

Latitudinal changes in siphonophore assemblages across the Atlantic sector of the Southern Ocean

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Siphonophores are commonly considered to be useful indicators of water masses and water-mass movement, but their employment as such across the wider Southern Ocean has not so far been attempted. We redress this here using archived samples, collected during January–February 1993 along a transect from Cape Town to the South African National Antarctic Expedition (SANAE) base in Antarctica, and compare the patterns generated with those determined from a prior analysis of whole assemblages at lower taxonomic resolution. Twenty-one species were identified from 18 of the original 53 samples collected, and two distinct assemblages were confirmed as separated by the Sub-Antarctic Front. That to the south was characterised by low diversity and high abundance and was dominated by cold-water specialists, whereas that to the north comprised a larger number of subtropical and temperate species at low abundance. Assemblage structure was strongly influenced by the mixed layer depth, sea surface salinity and chlorophyll *a* concentration, as well as mesozooplankton biomass. Congruence with the whole-assemblage study was high, indicating that this taxon can be suitably employed as a proxy in studies such as this. The study emphasises the value of archived plankton samples and makes a plea for better curation.

Keywords: archived plankton samples, biogeography, *Dimophyes arctica*, diversity, mesozooplankton biomass, *Muggiaea bargmannae*, oceanography, Sub-Antarctic Front

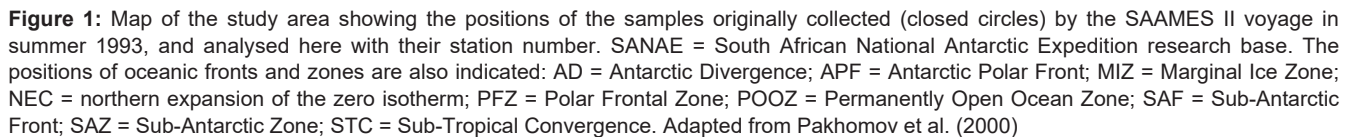
Introduction

The Southern Ocean extends southward from approximately 40° S to the Antarctic continent. 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 and Klinck 1986; Orsi et al. 1995; Ansorge et al. 2005). This eastward-flowing current is associated with four circumpolar 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, 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 Sub-Antarctic Front (SAF), the Sub-Antarctic Zone (SAZ), and the Sub-Tropical Convergence (STC) (Figure 1).

The Southern Ocean is considered 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). Productivity tends to be higher around islands

and at fronts, which can be attributed to aeolian transport (Korb et al. 2004) and an accumulation of phytoplankton through the convergence/divergence of different water masses (Olson and Backus 1985; Laubscher et al. 1993). The melting of sea-ice and the resuspension of shelf sediments also contribute iron into the Southern Ocean (Raiswell et al. 2008).

Copepods, ostracods and pteropods are frequently the most common components of zooplankton assemblages in the Southern Ocean (Pakhomov et al. 2000; Pakhomov and Froneman 2004), although salps and euphausiids can be locally important (Pakhomov et al. 2000; Hunt et al. 2011; Hauke et al. 2014). Mesozooplankton abundance and biomass tend to be highest in the region of the APF and the STC and lowest in the POOZ and the SAZ (Pakhomov et al. 2000; Pakhomov and Froneman 2004). Zooplankton assemblages are dominated by herbivores, detritivores and omnivores, and though carnivores generally make up only between 10% and 30% of the overall biomass, they may play a locally controlling role (Pakhomov et al. 1999). Chaetognaths tend to dominate assemblages in the SAZ, whereas siphonophores dominate those north of the STC (Pakhomov et al. 2000).



Several studies in the Atlantic and Indian sectors of the Southern Ocean have revealed that the STC, SAF,

This study uses all of the extant archived samples of zooplankton that were collected during the SAAMES II (South African Antarctic Marine Ecosystem Study) voyage in summer (January–February) of 1993, the full results of

which have been detailed by Pakhomov et al. (1999, 2000). In summary, and following Pakhomov et al. (1999, 2000), zooplankton samples were collected using a bongo net (mouth area 0.25 m², mesh size 300 µm) towed obliquely from 300 m to the surface, at stations situated approximately every 50 nautical miles along the World Ocean Circulation Experiment (WOCE) SR2 transect line, extending from Cape Town to the South African Antarctic base (i.e. SANA [South African National Antarctic Expedition]) (Figure 1). All nets were fitted with an electronic flowmeter, and samples were preserved in 4–6% buffered formalin on collection. Conductivity, temperature and depth (CTD) profiles were obtained at regular intervals of ~25' latitude, with water samples for the analysis of photosynthetic pigments being collected at the surface.

At the time of the voyage, Pakhomov et al. (1999, 2000) 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; the MIZ was located at 60° S and the pack ice at 69°10' S. Sea surface temperature (SST) gradually increased from a minimum at the AD northwards to the SAZ, and then increased rapidly (by ~7 °C) to the STC. The 'northern expansion of the zero isotherm' (NEC) was reached at ~54°10' S. Chlorophyll *a* concentrations (Figure 2) were highest at the ice-edge and within the MIZ; they decreased markedly between 60° and 51° S; and they were elevated at, and north of, the APF, the SAF and the STC (Pakhomov et al. 1999, 2000). Mesozooplankton biomass (Figure 2) was similarly patchy, with peaks in the MIZ, at the NEC, within the PFZ, at the southern proximity of the SAF,

and at the STC (Pakhomov et al. 1999, 2000). Carnivorous zooplankton biomass (i.e. amphipods, euphausiids, decapods, fishes, chaetognaths and jellyfish) remained low throughout the study (Figure 2). Pakhomov et al. (2000) described seven different assemblages of mesozooplankton within the Atlantic sector of the Southern Ocean, most of which coincided with the physical zones identified by the oceanographic data (Figure 1). These authors stressed the importance of the SAF as a biogeographic boundary (Pakhomov et al. 2000).

Laboratory analysis

All siphonophores were identified and counted from all the samples available, without subsampling, using a Leica S9i stereo microscope at various magnifications, following the methods of Totton (1965), Pugh (1999), Pagès and Gili (1992b) and Mapstone (2009). Specimens of the suborder Calycophorae were identified using, and counted from, the anterior nectophores of the polygastric stage. No members of the families Prayidae, Sphaeronectidae or Hippopodiidae were detected. Specimens of the suborder Physonectae were identified from their nectophores (*Halitemma* species were confirmed according to Pugh and Baxter [2014]), and in the absence of pneumatophores were simply regarded as present or absent. No specimens of suborder Cystonectae were collected. All species names were checked against the World Register of Marine Species (WoRMS 2019). When specimens were too damaged for full identification, counts were noted but excluded from further analysis.

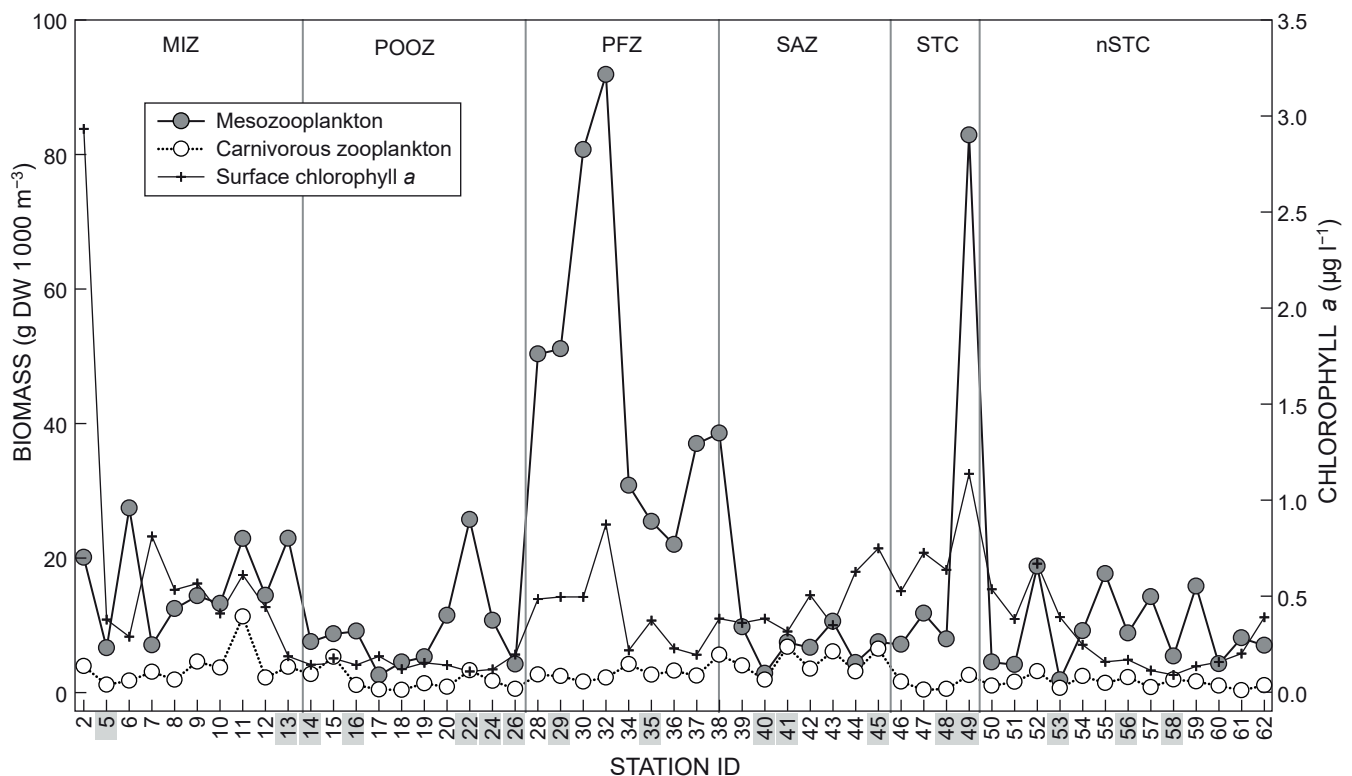


Figure 2: The distribution of mesozooplankton biomass, carnivorous zooplankton biomass, and surface chlorophyll *a* across the Southern Ocean at the time of the study (January–February 1993). The positions of sampling stations, along with the oceanic fronts and zones, are shown in Figure 1; nSTC = north of the Sub-Tropical Convergence. Stations studied here are shaded grey. Data from Pakhomov et al. (2000)

Abundances (ind. 1 000 m⁻³) were then estimated using the volume of water sampled by the net.

Numerical methods

The diversity of the siphonophore assemblages sampled at each station was determined using the Shannon Index (H'), following Roth et al. (1994).

To examine the similarity between the numerical composition of samples, data were first fourth-root-transformed and the Bray–Curtis resemblance computed between each (Clark and Gorley 2015). *Lensia cossack*, *L. pannikari* and *Muggiaea atlantica* were found at just one station in low abundance and were removed from the analysis. The resulting similarity matrix was visualised using both a cluster-analysis with group-average linkage, and nonmetric multidimensional scaling (nMDS), although only the results from the latter are shown here.

To test whether there was congruity between our data and those of Pakhomov et al. (2000), and to test for significant differences in the multivariate structure of assemblages in space, we used ANOSIM. The *a priori* areas (factors) tested were those identified by Pakhomov et al. (2000) from their broader study: MIZ, POOZ, PFZ, SAZ, STC and nSTC (north of the STC).

A distance-based linear model (distLM) was used to determine which of the measured environmental variables contributed to the structure of the observed siphonophore assemblages. The environmental variables included as inputs in the distLM were sea surface salinity (SSS), sea surface temperature (SST), chlorophyll *a* concentration, mixed layer depth (MLD) and mesozooplankton biomass. All variables were log₁₀(*x*+1)-transformed and normalised prior to use; the model was run in a sequential manner, and

significance reported relative to adj. R^2 . The outputs of the distLM were visualised using distance-based redundancy analysis (dbRDA).

Finally, the siphonophores responsible (>10%) for the identity of assemblages were determined using SIMPER. All statistical analyses were performed using PRIMER 7 and PERMANOVA+ (Clarke and Warwick 2001; Anderson et al. 2008; Clarke and Gorley 2015). Figures were created using Ocean Data View (ODV) software (Schlitzer 2020) and SigmaPlot 12.5.

Results

Abundance and diversity

Twenty-one species of siphonophores were collected: 19 Calycophorae and two Physonectae (Table 1). *Diphyes antarctica* and *Muggiaea bargmannae* shared a similar distribution in the south (Table 1; Figure 3), with densities between 19 and 25 ind. 1 000 m⁻³ and between 263 and 413 ind. 1 000 m⁻³, respectively. *Dimophyes arctica* was collected at all stations in abundances that were generally large but variable (avg. 137 ind. 1 000 m⁻³ [SD 152], max. 519 ind. 1 000 m⁻³), and was the only species collected at stations 14, 22, 24, 26 and 29.

In addition to *D. arctica*, three other species were found within the SAZ: *Eudoxoides spiralis*, *Lensia multicristata* and *L. hardy* (Table 1; Figure 3). All three of these species were also found at more northern latitudes, where they were generally more abundant. The balance of species was all found north of the STC (Table 1; Figure 3).

Species diversity (Figure 4) was generally lowest for stations within the POOZ (except station 16), the PFZ and the SAZ (Shannon H' <0.20) and was highest for

Table 1: Minimum–maximum abundance (ind. 1 000 m⁻³) of siphonophores in each of the *a priori* zones of Pakhomov et al. (2000), across the sampling area during January–February 1993. MIZ = Marginal Ice Zone; POOZ = Permanently Open Ocean Zone; PFZ = Polar Frontal Zone; SAZ = Sub-Antarctic Zone; STC = Sub-Tropical Convergence; nSTC = north of the Sub-Tropical Convergence

Species	Zone (No. of samples)					
	MIZ (2)	POOZ (5)	PFZ (2)	SAZ (3)	STC (2)	nSTC (4)
<i>Abylopsis eschscholtzii</i>					0–5.34	0–2.47
<i>Abylopsis tetragona</i>					0–3.56	0–2.47
<i>Chelophyes appendiculata</i>					0–3.56	1.80–22.27
<i>Dimophyes arctica</i>	4.10–176.24	11.76–519.21	14.05–380.56	17.50–306.50	32.06–133.30	37.78–157.00
<i>Diphyes antarctica</i>	0–18.55	0–25.43				
<i>Enneagonum hyalinum</i>					0–3.56	0–4.23
<i>Eudoxoides spiralis</i>				1.56–8.95	7.12–17.77	0–39.59
<i>Eudoxoides mitra</i>					1.78–10.69	0–81.64
<i>Lensia conoidea</i>						0–4.23
<i>Lensia cossack</i>						0–37.11
<i>Lensia fowleri</i>					0–1.78	0–17.32
<i>Lensia multicristata</i>			0–3.12	0–29.08	23.11–51.65	0–38.19
<i>Lensia hardy</i>				0–4.47	8.89–28.50	0–12.69
<i>Lensia hotspur</i>					0–5.34	0–22.27
<i>Lensia subtilis</i>					0–5.34	0–49.48
<i>Lensia meteori</i>					0–5.34	0–3.60
<i>Lensia panikkari</i>					0–1.78	
<i>Muggiaea atlantica</i>					0–8.90	
<i>Muggiaea bargmannae</i>	2.05–262.82	0–412.58				
<i>Halitemma rubrum</i>						Present
<i>Nanomia bijuga</i>					Present	

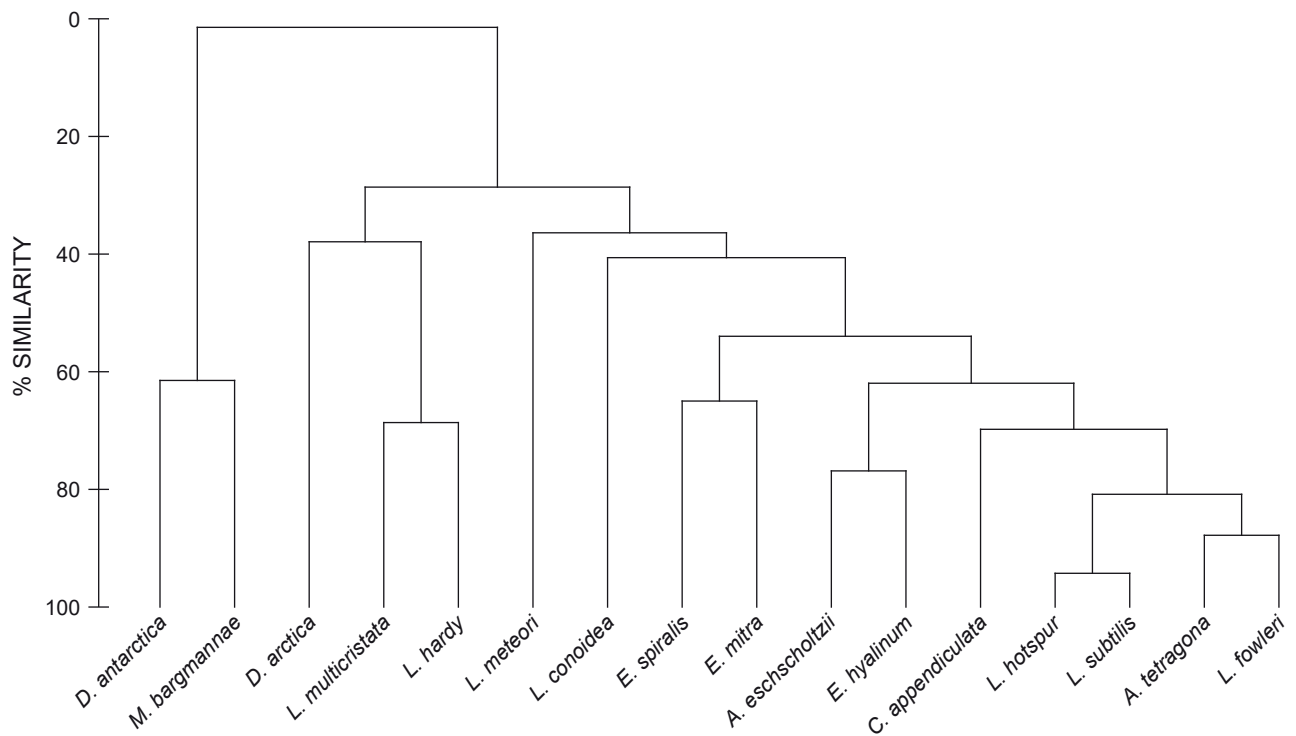


Figure 3: Cluster analysis (Bray–Curtis index, group-average linkage) showing the similarity in the distribution of siphonophore species across the Southern Ocean. See Table 1 for full species names

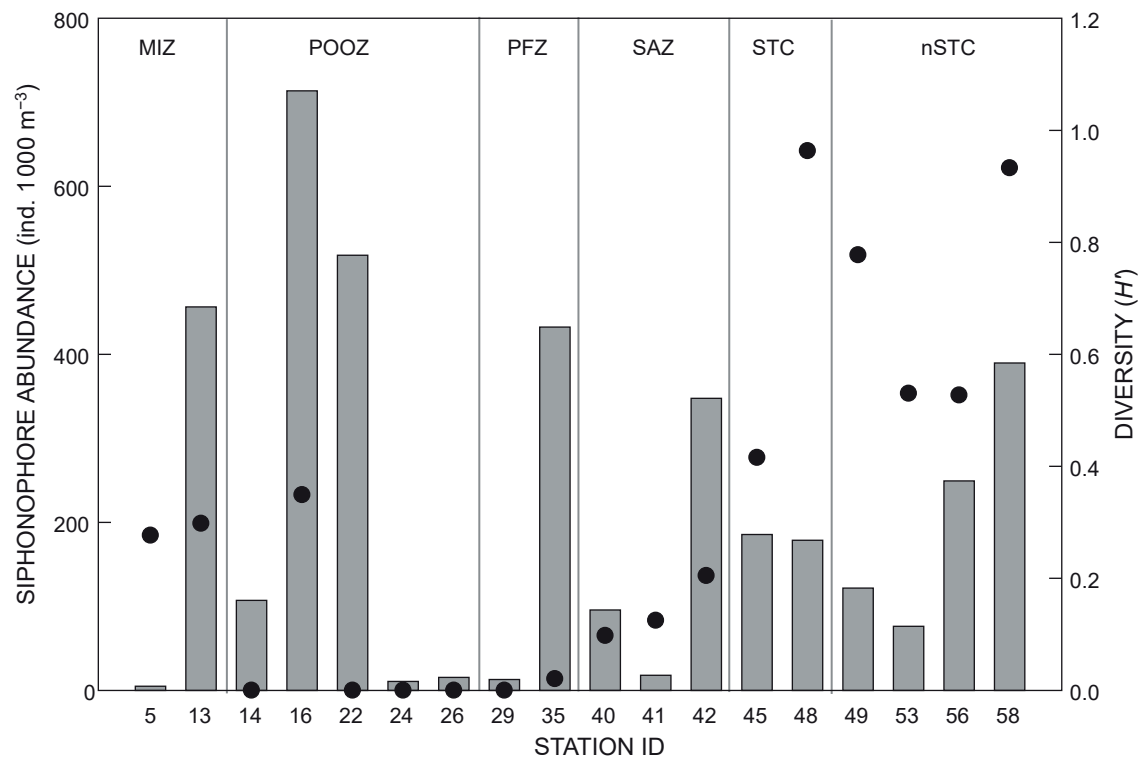


Figure 4: Changes in the abundance (grey bars) and diversity (black dots) of siphonophore assemblages across the Southern Ocean at the time of the study. The locations of the sampling stations and positions of the oceanic fronts and zones are shown in Figure 1; see Table 1 for abbreviations

stations within the STC (Shannon H' 0.42–0.96) and north of the STC (Shannon H' 0.53–0.93). The abundance of siphonophores varied across the transect (Figure 4), and samples with large numbers of individuals were noted both close to the Antarctic continent (in the MIZ and POOZ) and farther north (in the STC and nSTC). Variability in the dataset was conspicuous (Table 1; Figure 4)

Siphonophore assemblages

Results of the ANOSIM indicate a significant agreement (global $R = 0.471$, $p < 0.05$) between the siphonophore assemblages identified here and those of the *a priori* defined regions of Pakhomov et al. (2000). This is illustrated in the nMDS plot (Figure 5), from which the significance of the SAF, around station 40, is apparent, with assemblages to the south (Group A) and to the north (Group B) being resolvable at the 31.3% similarity level.

The SIMPER results indicate an average dissimilarity of 66.2% between Groups A and B. The main species contributing to this dissimilarity were *E. spiralis* (14.5%), *L. multicristata* (13.8%), *D. arctica* (12.1%) and *L. hardy* (11.1%) (Figure 6). The stations in Group A had an average similarity of 56.9%, with *D. arctica* contributing to 95.6% of the group's identity at an average abundance of 158.98 ind. 1 000 m⁻³ (SD 188.20). Although samples in Group A exhibited low diversity (Shannon $H' \leq 0.35$) they had the highest average abundance (262.05 ind. 1 000 m⁻³ [SD 294.85]). Stations within Group B were 52.1% similar to each other, with *D. arctica* (43.8%), *E. spiralis* (17.6%), *L. multicristata* (13.9%) and *L. hardy* (10.4%) making the greatest contributions to group identity (Figure 6). In Group B, average siphonophore abundance was 185.80 ind. 1 000 m⁻³ [SD 136.95], and siphonophore diversity tended to be highest at stations within the STC and north of the STC (see section above).

The results of the marginal tests indicate that all environmental variables except mesozooplankton biomass were significantly linked to the structure of siphonophore assemblages along the transect (Table 2): the final distLM incorporated SSS, SST, MLD and chlorophyll *a* concentrations (adj. $R^2 = 0.53$) (Table 3). The dbRDA plot (Figure 7) explains 90.8% of the fitted variation and 57.9% of total variation, and a latitudinal signal can clearly be seen moving from top-right through bottom-centre to top-left. Interestingly, the southern stations in the POOZ grouped with the MIZ stations, whereas the northern stations grouped with the PFZ stations. Stations of the SAZ, STC and nSTC showed the greater dispersion.

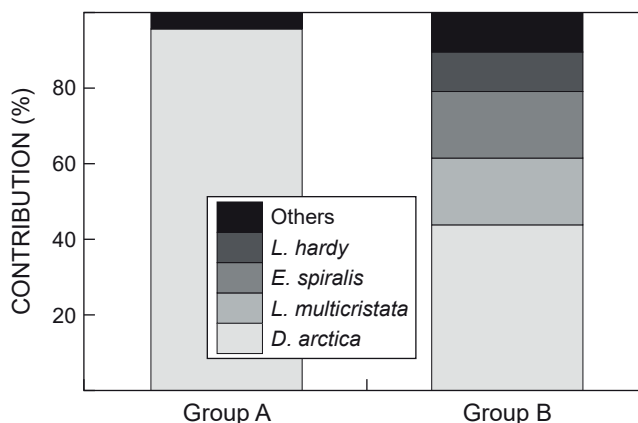


Figure 6: Percentage contribution of the main siphonophore species responsible for the similarities within samples to the south (Group A) and to the north (Group B) of the Sub-Antarctic Front. Results obtained from the SIMPER analysis. See Table 1 for full species names

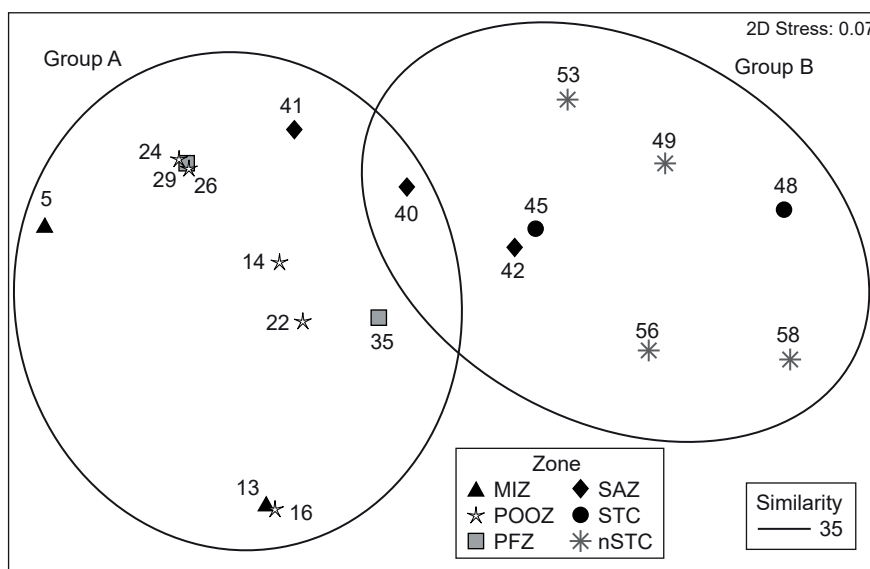


Figure 5: Nonmetric multidimensional scaling plot showing similarity between the siphonophore assemblages of the different stations sampled across the Southern Ocean at the time of the study. Location of the stations and the identity of *a priori* zones (following Pakhomov et al. [2000]) are given in Figure 1. The circles encompass those stations with a 35% similarity to each other, as identified by cluster analysis

Discussion

Most published studies have examined the siphonophore assemblages in the western Atlantic or Pacific sectors of the Southern Ocean (Pagès and Kurbjeweit 1994; Pagès et al. 1996; Pagès and Schnack-Schiel 1996; Pugh et al. 1997; Toda et al. 2010; Toda et al. 2014; reviewed by Lindsay et al. 2014). Few authors have studied siphonophores from the eastern sector (150° E to 30° W), Pagès et al. (1994) having studied assemblages in the Weddell Sea.

It is noteworthy that Pakhomov et al. (1999, 2000) reported only three species of siphonophore (*Dimophyes arctica*, *Diphyes antarctica* and *Melophysa melo*) from their analysis of the full 53 samples collected, whereas we found 21 species from only 18 samples. The absence of *M. melo* from our samples reflects the fact that we did not have access to all material, whereas the absence of more species from Pakhomov et al. (1999, 2000) reflects their subsampling approach to analysis. Regardless, the species identified here are not unknown from the sampling area (Lindsay et al. 2014), and indeed the results are similar to those of other studies conducted in the Southern Ocean (e.g. Pagès et al. 1994; Pagès and Schnack-Schiel 1996; Toda et al. 2014) and/or in the area of the STC (e.g. Pagès and Gili 1992a; Pakhomov et al. 1994). The diversity of siphonophore assemblages in our study was generally lowest at stations close to the Antarctic continent and increased northwards, as likewise observed by Toda et al. (2014) off Adélie Land. Similar observations have been made by numerous authors working on a variety of plankton taxa (as reviewed by Atkinson et al. 2012) and are often related to temperature (Atkinson et al. 2012). It is worth noting that our sampling was conducted down to 300 m only, which might have limited the number

of species encountered, as siphonophores have often been observed at depths deeper than 1 000 m in oceanic regions around Antarctica (Toda et al. 2010, 2014; Lindsay et al. 2014). Rather than comment on the comparative distribution of all species collected here, we confine our discussion to noteworthy observations linked to species associations (Figure 3).

Muggiaea bargmannae and *D. antarctica* are clearly Polar specialists, reaching greatest abundances in or south of the POOZ (Pagès et al. 1994; Pagès and Kurbjeweit 1994), though *D. antarctica* has been recorded in the PFZ (Pakhomov et al. 1994; Pagès et al. 1996) and around South Georgia (Atkinson and Peck 1988; Clarke et al. 1992). The close association between these two species (Figure 3) has been reported previously (Pagès et al. 1994; Pagès and Kurbjeweit 1994; Toda et al. 2014). Even though Lindsay et al. (2014) did not report any *D. antarctica* south of the POOZ—a fact they attributed to a lack of taxonomic expertise—Hunt et al. (2011) regularly observed the species in the epipelagos of the Lazarev Sea through the summers of 2004–2009. Interestingly, however, Hunt et al. (2011) failed to report any *M. bargmannae*.

Dimophyes arctica is distributed from the North Pole to the South Pole (Pagès et al. 1994) and was collected here in all samples. Although this species can tolerate a wide range of temperatures (−1.13 to 22.05 °C), and is usually more abundant at colder rather than warmer temperatures (Totton 1954; Pagès et al. 1994), rarely is it common at the ice-edge (Pagès et al. 1994). The maximum densities of *D. arctica* reported here are much higher than those reported from the area by Hunt et al. (2011) or Toda et al. (2010, 2014), yet are similar to those of Pagès et al. (1994) and Panasiuk-Chodnicka et al. (2014). While these differences may simply reflect patchiness in distribution, it is more likely that they are an artefact of sampling. The anterior nectophores of *D. arctica* are usually quite small (Mapstone and Arai 1992; Hosia and Bamstedt 2008). As a consequence, this species will be retained more efficiently by nets with a smaller rather than larger mesh size. Hunt et al. (2011) and Toda et al. (2010, 2014) used nets with a mesh size of >500 µm, whereas Pagès et al. (1994), Panasiuk-Chodnicka et al. (2014) and the present study used nets with meshes of <500 µm.

Numbers of *D. arctica* decline north of the PFZ, and though it is found around both the west coast (Pagès and Gili 1992a) and southeast coast (Thibault-Botha et al. 2004) of South Africa, it is not common there. The same northerly-declining trend was observed between the Strait

Table 2: Results of the distance-based linear model marginal tests for the abundance and composition of siphonophore samples collected at 18 stations between Cape Town, South Africa, and the SANAE base in Antarctica during January–February 1993, with sea surface salinity, sea surface temperature, mixed layer depth, surface chlorophyll *a* concentration, and mesozooplankton biomass as predictors. SS = sum of squares

Variable	SS (trace)	Pseudo- <i>F</i>	<i>p</i> -value	Proportion
Surface salinity	12 505	11.093	0.001	0.409
Surface temperature	13 361	12.444	0.001	0.438
Mixed layer depth	7 702	5.396	0.002	0.252
Chlorophyll <i>a</i>	4 919	3.072	0.028	0.161
Zooplankton biomass	283	0.145	0.972	0.009

Table 3: Results of the distance-based linear model sequential tests for the abundance and composition of siphonophore samples collected at 18 stations between Cape Town, South Africa, and the SANAE base in Antarctica, during January–February 1993, with sea surface salinity, sea surface temperature, mixed layer depth, and surface chlorophyll *a* concentration as predictors. df = degrees of freedom; SS = sum of squares

Variable	Adjusted <i>R</i> ²	SS (trace)	Pseudo- <i>F</i>	<i>p</i> -value	Cumulative variance	Residual df
+ Surface salinity	0.402	13361	12.444	0.001	0.437	16
+ Surface temperature	0.483	3242	3.490	0.010	0.544	15
+ Mixed layer depth	0.507	1535	1.732	0.160	0.593	14
+ Chlorophyll <i>a</i>	0.527	1346	1.582	0.216	0.638	13

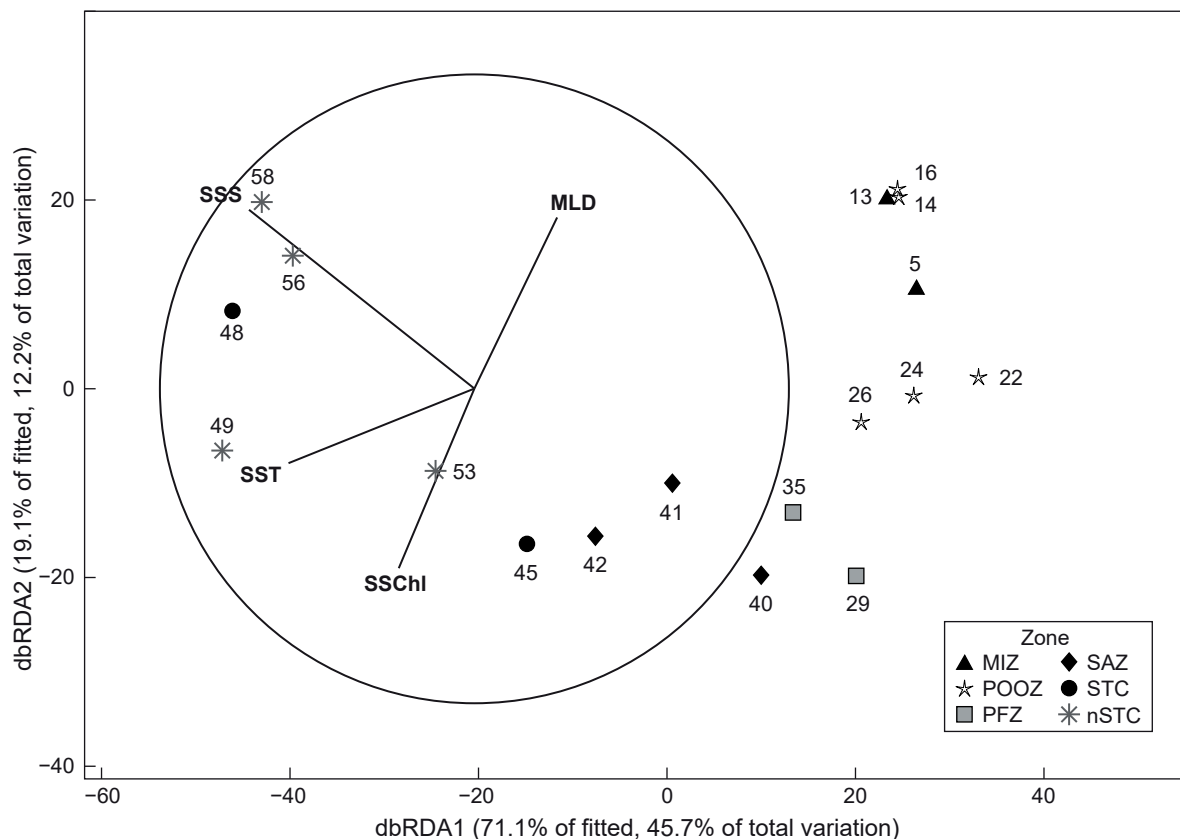


Figure 7: Multivariate multiple regression distance-based redundancy analysis performed on the siphonophore samples collected in the Southern Ocean, during summer (January–February) of 1993, and environmental predictors; vectors show the direction and strength of the environmental gradients. Location of stations and the identity of *a priori* zones (following Pakhomov et al. [2000]) are shown in Figure 1. MLD = mixed layer depth; nSTC = north of the Sub-Tropical Convergence; SSChl = sea surface chlorophyll *a* concentration; SSS = sea surface salinity; SST = sea surface temperature

of Magellan (50–52° S: Palma et al. 2018a) and the Chiloé Island Sea (42–44° S: Palma et al. 2018b) with average abundance decreasing from 806 to 5.8 ind. 1 000 m⁻³.

The balance of species shared a more northerly distribution in the sampling area; they are widespread and are commonly reported in temperate and subtropical assemblages (e.g. Pugh 1999; Pagès and Gili 1992a; Thibault-Botha et al. 2004). Notably, *Eudoxoides spiralis*, *Lensia hardy* and *L. multicristata* (not previously recorded in the region [Lindsay et al. 2014], or else recorded in a much deeper water layer [Hauke et al. 2014]) occurred farther south than the others, albeit at relatively low abundances, which could possibly be a result of the species' ability to occupy a wider range of temperatures and salinities (Sanvicente-Añorve et al. 2009).

The increase in siphonophore diversity noted from south to north is in contrast to the lack of any such trend reported by Pakhomov et al. (2000), who only noted peaks in diversity at frontal features, which they attributed to mixing and the development of ecotones. Strict comparisons between our results and those of Pakhomov et al. (2000), in the context of diversity, are problematic owing to the pronounced differences in taxonomic resolution employed in each study.

While there is largely good agreement between the distribution of distinct siphonophore assemblages and

prevailing circulation and/or water-mass structure in general (e.g. Grossmann and Lindsay 2013; Grossmann et al. 2014), the clearest biogeographic break is seen just south of the SAF. This separates low-diversity assemblages dominated by Antarctic and cold-water species to the south, from high-diversity, temperate and subtropical assemblages to the north (Figure 6), the latter being influenced by interactions with the Agulhas retroflexion (Pakhomov et al. 1994; Pakhomov et al. 2000). Unlike Pakhomov et al. (2000), we could not clearly distinguish between Antarctic and sub-Antarctic assemblages at the APF, which could be attributable to both the paucity of samples examined here and the general scarcity of taxa in waters to the south of the APF (Atkinson et al. 2012). That said, Pakhomov et al. (2000) noted that the assemblages they identified to the south of the APF were “faunistically coherent, but the contribution of dominant species and developmental composition of copepod species differ greatly, which may be ascribed to the water-mass modifications in the area investigated” (Pakhomov et al. 2000, p 1677).

Our results suggest that chlorophyll *a* concentrations, surface temperature and salinity, and MLD all influence the structure of siphonophore assemblages in the Southern Ocean, and indeed the best sequential distLM accounted for ~57.9% of total variation (adj. R^2 = 0.52) (Table 3).

While this finding is in contrast to the results of Pakhomov et al. (2000), who did not explain their observations of assemblage structure using any environmental variables, it can likely be explained by the univariate analytical methods those authors employed. Pakhomov et al. (2000) did note a strong latitudinal structure to assemblages, and in our study latitude is strongly linked to the distribution of the measured environmental variables. In addition, our findings agree with those of previous studies on siphonophores (Hsieh et al. 2013). Salinity (and temperature) are widely understood to affect the geographic and vertical distribution of siphonophores (Pugh 1975; Sanvicente-Añorve et al. 2009; Grossmann and Lindsay 2013; Grossmann et al. 2014), and tolerant species can dominate large areas (Sanvicente-Añorve et al. 2009). In the present study, this might apply to *D. arctica*, and to a lesser extent *E. spiralis*, *L. hardy* and *L. multicristata*. It is interesting that zooplankton biomass *per se* played no role in structuring the siphonophore assemblages observed (Tables 2 and 3), because biomass is known to influence the development of assemblages elsewhere (e.g. Lo et al. 2012). This could in part be due to the underrepresentation of small zooplankton, which have been shown to positively influence the development of siphonophore assemblages elsewhere (e.g. Mills 1995; Kršinić and Njire 2001; Lo et al. 2012; Blackett et al. 2015).

We set out to describe siphonophore assemblages along a transect across the Atlantic sector of the Southern Ocean, from Cape Town to the Antarctic continent, which we have accomplished, though perhaps not at the resolution we had originally hoped for because some archived samples could not be located. Archived plankton samples represent an irreplaceable resource for future research on matters not imagined at the time of their costly collection. An example is the use of DNA technologies to mine archived CPR silks to unravel some of the mysteries behind regime shifts in the North Sea (Kirby and Lindley 2005; Kirby et al. 2007), or the spread of cholera (Vezzulli et al. 2016). Plankton samples have a vital role to play in providing baseline data to map change, and as such deserve to be properly maintained and curated by an institution other than that involved in their initial collection. Sample curation for posterity is a responsibility beyond that of the original research collectors, and it is with some sense of relief that the South African National Biodiversity Institute (SANBI) and the then Department of Science and Technology have embarked on a Natural Science Collections Facility (NSCF). Although the NSCF, which was launched in 2017, aims to develop a virtual facility, with the central coordinating hub based at SANBI (Coetzer and Hamer 2019), there remains an urgent need to promote and preserve archives that exist precariously outside dedicated institutions.

Our other research aim was to test whether spatial patterns determined at one taxonomic resolution for an entire assemblage would be reflected in a more-detailed analysis of a small subset of the assemblage. Ecology textbooks indicate that the use of a taxocene is appropriate in studies of community ecology because of a lack of community-wide expertise in taxonomy (e.g. Morin 2011). Rarely, however, do we have an opportunity to test this or assess the level of appropriateness. Our data provide a high level of support for the use of siphonophores as

a proxy for the entire zooplankton assemblage, albeit necessarily at a coarse level of resolution in studies such as this.

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