Research Article

Siphonophore community biodiversity and spatio-temporal distribution concerning the oceanographic parameters in the Patagonian Fjord Ecosystem during the winter season

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ABSTRACT. This study describes the spatial distribution and abundance of siphonophores concerning oceanographic variables (temperature, salinity, and dissolved oxygen) in the northern Chilean Patagonian Fjord Ecosystem, from Guafo Passage (43º30'S) to Elefantes Gulf (46º40'S) during the winter of 2012. Twelve species were identified, ten belonging to suborder Calycophorae and two assigned to suborder Physonectae. The species *Chelophyes appendiculata* and *Sphaeronectes gamulini* are new records for this study area. Dominant species were *Muggiaea atlantica* (63.15%), *Lensia conoidea* (21.85%), and *Sphaeronectes koellikeri* (9.91%). Species richness showed a negative latitudinal gradient, and the highest densities were found in North Moraleda Channel (5316 ind 1000 m^{-3}) and the lowest in South Moraleda Channel, near Elefantes Gulf (71 ind 1000 m^{-3}). Some species showed a significant and positive association with some oceanographic variables, e.g., *M. atlantica* showed a positive association with dissolved oxygen, *L. conoidea* with temperature and negative association with dissolved oxygen, *Sphaeronectes fragilis*, *S. koellikeri,* and *C. appendiculata* showed a positive association with salinity. Eudoxids (sexual reproductive stage) were found for *M. atlantica*, *L. conoidea,* and *Dimophyes arctica,* indicating that the PFE conditions are suitable for some siphonophore species even in winter.

Keywords: siphonophores; community structure; spatial distribution; Patagonian Fjord Ecosystem; austral winter; southwestern Pacific

INTRODUCTION

The study of the gelatinous zooplankton and the increase of its negative interactions between their blooms, human activities, and ecosystem services (e.g. fisheries, aquaculture, tourism) is of great interest (Brodeur et al. 2002, Acuña et al. 2011, Baxter et al. 2011, Purcell 2012, Canepa et al. 2013, 2020, Condon et al. 2013, Mianzan et al. 2014). Gelatinous zooplankton, particularly planktonic cnidarians, are known as voracious predators with a high capacity for ingesting fish eggs, larvae, and juveniles, having negative effects on fisheries (Purcell 1981, Purcell et al. 2007), addressing the importance of understanding their distribution, spatio-temporal variability in abundance and relationship with present and future oceano-graphic conditions. The siphonophores are an important group of planktonic cnidarians, present in all marine ecosystems (Pagès & Gili 1992, Hosia & Båmstedt 2008, Silva & Palma 2008, Kenneth et al. 2011, Lindsay et al. 2014, Mapstone 2014). They are important consumers of ichthyoplankton and zooplankton in the spring season (Purcell 1981, 1997, Purcell & Arai 2001). Most species are pelagic and inhabit oceanic conditions. Some can adapt to a wide range of environmental conditions inhabiting coastal and estuarine waters, deep waters, and even benthos (Palma & Silva 2004, Hosia 2007, Hosia & Båmstedt 2008, Silva & Palma 2008, Mapstone 2014, Oliveira et al. 2016, Palma et al. 2018a,b).

Along the southeastern Pacific Ocean, the siphono-phores have been studied in northern Chile (Pagès et al.

2001, Palma & Apablaza 2004, Apablaza & Palma 2006), central Chile (Palma 1973, 1977, 1984, 1994, Palma & Rosales 1995, Ulloa et al. 2000), oceanic islands (Juan Fernández Archipelago, Palma 1985; Rapa Nui Island, Palma 1999, Palma & Silva 2006) and especially in the Patagonian Fjord Ecosystem (PFE) (Palma et al. 1997, 2007, 2011, 2014, 2018a,b, Palma & Silva 2004, Palma 2008, Villenas et al. 2009). Due to strong seasonal, latitudinal, and vertical variations in oceanographic conditions, plankton communities are affected by high spatial heterogeneity throughout the PFE (Palma & Silva 2004, Silva & Palma 2008, Valdenegro & Silva 2008), influencing the variability of the composition, distribution and the abundance of siphonophore community. Along the PFE, 20 species of siphonophores have been identified of the 56 species recorded along the Chilean coast and 177 species recorded worldwide (Mapstone 2015, Oliveira et al. 2016). The most abundant species on the Chilean coast are *Muggiaea atlantica* and *Sphaeronectes koellikeri*, which show high abundances associated with a coastal distribution. However, in the PFE, the most abundant species are *M. atlantica*, *S. koellikeri*, and *Lensia conoidea*, which biology and ecology have been widely described, particularly in the Norwegian fjords (Hosia 2007, Hosia & Båmstedt 2008). Besides, these species are very interesting in their ecological role as competitors and predators of other zooplankton species, including eggs and larval stages of fish with commercial interest (Purcell 2012).

In the northern sector of the PFE, from Guafo Passage (GP; 43º30'S) to Elefantes Gulf (EF; 46º40'S), a total of 11 species of siphonophores have been found, of which *M. atlantica*, *L. conoidea*, and *S. koellikeri* were the most abundant species (Palma & Silva 2004, Palma 2008). Spatial analysis has shown that *L. conoidea* is mostly found in deeper and less oxygenated waters. *S. koellikeri* is primarily associated with high salinity, whereas *M. atlantica* is mostly in shallower, less saline, and more oxygenated waters (Palma et al. 2014, 2018a,b). Most information has been addressed during campaigns conducted in the summer-spring season, with a lack of monitoring effort during the winter season. Thus, understanding the abundance and spatio-temporal variability is needed during the low productive season.

Palma et al. (2018a,b) found that temperature and dissolved oxygen were the most important variables in describing the distribution of the different siphonophore species. Understanding the environmental forcing on the communities of siphonophores in the PFE has allowed establishing, in general, higher siphonophore abundance when the temperature is higher, associated with spring-summer periods (Boltovskoy

1999, Palma et al. 2011, 2014b, 2018a,b). Nonetheless, the water column stability seems to be an important factor, increasing the siphonophore density associated with a stratified water column (Palma et al. 2018a,b).

In this study zone, the northern PFE from GP to EG, the association between siphonophore abundance, the oceanographic variables, and the environmental drivers of community composition during the winter season is still poorly understood. The only study conducted in winter corresponds to the northern Patagonian Fjords between Puerto Montt and GP (Palma et al. 2011). Thus, this study aims to contribute to the understanding of the siphonophore community composition, abundance and spatial distribution, and environmental association in the northern Patagonian Fjords during winter conditions.

MATERIALS AND METHODS

Study area

The Oceanographic National Committee (CONA, by its spanish acronym) and the Hydrographic and Oceanographic Service of the Navy (SHOA, by its spanish acronym) initiated the "Cruises for Marine Research in Remote Areas Program" (CIMAR, by its spanish acronym) to study in a multidisciplinary way oceanography, biodiversity, and underwater morphology of remote areas which have important and strategic value for the socio-economic development. By now, 25 research campaigns have been carried out, most of them in different zones of northern Chilean PFE and four of them close to the Chilean Islands.

The PFE extends from Puerto Montt (41°S) to Cape Horn (55°S), encompassing around 84,000 km of coastline, 1600 km in length, and a total area of ~240,000 km² of complex topography with highly variable oceanographic and atmospheric conditions, constituting a structurally and functionally unique inland water ecosystem by semi-enclosed highly haline-stratified areas (Palma & Silva 2004, Silva & Palma 2008, Pantoja et al. 2011).

This study will focus on the research campaign CIMAR 18, carried out onboard the R/V Abate Molina between June 16 and July 8, 2012, during the austral winter season. Along a latitudinal transect, 23 oceanographic stations were distributed in the northern Patagonian fjords from GP (43º30'S) to EG (46º40'S), including Aysen Fjord (45º17'-45º28'S) and Puyuhuapi Channel (44º56'-44º26'S) (Fig. 1).

Sampling

Oceanographic and zooplankton data were collected in each of the 23 sampling stations. Temperature, salinity, and dissolved oxygen were measured with a Seabird plus 19 CTD. Zooplankton samples were collected through oblique tows with a Tucker trawl net (mouth
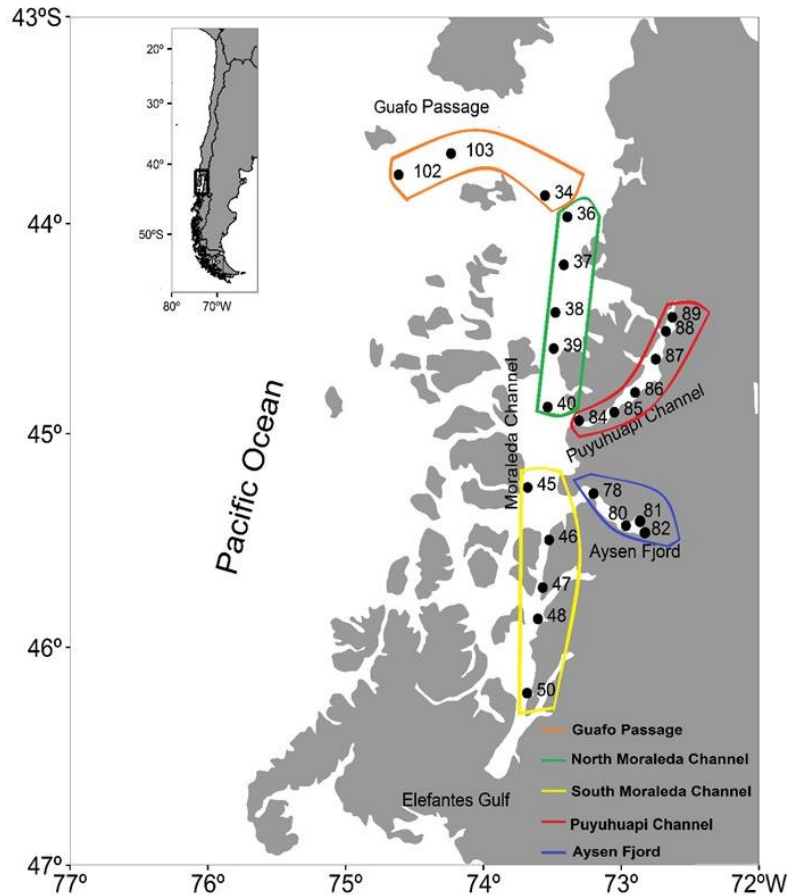
Figure 1. Study area showing the different sampling areas and their sampling stations during the cruise CIMAR-18 in northern Patagonia.

size 1 m² and mesh 300 mm), equipped with digital flowmeters to estimate the volume filtered during each trawl. For detailed information on the volumes filtered per station and their mean temperature, salinity, and dissolved oxygen, see Table S1. Three strata were considered, surface (0-25 m), middle (25-50 m), and deep (50-150 m), except in stations 45, 48, and 81, where the bottom depth was 100 m. The zooplankton samples were preserved immediately on board in a 5% solution of formaldehyde in seawater buffered with borax.

Statistical analysis

The zooplankton identification was carried out until the most specific taxonomical level, following Totton's (1965) and Pugh's (1999) works. The siphonophores were sorted, and the nectophores (asexual polygastric stage) and eudoxids (sexual reproductive stage) were identified and counted. Abundances of nectophores and eudoxids are given separately. For the statistical analysis, only nectophores were considered. Calculations of total abundance were standardized using the

volume of filtered seawater to individuals per 1000 m⁻³. Total abundance for suborder Calycophorae was estimated considering the highest number of anterior *vs.* posterior nectophores. In contrast, total abundance for suborder Physonectae was estimated by considering one colony of *Pyrostephos vanhoeffeni* to have 20 pairs of nectophores (Totton 1965).

Two commonly used community indices, dominance (DO) and frequency of occurrence (FO), were used to describe the siphonophore community (Palma et al. 2011, 2014, 2018a,b). The DO was calculated as each species percentage over the total individuals collected, and the FO represented the percentage of each species over the total number of stations sampled. Dominant species were species with a DO >5%.

As the oceanographic variables were measured at different depths than zooplankton samples, the weighted means of the environmental variables were calculated for the zooplankton samples range, following:

$$X_{ij} = \frac{\Sigma Z_{jk} * C_{ijk}}{\Sigma Z_{jk}}$$

where X_{ij} is the weighted mean of the i-th parameter at the j-th station, Z_{jk} is the k-th depth at the j-th station, C_{ijk} is the mean of the i-th parameters of the delta of the k-th depths at the j-th station.

Before using formal statistical analysis, the exploratory data analysis (EDA) suggested by Zuur et al. (2010) was conducted on the environmental and biological datasets to evaluate outliers and proper family distribution of the variable and homoscedasticity to avoid further statistical problems. All analyses were performed using R Statistical Software (v.3.4.0; R Core Team 2017). The siphonophore community structure was characterized through a non-metric multidimensional scaling (nMDS) (Clarke & Warwick 1994) via the function *metaMDS* from the "vegan" package (v.2.4.4; Oksanen et al. 2017). The role of the oceanographic variables over this community structure was analyzed through a canonical correspondence analysis (CCA) (Ter Braak 1986) via the *cca* function from the "vegan" package (v.2.4.4; Oksanen et al. 2017). The stepwise optimal model was achieved by a backward model selection using permutation tests with the *ordistep* function from the "vegan" package (v.2.4.4; Oksanen et al. 2017).

The association between each dominant species (DO >5%) and the environmental variables were evaluated through regression analysis. Collinearity assumption, i.e. the avoidance of auto-correlated explanatory variables, was analyzed through the variance inflation factor using the *vif* function from the "car" package (v2.1.5; Fox & Weisberg 2011). Due to the nature of species data (i.e. count numbers), generalized linear models (GLMs) with a negative binomial error family distribution and a log 'link' function were fitted using the *glm.nb* function from the 'MASS' package (v7.3.47; Venables & Ripley 2002). The sampled volume of seawater (log-transformed) was used as an offset inside the GLMs because of its high variability between stations (data not shown). The optimal model was achieved using a backward selection procedure until all explanatory variables were significant (Zuur et al. 2009). Oceanographic information was graphically inspected using ODV4 (Ocean Data View 4.7, 2015).

RESULTS

Hydrography

a) Guafo Passage (Fig. 2). It is the opening towards the Pacific Ocean. It presented homogeneous conditions through the whole transect, with an inverted vertical thermal distribution with lower temperature (9.4-10ºC) at the surface, increasing with depth, with a maximum of 10.5ºC at 55 m (Fig. 2a). Salinity values showed low variability in-depth, with 33 at the surface and 34 at 150 m, except in St. 34, where the surface salinity dropped to 32 (Fig. 2b). The dissolved oxygen distribution was stratified and fluctuated between 6.5 mL L^{-1} on the surface and 3 mL L^{-1} at 150 m (Fig. 2c).

b) Moraleda Channel to Elefantes Gulf (Fig. 3). It presents a characteristic latitudinal transect. At St. 45, temperature, salinity, and dissolved oxygen showed a break, dividing the zone into two hydrographic basins. The inverted vertical thermal distribution was found in both basins, with temperature values increasing from 9ºC at the surface to 10ºC at 100 m (Fig. 3a). The salinity gradient decreased from the north (32.5) to the south (26.5; Fig. 3b). The northern basin showed more homogeneous salinity conditions with a mean of 32.5 (Fig. 3b), while in the southern basin, the salinity increased from 26.5 at the surface to 31 at 150 m. The dissolved oxygen was lower in the northern basin than in the southern basin (5.0 *vs.* 5.5 mL L^{-1}; Fig. 3c).

c) Puyuhuapi Channel (Fig. 4). The presence of a two-layer structure characterizes the channel, the superficial layer (0-50 m) showed lower values of temperature and salinity and higher values of dissolved oxygen than the deeper layer (5.5 *vs.* 10.0ºC; 26 *vs.* 34; 6.5 *vs.* 4 mL L^{-1}, respectively; Fig. 4). At the head of the channel, the temperature showed a maximum of 10.5ºC at 100 m depth, whereas the mouth was 9.75ºC (Fig. 4a). Below 50 m, a more homogeneous layer was found with a mean of 10ºC and 34 of salinity (Fig. 4b). A minimum dissolved oxygen concentration layer (3.5 mL L^{-1}) was found at 150 m depth at St. 89 (Fig. 4c).

d) Aysen Fjord (Fig. 5). The fjord presented a high stratified two-layer structure. The surface layer was broader at the head of the fjord (0-50 m), and it narrows as it approaches the mouth of the fjord. The surface waters were, on average colder (9.2ºC), less salty (21.5), and more oxygenated (6 mL L^{-1}) than deeper waters (32.5, 4 mL L^{-1}, 11ºC; Fig 5). Both the halo- and thermocline were present between 25 and 50 m depth. Temperature and salinity increased with depth, showing a temperature of 11.5ºC and a salinity of 34 at 100 m at the head of the fjord (Figs. 5a,c); however, the oxycline was not evident with a continuous decrease in dissolved oxygen concentration with depth. This decrease was more pronounced in the head of the fjord than at the mouth (Fig. 5b).

Taxonomic composition

The siphonophore community was represented by 12 species, 10 belonging to the suborder Calycophorae and 2 to the suborder Physonectae. The species *Sphaeronectes gamulini* and *Chelophyes appendiculata* constitute new records for this geographic area.
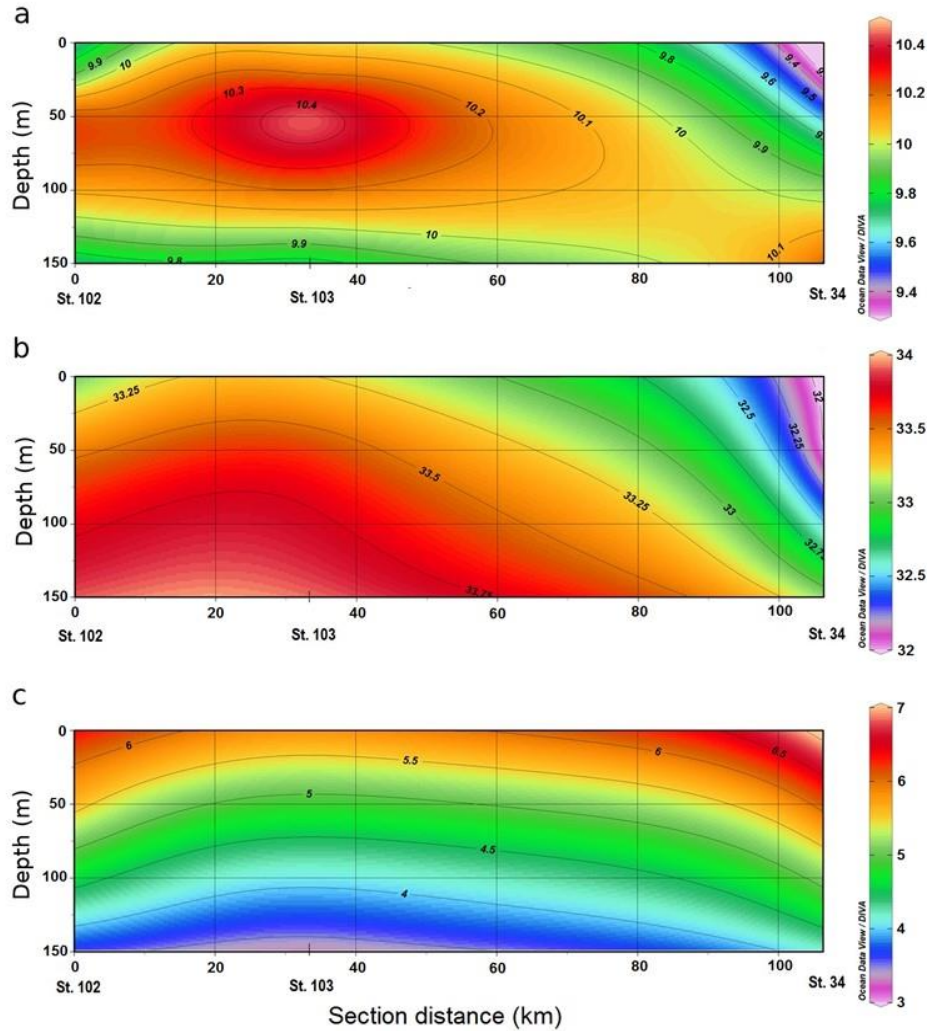
Figure 2. Vertical distribution of oceanographic parameters along the Guafo Passage. a) Temperature (°C), b) salinity and c) dissolved oxygen (mL L^{-1}).

The three dominant species (DO >5%) were, in descending order: *Muggiaea atlantica* (63.15%), *Lensia conoidea* (21.85%), and *Sphaeronectes koellikeri* (9.91%). The rest of the species (9) accounted for the remaining 5.1% of dominance (Table 1). Eudoxids were only found for *M. atlantica, L. conoidea,* and *Dimophyes arctica*. For *D. arctica,* no nectophores were found, so this species will not be considered in the statistical analysis.

Siphonophore community

The siphonophore community structure was represented using a non-metric multidimensional scaling nMDS (Fig. 6), showing species belonging to discrete groups of stations (polygons). In this analysis, stations are grouped based on the similarity in species composition. Those with a representation (proportional abundance) higher than the mean for one station are placed near that station. Most species were present in the Northern Moraleda Channel (NMC). *L. conoidea* was associated with Aysen Fjord (AF), while *M. atlantica* was represented in two polygons, Southern Moraleda Channel (SMC) and Puyuhuapi Channel (PC). *Sphaeronectes fragilis* showed a weak association with PC and *S. koellikeri* to the NMC (Fig. 6). The rest of the species were present in only one station or showed low abundance.

Spatial distribution patterns of the siphonophore community

A north-south gradient of species richness was present. Most species were found in GP and NMC, while at EG and AF, only two or three species were present (Fig. 6, Table 2). The species abundance had a similar distribu-
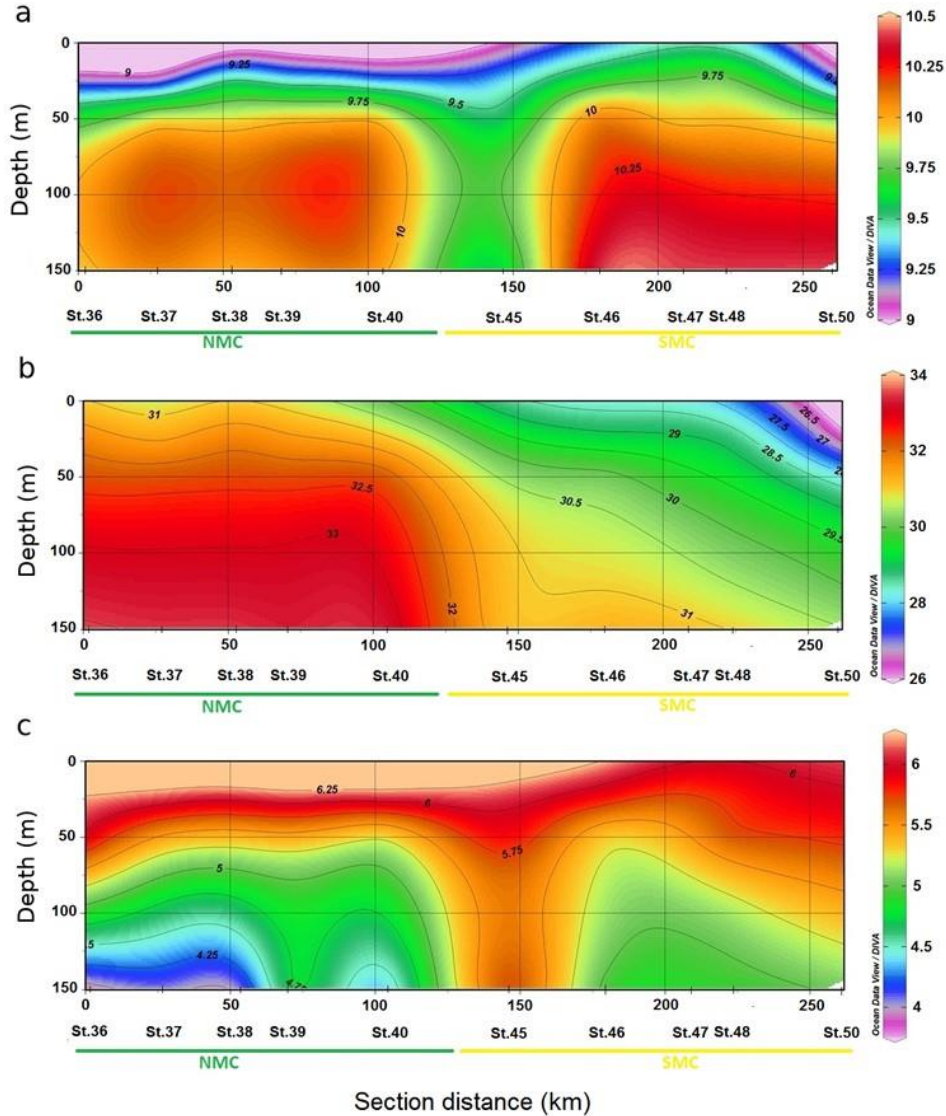
Figure 3. Vertical distribution of oceanographic parameters along the Moraleda Channel. a) Temperature (°C), b) salinity and c) dissolved oxygen (mL L^{-1}). NMC: North Moraleda Channel, SMC: South Moraleda Channel.

tion showing a north-south gradient with values decreasing from 5316 ind 1000 m^{-3} in Moraleda Channel (St. 40) to 71 ind 1000 m^{-3} in EG (St. 50) (Table 2), except for two stations of the northern basin (St. 34 and 36), where similar low values of abundance were found as in EG (315 and 210 ind 1000 m^{-3}). The mean abundance per station was 1950 ind 1000 m^{-3} (Table 2).

M. atlantica was the most abundant species (DO 63.15%) and had the broadest geographic coverage (FO 87%) (Table 1), being present in every station except at the head of AF (St. 80, 81, and 82) (Fig. 7a, Table 2). In general, *M. atlantica* showed high-density values (mean of 1232 ind 1000 m^{-3}) with a range of non-zero abundance between 5 and 3315 ind 1000 m^{-3}. Its maximum densities were found in Moraleda Channel,

with 4743 ind 1000 m^{-3} (St. 40) (Fig. 7a, Table 2). *M. atlantica* was present as well in its reproductive stage. A high amount of eudoxids were found in Moraleda Channel, but its maximum was reached in PC with 979 eudoxids 1000 m^{-3} (Table 2). Eudoxids of this species were present in most stations where the number of nectophores was high, but in one station in AF where no nectophores of *M. atlantica* were found (St. 80), still, 42 eudoxids were found.

L. conoidea showed a DO (21.8%) and a FO (82.6%) (Table 1) and presented a contrasting horizontal distribution to *M. atlantica* (Figs. 7a-b). The highest densities were found in AF (estuarine waters), where its maximum abundance reached 3844 ind 1000 m^{-3} in St. 80. Its lowest abundance was found in oceanic waters (area of GP), absent in St. 102, 36, and 34
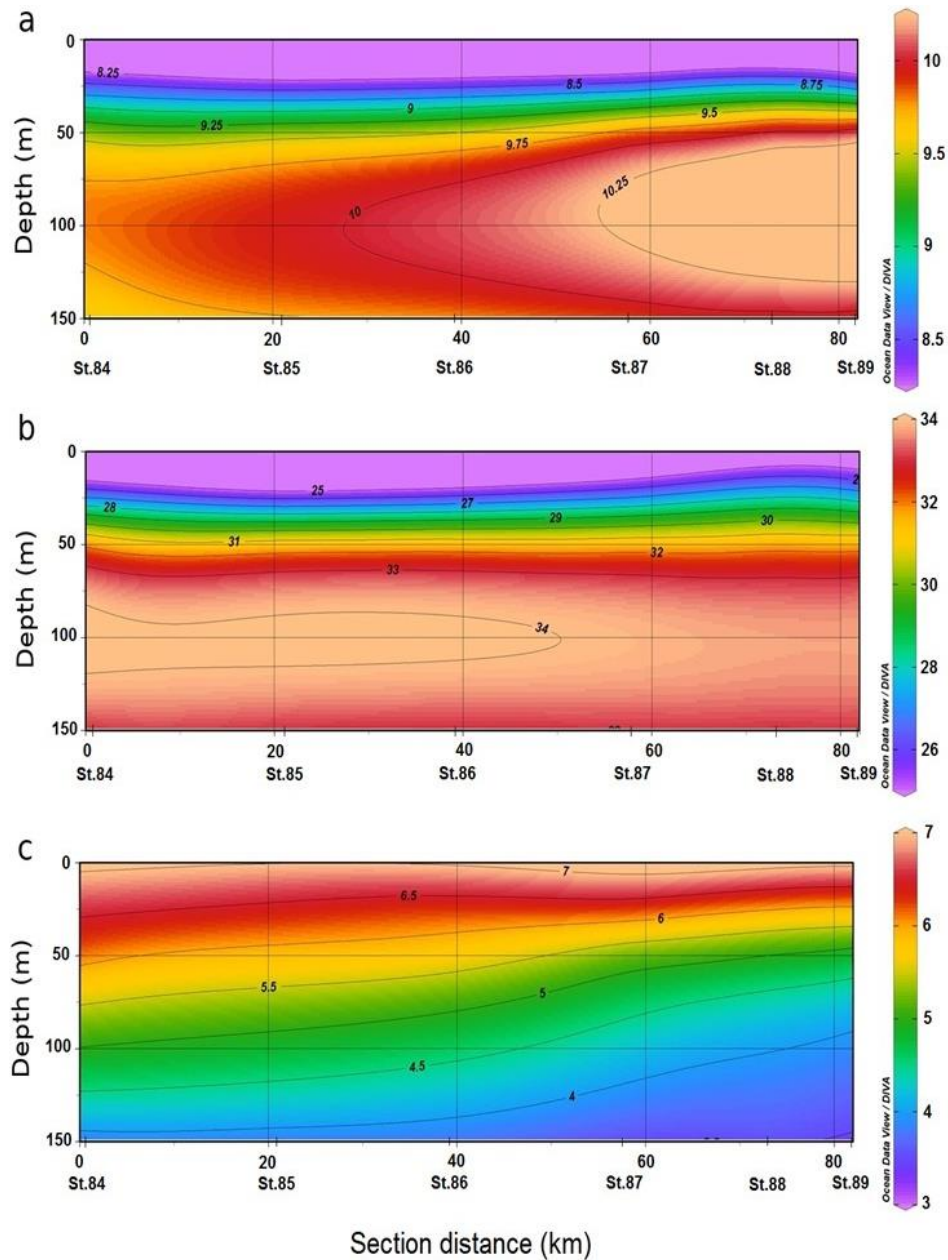
Figure 4. Vertical distribution of oceanographic parameters along the Puyuhuapi Channel. a) Temperature (ºC), b) salinity and c) dissolved oxygen (mL L^{-1}).

(Fig. 7b, Table 2). The mean abundance per station was 426 ind 1000 m^{-3} (Table 1). The reproductive stage of *L. conoidea* was also present. Of the species which presented eudoxids (*M. atlantica*, *L. conoidea* and *D. arctica*), *L. conoidea* showed the highest dominance (DO 57%) and broadest geographic coverage (FO 65%) (Table 1). In the SMC and PC *L. conoidea* showed higher eudoxid abundance than nectophore abundance (Table 2).

S. koellikeri (DO 9.9% and FO 69.6%) showed an average density of 79 ind 1000 m^{-3} and had its highest density in GP, with the highest abundance in St. 102 with 1455 ind 1000 m^{-3} (Tables 1-2). It was absent along AF and in the rest of estuarine waters, except for St. 48 (EG), where we found 11 ind 1000 m^{-3} (Fig. 7c, Table 2).
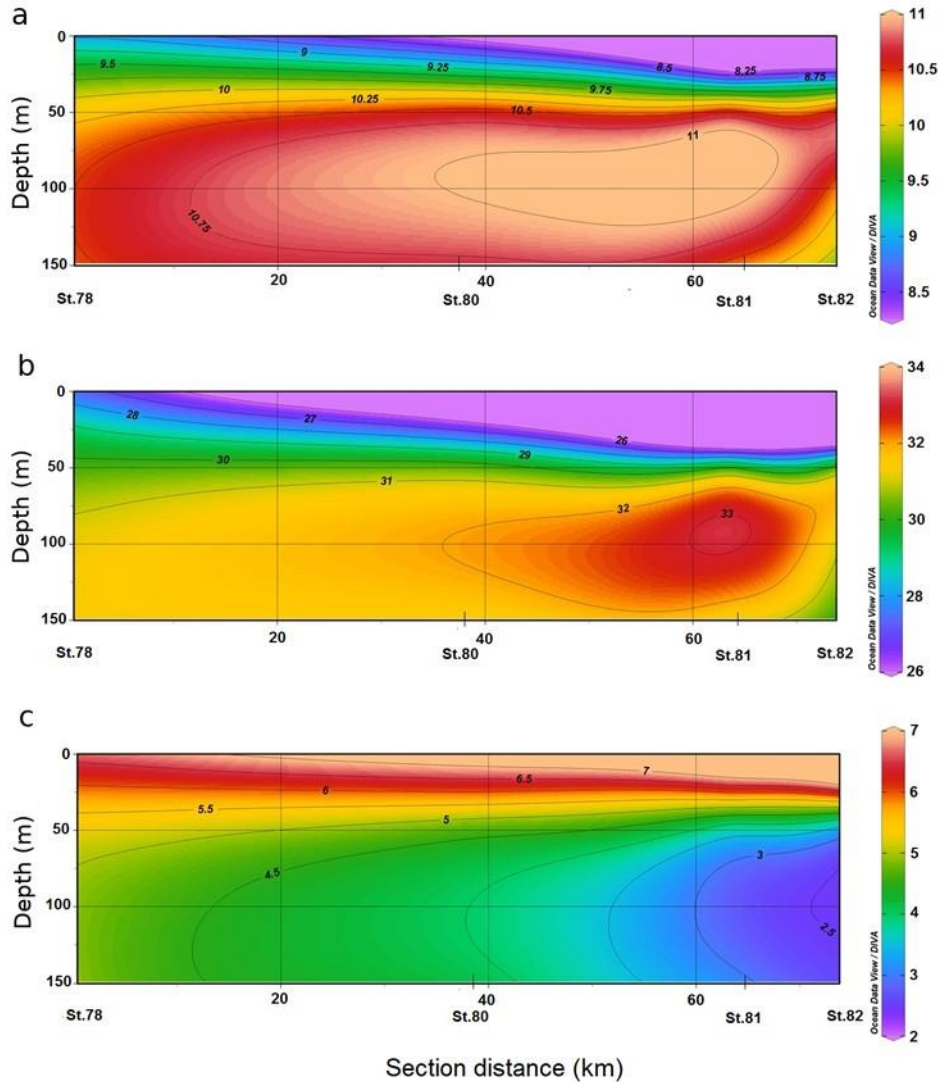
Figure 5. Vertical distribution of oceanographic parameters along the Aysen Fjord. a) Temperature (ºC), b) salinity and c) dissolved oxygen (mL L^{-1}).

Relationship with the oceanographic variables

From the univariate (i.e. species-specific) perspective, the abundance of the siphonophores was modeled (as the response variable) using the oceanographic variables: temperature (ºC), salinity, dissolved oxygen (mL L^{-1}), and depth (m) (as explanatory variables). Depth was only significant in the GLM for *M. atlantica* and *L. conoidea.* For *M. atlantica* and *L. conoidea* all the environmental variables were significant to explain their variability (44.9 and 74.8%, respectively). *M. atlantica* showed a non-linear response to all parameters (quadratic terms) except for temperature, where the highest abundances were negatively correlated with temperature and positively with depth (Table 3). A unimodal response was found concerning salinity and dissolved oxygen, where the highest

densities of *M. atlantica* were detected at ~31.2 and ~5.2 mL L^{-1}, respectively (Fig. 8a). *L. conoidea* abundance showed a non-linear response with all parameters (cubic terms). High temperatures and depth favored species abundance and dissolved oxygen and salinity showed a negative effect (Fig. 8b). For *S. koellikeri,* temperature, salinity, and dissolved oxygen were significant, explaining up to 70% of its variability. This species showed a positive correlation with salinity, appearing in waters with salinity values higher than 32.5 and showing a unimodal response to dissolved oxygen, where the highest densities were found between 4.5-5.5 mL L^{-1} (Fig. 8c).

From the multivariate (i.e. community composition) perspective, temperature, salinity, and dissolved oxygen proved significant in the amount of inertia ex-

Table 1. Total number of individuals (n), mean abundance per station (average in ind 1000 m^{-3}), non-zero (range of non-zero abundance in ind 1000 m^{-3}), dominance (DO), frequency of occurrence (FO) of siphonophore species for nectophores(eudoxids) along the study area. -- No nectophores(eudoxids) have been found.

| Species	n	Average	Non-zero	DO(%)	FO(%)
Muggiaea atlantica	28334(3498)	1232(152)	5 - 3315(6 - 943)	63.1(43)	87(61)
Lensia conoidea	9802(4662)	426(203)	6 - 2168(11 - 443)	21.8(57)	82.6(65)
Sphaeronectes koellikeri	4444(--)	193(--)	4 - 1222(--)	9.9(--)	69.6(--)
Sphaeronectes fragilis	1812(--)	79(--)	4 - 443(--)	4.0(--)	69.6(--)
Sphaeronectes gamulini	292(--)	13(--)	5 - 55(--)	0.7(--)	34.8(--)
Sphaeronectes irregularis	72(--)	3(--)	6 - 54(--)	0.2(--)	13(--)
Chelophyes appendiculata	58(--)	3(--)	5 - 24(--)	0.1(--)	8.7(--)
Dimophyes arctica	--(36)	--(2)	--(15 - 21)	--(0.45)	--(9)
Rosacea plicata	23(--)	1(--)	23 - 23(--)	0.1(--)	4.3(--)
Lensia sp.	22(--)	1(--)	5 - 18(--)	0.05(--)	8.7(--)
Agalma elegans	7(--)	0.3(--)	1 - 2 (--)	0.02(--)	21.7(--)
Pyrostephos vanhoeffeni	1(--)	0(--)	1 - 1(--)	0.002(--)	4.3(--)
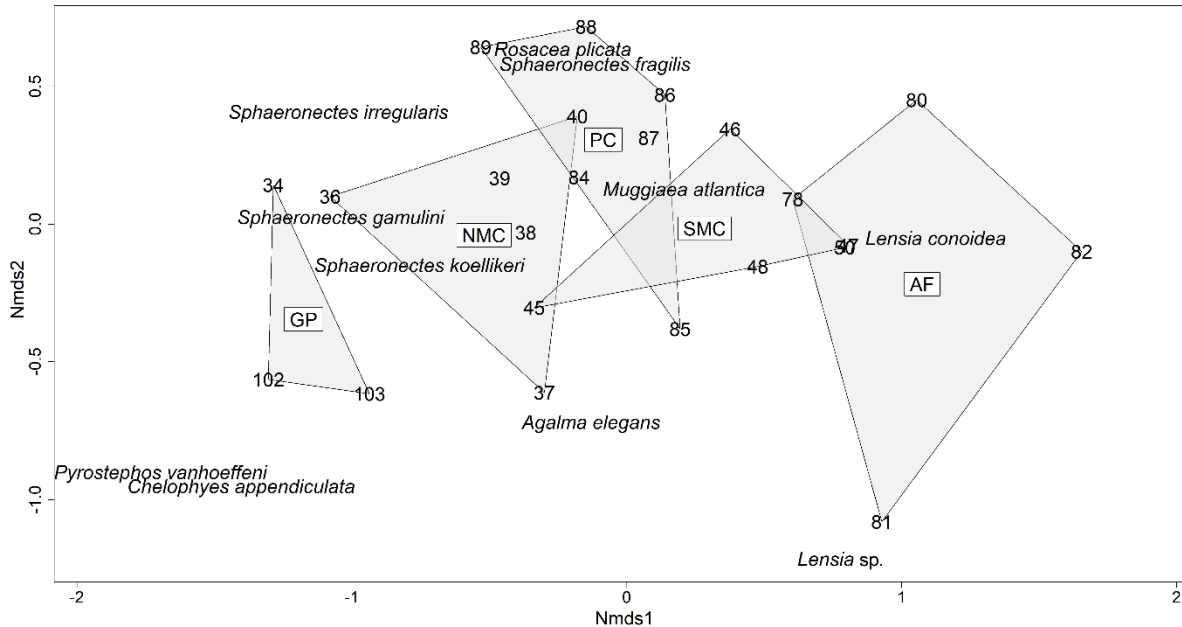
Figure 6. Siphonophore community structure represented by a non-metric multidimensional scaling (nMDS). The numbers represent the sampling stations. The polygons represent the different sampling zones as GP: Guafo Passage, NMC: North Moraleda Channel, PC: Puyuhuapi Channel, SMC: South Moraleda Channel, AF: Aysen Fjord.

plained for all dominant species (Table 4). The most adequate multivariate model (following the stepwise backward model selection using permutation) showed total inertia of 93.44%, with the first axis explaining up to 69.56% of the total variability and the second axis explaining up to 23.88% (Fig. 9). Most species showed a positive association with salinity. The dominant species, *M. atlantica* was attributed to stations from all depths with a positive response to dissolved oxygen, salinity, and low temperature. *L. conoidea* was associated with stations with more depth and high

temperature, while *S. koellikeri* was strongly associated with salinity (Fig. 9). A positive association with salinity was found for the other non-dominant species, such as *Chelophyes apendiculata*, *S. fragilis* and *Agalma elegans*. A similar relationship was found with *Rosacea plicata* and dissolved oxygen (Fig. 9).

DISCUSSION

A total of 12 species of siphonophores were recorded. *Sphaeronectes gamulini* and *Chelophyes appendiculata*

Table 2. Mean abundance per station of nectophores(eudoxids) of the siphonophores species collected in the study area (ind 1000 m^{-3}). Ma: *Muggiaea atlantica*, Lc: *Lensia conoidea*, Sk: *Sphaeronectes koellikeri*, Sf: *S. fragilis*, Si: *S. irregularis*, Sg: *S. gamulini*, Pv: *Pyrostephos vanhoeffeni*, Ae: *Agalma elegans*, Rp: *Rosacea plicata*, Ca: *Chelophyes appendiculata*. -- No nectophores(eudoxids) have been found.

| Area	Station	Total	Ma	Lc	Sk	Sf	Si	Sg	Pv	Ae	Rp	Ca	Da
Guafo Island	102	1582(--)	64(--)	--(--)	1455(--)	6(--)	--(--)	24(--)	1(--)	--(--)	--(--)	35(--)	--(--)
Guafo Passage	103	671(--)	44(--)	40(--)	554(--)	5(--)	--(--)	5(--)	--(--)	--(--)	--(--)	25(--)	--(--)
N Peligroso Islet	34	315(--)	77(--)	--(--)	188(--)	--(--)	13(--)	38(--)	--(--)	--(--)	--(--)	--(--)	--(--)
Moraleda Channel	36	210(--)	7(--)	--(--)	160(--)	14(--)	--(--)	30(--)	--(--)	--(--)	--(--)	--(--)	--(--)
Moraleda Channel	37	2778(775)	1949(775)	25(--)	802(--)	--(--)	--(--)	--(--)	--(--)	2(--)	--(--)	--(--)	--(--)
Moraleda Channel	38	4080(444)	3479(444)	6(--)	360(--)	207(--)	--(--)	29(--)	--(--)	1(--)	--(--)	--(--)	--(--)
Moraleda Channel	39	2709(--)	2146(--)	27(--)	362(--)	120(--)	54(--)	--(--)	--(--)	1(--)	--(--)	--(--)	--(--)
Moraleda Channel	40	5316(559)	4743(513)	22(46)	298(--)	231(--)	--(--)	--(--)	--(--)	--(--)	24(--)	--(--)	--(--)
SW Churrecue Island	45	3841(320)	3530(262)	132(58)	26(--)	37(--)	--(--)	116(--)	--(--)	2(--)	--(--)	--(--)	--(--)
Costa Channel	46	1521(673)	1414(59)	73(613)	--(--)	35(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)
Costa Channel	47	987(994)	645(15)	342(979)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)
Elefantes Gulf	48	642(228)	390(19)	242(209)	11(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)
Elefantes Gulf	50	71(66)	52(--)	20(51)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(15)
Aysen Fjord	78	2924(1042)	1309(252)	1605(789)	--(--)	12(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)
Aysen Fjord	82	760(437)	--(--)	760(437)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)
Aysen Fjord	81	2413(334)	--(--)	2412(334)	--(--)	--(--)	--(--)	--(--)	--(--)	1(--)	--(--)	--(--)	--(--)
Aysen Fjord	80	3892(301)	0(42)	3844(258)	--(--)	49(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)
Puyuhuapi Channel	84	4889(1137)	4591(979)	11(157)	102(--)	148(--)	--(--)	39(--)	--(--)	--(--)	--(--)	--(--)	--(--)
Puyuhuapi Channel	85	1649(505)	1563(43)	56(462)	27(--)	5(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)
Puyuhuapi Channel	86	774(46)	753(46)	--(--)	4(--)	18(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)
Puyuhuapi Channel	87	1499(204)	1116(22)	158(161)	30(--)	197(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(21)
Puyuhuapi Channel	88	564(91)	249(--)	15(91)	22(--)	281(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)	--(--)
Seno Ventisquero	89	773(32)	225(20)	21(11)	51(--)	457(--)	6(--)	14(--)	--(--)	--(--)	--(--)	--(--)	--(--)
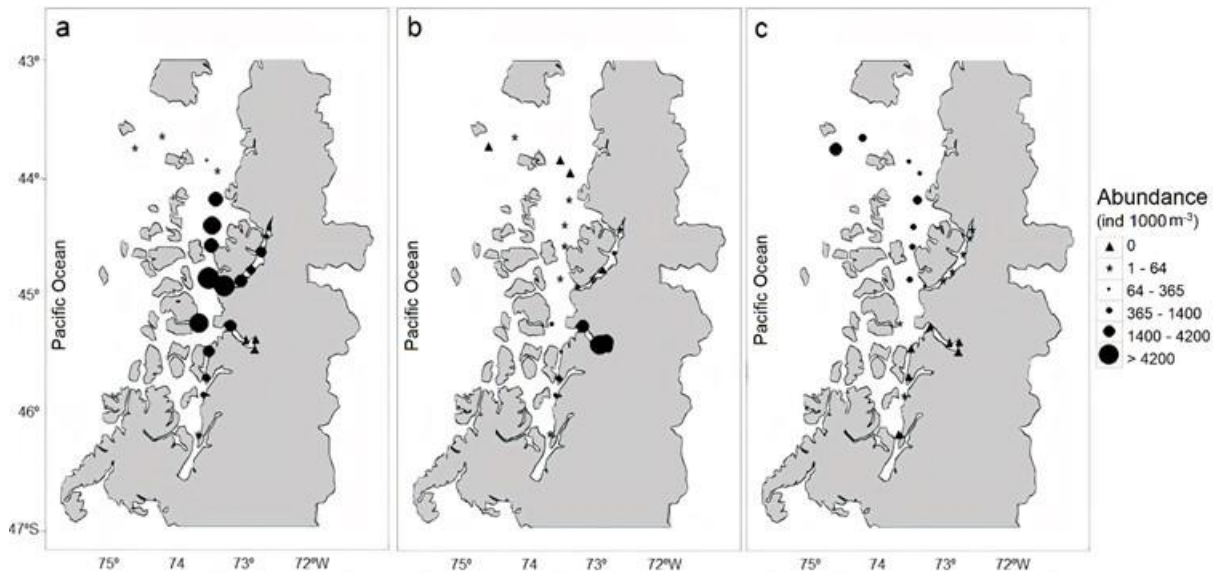
Figure 7. Spatial distribution of the dominant species in the study area. a) *Muggiaea atlantica*, b) *Lensia conoidea* and c) *Sphaeronectes koellikeri*.

were registered for the first time in this geographic area. Both species have been recorded in Chilean central waters, off Valparaíso (Palma 1973, 1984). However, only *C. appendiculata* was recorded in the Patagonian Fjords, between Penas Gulf and Trinidad Channel (Palma & Silva 2004, Palma 2008, Palma et al. 2014).

Siphonophores community structure

Along the whole PFE (41º20'-55º58'S), 20 siphonophore species have been described, of which 17 belong to the suborder Calycophorae and three to the suborder Physonectae (Palma et al. 2018a). Thus, the species richness along the PFE seems low compared to

Table 3. Statistical summary of generalized linear models for the dominant species, using a negative binomial family error distribution. The statistical test values (Z score) and the significance level are shown. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. ns: not significant, Temp: temperature, Sal: salinity, DO: dissolved oxygen, ^{2}quadratic term of the explanatory variable.

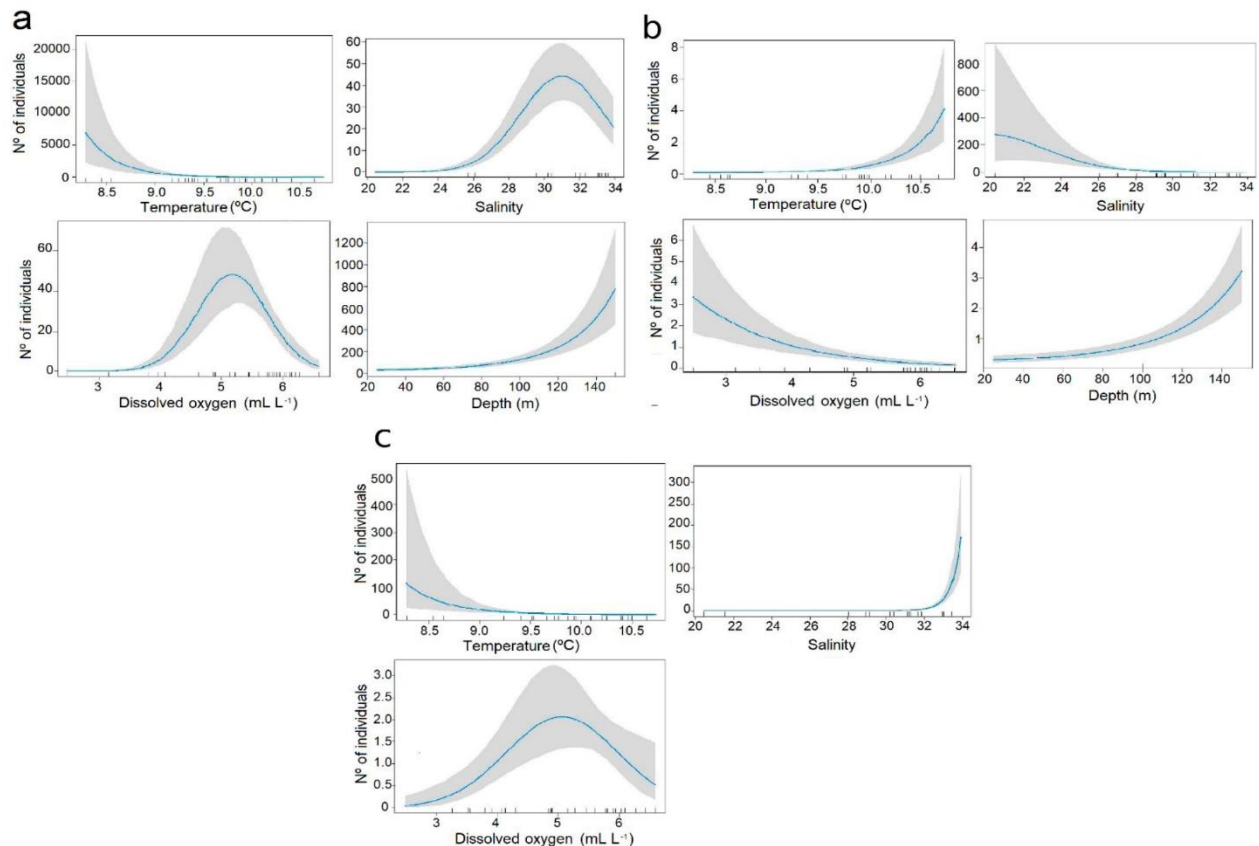| Oceanographic parameters	*Muggiaea atlantica*	*Lensia conoidea*	*Sphaeronectes koellikeri*
Temp/Temp^2	-10.3*** / ns	-2.4* / 2.8**	-5.4*** / ns
Sal/Sal^2	7.9*** / -7.6***	4.5*** / -6.2***	-4.5*** / 5.8***
DO/DO^2	10.5*** / 9.7***	-6.1*** / ns	3.2*** / -3.0***
Depth/Depth^2	ns / 9.3***	ns / 8.2***	ns / ns

Figure 8. Functional responses of dominant species of siphonophores. a) *Muggiaea atlantica*, b) *Lensia conoidea*, and c) *Sphaeronectes koellikeri* to the oceanographic parameters in winter 2012. The continuous blue line indicates the generalized linear model fit, and in grey, the areas of confidence intervals of the model.

Table 4. Results of the permutations of the canonical correspondence analysis (CCA) for the community of siphonophores. Values of the statistical test (F) and *P*-values for (*P*) the oceanographic parameters. $*P$-value < 0.05, $**P$-value < 0.01, $***P$-value < 0.001.

CCA	F-value	P-value
Temperature	6.2395	0.016*
Salinity	19.2287	0.001***
Dissolved oxygen	8.6998	0.002**

the 177 species of siphonophores recorded worldwide (Mapstone 2015). Only 12 species were found in the study area, indicating low species richness. Sipho-

nophores of this geographical area from GP (43°30'S) to EG (46°40'S) had previously been studied in spring (October-November) for different years (Palma & Rosales 1997, Palma et al. 2007) describing the presence of 11 or 12 species. Zooplankton sampling carried out during the winter season (June-July) showed that the species richness in winter is comparable to spring for this geographical area (Palma et al. 2007). However, five species have appeared in this study area during different springtimes that have not been found in the winter periods, such as *Abylopsis tetragona*, *Eudoxoides spiralis*, *Physophora hydrostatica*, *Vogtia pentacantha*, and *V. serrata*. These species are none
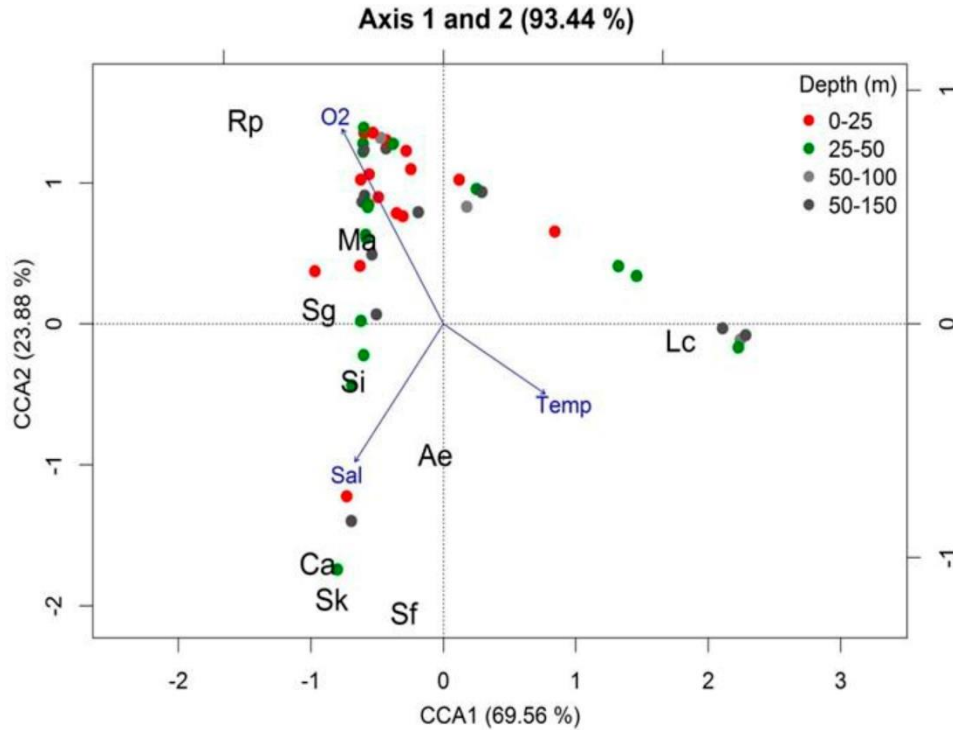
Axis 1 and 2 (93.44 %)

Figure 9. Canonical correspondence analysis (CCA) (tri-plot) shows the siphonophores community's association with the different oceanographic parameters. Ma: *Muggiaea atlantica*, Lc: *Lensia conoidea*, Sk: *Sphaeronectes koellikeri*, Sf: *Sphaeronectes fragilis*, Si: *Sphaeronectes irregularis*, Sg: *Sphaeronectes gamulini*, Pv: *Pyrostephos vanhoeffeni*, Ae: *Agalma elegans*, Rp: *Rosacea plicata*, Ca: *Chelophyes appendiculata*. Temp: temperature, Sal: salinity, O_2: dissolved oxygen.

dominant and sometimes described as occasional or visiting species (Palma & Rosales 1997, Palma et al. 2007).

The average abundance per station in the winter season of 2012 was similar to the spring season for other years (Palma & Rosales 1997, Palma et al. 2007). The interior waters are known to be highly fertile in spring, which favors the abundance of siphonophores (Palma & Silva 2004). In winter, a microbial loop maintains a high level of productivity in the ecosystem (Pantoja et al. 2011, Iriarte et al. 2013). So, one reason that explains these high abundances of siphonophores in winter might be due to the productivity in these areas, which allows reproductive stages for some species even in winter and possibly as a long-term response of the siphonophore abundance in recent years (Condon et al. 2013, Palma et al. 2018a,b). In the last decades, massive gelatinous plankton blooms have been reported in coastal areas, and the abundance of gelatinous organisms has been linked to climate conditions (Condon et al. 2013, D'Ambrosio 2018). The intra-season (winter) comparisons showed that the siphonophore community during the winter of 2007 (C13F) represented only half of the abundance that was

found in the same study area compared to the present study, during the winter of 2012 (Palma et al. 2007). When comparing the two surveys conducted during winter along the same area (i.e. C13F in 2007 and C18F in 2012, this study), we can see that the total abundance of siphonophores has doubled in just five years, indicating a possible (even though, difficult to prove) long-term increase response of the siphonophore community to oceanographic variables.

The majority of the identified siphonophore species are common in the Patagonian Fjords (Palma & Silva 2004, Palma et al. 2007, 2011, 2014, 2018a,b). For *Dimophyes arctica*, no nectophores were found, and just a few eudoxids (sexual reproductive stage) were present, reflecting its presence in the study area. This species was dominant during the first cruise (C1F, 1995), and since then, it has shown a constant decrease in abundance (Palma & Silva 2004, Palma et al. 2007, 2018a,b). Thus, the increase mentioned above does not represent the whole community, showing inter-specific differences in abundance variability, which is important since not only the abundance of siphonophores seems to be changing but also their community composition.

In several northern and central Patagonian Fjords studies, only eudoxids of *D. arctica* have been found (Palma & Silva 2004, Palma et al. 2007, 2018a). Still, some nectophores were found south of the channels (Palma et al. 2018b). *D. arctica* is a cosmopolitan species inhabiting all latitudes (Mapstone 2014), but more frequent in cold waters and known as a typical species of Antarctic waters (Totton 1965, Pagès & Gili 1992, Palma & Silva 2004). The absence of nectophores and its decrease in abundance could be related to a temperature increase. During the C1F, the temperature ranged between 8 and 10ºC (Palma & Rosales 1997). The temperature of the PFE southern channels, where *D. arctica* was found, oscillated between 5 and 9ºC (Palma et al. 2018b), while in this study, the temperature oscillated between 9 and 10.5ºC. Nevertheless, it is important to mention that C1F was conducted during the spring-summer season, while this study was conducted during the austral winter, reinforcing the idea of a substantial temperature increase.

Muggiaea atlantica is always the most dominant species in winter and spring, normally followed by *Lensia conoidea*. Therefore, the siphonophore community is often described as a mono- or bi-specific population represented by these two species (Palma & Silva 2004, Palma et al. 2007, 2014, 2018a,b). In the spring of 2003 (Palma et al. 2007), and in this study area, *S. koellikeri* was dominant (DO 9.9%). In other cruises carried out in the same area, *Pyrostephos vanhoeffeni* had always been a dominant species, but with low percentages (DO 5-6%) (Palma & Rosales 1997, Palma et al. 2007), but in this study, only one specimen was found (Table 1). *P. vanhoeffeni* is also a cold-water species from the Antarctic and Subantarctic waters (Totton, 1965, Mapstone 2014,). Thus, its decrease and the decrease of *D. arctica* reflect changes in the community structure, which may be due to changes in temperature regimes. The non-dominant species accounted for 5.1% of the total, from which *S. fragilis* accounted for the highest percentage (4.04%) (Table 1). Also, in the other studies in spring, this species was the most abundant non-dominant species (Palma & Rosales 1997, Palma et al. 2007).

A north-south species richness gradient was found (Fig. 6), decreasing towards the south to only two species (*M. atlantica* and *L. conoidea*) and a few eudoxids of *D. arctica* (Table 2). The extreme conditions, such as the low temperatures and the great salinity gradient found during the winter season in this fjord area, can generate conditions favorable for these two species. In previous studies, it was observed that *M. atlantica*, as well as *L. conoidea*, can adapt to this salinity and temperature gradients because they are euryhaline and eurythermal species, showing a wide range of spatial distribution (Palma & Silva 2004, Hosia & Båmstedt 2007, 2008, Baxter et al. 2011).

The highest abundance of *L. conoidea* was found in AF, where the other dominant species were absent (Fig. 7, Table 2). However, the three dominant species were found coexisting in most stations (Fig. 7, Table 2), *L. conoidea* could eventually exploit the oceanographic conditions present in this fjord, thus avoiding competition with the others. This has been observed, especially with *M. atlantica* and *L. conoidea*, as these species depend on the availability and abundance of their prey (Palma & Rosales 1997, Palma & Silva 2004, Hosia & Båmstedt 2008). Palma et al. (2018a,b) described that the more surface distribution of *M. atlantica*, the deeper the distribution of *L. conoidea*. However, most eudoxids (reproductive stage) of *L. conoidea* were found in the SMC and PC (Table 2) and not in AF, indicating that *L. conoidea* can exploit the oceanographic conditions present in AF even if they are not in its optimal range needed for its reproduction. For *L. conoidea*, higher stratification influences their reproductive stage, showing high eudoxids abundances in PC, AF, and SMC. In the NMC, *M. atlantica* eudoxids were more abundant. Since we found eudoxids in the winter season, these three species could have a longer reproductive period than the rest of the siphonophores in the study area. On the other hand, it could also mean that these three species' developmental stages (eudoxids) can live for a long time in the water column, even in winter, due to favorable living conditions. For *M. atlantica* it has been described that higher temperature causes the release of eudoxids (Purcell 2005). The number of eudoxids produced increases with the amount of food ingested while they rapidly vanish in case of fasting (Purcell 1981). It could indicate that this species found suitable thermal conditions for reproduction in the PFE, even in winter.

Spatial distribution of the siphonophore community

The highest abundance of siphonophores was found in Moraleda Channel and specifically in St. 40, where all three dominant species were present, and additionally, *S. fragilis* was also recorded (Table 2). This high abundance of siphonophores in the Moraleda Channel has been described previously in springtime (Palma & Rosales 1997, Palma et al. 2007). Marín & Delgado (2004) and Palma et al. (2007) have found a high amount of zooplanktonic biomass accumulating in the Moraleda Channel. They suggest that the Meninea Constriction, a geomorphological structure located in front of the Meninea Island (45°16'S, 73°37'W) with a low depth (50 m) (Silva et al. 1995), generates a constrained water flow between the northern and

southern basins which increases the species' residence time. The higher stability of the water column followed by a strong halocline is another argument for the high abundance in Moraleda Channel. On the other hand, the lowest abundance (71 ind 1000 m^{-3}) of siphonophores was found in the most southern part of the study area (EG; St. 50), where just two of the dominant species were present (*M. atlantica* and *L. conoidea*, Table 2). The density of both species was low, and no other non-dominant species could be found in this station. This low abundance can be associated with very cold, turbid, and low salinity estuarine waters that present low productivity (Iriarte et al. 2013), originating from the northern Ice Fields Glacier (Palma & Silva 2004). As well as in spring, low abundance (210 and 315 ind 1000 m^{-3}) were also found between the entrance from GP and in the NMC (Sts. 36 and 34 respectively, Table 2) due to the water column instability created by the inflow of ocean water mixing with the low import of freshwater (Palma & Silva 2004, Palma et al. 2007).

The northern basin where all species were found was the area where the highest diversity of species was registered (Table 2), reflecting the need for ocean waters influx in the wintertime for siphonophores. At the same time, it highlights the ease of some species (*L. conoidea* and *M. atlantica*) in adapting to a wide variety of oceanographic conditions. In winter and spring, only a few species have been able to adapt successfully to the strong oceanographic temperature and overall salinity gradient typical of the PFE (Palma & Silva 2004, Palma et al. 2007, 2018a,b).

Oceanographic conditions

The dynamics of the oceanographic conditions associated with the inter-seasonal variability (i.e. spring-summer *vs*. autumn-winter) in those remote areas is an interesting aspect that has been infrequently studied (Silva & Guzmán 2006, Pantoja et al. 2011) compared to other areas and/or periods. Therefore, we describe the main differences between oceanographic conditions from those two seasons to show the specific species' response to the oceanographic variables such as temperature, salinity, and dissolved oxygen afterward. The temperature variability associated with wintertime in our study agrees with what has been previously found, showing the typical vertical thermal inversion of the water column for the winter season (Silva & Guzmán 2006). The colder superficial water layer does not sink to depth because of its low salinity, producing less dense waters, floating over the more saline, warmer, and less oxygenated waters (Silva & Reinoso 2013). Also, surface waters showed higher variability than deeper waters. The temperature associated with the PC and AF showed the classical two-layer water

structure. The low temperature at the surface - subsurface layer was prominent near the inland waters, highlighting the role of the less saline and much colder waters from the inner part of the fjords. Salinity between GP and EG is similar between the two seasons, while PC and AF suffer big variations in salinity because of the main rivers draining into those channels, overall during the spring-summer season, imposing changes on the physical-chemical structure of the water mass (Gonzalez et al. 2011). The dissolved oxygen variability associated with the inter-season is small. The stratification (i.e. higher concentration values occur at the surface and decrease with depth) is evident in both periods, with a stronger oxycline in spring-summer seasons than in autumn-winter periods (Silva & Guzmán 2006).

Response to the oceanographic variables

The uni-modal response of some species to certain ranges of the physical and chemical variables indicates the optimal conditions for their development and survival. *S. koellikeri*, *S. fragilis*, and *C. appendiculata* showed an association with salinity (Figs. 8c, 9), explaining the higher abundance in GP. *M. atlantica* also showed a positive association with salinity and dissolved oxygen (Fig. 9), while in the univariate model, the response was unimodal (Fig. 8a). In other studies, *M. atlantica* response to salinity has been described as positive in one case (Palma & Rosales 1997) and negative in another (Palma et al. 2007). In our study *M. atlantica* showed a unimodal response with the highest abundances between 22-33 of salinity and 3.5-5.5 mL L^{-1} of dissolved oxygen (Fig. 8a), being well adapted to the estuarine conditions of the study area.

L. conoidea appeared in higher densities in waters with higher temperatures and lower salinity and dissolved oxygen (Figs. 8b, 9). This distribution pattern according to the oceanographic variables is in agreement with other areas of the Patagonian waters of southern Chile, where their abundance decrease from north to south in the PFE (Palma & Silva 2004, Palma et al. 2007, 2018a,b) and as well as in the Norwegian fjords (Hosia & Båmstedt 2007, 2008).

The interpretation of the environmental variables for the three-dominant species (*M. atlantica*, *L. conoidea*, and *S. koellikeri*) showed that *M. atlantica* and *L. conoidea* could adapt to the estuarine conditions, whereas *S. koellikeri* has preferences for higher salinity waters (Figs. 8,9), explaining thus the dominance of *M. atlantica* and *L. conoidea* along the PFE. In the last years, more frequently massive blooms of gelatinous zooplankton, overall the expansion of *M. atlantica* in different regions, for example, in the PFE, Mondego

estuary, and the western English Channel are reported (Condon et al. 2013, Blackett et al. 2014, D'Ambrosio 2018, Palma et al. 2018a,b).

This study contributes valuable information about the siphonophore distribution and community structure in the PFE for the austral winter, reporting two new species for the study area. We have shown that the distribution of siphonophores is influenced by some oceanographic conditions, being temperature and salinity the main drivers for this pattern. In addition, the presence of eudoxid stages in winter is an important finding contributing to the knowledge of the life cycle or reproduction in winter for some species. Based on the new records and comparing the variability of interannual abundances, we suggest a possible community composition change and a long-term increase of some specific siphonophore species. Nevertheless, further research in these remote areas is needed overall during winter.

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Supplementary material

Table S1. Mean temperature (ºC), mean salinity, and mean dissolved oxygen (DO) (mL L^{-1}) concentration and volumes filtered (m^3) for each station.

Area	Station	Temperature (ºC)	Salinity	DO (mL L^{-1})	Volume (m^3)
Guafo Island	102	9.85	33.73	4.32	311.59
Guafo Passage	103	9.95	33.79	3.91	301.31
N Peligroso Islet	34	9.96	32.75	4.87	244.11
Moraleda Channel	36	9.77	33.05	4.64	227.20
Moraleda Channel	37	9.90	32.92	4.65	293.63
Moraleda Channel	38	9.90	33.02	4.55	320.44
Moraleda Channel	39	9.94	32.84	5.16	272.99
Moraleda Channel	40	9.93	32.81	4.76	288.42
SW Churrecue Island	45	10.27	30.75	5.11	302.08
Costa Channel	46	10.22	30.57	5.12	289.82
Costa Channel	47	10.07	29.69	5.44	180.75
Elefantes Gulf	48	9.53	27.33	5.87	114.59
Elefantes Gulf	50	10.45	30.43	4.54	188.48
Aysen Fjord	78	9.64	26.09	3.93	98.90
Aysen Fjord	82	9.99	28.56	3.67	225.76
Aysen Fjord	81	10.11	29.36	3.72	334.94
Aysen Fjord	80	9.50	30.54	5.89	193.39
Puyuhuapi Channel	84	9.35	31.84	4.68	296.17
Puyuhuapi Channel	85	9.46	31.54	4.60	351.30
Puyuhuapi Channel	86	9.50	31.57	4.55	402.57
Puyuhuapi Channel	87	9.65	31.76	4.27	245.89
Puyuhuapi Channel	88	9.76	31.96	4.20	240.18
Seno Ventisquero	89	9.73	31.91	4.10	295.78