Zonal variability of pelagic Siphonophora (Cnidaria) in the atlantic sector of the southern ocean

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A B S T R A C T

Siphonophores have a widespread distribution in the world oceans, can be very abundant in some areas, and can have a significant impact on other pelagic animals. In this work, siphonophores from the Atlantic sector of the Southern Ocean were studied. Zooplankton organisms were collected at 35 stations in December 2009. Thirty different species were found: 2 physonects and 28 calycophorans. Total abundances of siphonophores varied with latitude; maximum numbers were observed in the northern part of the transect, in the vicinity of South Africa, where *Muggiaea atlantica* was the dominant species. To the south, the contribution of *Eudoxoides spiralis* and *Lensia subtilis* increased. In the whole investigated region, the most numerous siphonophore was *Dimophyes arctica*. Based on our results, it can be assumed that in the Atlantic sector of the Southern Ocean probably exist two Siphonophora biodiversity spots, probably exist in the Benguela Current region and the Subtropical Convergence region. Moreover, our results show that the Southern Subtropical Convergence seems to be a very strong biogeographical barrier for many tropical and temperate Siphonophora species.

1. Introduction

Siphonophores (Cnidaria) are very complex and highly polymorphic gelatinous organisms, living in oceanic waters of full salinity. Currently, almost 190 valid species are known (WoRMS Editorial Board 2020, n.d). In the twentieth and twenty first centuries many papers covered siphonophores, across several disciplines including systematics (Dunn et al., 2005; Haddock et al., 2005; Panasiuk et al., 2019), reproduction (Carré and Carré, 1991) and ecology in general (Pugh, 1974; Purcell, 1980; Haddock, 2004; Palma et al., 2007; Rossi et al., 2008; Wen-Tseng et al., 2013; Panasiuk-Chodnicka et al., 2014; Mańko et al., 2015). However, the fragility of siphonophore colonies still causes problems during collection, as their bodies are easily broken with traditional sampling nets, and mainly for this reason they have often been poorly studied.

The majority of Siphonophora have a broad, cosmopolitan distribution, living in all three great oceans (Pugh, 1999; Mapstone, 2014), but some taxa exhibit specific geographical ranges (Mapstone, 2014) with many small siphonophore species living in the superficial layer,

and larger taxa inhabiting deeper parts of the ocean (Robison, 2004). Siphonophores can be so abundant in some areas of the global ocean, that they form one of the major components of the zooplankton (Pakhomov et al., 2000), and are the dominant group among planktonic predators (Pugh, 1974). Swarms of siphonophores can have a significant impact on other pelagic organisms, e.g. small fishes, ichthyoplankton, and can even cause massive mortalities of farmed fish (Greve, 1994; Licandro et al., 2012).

In recent years, blooms of gelatinous zooplankton have been recorded (Richardson et al., 2009; Brotz et al., 2012; Purcell, 2012), and/ or shifts in their distribution noted (Palma and Silva, 2004; Attrill et al., 2007; Sanvicente-Añorve et al., 2007). The presumed causes of this phenomenon include climate change, introduction of non-indigenous species, eutrophication, and overfishing (Purcell, 2012). It should be emphasaized that gelatinous zooplankton blooms are usually a natural phenomenom, and a typical aggregations have been observed in some areas due to the anthropogenic factors which were mentioned above.

The Southern Ocean is sometimes excluded from detailed siphonophore studies, but Pugh (1999) described Siphonophora in the South

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Atlantic region, Alvariño (1971) and Alvariño et al. (1990) studied taxonomic composition in the southern part of the Pacific and the Atlantic oceans, and Pagès and Gili, 1992 in the Benguela Current region. Additionally, Pagès and Orejas (1999), Palma and Silva (2004, 2006), and Palma et al. (2011) studied the distribution of siphonophores in the Magellan region and in the fjords and channels of southern Chile. Selected publications have also focused on siphonophores of the Antarctic, including the Weddell Sea, where Boysen-Ennen and Piatkowski (1988) studied zooplankton composition, while Pagès and Kurbjeweit (1994) focused on vertical distribution and abundances of siphonophores, as did Panasiuk-Chodnicka and Żmijewska (2010) and Panasiuk-Chodnicka et al., 2014 in the Croker Passage. Additionally, Toda et al. (2010) studied vertical distribution in the Indian sector of the Southern Ocean. In the investigated area, partial studies on cnidarians have been previously carried out by Pakhomov et al. (1994), Pakhomov et al. (1999), Pagès et al. (1996), and by Gibbons and Thibault-Botha (2002), and Hissmann (2005) close to the African continent.

Due to the abiotic and biotic changes in the Antarctic environment, which have been observed for many decades, induced by climate changes and other antropogenic factors, it is important to observe the distribution patterns of zooplanktonktonic organisms, including jellyfish, and siphonphores. Thus, our study sets out to characterize the link between the distribution and abundance patterns of siphonophores in relation to the location of hydrological zones/sectors in the Atlantic sector of the Southern Ocean, and to define latitudinal variability of Siphonophora assemblages in this region.

2. Material and methods

2.1. Sampling

Zooplankton organisms were collected during the R/V "Akademik Ioffe" cruise in December 2009 (Fig. 1). In summary 35 stations in the Southern Ocean were sampled along the transect, to a maximum depth of 300 m (Table 1). Due to technical problems at some sampling stations it was not possible to quantify the stratification of the water column. Therefore, samples at these stations were taken from layers of 300–0 m, 200–0 m or 100-0. A WP2 plankton net was used with a mesh

Table 1
Geographical position and depth ranges of zooplankton samples.

Station	Latitude	Longitude	Depth ranges [m]
97	33° 57.1' S	17° 33.3' E	300–0
98	33° 58.1' S	17° 18.2' E	300–0
99	33° 59.2' S	16° 58.4' E	200–0
01	34° 1.7' S	16° 12.1' E	300–200, 200–100, 100–0
02	34° 3.1' S	15° 47.7' E	300–200, 200–100, 100–0
03	34° 4.4' S	15° 24' E	300–200, 200–100, 100–0
07	34° 43.5' S	14° 13.2' E	300–200, 200–100, 100–0
11	35° 56.1' S	13° 29.8' E	200–100, 100–0
15	37° 7.1' S	12° 44.4' E	300–0
18	38° 6.1' S	12° 9.3' E	300–0
19	38° 18.3' S	11° 57.4' E	200–0
23	39° 29.2' S	11° 8.6' E	300–200, 200–100, 100–0
27	40° 39.5' S	10° 17.8' E	100–0
31	41° 49.4' S	9° 25.1' E	300–200, 200–100, 100–0
33	42° 24.0' S	8° 57.8' E	300–200, 200–100, 100–0
35	42° 58.8' S	8° 30.1' E	300–200, 200–100, 100–0
40	44° 24.7' S	7° 18.1' E	300–200, 200–100, 100–0
41	44° 41.6' S	7° 3.4' E	200–100, 100–0
43	44° 58.8' S	6° 48.3' E	300–200, 200–100, 100–0
44	45° 15.8' S	6° 33.0' E	300–0
45	45° 49.6' S	6° 2.1' E	300–200, 200–100, 100–0
47	46° 23.3' S	5° 30.6' E	300–200, 200–100, 100–0
52	47° 46.7' S	4° 8.2' E	300–0
54	48° 19.6' S	3° 34.1' E	300–0
60	49° 57.4' S	1° 46.2' E	300–200, 200–100, 100–0
62	50° 26.6' S	1° 8.4' E	300–0
63	50° 45.6' S	0° 49.2' E	300–0
64	51° 1.5' S	0° 29.9' E	300–0
65	51° 17.2' S	0° 10.2' E	300–200, 200–100, 100–0
68	52° 16.2' S	0° 0.0' E	300–200, 200–100, 100–0
74	54° 15.0' S	0° 0.15' W	200–100, 100–0
76	54° 54.4' S	0° 0.1' W	300–0
78	55° 34.2' S	0° 0.0' E	300–200, 200–100, 100–0
80	56° 13.78S	0° 0.6' W	200–100, 100–0
82	56° 53.4S	0° 0.0' E	200–100, 100–0

size of 200 μm. The water flow rate through the nets was recorded using a flowmeter. The material was immediately preserved in a 4% solution of buffered formalin. The investigated area was divided into eight characteristic zones following Demidov et al., 2012a, Demidov et al., 2012b) who also investigated this region, based on the phytoplankton
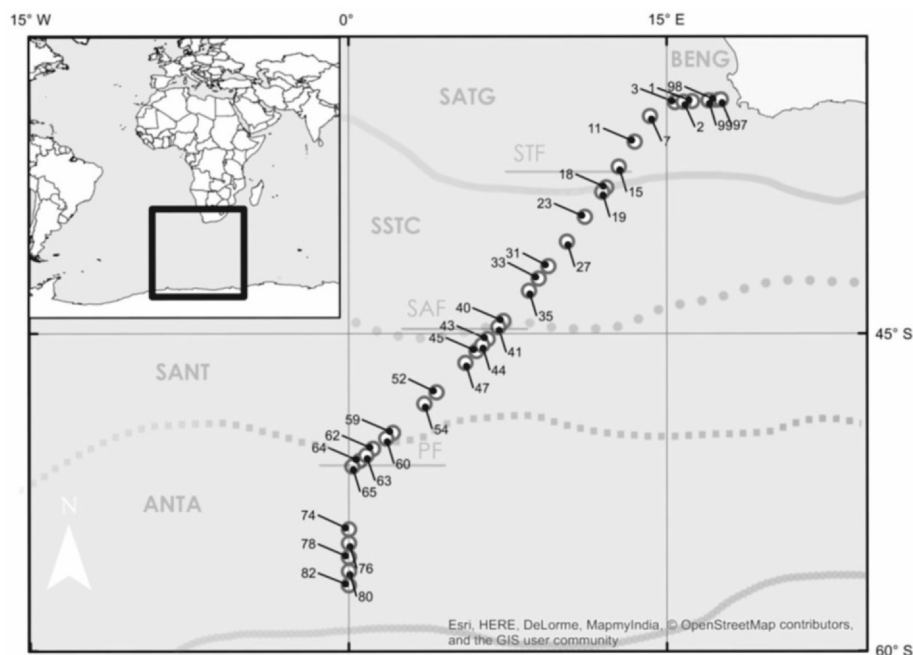

Fig. 1. Geographical position of sampling stations, with the distinguished positions of the main hydrological zones.

and chlorophyll *a* concentration values (obtained during the same cruise). The following zones have been identified: Benguela Current (hereafter BENG); Southern Subtropical Gyre (hereafter SATG); Subtropical Front (hereafter STF); Southern Subtropical Convergence (hereafter SSTC); Subantarctic Front (hereafter SAF); Subantarctic Surface Water (herafter SANT); Polar Front PF (hereafter PF); Antarctic Surface Water (hereafter ANTA).

2.2. Analyses of siphonophora diversity, abundance and distribution

Identification of siphonophores followed Margulis and Alekseev (1985), Pugh and Harbison (1987), Pagès and Gili, 1992), Pugh (1999), Bouillon et al. (2004) and Mapstone (2009). Polygastric stages of the diphyid siphonophores were counted by calculating the anterior nectophore number, and the number of eudoxid bracts was used for calculating the eudoxid stage abundance. In the genus *Rosacea* there are two nectophores per colony, therefore two nectophores in a sample were counted as a single colony. Hippopodiidae number of colonies were counted dividing the number of nectophores by 10. For physonect siphonophores, both pneumatophores and nectophores were counted. In the case of the Agalmatidae, if there were only few nectophores in a sample they were calculated to be from a single colony. *Pyrostephos vanhoeffeni* was represented during our study only by small nectophores, therefore 10 nectophores were estimated as a single colony. *Cordagalma ordinatum* colonies were calculated following to the estimates of Bouillon et al. (2004), and Hosia and Båmstedt (2008). The relative abundance by species was standardized as the number of ind. m^{-3}. For all statistical analyses of Siphonophora distribution only numbers of colonies were used.

Multivariate statistical analysis of siphonophore community abundance data were carried out using the PRIMER 7 software package (Clarke and Gorley, 2006; Clarke and Warwick, 2001). Obtained abundances of taxa were square root transformed prior to analysis. Similarities between samples were examined using the Bray and Curtis, 1957 index, depicted as a non metric multidimensional scaling (Bray and Curtis, 1957). A non–metric hierarchical CLUSTER routine was conducted to visualise a cluster tree with complete linkage to detect groupings within the abundance patterns. In addition, a SIMPER analysis, which determines the contribution of each species within hydrological zones from the investigated transect (Clarke and Gorley, 2006) allowed estimation of species ecological characteristics. A redundancy analysis (dbRDA) provided an ordination of fitted values using the multiple regression of the relationship between siphonophore community structure and the variables. Vector overlays on dbRDA ordination diagrams were used to aid in determining the strength and direction of the relationship between variables and redundancy analysis axes. The length of each vector corresponds to the size of the effect the variable had on the construction of dbRDA axes (Anderson et al., 2008).

3. Results

During our study 26 species of siphonophores were identified (Table 2). The most numerous species along the investigated transect were *Dimophyes arctica* (mean 88 ind. m^{-3}), *Eudoxoides spiralis* (mean 8 ind. m^{-3}), *Lensia* sp. and *Muggiaea atlantica* (14 ind. m^{-3} and 32 ind. m^{-3} respecively) (Table 2, Fig. 2). The widest distribution was observed for *D. arctica* (Table 2, Fig. 2). *L. conoidea, L. subtilis,* and L. *achilles* had also wide ranges of occurrence but were recorded only northwards of the SAF (Table 2, Fig. 2). Other observed species were limited to their specific regions. In the BENG zone, *Diphyes bojani, E. mitra, M. atlantica, L. hotspur, L. companella, L. cossack, Heteropyramis maculata, Abylopsis eschscholtzii, A. tetragona*, Agalmatidae colonies, and *Amphicaryon* sp. were recorded (Table 2, Fig. 2). In more open waters, of the SATG and SSTC zones, a number of oceanic species, including L. *fowleri, L. multicristata, Chelophyes appendiculata, Sulculeolaria turgida, S. chuni,* and *Cordagalma cordiformis* were found (Table 2, Fig. 2).

Table 2
Mean abundance [± SD] of individuals [ind. m^{-3}] of Siphonophora and their zone of occurrence.

Species	Mean abundance [± SD]		Zone
	Col.	Ex.	
Dimophyes arctica	88.29 ± 173.46	82.03 ± 117.55	BENG, STF, SSTC, SAF, SANT, PF, ANTA
Diphyes bojani	3.62 ± 21.44	–	BENG
Eudoxoides spiralis	8.62 ± 19.24	22.31 ± 68.29	BENG, SATG, STF, SSTC
Eudoxoides mitra	1.38 ± 4.74	3.29 ± 11.64	BENG, SSTC
Muggiaea atlantica	32.03 ± 139.22	24.42 ± 114.53	BENG
Muggiaea sp.	1.61 ± 9.51	–	BENG
Lensia conoidea	3.53 ± 10.35	–	BENG, SATG, SSTC, SAF
Lensia hotspur	1.64 ± 5.91	–	BENG
Lensia subtilis	19.84 ± 48.42	17.94 ± 51.79	BENG, SATG, SSTC
Lensia companella	0.47 ± 1.94		BENG
Lensia cossack	–	1.57 ± 8	BENG
Lensia meteori	1.06 ± 3.07	–	BENG, SSTC
Lensia achilles	1.18 ± 4.19	–	BENG, SSTC, SAF
Lensia fowleri	0.24 ± 1.41	–	SSTC
Lensia multicristata	2.08 ± 5.98	–	SSTC, SAF
Lensia subtiloides	0.92 ± 5.43	0.37 ± 2.17	SAF
Lensia sp.	13.81 ± 33.25	1.49 ± 6.16	BENG, SATG, SSTC, SAF
Chelopyes appendiculata	–	1.28 ± 5.68	SATG, SSTC
Sulculeolaria turgida	0.17 ± 1.03	–	SSTC
Sulculeolaria chuni	0.17 ± 1.03	–	SSTC
Heteropyramis maculata	–	0.24 ± 1.42	BENG
Abylopsis tetragona	–	0.73 ± 4.34	BENG
Abylopsis eschscholtzii	0.3 ± 1.78	0.38 ± 2.28	BENG
Abylidae unind.	–	0.56 ± 2.34	BENG
Vogtia glabra	0.24 ± 1.42		BENG
Rosacea plicata	0.4 ± 1.92	0.9 ± 5.33	SANT
Rosacea sp.	–	1.2 ± 5.94	SSTC, SANT
Prayidae unident.	1.06 ± 2.78	1.87 ± 6.65	BENG, SSTC, SANT
Agalmatidae unind.	0.48 ± 1.97	–	BENG
Pyrostephos vanhoeffeni	0.02 ± 0.08	–	SSTC, SANT
Cordagalma ordinatum	0.08 ± 0.46	–	SATG

Pyrostephos vanhoeffeni and species in the genus *Rosacea* were among siphonophores inhabiting colder waters, although *Rosacea* sp. was also observed in the SSTC zone (Table 2). During the sampling period, most of the common siphonophore taxa were associated with subtropical zones and the Benguela Current region, whilst a few species were observed within the southern zones SANT, ANTA and PF (Fig. 3, Table 3).

Cluster analysis distinguished 8 groups within the siphonophore community in the analyzed period along the Atlantic Sector of Southern Ocean transect (Fig. 4). Groups **a–e** should be considered separately – each of them was composed of only one unique station. The widest group **f** consisted mostly of stations from the southern part of the transect: the SANT, PF, and ANTA zones. In 40% it was similar to group **g** which included the SSTC and SAF. Group **h** was composed of typical "warmer" zone species (SSTC, STF, SATG, and BENG).

The siphonophore data, analyzed using a DistLM (Distance-based Linear Model), showed association with the vectors for the sea surface temperature (SST) and concentration of chlorophyll *A*. *axis* 1 of the dbRDA accounted for 91% of fitted variation (23% of the total variation) and correlated with temperature (Fig. 5). Vector overlays indicated visible patterns in siphonophore distribution grouping coinsiding with temperature. The most northern tropical and subtropical zones created one "warm" group (BENG, SATG, STF, SSTC), and "cold"
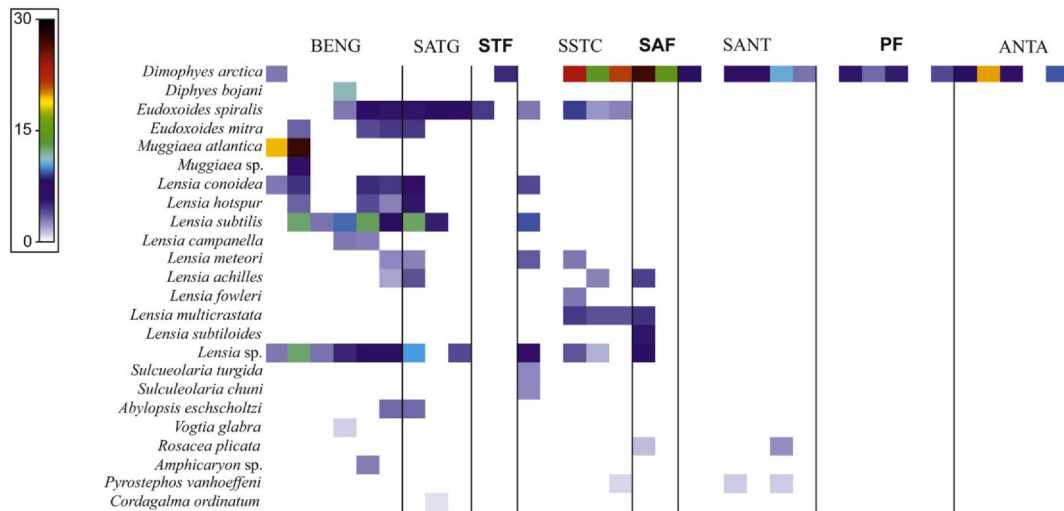
Fig. 2. Shade plot indicating zones of occurrence and abundances [ind. m^{-3}] of Siphonophora.

groups consisted of SANT, ANTA and PF zones. Chl *a* axis explained only 2.2% of total variation. However, the model accoubted for 25.7% of the total variation in the distribution data, and therefore it should be interpreted conservatively (Fig. 5).

Considering the distribution of siphonophore species, six were the most characteristic for the investigated region, and therefore were analyzed in detail, including: *Dimophyes arctica*, *Muggiaea atlantica*, *Eudoxoides spiralis*, *Lensia conoidea*, *Lensia subtilis*, and *Pyrostephos vanoheffeni*. *D. arctica* was the most numerous species at stations 40 and 31, which were located in the SAF and SSTC zones, respectively. It was also present at stations 35 and 76, and few other sites in smaller numbers (SSTC and ANTA zones) (Fig. 6). *M. atlantica* occurred only in the BENG zone, and it was especially abundant at the station 98 (Fig. 6). *E. spiralis* was the most abundant at stations 31 and 2 (SSTC and BENG zones respectively) (Fig. 6). This species was also present at stations in the SATG and SAF zones, but it was represented by a few individuals only (Fig. 6). *L. conoidea* had the largest abundance at the station 7 (SATG zone), followed by approximately two times smaller numbers in several stations in the BENG and SATG: 98, 2, 3, and 23. On the other hand, *L. subtilis*, the most abundant species within *Lensia* genus in this

study, displayed maximum numbers at stations 98, 2 (BENG zone), and 7 (SATG zone) (Fig. 6). *L. subtilis* was also identified along the the transect stations in the SSTC (Fig. 6). *P. vanhoeffeni*, on the other hand, was found in more southern waters. Its highest abundances were observed in the SANT zone (stations 45 and 52), while a few specimens were noted in the SSTC.

4. Discussion

Though the south-eastern sector of the Atlantic and the Southern Ocean have not been well studied for Siphonophora, some authors have investigated these areas. For example, Pugh (1999) in the South Atlantic region described 3 cystonect, 19 physonect, and 74 calycophoran species of which all taxa were also registered in this study. Almost all taxa described in this work were found previously around South Africa (north of 36°S), and in the Benguela Current region (Pagès and Gili, 1992; Thibault-Botha and Gibbons, 2005). However, the number of species observed here do not match the total species richness found by other workers, including Pagès and Gili (1992) in the Benguela Current region (3 cystonects, 8 physonects, 41 calycophores), and
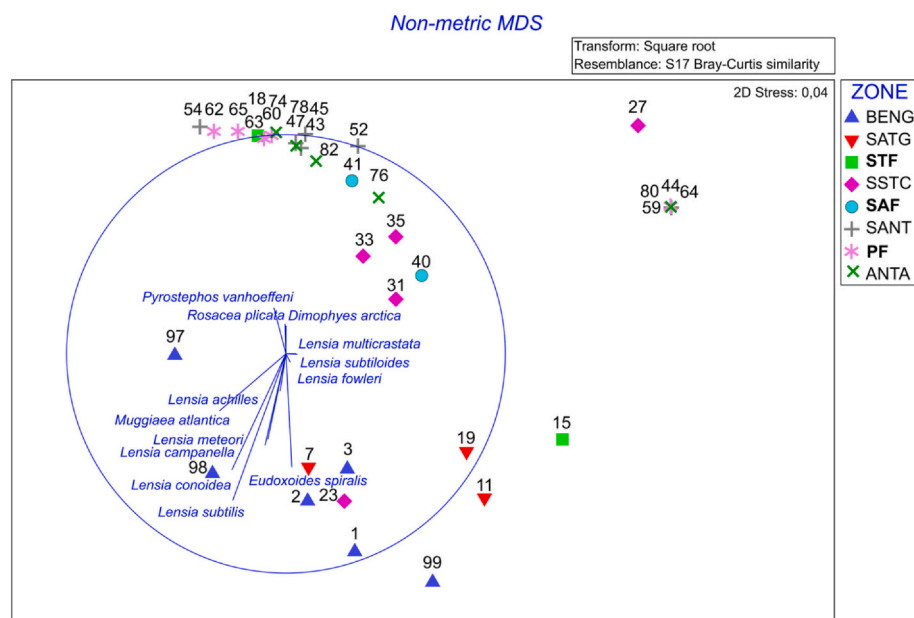

Fig. 3. Ordination diagram of non – metric multidimensional scaling (nMDS) of Siphonophora species abundances with vector projections of main species.

Table 3
Percentage contribution of siphonophores within investigated zones based on the SIMPER analysis.

	BENG	SATG	STF	SSTC	SAF	SANT	PF	ANTA
Species	Percentage [%]							
Dimophyes arctica	–	–	–	57.22	100	98.71	100.00	100.00
Lensia sp.	34.16	10.98		7.77	–			
Lensia subtilis	33.53	13.43	–	–	–	–	–	–
Lensia conoidea	9.79	–	–	–	–	–	–	–
Lensia campanella	1.42	–	–	–	–	–	–	–
Lensia hotspur	3.39	–	–	–	–	–	–	–
Lensia multicristata	–	–	–	13.90	–	–	–	–
Lensia meteori	–	–	–	2.87	–	–	–	–
Muggiaea atlantica	7.82	–	–	–	–	–	–	–
Eudoxoides spiralis	5.68	75.59	–	18.24	–	–	–	–
Eudoxoides mitra	4.21	–	–	–	–	–	–	–
Pyrostephos vanhoeffeni	–	–	–	–	–	1.29	–	–

Thibault-Botha and Gibbons (2005) off the east coast of South Africa (more than 50 species). Although the majority of these records were epipelagic, there was also a rich assemblage of deep-water taxa, which were not collected during this study, likely due to the sampling method and depth range covered.

The reason for the higher number of species in the African region is probably due to a complex circulation pattern in this area which includes three currents, many eddies and small gyres (Lutjeharms and Ansorge, 2001; Arruda et al., 2014), forming a unique ecotone where distinct assemblages are mixed. In more southern areas, it is quite difficult to find any detailed literature data about species composition and diversity of siphonophores. There are only some published data from the Subtropical and Antarctic Polar Fronts (Pakhomov et al., 1999), with 17 taxa being described, and among them 16 of which were noted in the Subtropical Convergence Region (e.g. *Chelophyes appendiculata*, *Diphyes dispar*, *Muggiaea atlantica*, *Eudoxoides spiralis*), and only one – *Diphyes antarctica* – was recorded in the Polar Front Region (during our study *D. antarctica* colonies were also noted, but only in samples from

the Bongo net, thus they were not included in the presented analyses). Pakhomov et al. (1999, 2000) investigated almost the same region as in this study, but only mentioned Siphonophora as a group of animals, indicating only two to three species as examples. Therefore, it can be assumed that data from this region of the South Atlantic are still very fragmentary and selective (Table 4).

Throughout the entire research area *Dimophyes arctica* was the most common species. This cosmopolitan siphonophore inhabits the three great oceans as well as both polar regions, with a more epipelagic distribution at boreal and austral latitudes than at tropical latitudes (Pugh, 1974; Alvariño et al., 1990; Panasiuk-Chodnicka and Żmijewska, 2010; Panasiuk-Chodnicka et al., 2014; Mańko et al., 2015).

The calycophoran siphonophore *Muggiaea atlantica* typically lives in superficial waters (< 200 m, Pugh, 1999). Large blooms of *M. atlantica* can cause significant ecological and economic impacts: predation by this species caused a restructuring of the copepod community during an invasion of the Adriatic (Kršinic and Njire, 2001), and it was also identified as the causative agent of mass mortalities in farmed fish (Baxter et al., 2011). The geographical expansion of *M. atlantica* may have significant impacts on the ecological and economic productivity of newly colonised regions. In our study it was a dominant species among Siphonophora at the northernmost stations, and according to Ulloa et al. (2000) it is associated with Subantarctic Water or Equatorial Subsurface Water. The results of our study suggest that the southern limit of occurrence for this species might be as far south as the Polar Front (Table 4).

The other very abundant species, *Eudoxoides spiralis*, has a broad distribution in the temperate zone of the World Ocean (Pugh, 1974), and may dominate in some areas and seasons (Gasca and Suárez, 1991). It was the dominant species in the subtropical part of the investigated area, often together with *Lensia subtilis* – another species with a widespread distribution in the Atlantic (Pugh, 1974). *E. spiralis*, in opinion of Lindsay et al. (2014), occurs in high abundances to the north of the Antarctic Convergence, although during our study the SAF seemed to be its occurrence limit.

4.1. Main assemblages of siphonophores

BENG - Benguela Current

Three cystonects, 8 physonects, and 41 calycophorans are known to occur in the Benguela Current (Pagès and Gili, 1992). Among them,
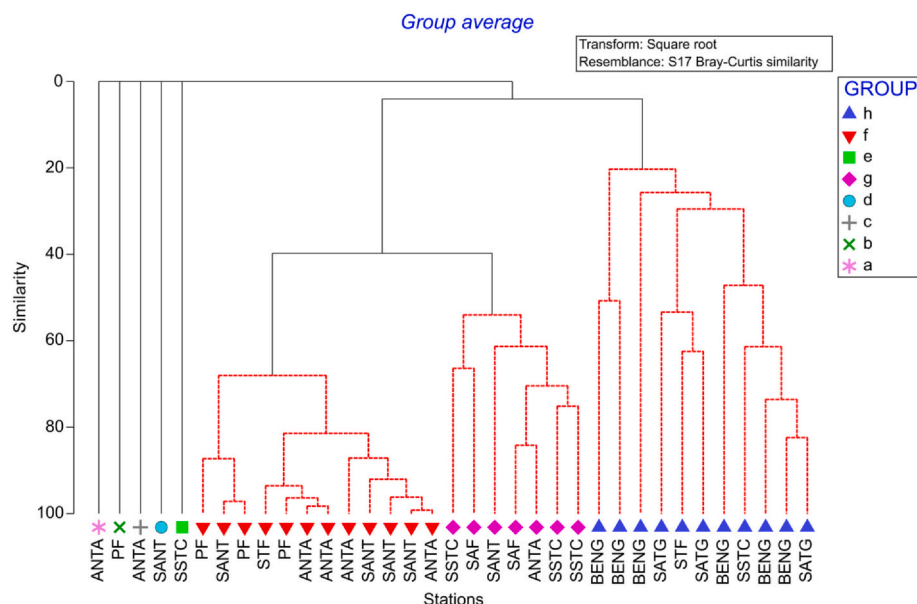

Fig. 4. Clustering dendrogram illustrating similarity between samples from different investigated zones.
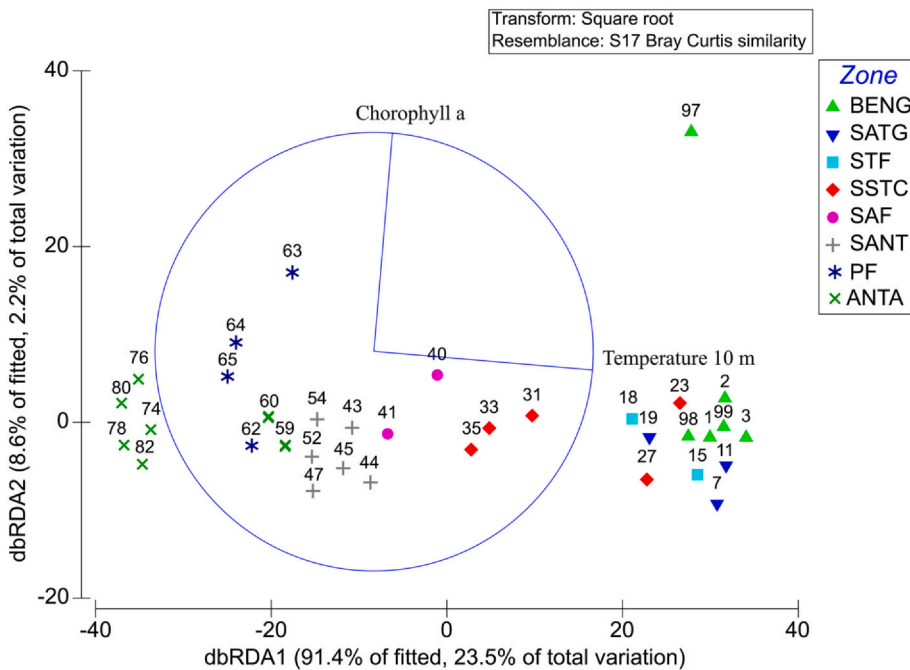
Fig. 5. DistLM plot of siphonophores abundance derived from a Bray – Curtis similarity matrix of data. To interpret the model visually, in a multi - dimensional space, we used distance based re- dundancy analysis (dbRDA) to show the relationship between species distribution and physical predictor variables. Numbers in parentheses indicate the per- centage of the total variation explained by each axis. Vectors represent strength of variables in model.

three physonect species and 25 calycophoran taxa were noted in the present study, although the investigated transect was quite short along the Benguela Current region, in comparison to the previous studies. For this zone the most typical siphonophores were *D. bojani, M. atlantica, E. mitra, L. hotspur, L. companella, L. cossack, H. maculata, A. tetragona, A. eschscholtzi, V. glabra*. Most of these species were previously registered in this region (Gibbons and Thibault-Botha, 2002).

SATG - Southern Subtropical Gyre

In the SATG zone the most characteristic species were *E. spiralis, L. conoidea, L. subtilis,* and *C. cordiformis. E. spiralis* is widely distributed on the shelf and in the oceanic zone throughout the region, very typical for the temperate regions of the three great oceans (Pugh, 1974). In case of *L. conoidea*, previous research conducted by other authors indicate that it is common in the region, and abundant in all seas (Alvariño, 1971). *L. subtilis* also has a world-wide distribution and inhabits temperate re- gions of all seas (Alvariño, 1971). It is very frequent and abundant in the southern Benguela region all year round both in the oceanic pro- vince and over the shelf (Pagès and Gili, 1992).

SSTC - Southern Subtropical Convergence

The second richest assemblage of siphonophores was recorded in the Southern Subtropical Convergence Zone. Most taxa recorded in this zone were also observed in the BENG, but species typical for this zone were – *L. multicristata, L. fowleri, S. turgida* and *S. chuni*. In the SSTC, *P. vanhoeffeni* was also observed (Table 3), and this is the most northerly record for this physonect in the present work. L. *fowleri* and *L. multi- cristata* are typical for the temperate regions of all three oceans (Mapstone, 2009). According to previous studies, *S. chuni* is a common species in equatorial and tropical regions (Gili, 1986). Moreover, Pagès and Gili (1992) mentioned that this species typically occurs (in the Benguela region) in warmer water from Angola. During this study *S. chuni* was observed only in the SSTC zone. *S. turgida* was noted by Pagès and Gili (1991) in the Benguela Current region. In much more open oceanic waters it was only recorded by several authors, e.g. Palma and Silva (2006). This allows assuming that our observations are some of the most southern records for this taxon.

SANT - Subantarctic Surface Water

R. plicata and *P. vanhoeffeni*, together with *D. arctica*, were the only

siphonophores recorded in this zone. *R. plicata* is a cosmopolitan species which occurs from the Bering Sea to the Antarctic, including the tropics (Alvariño et al., 1990; Mapstone, 2009). In the Atlantic *R. plicata* oc- curred at mesopelagic depths (Pagès et al., 1994), and this could ex- plain the absence of this species in the warmer waters north of the investigated transect. *P. vanhoeffeni* is a typical Antarctic taxon (Panasiuk et al., 2019), but it is also widely distributed in sub-Antarctic waters and even further north (Guerrero et al., 2013; Panasiuk- Chodnicka et al., 2014). In our opinion, *P. vanhoeffeni* is an Antarctic species but with a distribution strongly dependant on the Antarctic Circumpolar Current waters and its branches, and therefore it can be transported oceanwards of the coast (Lindsay et al., 2014). During our study this species has been observed even to the north of the SAF.

5. Conclusions

We can distinguish three major areas occupied by different assem- blages of siphonophores. The first area comprises the BENG, SATG, STF, and SSTC, and it is inhabited by warm water species. Among them are, for instance, *M. atlantica, E. spiralis,* and L. *subtilis*. In the second area, composed of the colder zones: the SANT, ANTA, and PF, very few si- phonophore taxa were observed: *R. plicata, P. vanhoeffeni,* and *D. arc- tica*. Between these two areas is the middle one, consisting of the SSTC and SAF with species living in both warm and cold waters. The SSTC zone is the only one area linked to former zones, however, it is located closer to the "cold" area. The middle area seems to be an ecotone in- tegrating warm and cold assemblages, where taxa with very different ecological preferences meet. We found here subtropical species (*E. spiralis, L. conoidea, L. subtilis*) and Antarctic species (*P. vanhoeffeni, R. plicata*), along with species observed in this area only (*L. fowleri, L. multicristata, L. subtiloides*). The only taxon recorded in all three major areas is *D. arctica*, known as typical cosmopolitan species. Results ob- tained during our study may suggest that some siphonophores pre- viously recorded only in the specific regions have broader distributions. Beside *Dimophyes arctica*, some species in the genus *Lensia* (i.e. L. *sub- tiloides*) and *Eudoxoides spiralis* seem to have more southern distribu- tion, based on the fact that their specimens/nectophores were collected far to the south of the STF area. Moreover, it can be assumed that the Southern Subtropical Convergence – in the case of siphonophore dis- tribution - is a much more restrictive hydrological barrier than was
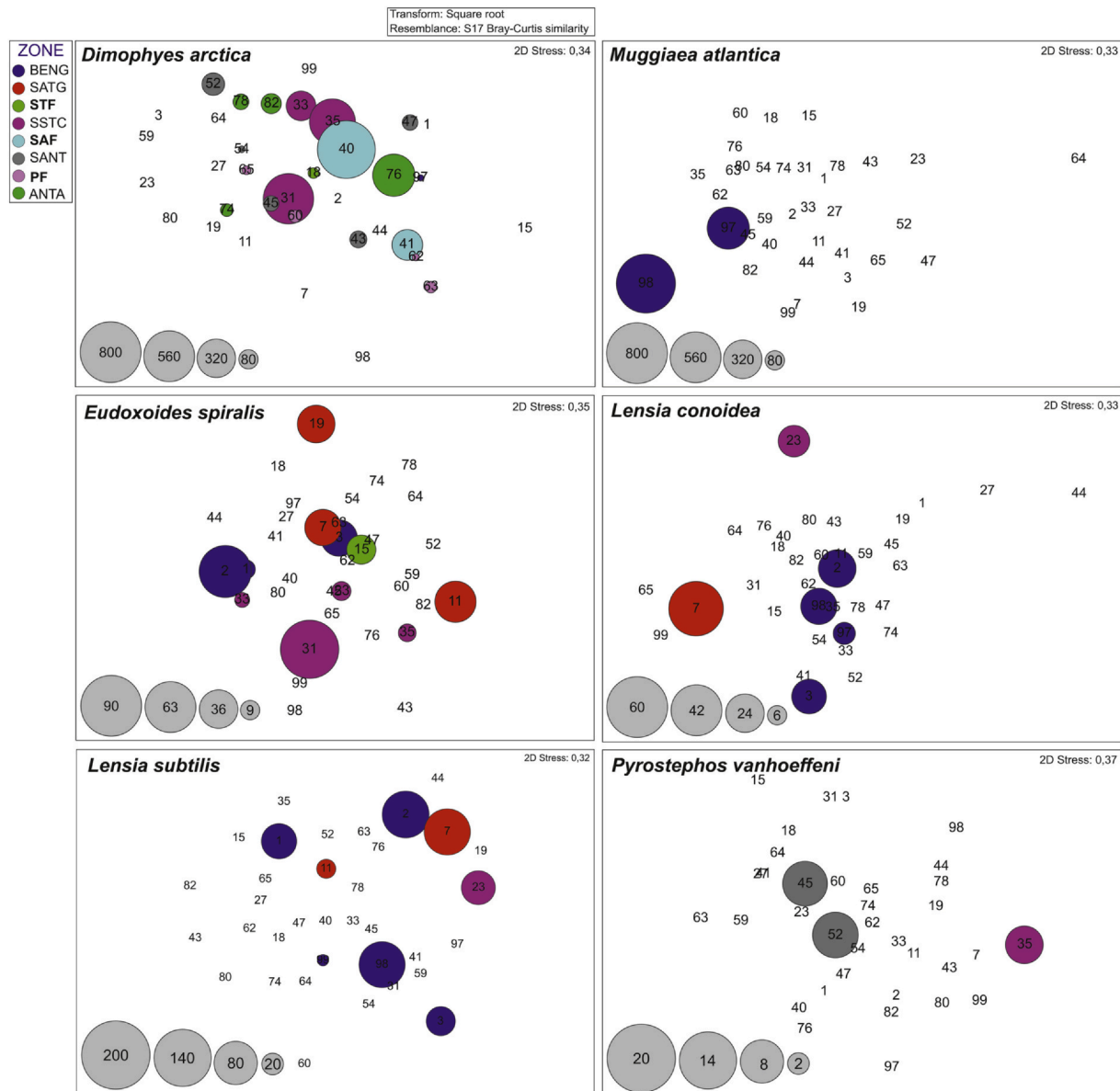
Fig. 6. Abundance [ind. m-3] of dominant siphonophores species represented as bubble plot overlay on nMDS plot of invstigated stations. nMDS plot prepared with Bray-Curtis similarity matrix. Larger bubbles indicate higher abundance.

previously thought, in comparison to the Polar Front. Moreover, the SSTC hydrological and ecological characteristics might create favourable conditions for siphonophores, judging by their higher biodiversity registered in this region, and not observed either in the northern or southern more open, oceanic waters.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Alvariño, A., 1971. Siphonophores of the Pacific ocean with a review of the world distribution. Bull Scripps Inst Oceanogr Univ Calif 16, 1–432.

Alvariño, A., Wojtan, J.M., Martinez, M.R., 1990. Antarctic siphonophores from plankton samples of the United States antarctic research program. Antarct Res. Ser. 49, 1–436.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA + for PRIMER: Guide to Software and Statistical Methods. PRIMER – E, Plymouth.

Arruda, W., Zharkov, V., Deremble, B., Nof, D., Chassignet, E., 2014. A new model of current retroflection applied to the westward protrusion of the agulhas current. J. Phys. Oceanogr. 44, 3118–3138.

Attrill, M.J., Wright, J., Edwards, M., 2007. Climate-related increases in jellyfish

frequency suggest a more gelatinous future for the North Sea. Limnol. Oceanogr. 52, 480–485.

Baxter, E.J., Rodger, H.D., McAllen, R., Doyle, T.K., 2011. Gill disorders in marine-farmed salmon: investigating the role of hydrozoan jellyfish. Aquac Environ Interact 1, 245–257.

Bouillon, J., Medel, M.D., Pagès, F., Gili, J.M., Boero, F., Gravili, C., 2004. Fauna of the mediterranean hydrozoa. Sci. Mar. 68, 5–438.

Boysen-Ennen, E., Piatkowski, U., 1988. Meso–and macrozooplankton communities in the weddell Sea, Antarctica. Polar Biol. 9, 17–35.

Bray, J.B., Curtis, J.T., 1957. An ordination of the upland forest communities of southern wisconsin. Ecol. Monogr. 27, 325–349.

Brotz, L., Cheung, W.L., Kleisner, K., Pakhomov, E., Pauly, D., 2012. Increasing jellyfish populations: trends in large marine ecosystems. Hydrobiologia 690, 3–20.

Carré, C., Carré, D., 1991. A complete life cycle of the calycophoran siphonophore *Muggiaea kochi* (will) in the laboratory, under different temperature conditions: Ecological implications. Philos. T. R. Soc. B 334, 27–32.

Clarke, K.R., Gorley, R.N., 2006. PRIMER V6: User Manual/Tutorial. PRIMER-E, Plymouth.

Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation, second edition. PRIMER-E, Plymouth.

Demidov, A.B., Mosharov, S.A., Gagarin, V.I., 2012. Phytoplankton production characteristics in the southern atlantic and the atlantic sector of the southern ocean in the austral summer of 2009 – 2010. Mar. Biol. 52, 226–238.

Demidov, A.B., Mosharov, S.A., Gagarin, V.I., 2012a. Meridional asymmetric distribution of the primary production in the atlantic sector of the southern ocean in the austral spring and summer. Oceanology 52 (5), 623–634.

Dunn, C.W., Pugh, P.R., Haddock, S.H., 2005. Molecular phylogenetics of the siphonophora (Cnidaria), with implications for the evolution of functional specialization. Syst. Biol. 54, 916–935.

Gasca, R., Suárez, E., 1991. Siphonophores (Cnidaria) of upwelling areas of the campeche bank and the mexican caribbean sea. Hydrobiologia 216/217, 497–502.

Gibbons, M.J., Thibault-Botha, D., 2002. The match between ocean circulation and zoogeography of epipelagic siphonophores around southern Africa. J. Mar. Biol. Assoc. U. K. 82 (05), 801–810.

Gili, J.M., 1986. Estudio Sistematico Y Faunistico De Los Cnidarios De La Costa Catalane. PhD thesis. Universitat Autónoma de Barcelona, Spain.

Greve, W., 1994. The 1989 german bight invasion of *Muggiaea atlantica*. ICES J. Mar. 51 (4), 355–358.

Guerrero, E., Gili, J.M., Rodriguez, C.S., Araujo, E.M., Canepa, A., Calbet, A., Genzano, G., Mianzan, H.W., González, R.A., 2013. Biodiversity and distribution patterns of planktonic cnidarians in San matías Gulf, patagonia, Argentina. Mar. Ecol. 34, 71–82.

Haddock, S.H., 2004. A golden age of gelata: Past and future research on planktonic ctenophores and cnidarians. Hydrobiologia 530, 549–556.

Haddock, S.H., Dunn, C.W., Pugh, P.R., 2005. A re-examination of siphonophore terminology and morphology, applied to the description of two new prayine species with remarkable bio-optical properties. J. Mar. Biol. Assoc. U. K. 85 (3), 695–707.

Hissmann, K., 2005. In situ observations on benthic siphonophores (Physonectae: Rhodaliidae) and descriptions of three new species from Indonesia and South Africa. Syst. Biodivers. 2 (3), 223–249.

Hosia, Aino, Båmstedt, Ulf, 2008. Seasonal abundance and vertical distribution of siphonophores in Norwegian fjords. J. Plankton Res. 30 (8), 951–962. https://doi.org/10.1093/plankt/fbn045.

Kršinic, F., Njire, J., 2001. An invasion by *Muggiaea atlantica* Cunningham 1892 in the northern adriatic sea in the summer of 1997 and the fate of small copepods. Acta Adriat. 42, 49–59.

Licandro, P., Souissi, S., Ibanez, F., Carré, C., 2012. Long-term variability and environmental preferences of calycophoran siphonophores in the Bay of Villefranche (northwestern mediterranean). Prog. Oceanogr. 97-100, 152–163.

Lindsay, D., Guerrero, E., Grossmann, M., Fuentes, V., 2014. Southern Ocean gelatinous zooplankton. In: De Broyer, C., Koubbi, P., Griffiths, H.J., Raymond, B., Udekem d Acoz, C. d' (Eds.), Biogeographic Atlas of the Southern Ocean. Scientific Committee on Antarctic Research, Cambridge, pp. 266–275.

Lutjeharms, J.R.E., Ansorge, I.J., 2001. The structure and transport of the Agulhas return current between South Africa and 70°E. J. Mar. Syst. 30, 1115–1138.

Mańko, M.K., Panasiuk-Chodnicka, A.A., Żmijewska, M.I., 2015. Pelagic coelenterates in the atlantic sector of the arctic ocean: species diversity and distribution as water mass indicators. Oceanol. Hydrobiol. St. 44 (4), 466–479.

Mapstone, G.M., 2009. Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific Waters. NRC Research Press, Ottawa, Ontario, Canada.

Mapstone, G.M., 2014. Global diversity and review of siphonophorae (Cnidaria: Hydrozoa). PLoS One 9 (2). https://doi.org/10.1371/journal.pone.0118381.

Margulis, R.Ya., Alekseev, D.O., 1985. The genus *Lensia* (Siphonophora, Calycophorae). Zool. Zh. 64 (1), 5–15.

Pagès, F., Gili, J.M., 1991. Vertical distribution of epipelagic siphonophores at the confluence between benguela waters and the angola current over 48 hours. Hydrobiologia 216/217, 355–362.

Pagès, F., Gili, J.M., 1992. Siphonophores (Cnidaria, Hydrozoa) of the benguela current (southeastern atlantic). Sci. Mar. 56, 65–112.

Pagès, F., Kurbjeweit, F., 1994. Vertical distribution and abundance of mesoplanktonic medusae and siphonophores from the weddell Sea, Antarctica. Polar Biol. 14, 243–251.

Pagès, F., Orejas, C., 1999. Medusae, siphonophores and ctenophores of the magellan region. Sci. Mar. 63 (1), 51–57.

Pagès, F., Pugh, P.R., Gili, J.M., 1994. Macro-and megaplanktonic cnidarians collected in the eastern part of the weddell Gyre during summer 1979. J. Mar. Biol. Assoc. U. K. 74, 873–894.

Pagès, F., White, M.G., Rodhouse, P.G., 1996. Abundance of gelatinous carnivores in the nekton community of the antarctic polar frontal zone in summer 1994. Mar. Ecol. Prog. Ser. 141, 139–147.

Pakhomov, A., Perissinotto, R., McQuaid, C.D., 1994. Comparative structure of the macro- zooplankton/micronekton communities of the subtropical and antarctic polar fronts. Mar. Ecol. Prog. Ser. 111, 155–169.

Pakhomov, E.A., Perissinotto, R., Froneman, P.W., 1999. Predation impact of carnivorous macrozooplankton and micronekton in the atlantic sector of the southern ocean. J. Mar. Syst. 19, 47–64.

Pakhomov, E.A., Perissinotto, R., McQuaid, C.D., Froneman, P.W., 2000. Zooplankton structure and grazing in the atlantic sector of the southern ocean in late austral summer 1993: Part 1. ecological zonation. Deep Sea Res. Part I: Oceanogr Res Pap 47 (9), 1663–1686.

Palma, S., Silva, N., 2004. Distribution of siphonophores, chaetognaths, euphausiids and oceanographic conditions in the fjords and channels of southern chile. Deep Sea Res. Part II, Top Stud Oceanogr 51 (6–9), 513–535.

Palma, S., Silva, N., 2006. Epipelagic siphonophore assemblages associated with water masses along a transect between chile and easter island (eastern south pacific ocean). J. Plankton Res. 28 (12), 1143–1151.

Palma, S., Apablaza, P., Soto, D., 2007. Diversity and aggregation areas of planktonic cnidarians of the southern channels of chile (boca del guafo to pulluche channel). Investig. Mar. 35 (2), 71–82.

Palma, S., Silva, N., Retamal, M.C., Castro, L., 2011. Seasonal and vertical distributional patterns of siphonophores and medusae in the chiloé interior sea, chile. Cont. Shelf Res. 31 (3), 260–271.

Panasiuk, A., Jażdżewska, A., Słomska, A., Irzycka, M., Wawrzynek, J., 2019. Genetic identity of two physonect siphonophores from southern ocean waters – The enigmatic taxon *Mica micula* and *Pyrostephos vanhoeffeni*. J. Mar. Biol. Assoc. U. K. 99 (2), 303–310.

Panasiuk-Chodnicka, A., Żmijewska, M.I., 2010. Cnidaria from Croker passage (antarctic peninsula) with a special focus on siphonophorae. Polar Biol. 33, 1131–1143.

Panasiuk-Chodnicka, A.A., Żmijewska, M.I., Mańko, M., 2014. Vertical migration of siphonophora (Cnidaria) and their productivity in the Croker Passage, the Antarctic. Pol. Polar Res. 35 (1), 115–131.

Pugh, P.R., 1974. The vertical distribution of the siphonophores collected during the SOND Cruise, 1965. J. Mar. Biol. Assoc. U. K. 54, 25–90.

Pugh, P.R., 1999. Siphonophorae. In: Boltovsky, D. (Ed.), South Atlantic Zooplankton. Backhuys Publishers, Leiden, pp. 465–511.

Pugh, P.R., Harbison, G.R., 1987. Three new species of prayine siphonophore (Calycophorae, Prayidae) collected by a submersible, with notes on related species. Bull. Mar. Sci. 41 (1), 68–91.

Purcell, J.E., 1980. Influence of siphonophore behavior upon their natural diets: evidence for aggressive mimicry. Sci. 209, 1045–1047.

Purcell, J.E., 2012. Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Annu. Rev. Mar. Sci. 4, 209–235.

Richardson, A.J., Bakun, A., Hays, G.C., Gibbons, M.J., 2009. The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol. Evol. 24, 312–322.

Robison, B.H., 2004. Deep pelagic biology. J. Exp. Mar. Biol. Ecol. 300, 253–272.

Rossi, S., Youngbluth, M., Pagès, F., Jacoby, C.A., Garrofé, X., 2008. Fatty acid trophic markers and trophic links among seston, crustacean zooplankton and the siphonophore nanomia cara in georges basin and Oceanographer Canyon (NW Atlantic). Sci. Mar. 72 (2), 403–416.

Sanvicente-Añorve, L., Alba, C., Alatorre, M.A., Flores-Coto, C., 2007. Cross-shelf and vertical distribution of siphonophore assemblages under the influence of freshwater outflows in the southern gulf of Mexico. Hydrobiologia 586 (1), 69–78.

Thibault-Botha, D., Gibbons, M.J., 2005. Epipelagic siphonophores off the east coast of South Africa. Afr. J. Mar. Sci. 27 (1), 129–139.

Toda, R., Moteki, M., Ono, A., Horimoto, N., Tanaka, Y., Ishimaru, T., 2010. Structure of the pelagic cnidarian community in Lützow–Holm Bay in the Indian sector of the southern ocean. Polar Sci. 4 (2), 387–404.

Ulloa, R., Palma, S., Linacre, L., Silva, N., 2000. Seasonal changes in the bathymetric distribution of siphonophores, chaetognaths and euphausiids associated to water masses off valparaíso, chile (Southeast Pacific). In: Farber, J. (Ed.), Oceanography in the Eastern Pacific. CICESE, Ensenada, pp. 72–83.

Wen-Tseng, L., Shwu-Feng, Y., Hung-Yen, H., 2013. Effects of summer mesoscale hydrographic features on epipelagic siphonophore assemblages in the surrounding waters of Taiwan, western north pacific ocean. J. Oceanogr. 69 (5), 495–509.

WoRMS Editorial Board 2020. World Register of Marine Species. Available from http://www.marinespecies.org at VLIZ. Accessed 2020-03-03. doi:10.14284/170.