Pakhomov et al. 1999). These groups were: the APF and south of it (Group 1), the PFZ (Group 2), and north of the SAF (Group 3). Group 3 was divided into two non-significantly different subgroups; the SAZ (Group 3a) and north of the STC (Group 3b; Table 2) (Pakhomov et al. 1999). Carnivores were more prevalent within the PFZ and least within the stations north of the STC (Pakhomov et al. 1999). Four species of euphausiids, *Thysanoessa macrura, T. vicina, T. gregaria*

Table 2: The physical zones and different carnivorous zooplankton assemblages (including average abundances and major contributing species) within the Atlantic sector of the Southern Ocean during January to February 1993. Modified from Pakhomov et al. (1999).

Physical Zones	Carnivorous Zooplankton	Average Abundances ± SD ind. 1000 m^{-3}	Major Contributors
MIZ			
POOZ			
	South of the APF (Group 1)	4452 ± 4661	*Thysanoessa macrura, Electrona antarctica, Notolepsis coatsi, Vibilia antarctica, Cyllopus magellanicus*
APF			
PFZ	PFZ (Group 2)	10949 ± 5745	*Thysanoessa vicina, Themisto gaudichaudi, Primno macropa, Melophysa melo*
SAF			
SAZ	SAZ (Group 3a)	4394 ± 2289	*Thysanoessa gregaria, Vinciguera attenuata, Bentosema suborbitale, Hymenodora glacialis*
STC			
nSTC	nSTC (Group 3b)	2240 ± 1664	*Nematoscelis megalops, Thysanoessa gregaria, Themisto gaudichaudi, Pasiphaea grandicula*

and *Nematoscelis megalo*ps accounted for most of the average similarity between the different groups (Table 2). The highest dissimilarity in carnivore assemblages were between the groups separated by the SAF (> 95%), while the lowest dissimilarity was between the Groups 3a and 3b (75%) separated by the STC (Table 2) (Pakhomov et al. 1999). The overall species diversity of carnivorous zooplankton within this sector was very low, and usually only one or two species dominated each sample by number and biomass (Pakhomov et al. 1999).

The PFZ is characterized by Antarctic and subantarctic species, with some subtropical taxa, while the Antarctic community persists south of the APF (Froneman et al. 2000). Zooplankton communities are, in general, similar in the STC to those found north of the STC, while the SAZ typically consists of species found in the PFZ as well (Pakhomov & McQuaid 1996; Froneman et al. 2000). The APF and SAF, including the STC, act as two circum-global zoogeographical boundaries (Deacon 1982; Pakhomov & McQuaid 1996; Pakhomov et al. 1999; Pakhomov et al. 2000). The SAF and STC (SAZ) separate the subantarctic and subtropical communities, while the APF separates the Antarctic and subantarctic communities (Deacon 1982; Pakhomov et al. 1999).

Similar boundaries are observed within the Indian sector of the Southern Ocean (Hunt & Hosie 2005). Hunt & Hosie (2005) investigated the zonal structure of zooplankton south of Australia and described five distinct zooplankton zones south of the STC, mostly corresponding with the different oceanic zones. These zones were: the AD to the shelf; the MIZ; the MIZ to the APF (POOZ); the PFZ; and the SAZ (Hunt and Hosie 2005). Although their study did not include the STC, the SAZ which ranges from the SAF to the STC acted as a strong biogeographic boundary and like that discussed by Pakhomov et al. (2000), the PFZ acted as a weak boundary (Hunt & Hosie 2005). Although there may be distinct assemblages across the region, most taxa generally have broad distributions, with most occurring in adjacent assemblages, and very few are restricted to a single area (Hunt & Hosie 2005). Individual species are not necessarily dependent on one specific region’s physical structure, mostly having a core region, but can be widely distributed far beyond their reproductive range (Angel 1988; Hunt & Hosie 2005).

1.3 Hydrozoa: Hydromedusae and Siphonophorae

There have been relatively few studies on the gelatinous zooplankton in the Southern Ocean, specifically hydrozoans. The class Hydrozoa is a very diverse group of ~ 3 720 species (WoRMS 2019) divided into the subclasses Hydroidolina (orders: Anthoathecata, Leptothecata and Siphonophoreae) and Trachylinae (orders: Actinulida, Limnomedusae, Narcomedusae and Trachymedusae).

Hydrozoans display either tetramerous, polymerous or biradial symmetry, and have an ecto- and endodermis separated by mesoglea. They possess a simple gastrovascular cavity, which lacks a pharynx/actinopharynx. Each medusae has a velum (except *Obelia*), which is essentially a membrane that extends inwards from the umbrellar margin and partly closes its opening. Hydrozoans are generally carnivorous, using nematocysts to capture their prey. When in high abundance, they are regarded as amongst the most important benthic and planktonic predators, being able to deplete and alter the local zooplankton community structure (Rees & Gershwin 2000). They feed on phytoplankton, zooplankton, protozoans, bacteria, dissolved organic matter and some have symbiotic relationships with intracellular algae (Rees & Gershwin 2000; Bouillon et al. 2006). Some also feed on fish larvae and juvenile fish (Rees & Gershwin 2000).

Hydrozoans are either holoplanktonic or meroplanktonic, meaning that individuals either complete their entire life cycle as free-swimming medusae, or have both a free-swimming sexual medusa stage and an asexual fixed polyp stage (Figure 3) (Boero et al. 1992; Boero & Bouillon

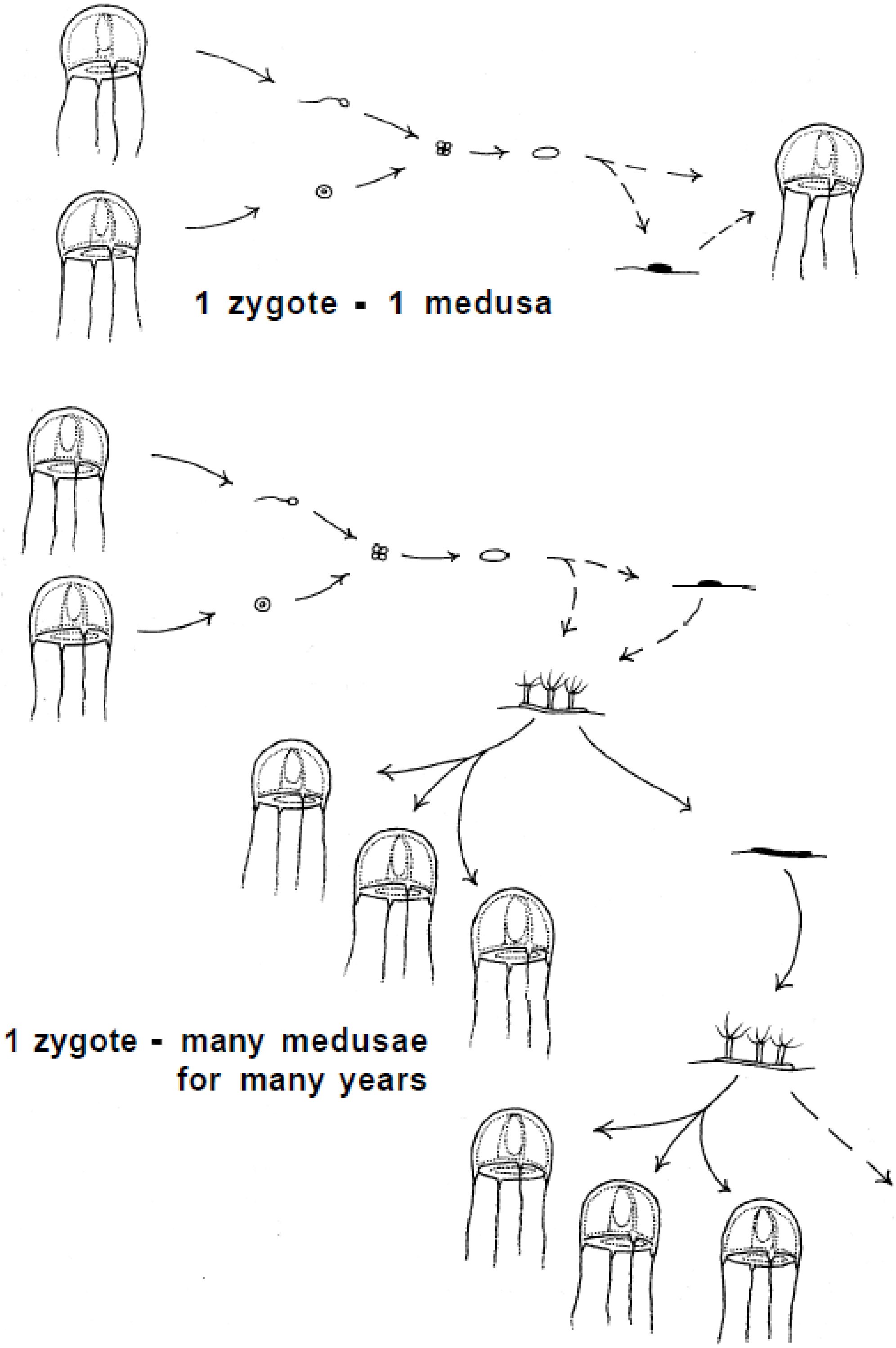

Figure 3: The life cycle of hydromedusae without (above) and with a polyp stage (below): from Boero et al. (1992).

1993). Some Narcomedusae and all Trachymedusae are holoplanktonic (Boero & Bouillon 1993). The fertilized eggs of the above-mentioned individuals develop into the planula and then directly into a medusae stage (Figure 3) (Boero et al. 1992). Most hydromedusae are negatively buoyant and must swim to maintain their position in the water column (Mills 1981). Hydromedusae have two different modes of swimming; “rowing” and “jetting” in which the modes of feeding differ for each (Colin et al. 2003). Rowing hydromedusae use the flow of water created while swimming to draw prey towards their tentacles, while jetting hydromedusae extend their tentacles while drifting to feed (Colin et al. 2003). Thus, rowing medusae spend the majority of their time swimming, while jetting medusae spend the majority of their time drifting (Colin et al. 2003).

Siphonophores are complex polymorphic hydrozoans, comprised of highly specialized zooids, each with a specific role contributing towards a functional individual (Totton 1965). Two clades within the monophyletic Siphonophorae are recognized: Cystonecta (5 species) and Codonophora. Cystonecta have a pneumatophore which can be rather large (*Physalia physalis*) allowing this particular species to float. Codonophora is divided into Physonectae (73 species) and Calycophorae (110 species) (Totton 1965; Pugh 1984; Mapstone 2015; WORMS). Physonectae have a small pneumatophore and a long stem divided into two regions (Totton 1965; Mapstone 2015). Firstly, the nectosome (immediately below the pneumatophore), which bears a number of asexual nectophores, or swimming bells, for locomotion (Totton 1965, Mackie 1987). Secondly, the siphosome, which bears a number of iterative units termed cormidia (Totton 1965; Mapstone 2015). Each cormidium comprises the main stem (of the siphosome), with several side branches bearing bracts, gastrozooids with tentacles, palpons (in most physonect species) and gonodendra, used for buoyancy, protection, feeding (including capturing prey) and reproduction Totton 1965; Mapstone 2015.

Siphonophores are also holoplanktonic (except Rhodaliidae), with two different forms, the sexual eudoxid and asexual polygastric organisms (Totton 1965; Pugh 1999). Eudoxids are

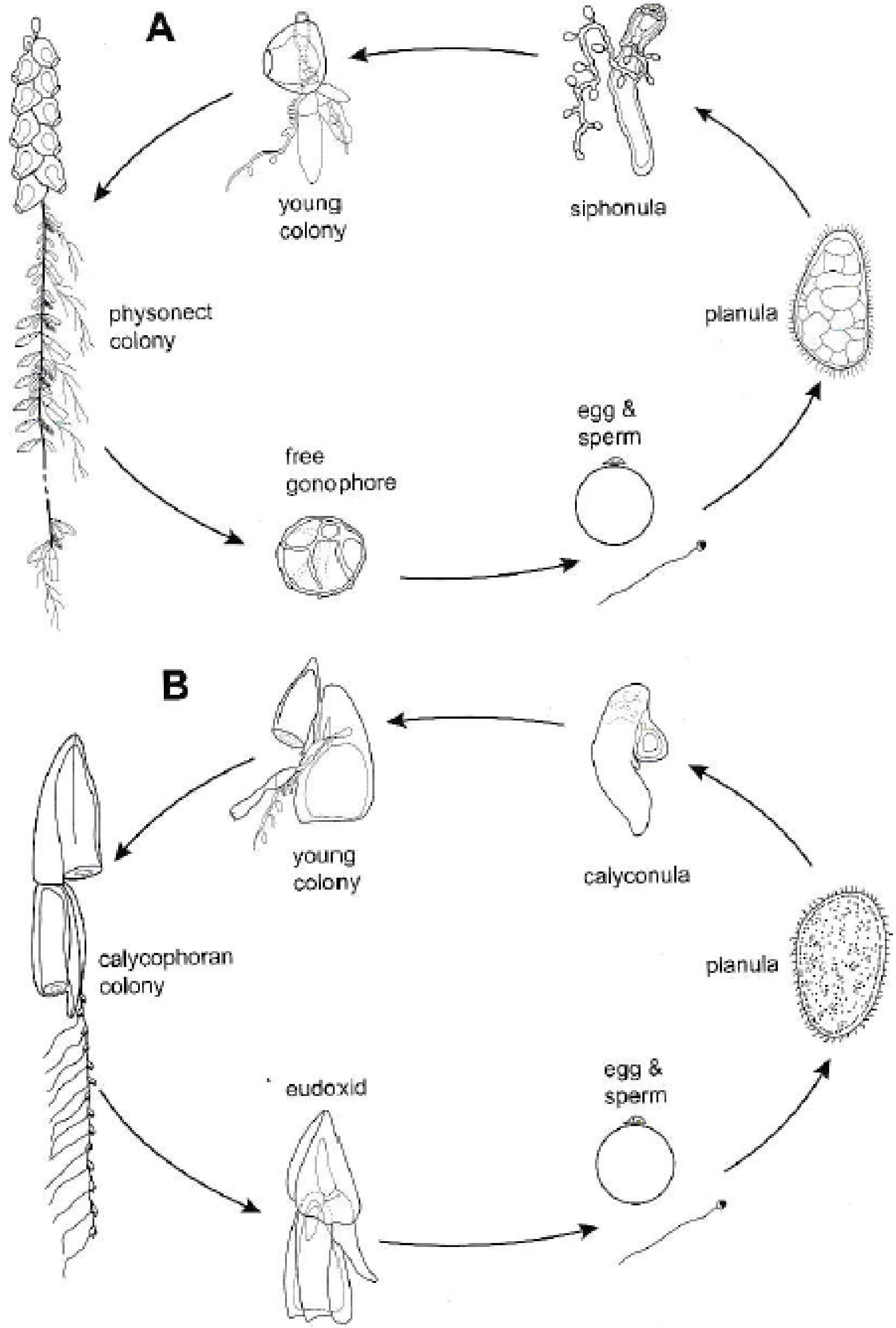

Figure 4: Life cycle of: A: a typical physonect (*Nanomia bijuga*); B: a typical calycophoran (*Lensia conoidia*): from Mapstone (2009).

composed of one male or female gonophore topped by a bract (Totton 1965). They remain on the polygastric form (Physonectae and Cystonectae) or are shed from the distal end of the cormidia of the polygastric organism and swim freely while dispersing gametes (most calycophorans, except Hippopodiidae, Prayidae and Sulculeolariinae) (Figure 4) (Mackie et al. 1987; Mapstone 2009).

Mackie et al. (1987) and Mapstone (2009) provide in-depth descriptions of siphonophore life cycles with regards to various taxa. In short, gametes are released directly into the water column where external fertilization takes place (Mapstone 2009). After fertilization (Figure 4) the divided cells develop into a planula, and within 24 hours develops into either a siphonula (physonects) or a calyconula (calycophorans) (Mackie et al. 1987; Mapstone 2009). The siphonula and calyconula are the larval stages of the colonial individual. During the early development in the siphonula either a larval bract or pneumatophore forms to provide buoyancy to the individual (Mackie et al. 1987; Mapstone 2009). In species such as *Nanomia bijuga* the pneumatophore develops first, followed by the tentacle of the first gastrozooid and a larval bract, and later the first nectophore (Mapstone 2009). In the calyconula, a bud for a larval nectophore is the first structure to form (Mackie et al. 1987; Mapstone 2009) while another bud forms to become the first gastrozooid (Mapstone 2009). This type of budding occurs consistently throughout the lifetime of codonophorans and is critical for colony growth (Mapstone 2009). There are typically two zones where budding takes place, where these buds in the one develops into nectophores and the other into siphosomal cormidia (Mapstone 2009). When the colony reaches maturity, these zones will become separated through the development of a nectosomal stem, as in long-stemmed physonects, but not in calycophorans (Mapstone 2009).

Since siphonophores are holoplanktonic they have a greater spatial distribution than other metagenic hydrozoans, which are often limited to the shelves around land masses (Mapstone 2015). Most species of siphonophores have a cosmopolitan distribution, mostly occurring in the open ocean, at various depths from the surface to at least 4 500 m and form colonies that may range between 1 mm to tens of meters in length, with some specimens exceeding 40 m (Dunn et al 2005; Robison 1995; Pugh 1999). Their mobility is affected by the size of the colony which therefore affects its feeding strategy (Silguero & Robison 2000). Siphonophores are often abundant, but they are also very fragile (Dunn et al. 2005; Dunn & Wagner 2006) making their collection difficult.

Siphonophores specifically, have a very specialized mode of feeding. They feed by means of nematocyst batteries (or pads in cystonects) on side branches from each tentacle of each cormidium (Totton 1965; Mapstone 2009; Mapstone 2014). These side branches are termed tentilla, and each comprises a pedicel, usually a nematocyst battery, and a terminal filament (Tottoan 1965; Mapstone 2009; Mapstone 2014). They extend their tentilla (on the tentacles) into the water column to form a relatively transparent net and passively wait to ambush their prey (Purcell 1980; Mapstone 2009). Some mimic shoals of smaller copepods, fish, or medusae which are lured towards their tentacles (Mapstone 2015). These stinging cells also possibly deter potential predators (Purcell & Arai 2001). Siphonophores contract their stem and tentacles to swim and then relax them to form a large net to feed (Mapstone 2015). Individuals often use a swirling motion to set the net which increases the effectiveness of capture (Mapstone 2015).

Some species of siphonophore are also known to undergo diel vertical migration (DVM) (Pugh 1977; Pugh 1984: Mackie et al. 1987; Pagès & Gili; 1991; Pagès et al. 1996). Pugh (1977) described that siphonophores either undergo slow or fast vertical migration. Slow vertical migration is when species occur either within or below a specific depth interval (for example 250 m) during the day and migrate above or through that interval during night (Pugh 1977). For example, *Chelophyes appendiculata, Hippopodius hippopus* and *Vogtia glabra* are known to follow this type of DVM (Pugh 1977). Fast vertical migrating species like the eudoxid of *Ceratocymba sagittate* migrate rapidly through the 250 m depth interval at sunrise or sunset (Pugh 1977). Although changes in light intensity is believed to affect the vertical migration of siphonophores (Pugh 1977; Pugh 1984), Pugh (1984) suggested that it is unlikely that siphonophores are able to sense small changes in light intensity. Their migration, however, is possibly a secondary response due to the migration of other zooplankton (Pugh 1977). Temperature could also possibly be a controlling factor but is likely not the case in areas which has very little changes in temperature with depth (Pugh 1984).

Studies on cnidarians with regards to species composition and horizontal and vertical distribution in the Southern Ocean have been conducted within the POOZ (55 °S) to the Weddell Sea Gyre (Pagès et al. 1994; Pagès & Kurbjeweit 1994; Pagès & Schnack-Schiel 1996; Pugh et al. 1997). Pagès et al. (1994) described that many siphonophores and hydromedusae have either an epi- (0 -500 m), meso- (500 – 1000 m) or bathypelagic (1000 – 2000 m) distribution. It is known that the epipelagic layer is generally the top 200 m of the water column but for the purpose of Pagès et al.'s (1994) study the first 500 m were regarded as the epipelagic layer. Pagès et al. (1994) suggested that the segregation of species between the above-mentioned pelagic zones could be due to the narrow range in temperature distributions (-1.77 °C to 1.99 °C) between 0 – 2000 m depths, while the coldest temperatures (<0 °C) were restricted to the top 200 m and the greatest number of species occurred within the 500 – 1000 m depth range (Pagès et al. 1994).

However, siphonophores (collected with a 450 µm mesh size) were most abundant in the epipelagic layer (10.7 ± 4.3 ind. 1000 m), and their abundance decreased with depth (2.6 ± 1.2 ind. 1000 m^{-3} at 500 – 1000 m and 1.6 ± 0.7 ind. 1000 m^{-3} at 1000 – 2000 m) (Pagès et al. 1994). The most abundant calycophoran species were also found in the epipelagic layer, being *Dimophyes arctica, Heteropyramis crystallina, Diphyes antarctica, Muggiaea bargmannae* and *Rosacea plicata* (Pagès et al. 1994). *Dimophyes arctica*, which has a widespread distribution, was found to be most abundant (6.2 ind. 1000 m^{-3}) from the POOZ to the eastern Weddell Gyre (Pagès et al. 1994). While species such as *Diphyes antarctica*, *Crystallophyes amygdalina* and *M. bargmannae* were mainly confined to the Weddell Sea (Pagès et al. 1994; Pagès & Kurbjeweit 1994).

1.4 Aims and Objectives

Despite multiple efforts to describe the zooplankton communities within the Southern Ocean (Foxton 1956; Deacon 1982; Pakhomov & McQuaid 1996; Rudjakov 1996; Errhif et al. 1997; Fransz & Gonzalez 1997; Perissinoto et al. 1997; Pakhomov et al. 1999; Atkinson & Sinclair 2000; Pakhomov et al. 2000; Froneman et al. 2000; Pollard et al. 2002; Pakhomov & Froneman 2004a; Pakhomov & Froneman 2004b; Hunt & Hosie 2005; Atkinson et al. 2012; etc.), little attention has been given to assemblages of siphonophores and hydromedusae, especially within the Atlantic sector. This study aims to describe the species composition, abundance and distribution of pelagic cnidarians, more specifically siphonophores along a transect from South Africa to Antarctica, to compliment work already done on other taxa and to provide descriptions of uncommonly described species. Understanding these cnidarians will provide us with a better insight into their role in the Southern Ocean ecosystem and will increase our understanding of the ecology of this region.

2 MATERIALS AND METHODS

Field Sampling

Samples were collected during the second cruise of the South African Marine Ecosystem Study (SAAMES II) from 17 January to 21 February 1993 onboard the RS *S.A. Agulhas* along the WOCE (World Ocean Circulation Experiment) SR2 line (Figure 1) (Pakhomov et al. 1999; 2000). Samples were collected every 50 nautical miles, except at major frontal areas where samples were collected every 20 nautical miles (Figure 1). All data related to the sampling methods and analysis of the environmental data and zooplankton other than siphonophores and hydromedusae were extracted from Pakhomov et al. (1999; 2000), as the original dataset was not available for re-analysis.

2.1 Environmental variables

Vertical profiles of salinity, temperature and depth were obtained using a Neil Brown MK II probe mounted on a rosette. Chlorophyll-*a* samples were collected at the surface water. A known volume (200 to 1000 ml) of water was filtered through Whatman GF/F filters. Pigments were extracted for 24 h using 8 mL of 90% acetone in polyethylene tubes, and fluorescence measured using a Turner 111 fluorometer (Strickland and Parsons 1968; Conover et al. 1986; Pakhomov et al. 2000). The Mixed Layer Depth (MLD) was determined from temperature:depth plots, as the upper layer of water with uniform temperature. See Pakhomov et al. (2000) for more details.

All relevant environmental data were extracted as accurately as possible from Pakhomov et al. (1999; 2000), using GetData Graph Digitizer software. Owing to gaps in sample coverage (see below), the locations of the various fronts and zones used here were those described by Pakhomov et al. (1999; 2000).

2.2 Zooplankton sampling and analysis

Zooplankton samples were collected using a Bongo net (300 µm mesh size; 0.25 m^2 mouth area). The net was towed obliquely between 300 m and the surface at a speed of between 1.5 to 3 knots with a Universal Underwater Unit fitted to the net. The volume of water filtered through the net was calculated using an electronic flowmeter, while taking into account the mouth area and ranged from 310 to 1315 m^3. Samples were then preserved in 4-6% buffered saline formalin. See Pakhomov et al. (2000) for more details.

Table 3: Latitude and longitude of all 19 samples examined here. The physical zonation, chlorophyll-*a* concentration and mesozooplankton biomass were extracted from Pakhomov et al. (1999, 2000).

Station Number	Latitude (°S)	Longitude (°E)	Zonation	Chl-*a* (mg m^{-3})	Mesozooplankton Biomass (g DW 1000 m^{-3})
5	66˚47'	00°00'	MIZ	0.378	6.56
13	60˚03'	00°00'	MIZ	0.187	22.83
14	59˚12'	00°00'	POOZ	0.142	7.46
16	57˚28'	00°00'	POOZ	0.142	9.03
22	53˚00'	00°00'	POOZ	0.107	25.64
24	52˚10'	00°46'	POOZ	0.118	10.65
26	51˚19'	02°06'	POOZ	0.196	4.13
29	50˚06'	03°09'	PFZ	0.495	51.08
34	48°03'	04°09'	PFZ	0.217	30.36
35	47˚23'	06°06'	PFZ	0.372	25.37
40	44˚48'	08°36'	SAZ	0.383	2.75
41	44˚25'	09°03'	SAZ	0.316	7.38
42	43˚44'	09°51'	SAZ	0.504	6.63
45	41˚40'	11°48'	STC	0.748	7.44
48	40˚49'	12°42'	STC	0.636	7.87
49	40˚24'	13°06'	nSTC	1.136	82.88
53	38˚04'	14°57'	nSTC	0.391	1.79
56	36˚49'	16°09'	nSTC	0.168	8.75
58	36˚00'	17°06'	nSTC	0.090	5.32

2.3 Laboratory Analysis

To complement what has been already published (Pakhomov et al. 1999; 2000), hydrozoans were studied from 19 of the 53 samples collected (Table 3). These 19 samples were the only ones available to me for analysis. All hydrozoans were examined under a Leica S9i dissecting microscope and specimens were identified using appropriate literature (Totton 1965; Pugh 1999; Pages & Gili 1992a; Mapstone 2009). Hydromedusae were identified based on the whole organism, while siphonophores were identified from nectophores (only anterior nectophores of calycophorans) of the polygastric stage (except for Abylidae, within which the eudoxid stages were also identified). Species names were checked against the World Register of Marine Species (WoRMS 2019). Counts of siphonophores were based only on the anterior nectophores of Calycophorae, except for Hippopopidae which may have up to 15 identical nectophores, and Prayidae which carry between two to four nectophores. These last two taxa were simply recorded as present or absent. The abundance of eudoxids was estimated by counting either gonophores or bracts, when identifiable, and the greater of the two counts for any species in a sample was employed. Physonectae were also only regarded as present or absent, as each individual may have more than one nectophore: definitive counts can only be determined with a knowledge of the number of pneumatophores. No species of Cystonectae were collected. When specimens were too damaged for proper identification, counts were noted but excluded from further analysis. Abundances (ind. $1000m^{-3}$) were then estimated using the volume of water sampled by the net.

2.4 Numerical Methods

All statistical analyses were performed using PRIMER 6 & PERMANOVA + and PRIMER 7 & PERMANOVA + (Clarke & Warwick 2001; Clarke & Gorley 2006; Anderson et al. 2008). Environmental data (mesozooplankton biomass, chl-*a*, sea surface temperature (SST), sea surface salinity (SSS) and mixed layer depth (MLD)) were $\log_{10}$ transformed, normalized and a distance matrix was computed between samples based on Euclidean distance. This matrix was visualized using a two-dimensional non-metric multi-dimensional scaling (nMDS) plot with an overlaying CLUSTER analysis to group the different stations at different similarity distances.

Community attributes such as species richness and Shannon Diversity Index were calculated for each sample. The Shannon index was calculated using the following formulae:

$$H = -\sum_{i=1}^{s} p_i \; ln p_i$$

Hydromedusae were very rare and were usually too damaged to be identified beyond order level, and therefore they were excluded from further statistical analysis; as too were rare species of siphonophores (a single specimen occurring in a single sample: *Lensia panikkari*, *Halistemma rubrum* and *Nanomia bijuga*). The densities of the remaining species were root-root transformed, and a Bray-Curtis resemblance matrix was computed between both samples and species. These matrices were visualized using non-metric multi-dimensional scaling (nMDS) plots. The first containing an overlaying CLUSTER analyses indicating the percentage similarity of each group and the second displaying the species data as a vector to visualize how the species were distributed between the different stations.

Another three non-metric multi-dimensional scaling (nMDS) plots with overlaying CLUSTER analyses were computed, which displays the groupings of siphonophore densities at each station into the different *a priori* described zones/assemblages within the Atlantic sector of the Southern Ocean described by Pakhomov et al. (1999: 2000), on one hand the physical zones predicted by the environment and on the other hand the mesozooplankton and carnivorous zooplankton zonation patterns predicted by the distribution of the different mesozooplankton and carnivorous species assemblages respectively (Pakhomov et al. 1999, 2000). ANOSIM analyses were used to determine how similar the *a priori* described mesozooplankton and carnivorous zooplankton zonation were to those of siphonophores between the different physical, mesozooplankton and carnivorous zones described by Pakhomov et al. (1999; 2000).

A Similarity Percentage (SIMPER) analysis was used to determine the average similarity/dissimilarity between the different physical zones using abundance data, and identified which species were responsible for this similarity/dissimilarity.. The SIMPER routine breaks down the average Bray-Curtis similarities between all groups of species within each sample and transforms the data into percentage contribution of each species (Clarke & Gorley 2006).

In order to describe the siphonophore assemblages present within the Atlantic sector of the Southern Ocean, two non-metric multi-dimensional scaling (nMDS) plots were computed using both the Bray-Curtis resemblance matrix of the siphonophore densities between stations and the Euclidean distance matrix of the environment between stations. Both contained an overlaying CLUSTER analysis which identified the different groups of siphonophores present. A SIMPER analysis was used to determine the average similarity/dissimilarity between these assemblages and to highlight the species responsible.

Finally, to determine how the different environmental factors (Chl-*a*, mesozooplankton biomass, MLD, SSS and SST) were responsible for the pattern observed within the siphonophore resemblance matrix, the data were analyzed using a Distance Based Linear Model (DistLM) (Anderson et al. 2008). The DistLM quantitatively measures and tests the variation in siphonophore distribution between stations using one or more environmental predictors. Firstly, marginal tests calculate the proportion of the variance in the siphonophore distribution pattern caused by each environmental predictor, where after this variation is partitioned according to a stepwise multiple regression model. The stepwise procedure starts with a null model and at first adds a variable that improves the selection criterion (Anderson et al. 2008). The procedure will continue in this fashion, but after every step, it attempts to improve the criterion by removing a variable (Anderson et al. 2008). When no more improvements can be made by adding or removing a variable, the procedure stops (Anderson et al. 2008). This DistLM was visualized using a distance-based redundancy analysis (dbRDA) which performs an ordination of the fitted values from the above-mentioned multiple regression model (Anderson et al. 2008). Adjusted R^2 was used to explain the variation in siphonophore distribution as it provides a more useful criterion for model selection than R^2 (Anderson et al. 2008).

3 RESULTS

3.1 Physical Environment

During the SAAMES II voyage temperature and salinity data identified the AD at 66°10’S, the APF at 50°10’S, the SAF at 45°S and the STC at 41°40’S (Pakhomov et al. 2000). The MIZ was located at 60°S and the pack ice at 69°10’S (Pakhomov et al. 2000). In summer (January – February 1993), SST varied greatly across the transect with values ranging from 1.1°C in the south at the AD to 20.3°C just north of the STC (Figure 5). Temperatures gradually increased north of the AD to the position of the SAZ, and then increased rapidly (by ~7 °C) to the STC (Figure 5). The 0 °C isotherm (NEC) extended from the Antarctic mainland to 53°S at depths of more than 300 m close to the mainland, and to between 100 to 200 m further north (Figure 5).

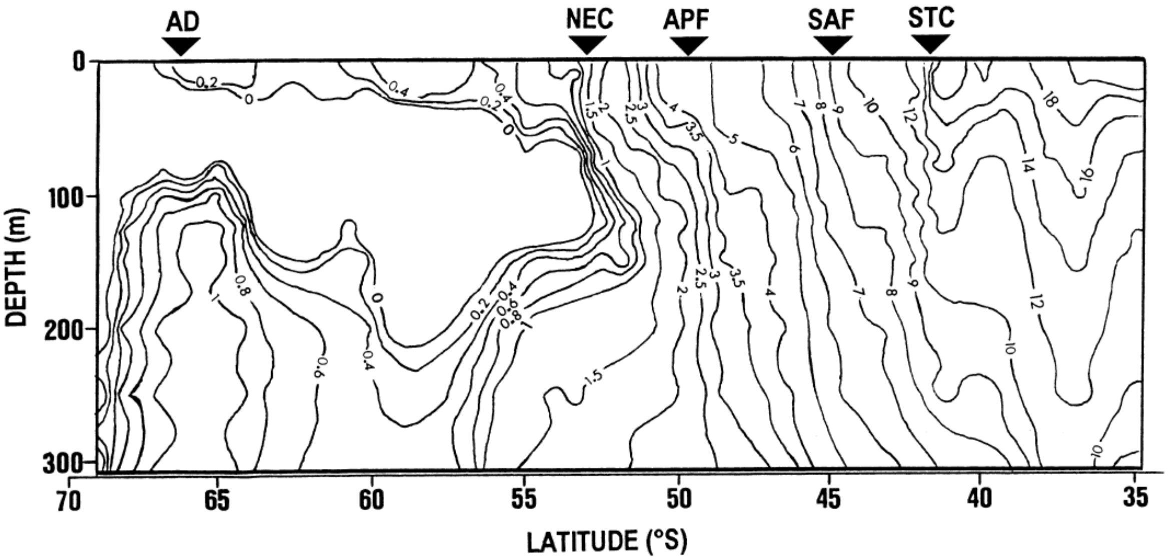

Figure 5: Vertical temperature profile across the SAAMES II transect during the months January to February 1993 from Pakhomov et al. (2000). See Table 1 for physical zone descriptions.

The mixed layer depth (MLD) exceeded 300 m depth in the MIZ and in the southern extent of the POOZ (Figure 6). Further north, the MLD varied between 30 – 50 m towards the northern extent of the SAZ, while the STC and nSTC had the shallowest MLD at 30 m and 10 m, respectively (Figure 6). Sea surface salinity (SSS) in the MIZ, POOZ and PFZ was, on average, ~33.8 and increased gradually to 34.1 in the SAZ and reached 35.6 in the nSTC.

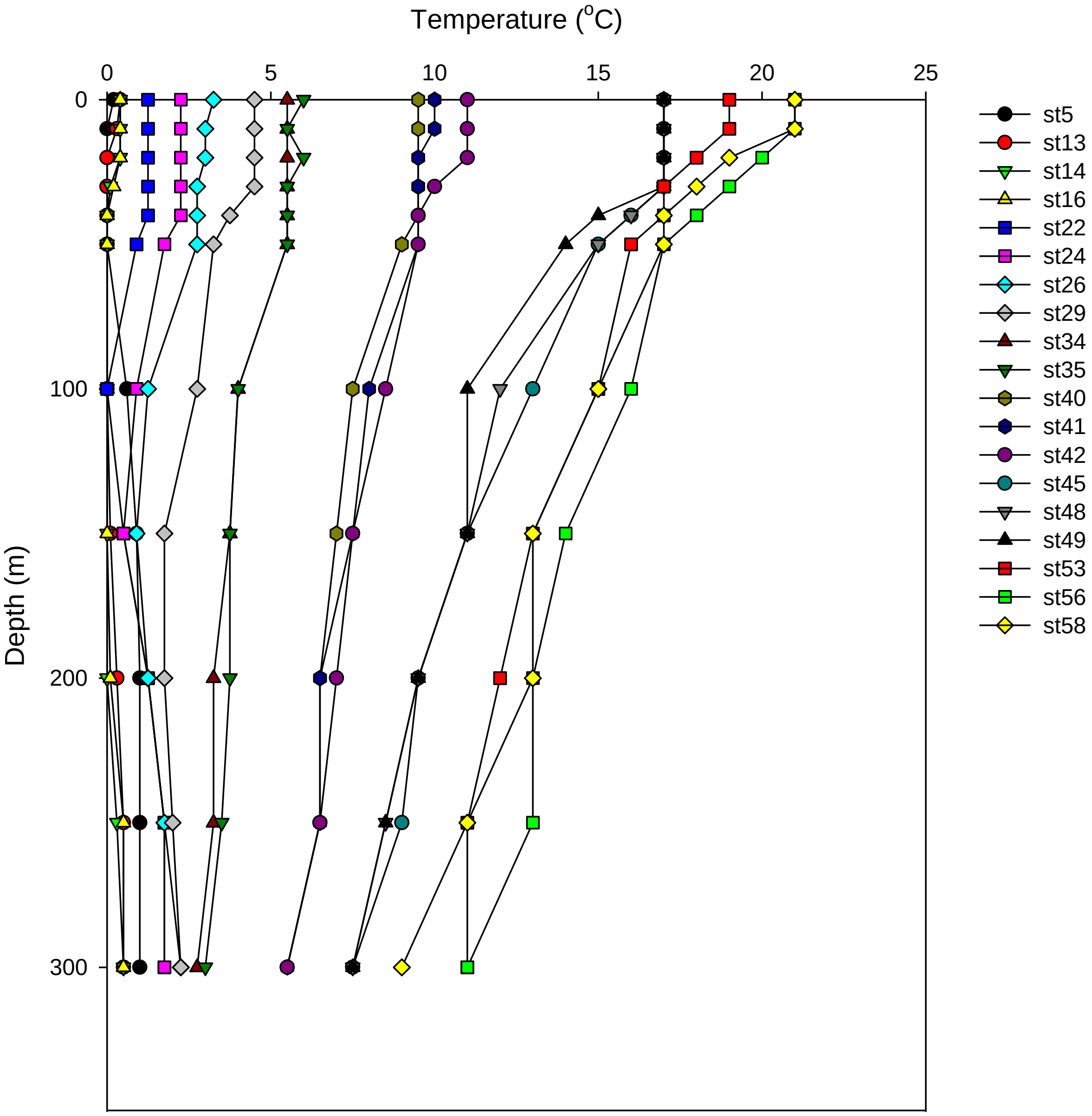

Figure 6: Temperature versus depth profiles of the 19 stations used during this study.

Across the 19 stations, surface chl-*a* values ranged from 0.09 mg m^{-3} to 1.14 mg m^{-3} (Table 3; Figure 7). Surface chl-*a* was 0.38 mg m^{-3} just south of the AD (station 5) and varied between 0.11 and 0.20 mg m^{-3} in the POOZ and towards the south of the APF. Elevated chl-*a* concentrations were observed in the regions of the PFZ and SAZ, ranging from 0.37 to 0.75 mg m^{-3}, with a maximum at 1.14 mg m^{-3} north of the STC (station 49). Concentrations further north of the STC steadily decreased from 0.39 mg m^{-3} at station 53 to 0.09 mg m^{-3} at station 58 (Figure 7).

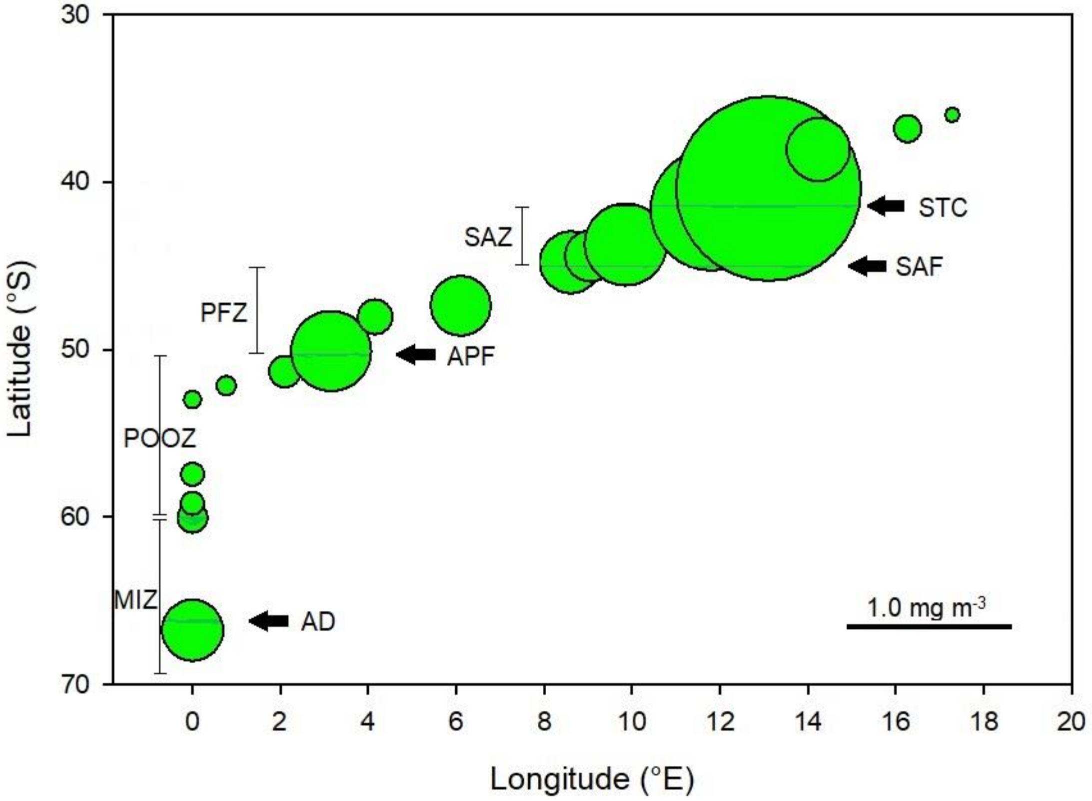

Figure 7: Bubble plot showing changes in concentration of surface chl-*a* across the stations used during this study along the SAAMES II transect. See Table 1 for physical zone descriptions.

The MDS plot of the environmental variables (Chl-*a*, MLD, SSS and SST) at each station displays a gradual movement from south to north (left to right, Figure 8), which indicates some separation of stations by the different physical zones identified by Pakhomov et al. (2000). The ANOSIM results indicate that that, overall, there was a significant difference (global R = 0.624, $p < 0.05$) between the environment of the different *a priori* regions defined by Pakhomov et al. (2000). The strongest differences in the environment were observed between the POOZ and the nSTC, the STC and the SAZ, while significance levels declined between regions towards the PFZ (Table 4). No clear differences were observed between samples south of the PFZ (Table 4).

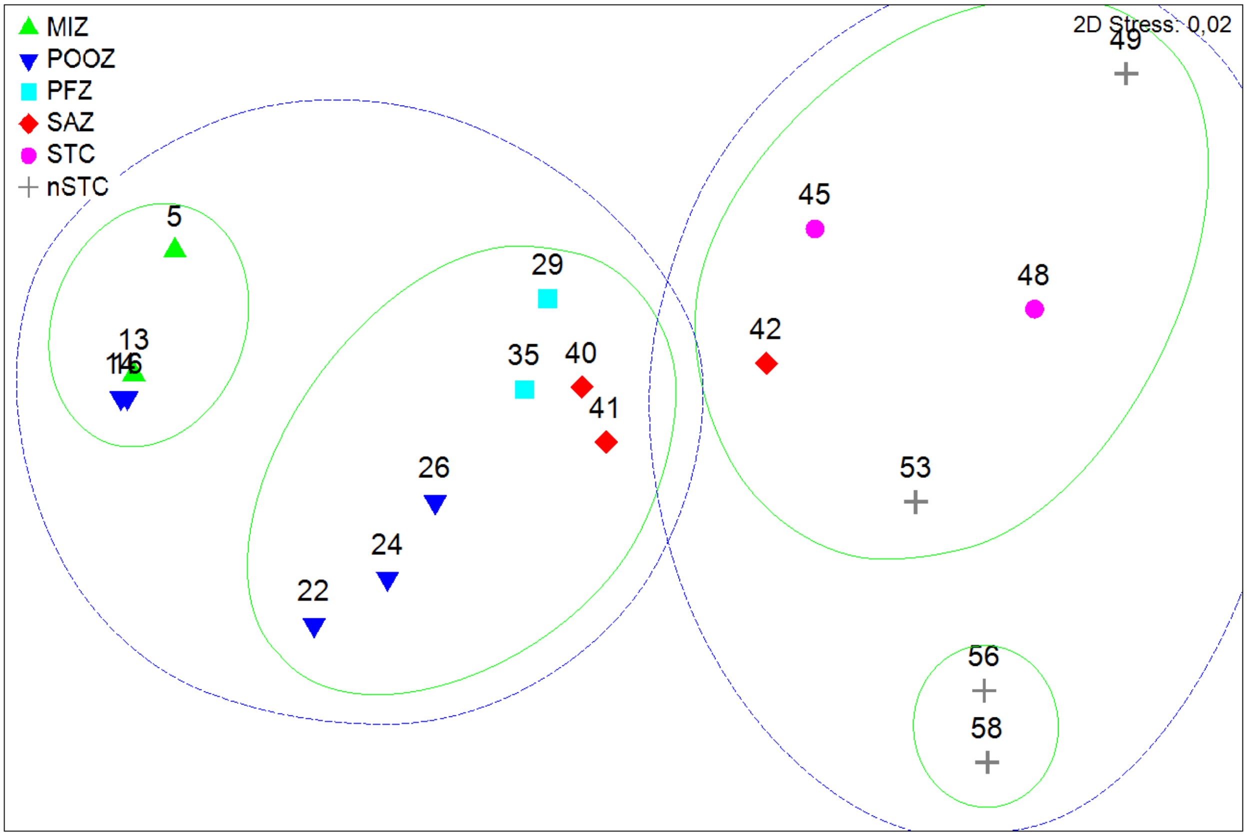

Figure 8: Two-dimensional non-metric multi-dimensional scaling (MDS) plot indicating the similarities in chlorophyll-*a*, mixed layer depth, sea surface salinity and sea surface temperature between the physical zones (identified in Table 1). Green line resembles a similarity distance of two and blue a distance of three, depicted from the CLUSTER analyses.

Table 4: ANOSIM results (R-values) for the differences in the environment (chlorophyll-*a*, mixed layer depth, sea surface salinity and sea surface temperature) between each a priori physical zone (see Table 1 for physical zone descriptions) described by Pakhomov et al. (2000). R-values in bold are significantly different ($p < 0.05$).

	MIZ	POOZ	PFZ	SAZ	STC	nSTC
MIZ	--					
POOZ	0.36	--				
PFZ	1.00	0.55	--			
SAZ	1.00	**0.73**	0.25	--		
STC	1.00	**1.00**	1.00	0.75	--	
nSTC	1.00	**0.90**	0.43	0.39	0.14	--

3.2 Biomass, Siphonophore Abundance and Diversity

Mesozooplankton biomass at the 19 stations is presented in Table 3. On average, mesozooplankton biomass values were highest within the PFZ (35.60 ± 13.63 g DW 1000 m^{-3}). Within the MIZ, the total mesozooplankton biomass decreased along a north- south axis with the lowest values recorded in the waters close to the Antarctic continent (from 22.83 to 6.56 g DW 1000 m^{-3}). A similar pattern was observed within the POOZ, where biomass was on average 8.25 ± 1.11 g DW 1000 m^{-3} in the south and 13.47 ± 11.03 g DW 1000 m^{-3} to the north. Biomass values were, on average, lower within the SAZ (5.59 ± 2.49 g DW 1000 m^{-3}), the STC (7.66 ± 0.30 g DW 1000 m^{-3}), and north of the STC (5.29 ± 3.48 g DW 1000 m^{-3}), except for station 49 which, just north of the STC, had the overall highest biomass (82.88 g DW 1000 m^{-3}) of all the stations.

Average carnivorous zooplankton biomass (Figure 9) was highest at the SAZ (4.0 ± 2.5 g DW 1000 m^{-3}), the STC (3.4 ± 4.2 g DW 1000 m^{-3}) and the PFZ (3.0 ± 1.0 g DW 1000 m^{-3}). The POOZ presented the second lowest carnivorous biomass throughout the transect (1.8 ± 1.1 g DW 1000 m^{-3}) with negligible variation (var. < 0.1 g DW 1000 m^{-3}) between its southern and northern

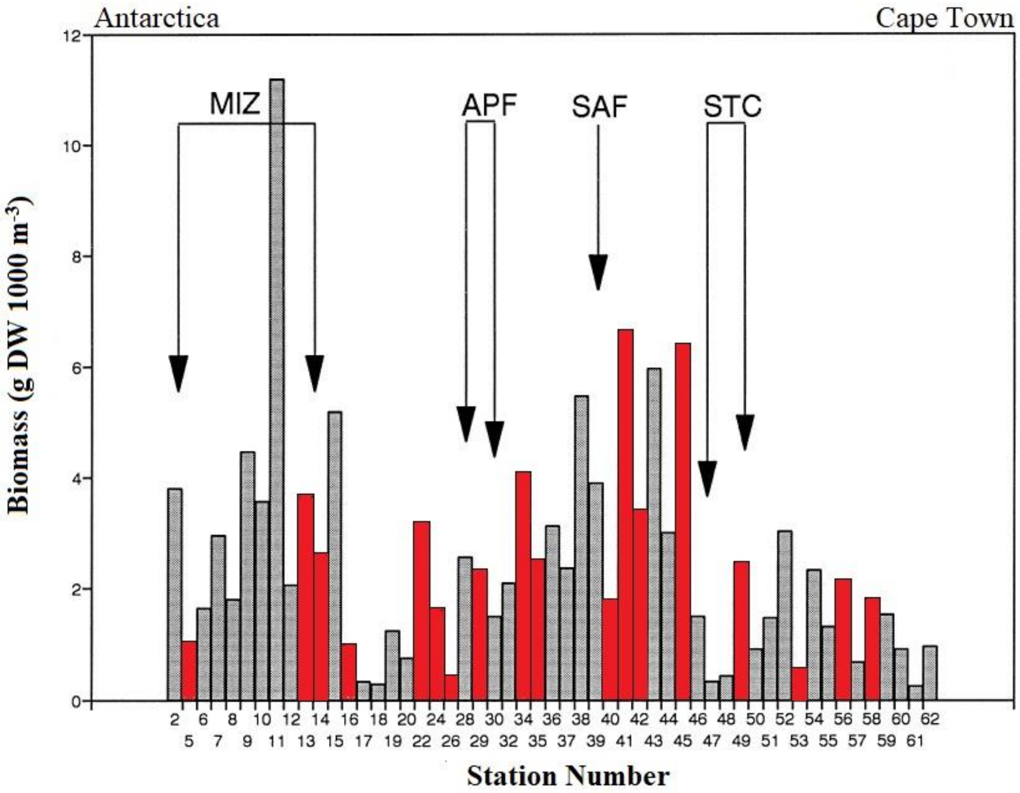

Figure 9: Carnivorous zooplankton biomass along the SAAMES II transect adapted from Pakhomov et al. (1999). The 19 stations analyzed in this study are indicated in red.

stations. Within the MIZ, there was an increase in carnivorous zooplankton biomass from south to north (from 1.1 to 3.7 g DW 1000 m^{-3}). Carnivores seemed to be least prevalent at the stations north of the STC, reaching a mean biomass of 1.8 (± 0.8) g DW 1000 m^{-3}.

Five different hydromedusae were collected, belonging to the orders Narcomedusae (1) and Trachymedusae (4) (Table 5). Specimens of hydromedusae were (in general) very badly damaged and at best could be placed into either order, family or genus. Twenty-one species of siphonophore were collected: 19 species of calycophorans and only two species of Physonectae

Table 5: Classification of hydromedusae and siphonophores collected between Antarctica and South Africa during January to February 1993. Individuals were identified to the lowest taxonomic rank possible.

Subclass	Order	Suborder	Family	Subfamily	Species
Hydroidolina	Siphonophorae	Calycophorae	Abylidae	Abylopsinae	*Abylopsis eschscholtzii* Huxley 1859
					Abylopsis tetragona Otto 1823
					Enneagonum hyalinum Quoy & Gaimard 1827
			Diphyidae	Diphyinae	*Chelophyes appendiculata* Eschscholtz 1829
					Dimophyes arctica Chun 1897
					Diphyes antarctica Moser 1925
					Eudoxoides spiralis Bigelow 1911
					Eudoxoides mitra Huxley 1859
					Lensia conoidea Keferstein & Ehlers 1860
					Lensia cossack Totton 1941
					Lensia fowleri Bigelow 1911
					Lensia hardy Totton 1941
					Lensia hotspur Totton 1941
					Lensia meteori Leloup 1934
					Lensia multicristata Moser 1925
					Lensia panikkari Daniel 1971
					Lensia subtilis Chun 1886
					Muggiaea atlantica Cunningham 1892
					Muggiaea bargmannae Totton 1954

Table 5 (continued)

Subclass	Order	Suborder	Family	Subfamily	Species
Hydroidolina	Siphonophorae	Physonectae	Agalmatidae	N/A	*Halistemma rubrum* Vogt 1852
				N/A	*Nanomia bijuga* Delle Chiaje 1844
Trachylinae	Narcomedusae	N/A	N/A	N/A	Unknown
	Trachymedusae	N/A	N/A	N/A	Unknown
		Halicreatidae	N/A	N/A	Unknown
		N/A	Rhopalonematidae	N/A	Unknown
		N/A		N/A	*Rhopalonema* sp.

Table 6: The average abundance (ind. 1000 m^{-3} ± SD) of each species of siphonophore collected in each physical zones (number of stations) between Antarctica and Cape Town.

	MIZ (2)	**POOZ** (5)	**PFZ** (3)	**SAZ** (3)	**STC** (2)	**nSTC** (4)
Abylopsis eschscholtzii (Polygastric)					2.7 ± 3.8	0.6 ± 1.2
Abylopsis eschscholtzii (Eudoxid)					0.9 ± 1.3	0.6 ± 1.2
Abylopsis tetragona (Polygastric)					1.8 ± 2.5	1.1 ± 1.3
Abylopsis tetragona (Eudoxid)					1.8 ± 2.5	4.7 ± 5.4
Chelophyes appendiculata					1.8 ± 2.5	8.7 ± 9.6
Dimophyes arctica	90.2 ± 121.7	186.5 ± 214.7	197.3 ± 529.2	138.7 ± 150.0	82.7 ± 71.6	82.2 ± 55.5
Diphyes antarctica	9.3 ± 13.1	5.1 ± 11.4				
Enneagonum hyalinum					1.8 ± 2.5	1.7 ± 2.1
Eudoxoides spiralis					12.4 ± 7.5	13.1 ± 18.0
Eudoxoides mitra					6.2 ± 6.3	21.5 ± 40.2
Lensia conoidea						2.1 ± 1.7
Lensia cossack						9.3 ± 18.6
Lensia fowleri					0.9 ± 1.3	4.9 ± 8.4
Lensia multicristata			1.6 ± 2.2	9.7 ± 16.8	37.4 ± 20.2	24.8 ± 17.1
Lensia hardy				2.5 ± 2.3	18.7 ± 13.9	4.5 ± 6.0
Lensia hotspur					2.7 ± 3.8	9.8 ± 11.5
Lensia subtilis					2.7 ± 3.8	18.7 ± 23.8
Lensia meteori					2.7 ± 3.8	0.9 ± 1.8
Lensia panikkari					0.9 ± 1.3	
Muggiaea atlantica					4.5 ± 6.3	
Muggiaea bargmannae	132 ± 184.4	82.5 ± 184.5				

(Table 5). Table 6 provides the average abundance of siphonophores at the different fronts/zones, however since only one nectophore of *Nanomia bijuga* and two of *Halistemma rubrum* were collected in total, and no pneumatophores were observed, it was not possible to estimate their abundance.

Dimophyes arctica was collected at all stations (except at station 34 where no hydrozoans were recorded) in generally large, but variable abundances (avg.: 137 ± 152 ind. 1000 m^{-3}, max. = 519 ind. 1000 m^{-3}). It was the only species collected at stations 14, 22, 24, 26 and 29. Species richness was relatively low from the MIZ to south of the SAZ (Figure 10A) and only three other species were collected within this area: *Diphyes antarctica, Lensia multicristata* and *Muggiaea bargmannae*. *Diphyes antarctica* was only present at stations 13 (19 ind. 1000 m^{-3}) in the MIZ and 16 (25 ind. 1000 m^{-3}) within the southern POOZ. Assemblages from the two above mentioned stations, as well as at station 5 included *M. bargmannae*. Only one individual of the latter species was collected at station 5, but higher abundances were collected within the northern station of the MIZ (262.8 ind. 1000 m^{-3}) and at station 16 (412.6 ind. 1000 m^{-3}). Only two individuals of *L. multicristata* were found at one station (station 35) in the PFZ, but it occurred more commonly between the SAZ and Cape Town (avg.: 34 ± 10 ind. 1000 m^{-3}).

Species richness increased north from the SAZ, within which more temperate species such as *Eudoxoides spiralis*, *Lensia multicristata* and *L. hardy* were also collected (Table 6; Figure 10A). The area north of the STC had the highest species richness containing 19 out of the 21 species collected (Table 6; Figure 10A). *Abylopsis tetragona*, *Chelophyes appendiculata*, *Eudoxoides spiralis, E. mitra, Lensia fowleri, L. multicristata, L. hardy, L hotspur, L. subtilis* and *L. meteori* occurred commonly throughout this area. *Dimophyes arctica* dominated assemblages in this

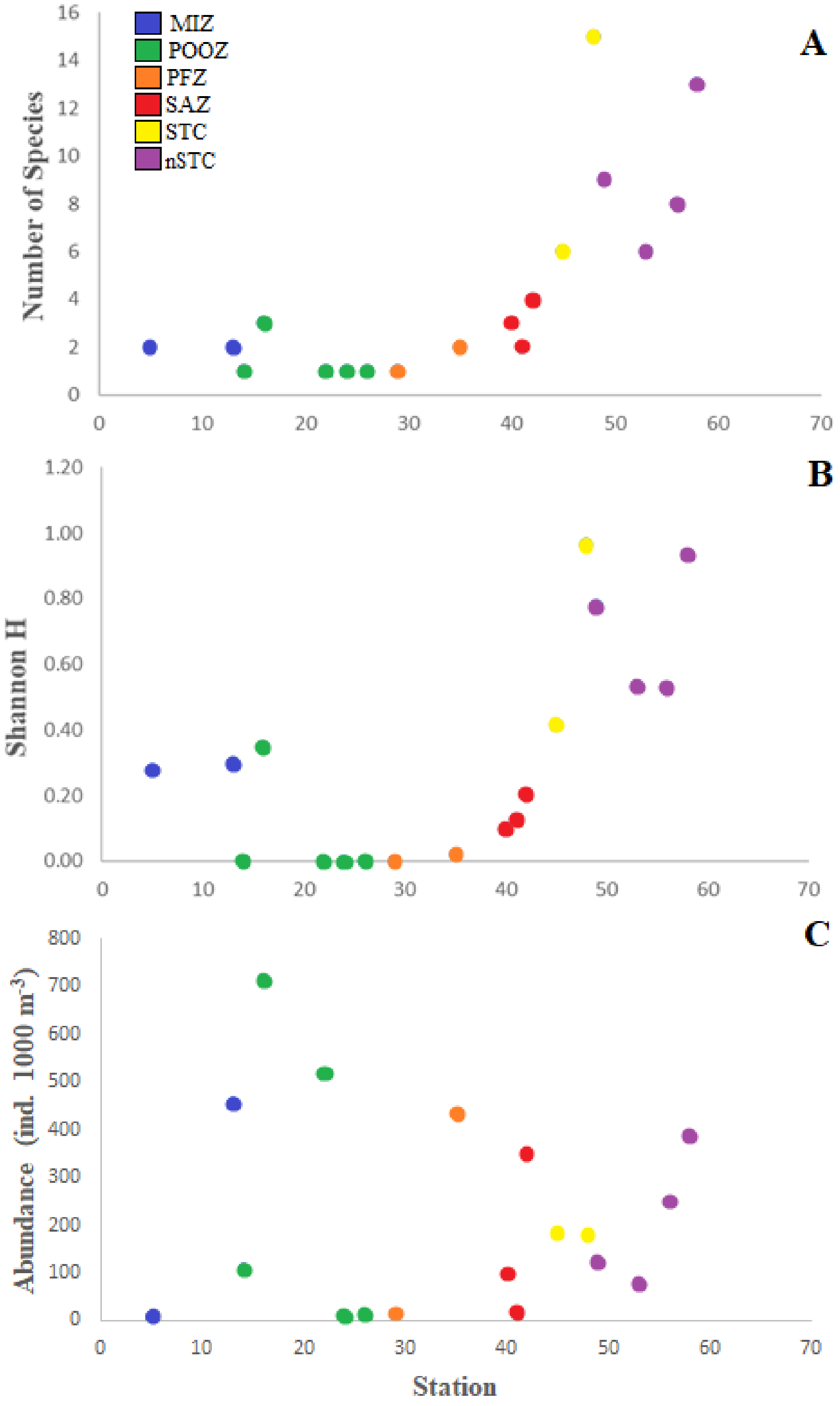

Figure 10 Siphonophore species richness (A), Shannon Diversity Indices (B) and average abundance (C) along the SAAMES II transect. See Table 1 for physical zone descriptions.

region, making up 40.9% of the total siphonophore abundance (avg.: 82 ± 54 ind. 1000 m^{-3}). Other major contributors were *L. multicristata* (14.38%; avg. abundance: 29 ± 17 ind. 1000 m^{-3}), *E. mitra* (8.14%; avg. abundance: 16 ± 32 ind. 1000 m^{-3}) and *E. spiralis* (6.39%; avg. abundance: 13 ± 14 ind. 1000 $m^{- 3}$). The only two physonects species; *Halistemma rubrum* and *Nanomia bijuga* were collected within this region.

Species diversity (Figure 10B) was lowest within the PFZ and the SAZ (Shannon H < 0.20), while the highest within the STC (Shannon H ranging from 0.42 to 0.96) and north of the STC (Shannon H ranging from 0.53 to 0.93). The STC and nSTC mostly contained similar species (Table 6), but species such as *Lensia pannikari, Muggiaea atlantica* and *Nanomia bijuga* were confined to the STC, while *L. conoidea, L. cossack*, and *Halistemma rubrum* were only found at the stations within the nSTC.

Average siphonophore abundances (Figure 10C) were highest in the MIZ (231.9 ± 319.2 ind. 1000 m^{-3}) and the POOZ (274.1 ± 322.9 ind. 1000 m^{-3}). The high standard deviations indicate that abundances varied markedly between the stations. Although high average abundances were observed within the MIZ, it should be noted that there were only two stations within this zone, of which the most southern station (station 5) had the overall lowest abundance (6.2 ind. 1000 m^{-3}) of all stations (Figure 10C). Siphonophore abundances increased towards the northern station (station 13) within the MIZ which coincides with the pattern observed in both mesozooplankton and carnivorous zooplankton biomass. Overall the PFZ had the lowest average siphonophore abundance (149.3 ± 246.5 ind. 1000 m^{-3}) (Figure 10C). Siphonophore abundances were, on average, 183.24 ± 4.77 ind. 1000 m^{-3} in the STC and 210 ± 140.90 ind. 1000 m^{-3} north of the STC, with the highest abundances occurring in the northern most stations of the nSTC (Figure 10C).

The MDS plot (Figure 11) displays the grouping of species amongst the different stations at a level of 70% similarity, indicating a clear spatial separation of species associations from north to south. Four distinct groups are visible: Group 1 (*Diphyes antarctica* and *Muggiaea bargmannae*); Group 2 (*Dimophyes arctica*); Group 3 (*Eudoxoides spiralis*, *Lensia hardy* and *L. multicristata*); and Group 4 (the remaining species; see Table 6). For example, polar species such as *D. antarctica* and *M. bargmannae* were grouped separately from those with a more tropical or subtropical distribution, while the ever-present *D. arctica* did not group with any cluster (Figure 11). Lastly, species with a larger spatial distribution, such as *E. spiralis* and *L. hardy* which occurred in all zones north from PFZ and *L. multricristata* which occurred within all the zones north of the POOZ

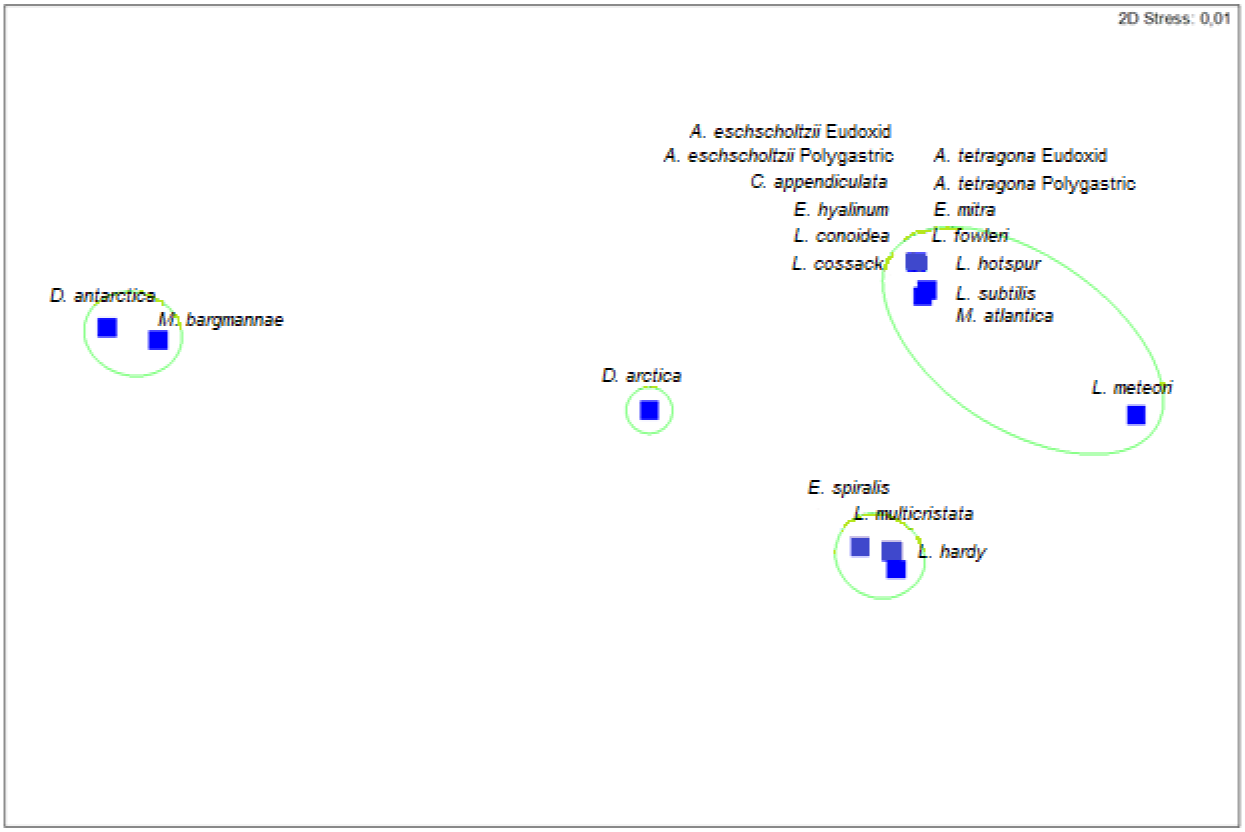

Figure 11: Two-dimensional non-metric multi-dimensional scaling (nMDS) plot indicating the groupings of siphonophore species between the different stations. Green clustering resembles groups at a 70% similarity.

were grouped together (Figure 11). Figure 12 provides a visual representation of how the different species were distributed between the different stations.

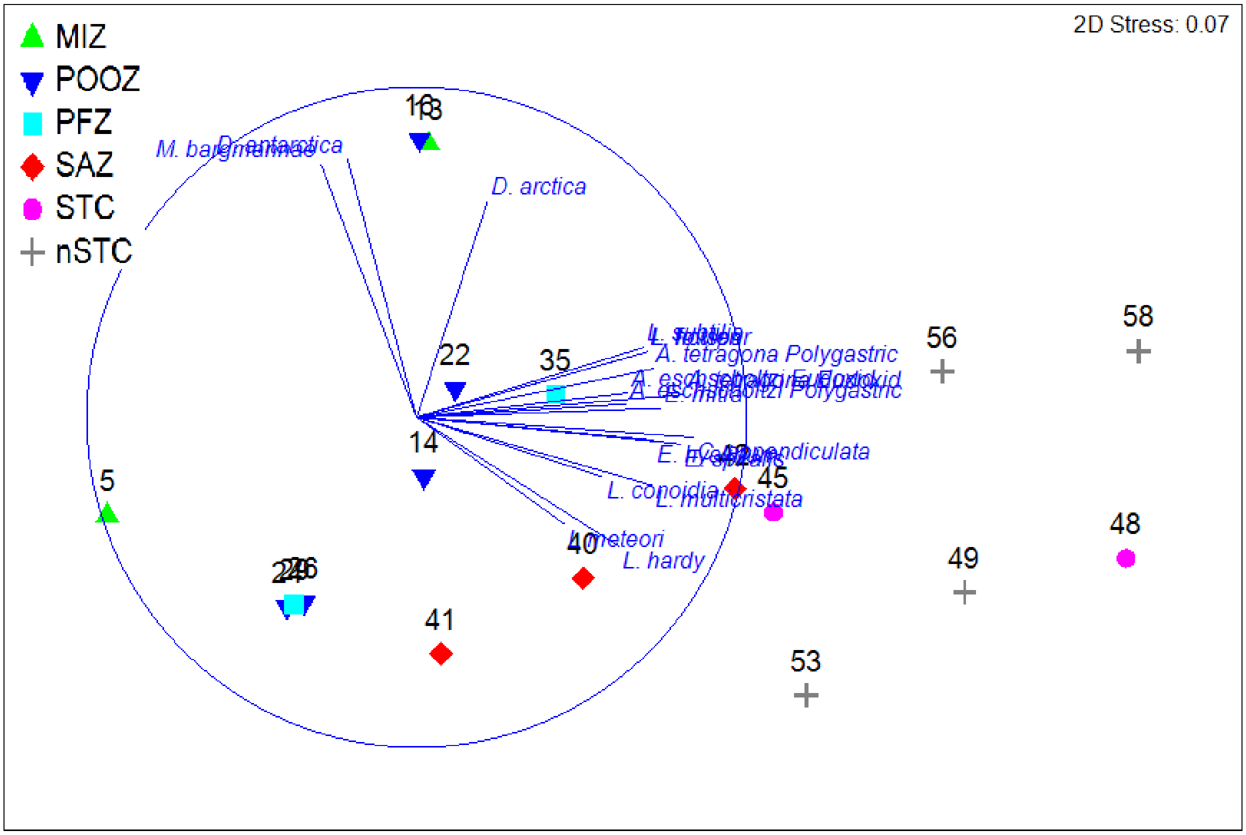

Figure 12: Two-dimensional non-metric multi-dimensional scaling (nMDS) plot of siphonophore densities between the different stations with an overlaying vector indicating the distribution of siphonophore species amongst the different stations. See Table 1 for physical zone descriptions.

3.3 Siphonophore assemblages

The MDS plot indicates some separation of the samples by *a priori* identified zones (Figure 13A). At the 35% similarity level, stations are grouped into two large groups (Figure 13A) either side of the SAF (except station 41). The ANOSIM indicates that, overall, there is a significant difference (global R = 0.48, $p < 0.05$) between the assemblages of the different *a priori* regions as defined by Pakhomov et al. (2000). Strongest differences were observed between assemblages of

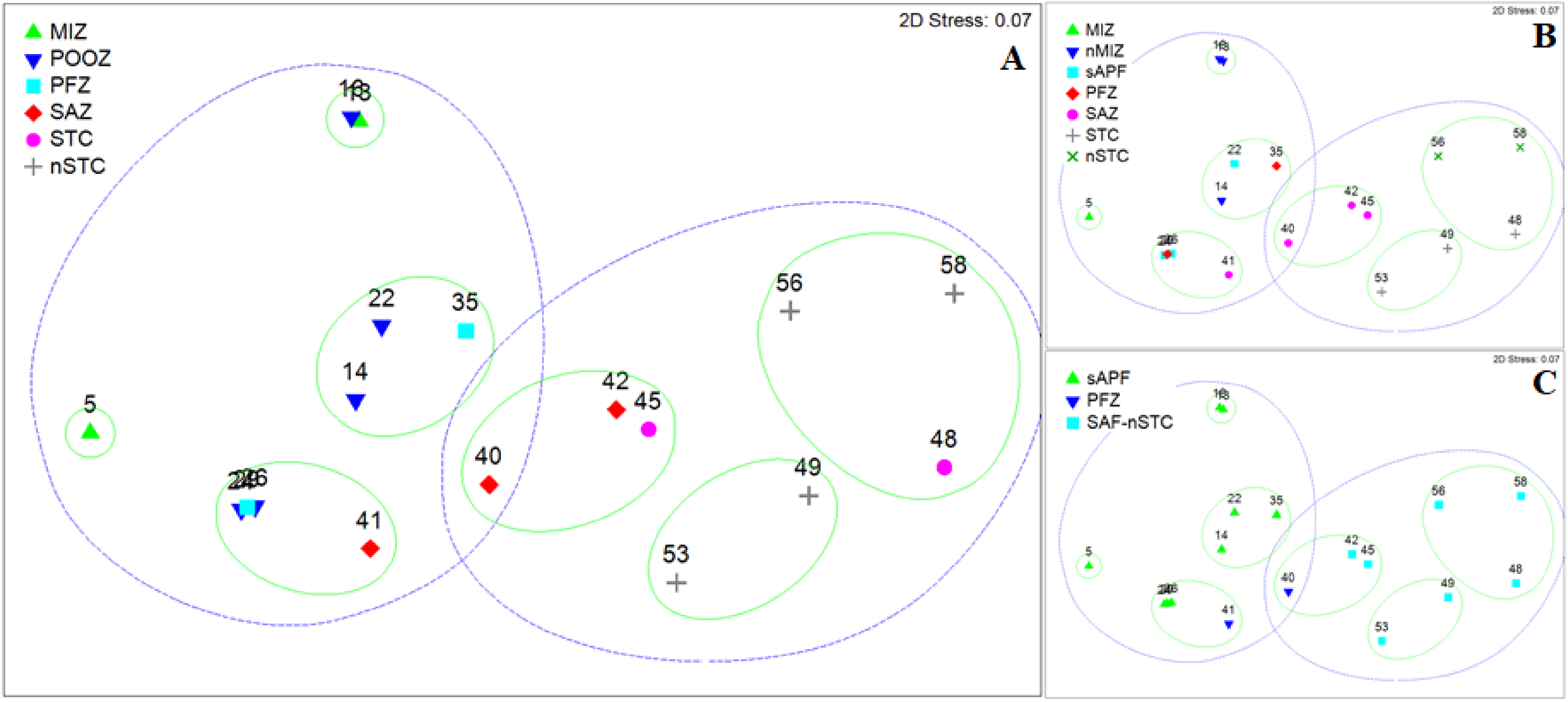

Figure 13: Two-dimensional non-metric multi-dimensional scaling (nMDS) plot indicating the similarities in siphonophore assemblages between the different physical zones (A), mesozooplankton assemblages (B) and carnivorous zooplankton assemblages (C) described by Pakhomov et al. (1999; 2000). Green clustering resembles groups at 62% similarity and blue at 35% similarity. See Table 1 for physical zone descriptions.

Table 7: The ANOSIM and SIMPER results for the differences in siphonophore assemblages between each *a priori* physical zone (see Table 1 for physical zone descriptions) described by Pakhomov et al. (2000). R-values in black and in bold where values were significantly different ($p < 0.05$). The blue numbers indicate the percentage similarity within each zone, while red numbers indicate the percentage dissimilarity between each physical zone.

	42.37	60.03	49.26	64.89	51.59	51.73
	MIZ	POOZ	PFZ	SAZ	STC	nSTC
MIZ	--	48.79	56.14	63.86	80.15	81.00
POOZ	0.20	--	33.84	47.85	73.92	75.35
PFZ	0.25	-0.16	--	44.82	67.98	70.46
SAZ	0.92	0.24	0.17	--	49.66	59.41
STC	1.00	**0.82**	0.50	0.50	--	40.72
nSTC	0.96	**0.89**	0.82	0.54	-0.39	--

the POOZ and both the nSTC and STC, with significance levels declining towards the SAZ (Table 7). There were no significant differences between samples south of the SAZ, though it should be remembered that in some cases the number of replicates per region were small. From the results of the SIMPER analysis, it is clear that the dissimilarity in the composition between *a-priori* zone pairs increased with increasing distance between them (Table 7). Thus, for example, communities at the MIZ were 49% dissimilar from those in the POOZ and 81% dissimilar from those at the nSTC. The species responsible for the identity of each *a priori* zone are shown in Figure 14 and their average abundances in Figure 15.

When the *a priori* zones were defined using Pakhomov et al.'s (1999; 2000) classifications derived from mesozooplankton and carnivorous zooplankton data, effectively similar results were generated. That said, there was a better fit with the mesozooplankton (global $R = 0.65$, $p < 0.05$) than with the carnivorous zooplankton data (global $R = 0.64$, $p < 0.05$). The MDS plots were used to divide the assemblages of each station into the respective groups of mesozooplankton (Figure 13B) and carnivorous zooplankton (Figure 13C). There is a clear separation of samples within the

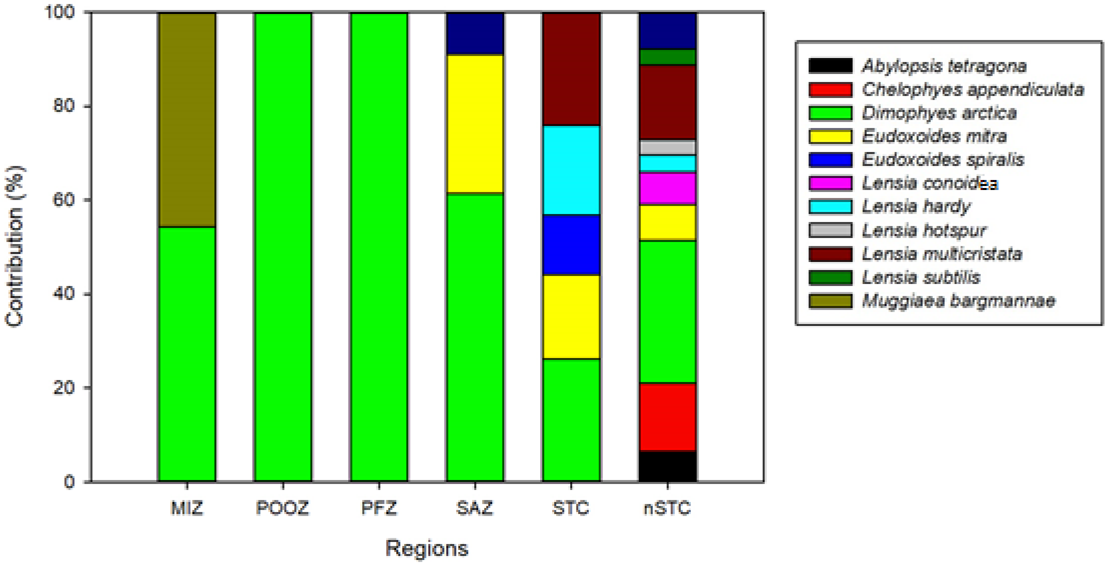

Figure 14: Percentage contribution of the main species of siphonophores responsible for the average similarity between samples within each physical zone as identified by the SIMPER analysis.

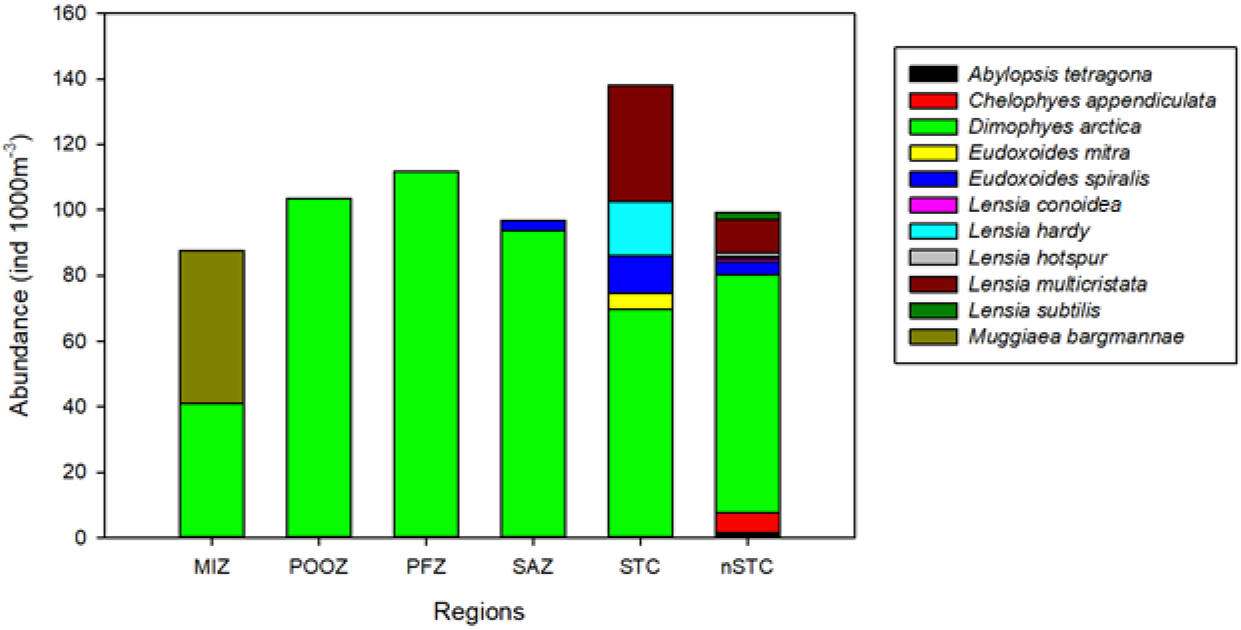

Figure 15**:** Average abundances of the major contributing species of siphonophore in each physical zone described by Pakhomov et al. (2000).

mesozooplankton groups from north to south between the nSTC, STC and the SAZ (Figure 13 B). However, south of the SAZ the groupings become less clear. The ANOSIM results revealed that significant differences between the assemblages were observed between the STC and the SAZ, and between the SAZ and nMIZ (Table 8). The groupings of carnivorous zooplankton indicate more separation between groups, clearly separating the three distinct groupings of zooplankton (Figure 13C). The ANOSIM results (Table 9) indicate that the group of the SAF to nSTC were significantly different to that of the PFZ as well as the group to the south of the APF (sAPF). However, there was no significant difference between the groups of the PFZ and the sAPF.

Table 8: The ANOSIM results for the differences in siphonophore assemblages between the different assemblages of mesozooplankton described by Pakhomov et al. (2000). See Table 1 for the mesozooplankton assemblage descriptions. R-values are listed in black numbers, while those in bold were significantly different ($p < 0.05$).

	MIZ	nMIZ	sAPF	PFZ	SAZ	STC	nSTC
MIZ	--						
nMIZ	0.79	--					
sAPF	0.11	0.41	--				
PFZ	0	0.33	-0.17	--			
SAZ	0.92	**0.72**	0.5	0.32	--		
STC	1	1	1	1	**0.63**	--	
nSTC	0.78	1	1	1	0.86	0.17	--

Table 9: The ANOSIM results for the differences in siphonophore assemblages between the different assemblages of carnivorous zooplankton described by Pakhomov et al. (1999). See Table 2 for the carnivorous zooplankton assemblage descriptions. R-values are listed in black numbers, while those in bold were significantly different ($p < 0.05$).

	sAPF	PFZ	SAF - nSTC
sAPF	--		
PFZ	0.06	--	
SAF - nSTC	**0.82**	**0.54**	--

Assemblages of siphonophores along the Atlantic sector of the Southern Ocean could be divided, most clearly, into two distinct assemblages (Figure 16). These two natural groupings (Group A (south) and Group B (north)) are separated by the SAF at the 35% similarity level, except for station 41 (Figure 16A). Group A consist of the southern area between the Antarctic continent and the SAF, while group B stretches from the SAF towards Cape Town. There is a clear separation of samples between stations from the north to south, moving east to west across the grid, with samples from similar zones being grouped more closely together. The structure of the physical environment can be interpreted to support this north:south separation at a 35% similarity interval, except for stations 40 and 41 (Figure 16B).

The SIMPER results indicate an average dissimilarity of 66.92% between Groups A and B with only *Dimophyes arctica* and *Lensia. multicristata* occurring in both groups. Species mainly contributing to this dissimilarity were *Eudoxoides spiralis* (13.89%), *L. multicristata* (13.20), *D. arctica* (11.82) and *L. hardy* (10.67). The stations within Group A had an average similarity of 56.69% with *D. arctica* contributing to 95.27% of the species composition and an average abundance of 173.02 ± 195.37 ind. 1000 m^{-3} across this region. Although group A had the lower diversity (avg. Shannon H = 0.10 ± 0.15), it had the highest average abundance (253.57 ± 276.58 ind. 1000 m^{-3}). Group B however, was 50.56% similar in species composition between stations with *D. arctica* (43.15%), *E. spiralis* (17.13%), *L. multicristata* (13.59%), and *L. har*dy (10.37%) having the largest contribution. Average siphonophore abundance were 185.85 ± 124.69 ind. 1000 m^{-3} within this region but siphonophore diversity (Figure 10B) was highest especially within the STC (avg. Shannon H = 0.69 ± 0.39) and north of the STC (avg. Shannon H = 0.69 ± 0.20).

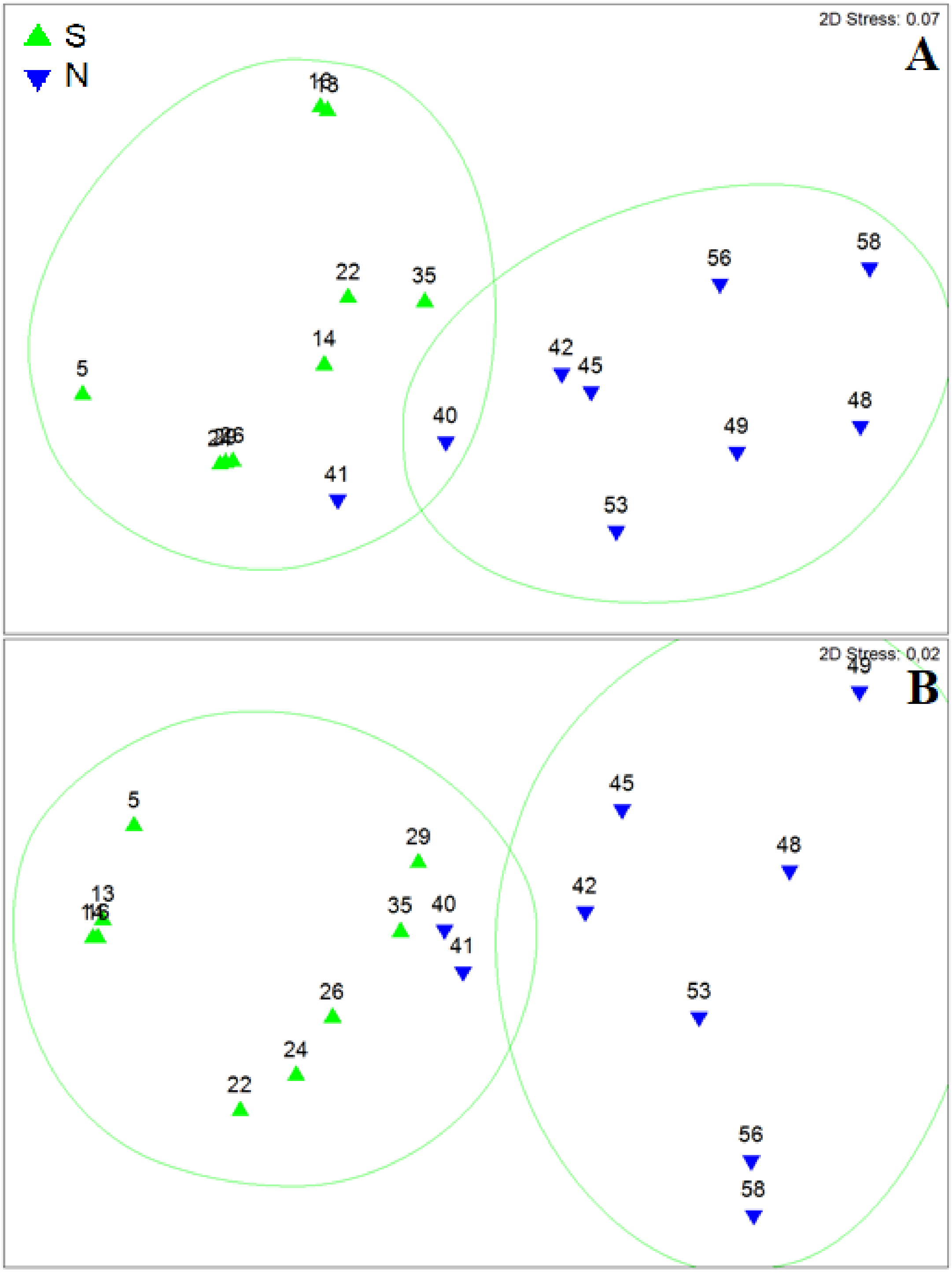

Figure 16: Two-dimensional non-metric multi-dimensional scaling (MDS) plots. (A) The similarities in siphonophore assemblages between two natural groupings: Group A (south) and Group B (north). (B) The similarities in the environment of between the two above mentioned groups. The green clustering indicates a 35% similarity within the respective groups.

Table 10: Distance Based Linear Model's marginal and sequential tests results.

Marginal Tests

Variable	Pseudo-F	Significance Level (P)
Chlorophyll-*a*	2,946	0,032
Mesozooplankton Biomass	0,180	0,964
Mixed Layer Depth	5,333	0,004
Sea Surface Salinity	12,991	0,001
Sea Surface Temperature	10,288	0,001
Sequential Tests		
Chlorophyll-*a*	1,497	0,227
Mesozooplankton Biomass	1,012	0,377
Mixed Layer Depth	1,560	0,186
Sea Surface Salinity	12,991	0,001
Sea Surface Temperature	3,474	0,007

The marginal test results of the Distance Based Linear Model indicate that chl-*a*, MLD, SSS and SST contributed to the structure of siphonophore assemblages along the transect (Table 10). Figure 17 displays a final DistLM (adj. $R^2 = 0.53$) for the physical zones (Figure 17A) described by Pakhomov et al. (2000) and the two different siphonophore assemblages (Figure 17B). The influence that each environmental variable (chl-*a*, mesozooplankton biomass, MLD, and SSS) has on the distribution of siphonophore densities between the different stations are also visible (Figure 17). This model explains 58.9% of the total variation and 92.1% of the fitted variation in siphonophore communities. The sequential test results indicate that when all environmental factors are simultaneously assessed to determine the variability in siphonophore abundances between the different groups, only SSS had an overall significant impact on their distribution (Table 10). Although SSS has the most significant impact on the distribution of siphonophores along the transect, other changes in the environment (chl-*a*, mesozooplankton biomass, MLD, and SST) are also linked to the variation observed between communities.

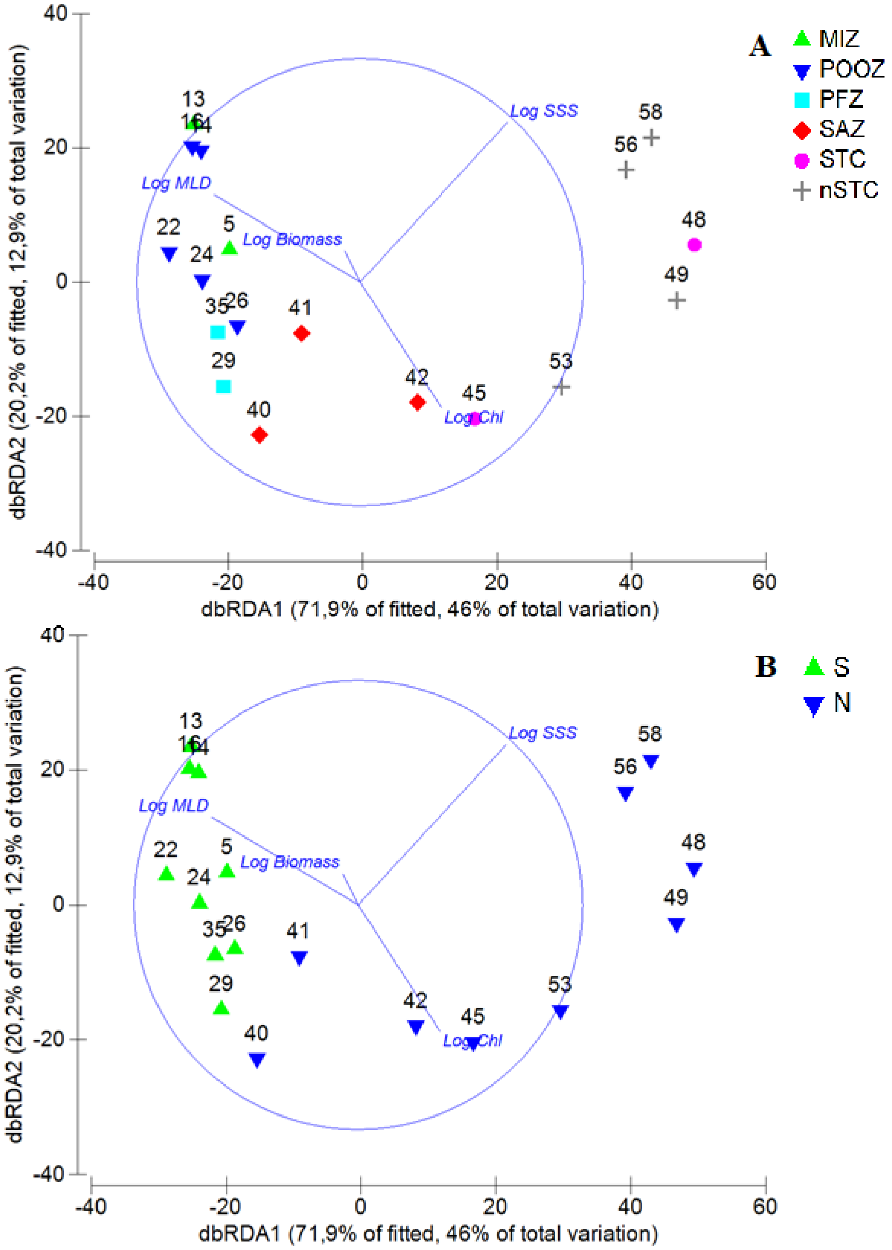

Figure 17: Distance Based Linear Matrix using a multivariate multiple regression (dbRDA) performed on siphonophore species composition according to the physical zones (A) identified by Pakhomov et al. (2000) as well as the two natural groupings (B): Group A (south) and Group B (north) Environmental predictors: chlorophyll-*a*, mesozooplankton biomass, mixed layer depth and sea surface salinity.

4 DISCUSSION

Pakhomov et al. (1999; 2000) found that the highest average abundances of zooplankton (meso- and crustacean carnivorous zooplankton) were associated with the frontal systems of the Southern Ocean. The PFZ was characterized by high abundances of mesozooplankton (84200 ± 21900 ind. 1000 m^{-3}) and carnivorous zooplankton (10949 ± 5745 ind. 1000 m^{-3}) (Pakhomov et al. 1999; 2000). Carnivores only contributed to a small proportion (between 10 and 30%) of the entire zooplankton stock and diversity along the transect was relatively low (Pakhomov et al. 1999). However, when studying the distribution of another carnivorous group, the siphonophores, results were different with maximum abundances found within the POOZ, where species diversity was lowest. The diversity of siphonophore communities was generally lowest close to the Antarctic continent and increased northwards, as observed by Toda et al. (2014) off the Adélie Land. Similar observations have been made by numerous authors working on a variety of planktonic taxa (as reviewed by Atkinson et al. 2012) and are often related to temperature (Atkinson et al. 2012). Although the average abundances of siphonophores within the STC and nSTC were in general lower (182.4 ± 154 ind. 1000 m^{-3} and 209.1 ± 223.0 ind. 1000 m^{-3} respectively) than those in the MIZ and POOZ (231.9 ± 319.2 ind. 1000 m^{-3} and 274.1 ± 410.6 ind. 1000 m^{-3} respectively), species diversity was at its highest (Shannon H: STC = 0.42 – 0.96; nSTC = 0.53 – 0.93 vs. MIZ = 0.28 – 0.30; POOZ = 0.00 – 0.35). A number of species of siphonophores exhibited a clearly restricted affinity to specific zones, while others had a wide distribution, found through several of the physical zones described by Pakhomov et al. (2000). Pakhomov et al. (1999; 2000) identified three species of siphonophores (*Dimophyes arctica, Diphyes antarctica* and *Melophysa melo*) within their samples, but *M. melo* was not present within the 19 samples analyzed here.

4.1 Group 1

The first of the four groups identified by the nMDS plot, included the Antarctic species *Diphyes antarctica* (Totton 1954) and bipolar species *Muggiaea bargmannae* (Totton 1954; Pagès et al. 1994), which were both confined to areas close to the Antarctic mainland, and were only collected up to the southern region of the POOZ. These species are clearly polar specialists. Overall, the average abundances of *D. antarctica* were much lower than those of *M. bargmannae* (Table 6). Both species occurred in higher average abundances within the southern POOZ (*D. antarctica*: 12.7 ± 18.0 ind. 1000 m^{-3} and *M. bargmannae*: 206.3 ± 291.7 ind. 1000 m^{-3}) than within the MIZ (*D. antarctica*: 9.3 ± 13.1 ind. 1000 m^{-3} and *M. bargmannae*: 132.4 ± 184.4 ind. 1000 m^{-3}). Pagès et al. (1994) however reported a decrease in *M. bargmannae* abundances from south to north (from the southern MIZ to the southern POOZ).

Nevertheless, these two species have already been reported in several studies within the Weddell Sea (Pagès et al. 1994; Pagès & Kurbjeweit 1994; Pagès et al. 1996; Pagès & Schnack-Schiel 1996), elsewhere (Lindsay et al. 2014, Maps 7a-b, see chapter 5), and in Lützow-Holm Bay within the Indian sector of the Southern Ocean (Toda et al. 2010). *Muggiaea bargmannae* was generally only found south of 60 °S (Pagès et al. 1994), although not always (Lindsay et al. 2014), and at every station within the Weddell Sea (Pagès & Kurbjeweit 1994; Pagès & Schnack-Schiel 1996), where it was also the most abundant species (avg.: 905.3 ind. 1000 m^{-3}) in the siphonophore community (Pagès & Kurbjeweit 1994). Toda et al. (2010) reported the same trend with *M. bargmannae* being the most abundant species collected in 2006 within the Lützow-Holm Bay, and at a significant lower level than within the Weddell Sea (avg.: 3.6 ind. 1000 m^{-3}; at depths up to 500 m). However, during 2005, *M. bargmannae* was only the third most abundant species of siphonophore collected within Lützow-Holm Bay, but in a higher average abundance (13.9 ind. 1000 m^{-3}; at depths up to 500 m) (Toda et al. 2010).

Pagès et al (1994) found *D. antarctica* to be the most abundant epipelagic species (avg.: 1.6 ind. 1000 m^{-3}) during their study in the eastern Weddell Sea during 1979. While this species has also been reported to occur in the PFZ within the South Georgia sector of the Southern Ocean, it appears to occur at very low abundances (avg.: 0.05 ind. 1000 m^{-3}) and only at depths between 600 and 800 m. Pakhomov et al. (1994) also recorded *D. antarctica* (identification not conclusive) within the regions of the STC and APF during another study in 1993 around the same period of this study, while Lindsay et al. 2014 found similar distributions but mostly in the Indian and Pacific sectors of the Southern Ocean.

4.2 Group 2

Overall, *Dimophyes arctica* was the most abundant species throughout, occurring at all stations and reaching highest abundances (up to 519.2 ind. 1000 m^{-3}) within the PFZ and the POOZ (Table 6). Pagès et al. (1994) described this species to occur within all latitudinal ranges, from the Arctic to the Antarctic, being able to accommodate to a wide range of temperatures (-1.13 to 22.05 °C), but being usually more abundant in the lower end of the range (Totton 1954; Pagès et al. 1994). This suggests we should expect to see more *D. arctica* at the higher latitudes, with decreased abundances towards lower latitudes. Within the Weddell Sea, this species has a similar spatial distribution to *M. bargmannae,* while occurring in average abundances of 76.1 ind. 1000 m^{-3} (Pagès & Kurbjeweit 1994). Within similar latitudinal ranges during this study, the abundance of *D. arctica* (90.2 ± 121.7 ind. 1000 m^{-3}) was very similar to that reported in the findings of Pagès & Kurbjeweit (1994), although the number of replicates in this study within the region were very low. Similar abundances (62 ind. 1000 m^{-3}) were also found in the Eastern Weddell Sea (Pagès et al. 1994). Within the eastern Weddell Sea, *D. arctica* was most abundant between 59 and 62 °S (max. 6.2 ind. 1000 m^{-3}), while abundances were lowest (0.93 ind. 1000 m^{-3}, up to 510 m) at the most southern station (66.5 °S) (Pagès et al. 1994). This species was also overall the second most abundant species collected in the Lützow-Holm Bay during 2005 (15.3 ind. 1000 m^{-3}) and 2006 (1.3 ind. 1000 m^{-3}) (Toda et al. 2010).

The abundance of *Dimophyes arctica* decreased north of the PFZ from 138.7 ± 150 ind. 1000 m^{-3} in the SAZ to 82.2 ± 55.5 ind. 1000 m^{-3} north of the STC (Table 6). Unfortunately, data for this species are scarce north of the POOZ with previous studies within the Atlantic Sector of the Southern Ocean not elaborating much. While Pakhomov et al. (1994) investigated the microzooplankton/micronecton communities across the APF and the STC, their samples within the APF were collected within two weeks after the sampling of this study, while those within the STC were collected during winter of the same year identified 16 species of siphonophores, but no *D. arctica* specimens. Since *D. arctica* was present at all stations sampled during this study and it was by far the most abundant species collected at each station (except at station 13), we would expect it to have been collected within the zones studied by Pakhomov et al. (1994).

Dimophyes arctica has been reported in much lower abundances within the Southern Benguela region in 1977 and 1978 (avg.: 1977: 0.14 ± 1.02 ind. 1000 m^{-3}; 1978: 0.31 ± 2.06 ind. 1000 m^{-3} respectively) (Pagès & Gili 1992b). Within the inshore waters off South Africa's west coast it was observed as far north as 30°S while up to 20°S offshore (Gibbons & Thibault-Botha 2002). However, it is important to note that the latter distributions are depicted from presence/absence data (Gibbons & Thibault-Botha 2002), but not in Thibault-Botha et al. (2004) which found *D. arctica* to occur along the east coast of South Africa between Algoa Bay (34°S, 26°E) and the Tugela River (29°S, 31°E).

4.3 Group 3

Both *Eudoxoides spiralis* and *Lensia hardy* occurred in the SAZ at low abundances (avg.: 4 ± 4.3 ind. 1000 m^{-3} and 2.5 ± 2.3 ind. 1000 m^{-3} respectively), reaching higher abundances within the STC (12.4 ± 7.5 ind. 1000 m^{-3} and 18.7 ± 13.9 ind. 1000 m^{-3} respectively) and nSTC (13.1 ± 18.0 ind. 1000 m^{-3} and 4.5 ± 6 ind. 1000 m^{-3} respectively). *Eudoxoides spiralis* has already been reported throughout the latitudinal range of the Southern Ocean (Lindsay et al. 2014) andin the vicinity of the STC (Pakhomov et al. 1994) and the Southern Benguela (12.6 ± 23.8 ind. 1000 m^{-3} and 6.0 ± 10.2 ind. 1000 m^{-3} in 1977 and 1978 respectively (Pagès & Gili 1992b). Their results were similar than those obtained during this study for both the STC (avg. abundance 12.4 ± 7.5 ind. 1000 m^{-3}) and nSTC. (13.1 ± 18.0 ind. 1000 m^{-3}) (Pagès & Gili 1992b). Pagès and Gili (1992) also collected *L. hardy* (0.09 ± 0.59 ind. 1000 m^{-3}and 0.32 ± 2.02 ind. 1000 m^{-3} in 1977 and 1978 respectively and *L. multicristata* only in 1977 (0.04 ± 0.42 ind. 1000 m^{-3}) within the Southern Benguela but at lower abundances collected within the region of the STC and nSTC during this study. *Lensia multicristata* had a broad distribution during this study, while average abundances increased from the PFZ (1.6 ± 2.2 ind. 1000 m^{-3}) to the STC (37.4 ± 20.2 ind. 1000 m^{-3}) (Table 6).

4.4 Group 4

This group consisted of tropical and subtropical species, confined to the STC and nSTC and showing lower abundances than the previous groups. Information on these species within the region are scarce. Several species: *Abylopsis tetragona, Chelophyes appendiculata* and *Muggiaea atlantica* have already been reported in the vicinity of the STC (Pakhomov et al. 1994), and most *A. eschscholtzii, A. tetragona, C. appendiculata, Enneagonum hyalinum, Eudoxoides mitra, Lensia connoidea, L. hotspur* and *M. atlantica* previously recorded within the Southern Benguela region in 1977 and 1978 (Table 11) (Pagès & Gili 1992b). It is important to note that *M. atlantica* was collected in large numbers within the Southern Benguela (up to 14380 ind. 1000 m^{-3}) (Pagès & Gili 1992b), while within this study it occurred only at station 48 and in very low numbers (8.9 ind. 1000 m^{-3}). However, all species within this group have previously been recorded by Gibbons & Thibault-Botha (2002) and many species are distributed throughout most of South Africa's coastline.

4.5 Siphonophore Assemblage Drivers

The Distance Based Linear Model revealed that chlorophyll-*a*, mesozooplankton biomass, mixed layer depth, sea surface salinity and sea surface temperature were all responsible for the

Table 11: Average abundances ± SD (minimum - maximum densities) (ind 1000 m^{-3}) of siphonophore species collected by Pagès and Gili (1992b) within the Southern Benguela region in 1977 (SB 1977) and 1978 (SB1978), and during this study in the Subtropical Convergence (STC) and north of the STC (nSTC).

Species	STC	nSTC	SB (1977)	SB (1978)
Abylopsis eschscholtzii	3.6 ± 5.0 (0 – 7.1)	1.2 ± 2.5 (0 – 4.9)	1.8 ± 4.9 (3.0 – 33.0)	6.1 ± 11.0 (3.0 – 78.0)
Abylopsis tetragona	3.6 ± 5.0 (0 – 7.1)	5.8 ± 6.3 (4.2 – 14.8)	0.4 ± 1.4 (3.0 – 9.0)	1.9 ± 4.5 (3.0 – 22.0)
Chelophyes appendiculata	1.8 ± 2.5 (0 – 3.6)	8.7 ± 9.6 (1.8 – 22.3)	1.4 ± 4.3 (4.0 – 28.0)	1.6 ± 7.0 (3.0 – 61.0)
Enneagonum hyalinum	1.8 ± 2.5 (0 – 3.6)	1.7 ± 2.1 (2.5 – 4.2)	0.1 ± 0.7 (0 – 4.0)	0.5 ± 1.3 (3.0 – 6.0)
Eudoxoides mitra	6.2 ± 6.3 (1.8 – 10.9)	21.5 ± 40.2 (4.2 – 81.6)	1.4 ± 3.1 (4.0 – 18.0)	2.5 ± 5.5 (3.0 – 26.0)
Lensia conoidea		2.1 ± 1.7 (1.8 – 4.2)	8.0 ± 24.6 (4.0 – 107.0)	10.0 ± 25.9 (3.0 – 165.0)

Lensia hotspur	2.7 ± 3.8 (0 – 5.3)	9.8 ± 11.5 (17.0 – 22.3)	2.5 ± 13.0 (5.0 – 101.0)	2.3 ± 12.0 (3.0 - 113.0)
Muggiaea atlantica	4.5 ± 6.3 (0 – 8.9)		653.7 ± 1103.6 (4.0 – 7040.0)	1386.2 ± 2591.2 (3.0 – 14380.0)

siphonophore assemblages observed during this study. This was already stated by Hsieh et al. (2013) where the mesoscale distribution of siphonophores were influenced by the nature of the surrounding water masses (temperature, zooplankton abundance, salinity and chlorophyll-*a*).

Mixed layer depth, SSS and SST however had the greatest impact on their distribution (Table 10). It has been previously stated that temperature and salinity affect the vertical and geographical distributions of siphonophore populations (Pugh 1975; Sanvicente-Añorve & Alba 2009). However, some species can dominate large areas by being able to survive within a wide range of salinities and temperatures (Sanvicente-Añorve & Alba 2009). This was observed for several species such as *Dimophyes arctica*, *Eudoxoides spiralis*, *Lensia hardy* and *L. multicristata*. Siphonophore vertical distribution is also affected by the thermocline, which tends to segregate species as they generally have specific temperature ranges (Pagès & Schnack-Schiel 1996).

There was a clear separation in the siphonophore communities north and south of the SAF within the Atlantic sector of the Southern Ocean (Figure 14A, B). The SAF has previously been described as a biogeographic boundary for zooplankton (Andrews 1966; Deacon 1982; Bekker 1985; Grachev 1991; Koubbi 1993; Froneman et al. 1995; Pakhomov et al. 1999; Pakhomov et al. 2000). Although other boundaries such as the STC and the APF have also been described as important biogeographic boundaries for zooplankton within the Southern Ocean (Rustad 1930; Deacon 1982; Pakhomov et al. 1999; Pakhomov et al. 2000), the effects of those were less clear during this study. The STC is known to separate temperate and Subantarctic communities, while the APF separates Subantarctic and Antarctic communities (Deacon 1982; Grachev 1991; Pakhomov et al 1994; Pakhomov & McQuaid 1996; Pakhomov et al 1999).

The STC is known to be a region of major latitudinal “disturbance” (Pakhomov et al. 1994; Pakhomov & Perissinotto 1997; Froneman et al. 1997; Pakhomov et al. 1999), due to spatial and temporal interactions between the Antarctic Circumpolar Current and the Agulhas retroflection system within which warm-core eddies are regularly generated in the STC area (Lutjeharms & Gordon 1987; Lutjeharms & valentine 1988; Duncombe Rae 1991; Pakhomov et al. 1999). These eddies cross the STC and surrounding waters, and influence the physical, chemical and biological properties of the Subantarctic region (Lutjeharms & Gordon 1987, Pakhomov et al. 1994; Pakhomov & Perissinotto 1997; Pakhomov et al. 1999). This injection of warm and more saline waters into the Subantarctic gives rise to the ability of more temperate siphonophore species to occur in larger areas in the Southern Ocean.

Sea surface salinity was similar in both the MIZ and the SAF (min 33.82, max 33.91), then increased from 34.13 to 35.62 further north of the SAF towards the nSTC. A sharp increase in SST was also observed across the SAF (from 5.8 south to 9.1 °C north of it) coinciding to the findings of Lutjeharms & Valentine (1984) where the SST increased from 5.1 to 9 °C across the front, with a mean temperature of 7 °C. Further north, within the STC there was an increase in species richness (from 6 to 17) from south to north. Sea surface salinity and SST also increased (salinity from 34.78 to 35.52 and temperature from 12.3 to 19.8 °C) from south to north. Seeing that there is a change in the siphonophore community composition at areas which experiences sharp changes in SSS and SST, it could be said that these variables strongly affect the distribution of siphonophores. Therefore, these changes could describe the sudden switch between Antarctic and Temperate species at the SAF as well as the high species diversity at the STC and north of the STC.

Froneman et al. (1995a) described two distinct microphytoplankton communities in the Atlantic sector of the Southern Ocean, north and south of the SAF, which comprised of different groups. These authors suggested that there is a close coupling between microplankton and mesozooplankton distribution. The biomass of mesozooplankton also affected the distribution of siphonophores (Figure 17). This could be due to various factors. Hsieh et al. (2013) described the distribution of siphonophores to be consistent with that of zooplankton abundance and that the distribution of zooplankton biomass affected the overall spatial distribution of siphonophores in the Taiwan Strait (TS). According to Pakhomov et al. (2000), copepods were the dominant taxa in the mesozooplankton of the Southern Ocean during this cruise. Since siphonophores mostly feed on copepods (Purcell 1981; Purcell 1997; Hsieh et al. 2013), their distribution could be largely affected by the distribution and abundance of copepods along the transect. Pugh (1986) stated the size, distribution and abundance of the potential prey population at any position and depth plays an important role in determining the specific siphonophore assemblage associated with it.

4.6 Conclusions

The siphonophore communities within the Atlantic Sector of the Southern Ocean are diverse and although it was not possible to provide in-depth patterns of zonation between the different physical zones described by Pakhomov et al. (2000), we observe at least a shift between the Antarctic and temperate communities throughout the Atlantic Sector. As previously mentioned, the different frontal systems within the Southern Ocean affect the distribution of phytoplankton and zooplankton (Rustad 1930; Andrews 1966; Deacon 1982; Bekker 1985; Grachev 1991; Koubbi 1993; Pakhomov et al. 1994; Froneman et al. 1995; Pakhomov and McQuaid 1966; Pakhomov et al. 1999; Pakhomov et al 2000) and while the importance of the SAF as a biogeographic barrier for siphonophore communities is clear, the effect of other major frontal systems on the distribution of these organisms is not yet fully resolved. This study provides supplementary information on the assemblage structure and diversity of siphonophores within the Southern Ocean, adding towards our understanding of the role these organisms may play within this vast ecosystem.

Unfortunately, due to the lack of available samples and access to the environmental data the results of this study remain limited. Proper curation of samples is crucial to ensure that archived samples are available to either supplement current data or to study changes over time. As a result, this will help us to understand how the ecosystems of the world's oceans are changing over time and help us to understand the effects of climate change. It is also important to consider further investigation into the species composition, abundance and distribution of siphonophores within the region. More intense sampling across the Southern Ocean is needed, with increased effort especially at the different frontal systems. Sampling also needs to take place at greater depths. Pagès et al. (1994) described that the species diversity of cnidarians is highest at depths between 500 and 1000 m. Calycophorans tend to have an epipelagic (0 – 500 m) distribution (Pages et al. 1994), but during this study sampling only took place within the first 300 m, possibly excluding valuable information on this group of holoplanktonic organisms. The fact that some species also undergo diel vertical migration (Pugh 1984) possibly limits the success rate of sampling if not a great enough depth is sampled, especially in areas like Antarctica where the sun does not set during summer. Siphonophores have been receiving a lot more attention over the past few decades and various new and more effective methods of sampling are being implemented. However, we need to continue improving research strategies in this field, which will help us to gain a better understanding of how these organisms operate, as well as their ecological roles in the various ecosystems throughout the world's oceans.

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5 *Muggiaea bargmannae* (Cnidaria: Hydrozoa: Siphonophorae) from the Antarctic waters in the Atlantic sector of the Southern Ocean

5.1 Abstract

Muggiaea bargmannae is a very poorly studied bipolar species of diphyid siphonophore, despite it being one of the dominant species of siphonophore in the vicinity of the Antarctic mainland. This study presents a morphological description of *M. bargmannae* as well its distribution and abundances in the Marginal Ice Zone (MIZ) and Permanently Open Ocean Zone (POOZ) within the Atlantic sector of the Southern Ocean during January to February 1993. During the present study, individuals of *M. bargmannae* were collected at three stations, two within the Marginal Ice Zone and one within the southern Permanently Open Ocean Zone. Abundances were very low within the southern part of the Marginal Ice Zone, but increased northward towards the southern Permanently Open Ocean Zone. There were also noticeable differences in the size and morphology of individuals, a new finding for this work, which is discussed.

Keywords: Diphyidae, nectophores, siphonophores, taxonomy

5.2 Introduction

The Suborder Calycophorae is a monophyletic clade within the Codonophora and consists of six families: Abylidae, Clausophyidae, Diphyidae, Hippopodiidae, Pryidae and Sphaeronectidae (Totton 1965). Calycophoran siphonophores possess nectophores and bracts (except in Hippopodiidae) but lack a pneumatophore (Totton 1965). Like the Cystonecta and Physonectae, Calycophorans have a stem (siphosome) supporting cormidia, which are essentially groups of zooids distributed in a repetitive or iterative fashion (Totton 1965; Mapstone 2015). Each of the three above mentioned suborders possess a cormidium containing a gastrozooid with a tentacle used for feeding, and one or more sexual zooids used for reproduction (Mapstone 2015). However, Calycophorans are monoecius and both sexes develop on the same individual, but at different times to prevent self-fertilization (Mapstone 2015). A cormidium containing a bract and a gastrozooid with sexual gonophores breaks away from the polygastric individual to form a free-swimming sexual eudoxid which persists as a separate individual (Totton 1965; Kirkpatrick & Pugh 1984).

The family Diphyidae consists of c. 45 species and they dominate the surface waters across the world’s oceans (Mapstone 2015). Diphyids consists of two dissimilar linearly aligned nectophores that are streamlined (Kirkpatrick & Pugh 1984; Mapstone 2015). In front is an anterior nectophore, which is followed by a smaller posterior nectophore (Figure 1) (Mapstone 2015). Diphyids’ stems are withdrawn into the hydroecium of the posterior nectophore, which is used for swimming (Mapstone 2015). These individuals are filled with a nectosac, have a moutplate adjacent to the ostium and are usually ridged (Mapstone 2009; Mapstone 2015). The anterior nectophore posseses a somatocyst, while the posterior does not (Totton 1965; Kirkpatrick & Pugh 1984; Mapstone 2015). The somatocyst is used for food storage and could also acts as a buoyancy organ (Mapstone 2009; Mapstone 2015). Diphyids’ stems possess multiple cormidia, each containing a bract, gastrozooid, tentacle and, when mature, a gonophore (Mapstone 2015).

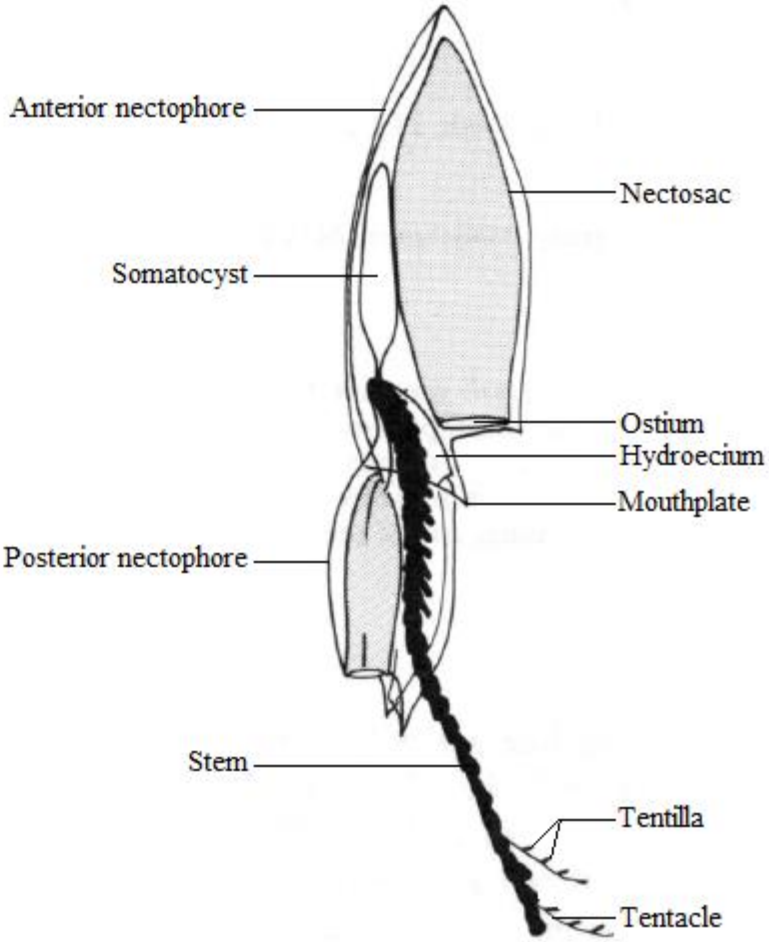

Figure 1: Polygastric stage of a Diphyid siphonophore (*Chelophyes appendiculata*) modified from Bone & Trueman (1982).

Individuals of the genus *Muggiaea* have pentagonal-shaped anterior nectophores, which develop a complete dorsal ridge but support no visible ostial teeth (Totton 1965). These individuals also do not develop a posterior nectophore (Totton 1965; Kirkpatrick & Pugh 1984). They have a deep hydroecium, a divided mouth plate and the somatocyst is positioned very close to the wall of the nectosac (Kirkpatrick & Pugh 1984). There are currently only four described species of the genus *Muggiaea: M. atlantica, M. bargmannae*, *M. delsmani* and *M. kochi* (Totton 1965). *Muggiea atlantica* and *M. kochi* are neritic and are seldom found in open waters (Kirkpatrick & Pugh 1984). *Muggiaea delsmani* occurs in the low salinity water of the Java Sea, and *M. bargmannae* is a bipolar species (Totton 1965).

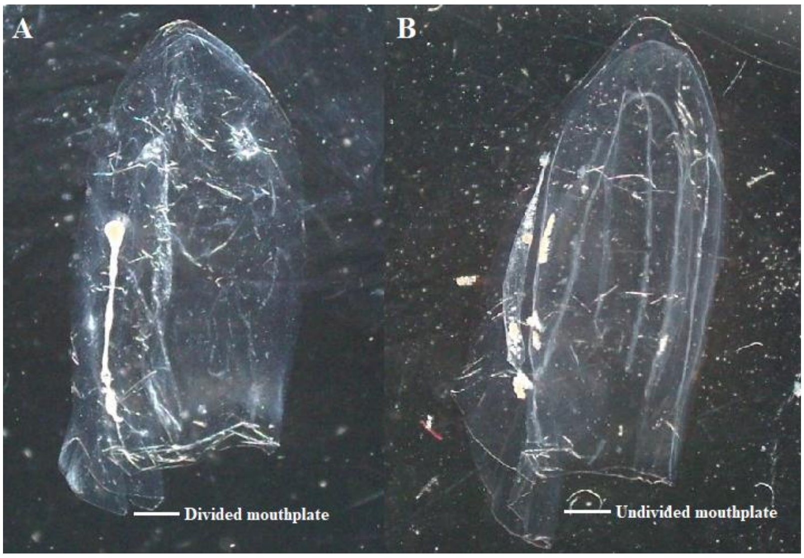

Figure 2: Anterior nectophore of *Muggiaea bargmannae* (A) and *Dimophyes arctica* (B) collected during the SAAMES II cruise from 17 January to 21 February 1993 onboard the RS *S.A. Agulhas* along the WOCE SR2 line.

Muggiaea bargmannae was first described by Totton (1954). He mentioned that *M. bargmannae* bears some resemblance to *Dimophyes arctica* (Figure 2) and can be mistaken for *D. arctica* when preserved in plankton trawls (Totton 1954). However, *M. bargmannae* can be separated from *D. arctica* by its divided mouth plate (Figure 2) (Totton 1954). This species has been reported in the coastal waters of Antarctica: in the Antarctic Peninsula (Panasiuk-Chodnicka & Żmijewska 2010; Correa 2013; Lindsay et al. 2014); the Weddell Gyre (Montú & Cordeiro 1986; Pagès et al. 1994; Pagès & Kurbjeweit 1994; Pagès et al. 1996; Pagès & Schnack-Schiel 1996; Lindsay et al. 2014); the Lazarev Sea (Lindsay et al. 2014); in and north of the Riiser-Larsen Sea (Pagès & Gili 1989; Lindsay et al. 2014); the Cosmonaut Sea (Lindsay et al. 2014); Lützow-Holm Bay (Toda et al. 2010); Adélie Land (Toda et al. 2014); Prydz Bay (Yang et al. 2016); the D' Urville Sea (Lindsay et al. 2014); and the East Kerguelen Island (Carlotti et al. 2015). Individuals have also been collected in the Arctic's Canada Basin

(Beaufort Sea) towards the Arctic sea (Kosobokova & Hopcroft 2010; Zhang & Lin 2001; Wang et al. 2014) and in the Greenland Sea (Richter 1994). It is important to note that individuals of *M. bargammae* have also been collected in Sagami Bay, Japan (Grossmann & Lindsay 2013), and the Sea of Japan (East Sea) (Park & Won 2004) which suggests that this species has a wider distribution than previously suggested by Totton (1954).

Pagès & Kurbjeweit (1994) found *M. bargmannae* to be the most abundant siphonophore across the Weddell Sea, reaching densities up 1172 ind. 1000 m^{-3} while mostly being concentrated between 100 and 500 m depths. Eudoxids of *M. bargmannae* were less abundant than asexual individuals, with densities up to 447 ind. 1000 m^{-3}. However, these individuals were collected exclusively below 200 m and were most prevalent between 200 and 500 m depth (Pagès & Kurbjeweit 1994). Pagès & Schnack-Schiel (1996) found lower abundances (up to 782.5 ind. 1000 m^{-3}) of *M. bargmannae* nectophores within the eastern Weddell Sea, but more eudoxids (up to 1390 ind. 1000 m^{-3}). They collected these individuals at all oceanic stations, occurring mostly below the thermocline (Pagès & Schnack-Schiel 1996). However, Pagès & Kurbjeweit (1994) found *M. bargmannae* to be concentrated in the thermocline and abundances decreased with an increase in depth. Only a few nectophores were collected in the upper cold-water (-1.8°C) (Pagès & Kurbjeweit 1994).

The vertical distribution of *Muggiaea bargmannae* is similar to that of *Dimophyes arctica* (Pagès & Kurbjeweit 1994). The vertical distribution of both the above-mentioned species were found to be similar to that of *Microcalanus pygmaeus*, which was the most abundant copepod collected in the Weddell Sea area (Kurbjeweit 1993; Pagès & Kurbjeweit 1994). Since copepods are the main prey items of siphonophores (Purcell 1981; Purcell 1997; Hsieh et al. 2013), we can believe that the vertical distribution of *M. bargmannae* and *D. arctica* are related to both the hydrography and their prey. However, the eudoxids of *M. bargmannae* are found below the thermocline in the mesopelagic area, which could suggest that temperature may be more important than prey availability when it comes to reproduction (Pagès & Kurbjeweit 1994). Even though *M. bargmannae* inhabits cold waters, it is believed that the eudoxids prefer temperatures above 0°C for reproduction (Pagès & Kurbjeweit 1994).

Muggiaea bargmannae is still poorly studied and there is little information regarding its morphology and distribution. Since these individuals occur at the two different poles it is difficult and expensive to obtain specimens for investigation. This study aims to elaborate on the morphology and distribution of the infrequently collected *M. bargmannae* within the Atlantic sector of the Southern Ocean.

5.3 Materials and Methods

Specimens of *Muggiaea bargmannae* were collected during the second cruise of the South African Marine Ecosystem Study (SAAMES II) from 17 January to 21 February 1993 onboard the RS *S.A. Agulhas* along the WOCE (World Ocean Circulation Experiment) SR2 line (Figure 3). The individuals studied were collected at station 5, 13 and 16 (Figure 3) within the Marginal Ice Zone (MIZ) and the Permanently Open Ocean Zone (POOZ). Specimens were collected using a Bongo net (300 µm mesh size; 0.25 m^2 mouth area). The net was towed obliquely between 300 m and the surface at a speed of between 1.5 to 3 knots, and the volume of water filtered through the net was calculated using electronic flowmeter data (Pakhomov et al. 1999; Pakhomov et al. 2000). Samples were then preserved in 4-6% buffered saline formalin (Pakhomov et al. 1999; Pakhomov et al. 2000) and individuals of *M. bargmannae* were identified using descriptions from Totton (1954) and Pugh (1999). Individuals were identified, photographed and measured using a Leica S9i stereo microscope and the Leica Application Suite (LAS) V4.12 software. An individual was also drawn using ibisPaint V5.5.5 software on a Samsung Galaxy Note 1 tablet.

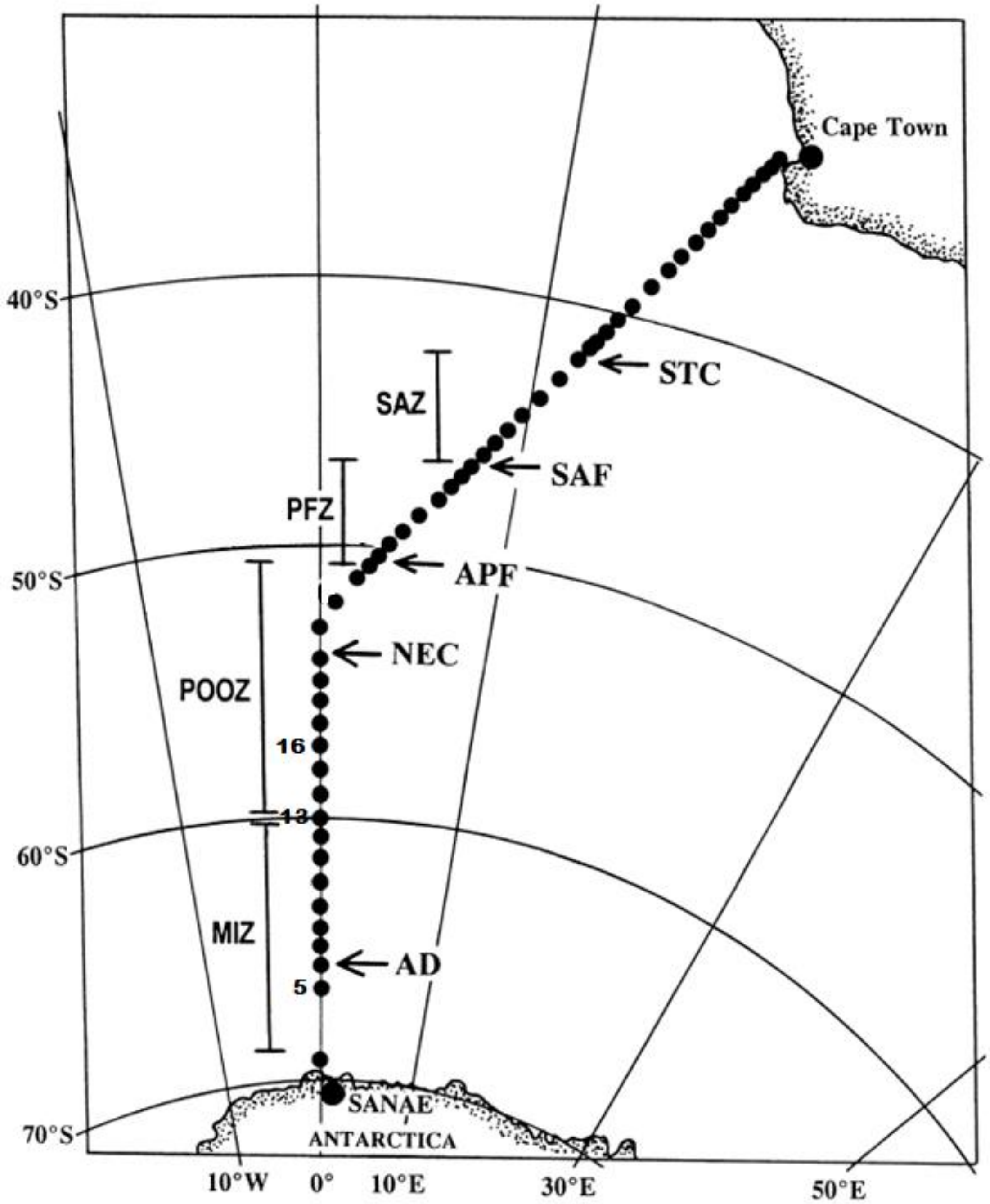

Figure 3: Cruise track of the SAAMES II voyage between South Africa and Antarctica, including the station positions *Muggiaea bargmannae* was collected. Edited from Pakhomov et al. (2000), STC: Subtropical Convergence, SAF: Subantarctic Front, APF: Antarctic Polar Front, NEC: northern expansion of the zero isotherm, AD: Antarctic Divergence, SAZ: Subantarctic Zone, PFZ: Polar Frontal Zone, POOZ: Permanently Open Ocean Zone, MIZ: Marginal Ice Zone.

5.4 Taxonomy

Phylum Cnidaria Verrill, 1965

Subphylum Medusozoa Petersen, 1979

Class Hydrozoa Owen, 1843

Subclass Hydridolina Collins, 2000

Order Siphonophorae Eschscholtz, 1829

Suborder Calycophorae Leuckart, 1854

Family Diphyidae Quoy & Gaimard, 1827

Subfamily Diphyinae Quoy & Gaimard, 1827

Genus *Muggiaea* Busch, 1851

Species *Muggiaea bargmannae* Totton, 1954

(Figures 4 – 6; Table 1)

Abbreviated Synonymy: *Muggiaea bargmannae* Totton, 1954: 121, text-figure 63; Totton, 1965: 183, text-figure 120; Pagès & Gili, 1989: 56; Pugh, 1999: 491, figure 3.75; Zhang & Lin, 2001: 254, figure 1; Park & Won, 2004: 183, figure 3 (A-C).

Examined material: Atlantic sector of the Southern Ocean, close to the Antarctic mainland. Thirty individuals collected at both station 13 (60°03’S-00°00’E) and 16 (57°28’S-00°00’E) from 17 January to 23 February 1993. In the area the sun does not set during above-mentioned months; therefore, collection times were insignificant. Sampling occurred within the upper 300 m of the water column and specimens were preserved in 4-6% buffered saline formalin. Collected during the second cruise of the South African Marine Ecosystem Study (SAAMES II) by Pakhomov et al. (1999; 2000).

Description: Anterior nectophore (Figures 4, 5) containing nectosac reaching near the apex of the nectophore. It has longitudinal folds instead of crest-like ridges. The hydroecium is shallow and the mouth plate divided and slanted. The somatocyst originates from the top of the hydroecium to halfway between nectosac. The somatocyst forms a bulge at the apex and generally contain oil droplet/s. Average measures (min-max) are listed in Table 1. Posterior nectophore is not developed (Totton 1954). No eudoxids were collected.

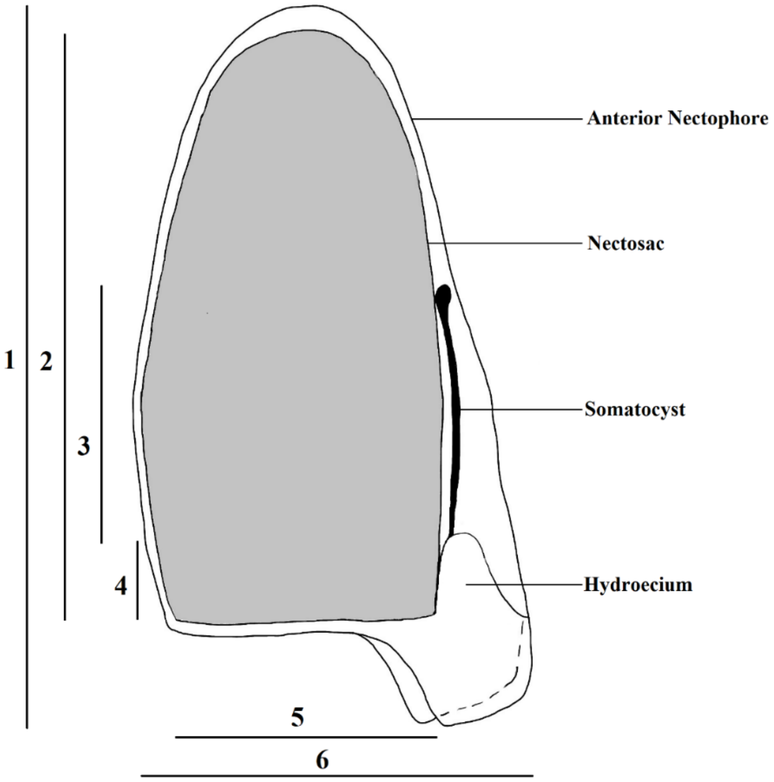

Figure 4: Measurements taken from *Muggiaea bargmannae* specimens collected during the SAAMES II cruise from 17 January to 21 February 1993 onboard the RS *S.A. Agulhas* along the WOCE SR2 line. 1: Anterior nectophore height; 2: Nectosac height; 3: Somatocyst length; 4: Hydroecium height; 5: Ostium width; 6: Anterior nectophore width.

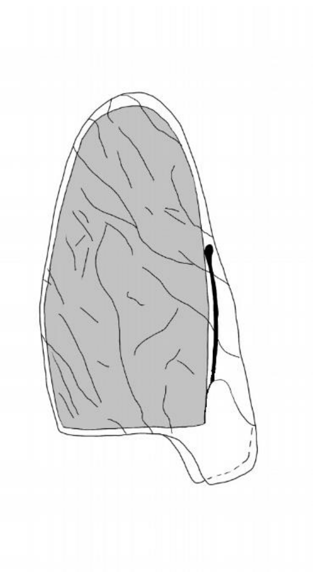

Figure 5: Illustration of *Mugiaea bargmannae* displaying the folds surrounding the nectophore.

Variation: A total of 60 individuals of *Muggiaea bargmannae* (30 ind. each from station 13 and 16) were measured from the Antarctic waters in the Atlantic Sector of the Southern Ocean. The morphology of the individuals was consistent with the descriptions of Totton (1954) and Pugh (1999). The various morphological features measured on each individual are shown in Figure 4.

Average measures of each feature from the two above-mentioned stations were very similar and individuals averaged 5.4 mm in height (Table 1). Pagès & Kurbjeweit (1994) described the nectopohores to be between 1-6 mm in height. However, during this study nectophores were never shorter than 3.48 mm and exceeded 6 mm (up to 7.27 mm) in height as described by Pagès & Kurbjeweit (1994). The height and width of *M. bargmannae* individuals examined during this study (Table 1) were similar to that described by Zhang & Lin (2001) which found the nectophore length and width to vary from 2.2-7.0 mm and 1.2-4.2 mm respectively. It is important to note the folds on the nectophore (Figure 5), a feature shared by all the individuals examined. The somatocyst in most cases also contained oil and varied in size and shape (Figure 6: Table 1). Totton (1954) described the somatocyst of *Muggiaea* *bargmannae* as being sausage-shaped when well-fed, however in Figure 6 it can be observed that in the individuals collected during this study the somatocyst thickens from the hydrocium towards the top and forms a "bulge".

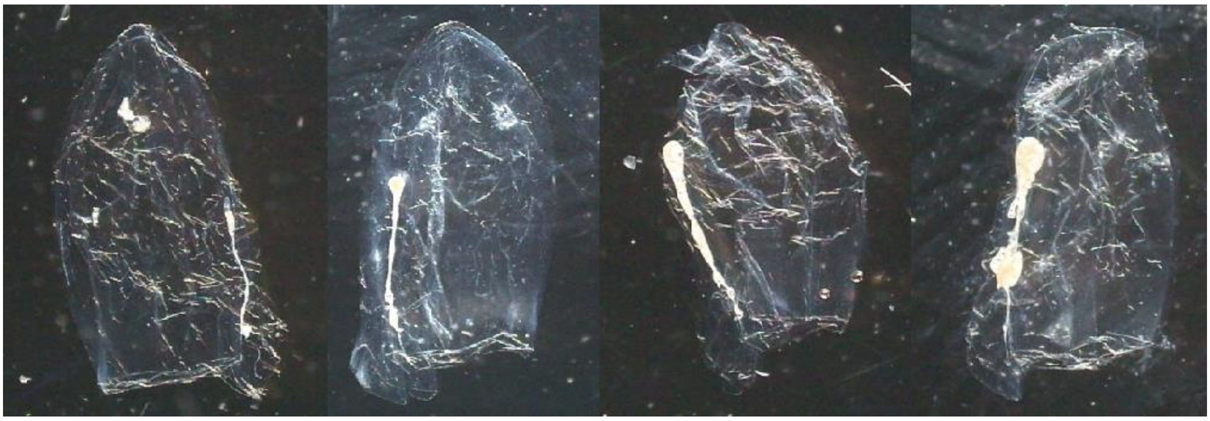

Figure 6: Different shapes and sizes of the somatocysts of *Muggiaea bargmannae* collected during the SAAMES II cruise from 17 January to 21 February 1993 onboard the RS *S.A. Agulhas* along the WOCE SR2 line.

Although no eudoxids of *Muggiaea bargmannae* were collected here, this could be due to the large mesh size (300 μm) used during collection. Pagès & Kurbjeweit (1994) described the eudoxids of *M. bargmannae* to be between 1-2 mm in length, and therefore would not have been collected by the nets used during this study. Another factor to consider is that the eudoxids are almost exclusively collected below 200 m and are mostly present below the thermocline (Pagès & Kurbjeweit 1994). By the odd chance that eudoxids might have been collected either by the net clogging up or individuals becoming stuck to other organisms, the thermocline of these stations was more than 300 m deep (data not shown) and since only the upper 300 m of the water column were sampled the eudoxid's could possibly have been missed.

Table 1: Average measures (minimum-maximum) in millimeters of the different morphological features of *Muggiaea bargmannae* collected during the SAAMES II cruise from 17 January to 21 February 1993 onboard the

RS *S.A. Agulhas* along the WOCE SR2 line. Refer to Figure 4 for visual representation of the morphological features measured.

Sample	13	16
Anterior Nectorphore Height	5,45 (3.48 - 7.27)	5,35 (3.58 - 6.85)
Anterior Nectophore Width	2,71 (1.74 - 3.72)	2,74 (1.84 - 3.62)
Hydroecium Height	0,73 (0.44 - 0.95)	0,72 (0.50 - 1.06)
Nectosac Height	4,60 (3.02 - 6.22)	4,52 (2.92 - 5.98)
Ostium Width	1,75 (1.05 - 2.57)	1,88 (1.19 - 2.49)
Somatocyst Length	1,88 (1.02 - 3,30)	1,85 (1.28 - 2,42)
Somatocyst Width	0,25 (0.04 - 0.47)	0,23 (0.04 - 0.36)

Geographic distribution: This species occurs around the Antarctic mainland: the Antarctic Peninsula(Panasiuk-Chodnicka & Żmijewska 2010; Correa 2013; Lindsay et al. 2014); the Weddell Gyre (Montú & Cordeiro 1986; Pagès et al. 1994; Pagès & Kurbjeweit 1994; Pagès et al. 1996; Pagès & Schnack-Schiel 1996; Lindsay et al. 2014); the Lazarev Sea (Lindsay et al. 2014); in and north of the Riiser-Larsen Sea (Pagès & Gili 1989; Lindsay et al. 2014); the Cosmonaut Sea (Lindsay et al. 2014); Lützow-Holm Bay (Toda et al. 2010); Adélie Land (Toda et al. 2014); Prydz Bay (Yang et al. 2016); the D' Urville Sea (Lindsay et al. 2014); and the East Kerguelen Island (Carlotti et al. 2015). It also occurs in the Arctic's Canada Basin

(Beaufort Sea) towards the Arctic sea (Zhang & Lin 2001; Kosobokova & Hopcroft 2010; Wang et al. 2014); in the Greenland Sea (Richter 1994); in Sagami Bay, Japan (Grossmann & Lindsay 2013); and the Sea of Japan (East Sea) (Park & Won 2004).

During this study, *Muggiaea bargmannae* was exclusively collected between 57°28’ S (Station 16; Figure 3) and 66°47’S (station 5). Within this area it was the most abundant species (169.4 ind. 1000 m^{-3}) of siphonophore. Average abundances of *M. bargmannae* were highest (412.6 ind. 1000 m^{-3}) at station 16 within the POOZ and abundances decreased from north to south. Station 13 had an abundance of 262.8 ind. 1000 m^{-3} and the most southern station within the MIZ (station 5) only delivered one individual of *M. bargmannae*. However, Pagès et al. (1994) found this species to increase in abundance from north to south (from the southern POOZ to the southern MIZ). Densities of *M. bargmannae* collected during this study (up to 412.6 ind. 1000 m^{-3}) was however substantially lower than those collected by Pagès & Kurbjeweit (1994) and Pagès & Schnack-Schiel (1996) (up to 1172 and 782.5 ind. 1000 m^{-3} respectively).

5.5 Conclusions

Muggiaea bargmannae is mostly confined close to the Antarctic mainland and is usually the dominating species of siphonophore in the area occurring in high abundances. Not much data on the horizontal and vertical distribution of these organisms are available and descriptions of the eudoxid stage is lacking. The morphology of the individuals between the two different stations were very similar and mostly agreed to what has been previously described. Although Totton (1954) described the somatocyst to be sausage-shaped, it was not observed in individuals collected during this study. Increasing the sample size should allow us to determine whether the somatocyst in fact varies in its morphology or if these individuals examined during this study were not as “well-fed” for the somatocyst to become sausage-shaped.

This study presents the distribution, abundances and important morphological measures of *Muggiaea bargmannae* which can be used to elaborate on this species and compare them to other specimens being collected in the future. In future better curation of samples is needed to ensure that these individuals are not as damaged from fixation. Future studies aiming towards the collection of *M. bargmannae* should consider a smaller mesh size (≤ 100 µm) to include the collection of the eudoxid stage. Sampling at greater depth's is also required, especially when the thermocline is very deep, allowing us to better understand how these organisms operate throughout the water column.

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