

Siphonophores in fjords and channels in southern Patagonia: biodiversity, spatial distribution and environmental association

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This study characterizes the abundance and spatial distribution of siphonophores between the Trinidad Channel (50°06'S) and the Strait of Magellan (52°45'S) in southern Chile, during October–November 2009. Ten species were identified, of which Agalma elegans, Rosacea plicata and Sphaeronectes fragilis are new records for this region. Dominant species showed similar dominance values e.g. Lensia conoidea (26.3%), Dimophyes arctica (24.6%), Lensia meteori (22.2%) and Muggiaea atlantica (20.7%). Eudoxids of L. conoidea and D. arctica represented 97.3% of all eudoxids collected and they were mainly collected in estuarine waters. The highest densities were found in estuarine waters (high vertical stratification and low temperature, salinity and dissolved oxygen values). On the other hand, the lowest densities were found in coastal areas influenced by permanent influx of Sub-Antarctic waters from the Pacific (greater instability and vertical mixing, higher temperatures, salinity and dissolved oxygen values). Temperature and dissolved oxygen were the most important environmental variables. In general, all the dominant species showed a positive association with temperature and a negative association with dissolved oxygen (with the exception of L. meteori). The vertical distribution showed that M. atlantica was mainly distributed in the first 50 m, in association with estuarine waters, while L. conoidea, L. meteori and D. arctica were mainly found in the deeper layer (50–200 m) and in association with modified Sub-Antarctic waters. The comparison of the results obtained in the springs of 1996 and 2009 showed a significant increase in abundance.

Keywords: Siphonophores, gelatinous zooplankton, spatial distribution, Patagonian Fjord Ecosystem, community analysis, environmental association, CCA, GLM, southern Chile

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INTRODUCTION

The Patagonian Fjord Ecosystem (PFE) in southern Chile extends from Puerto Montt (41°20'S) to Cape Horn (55°58'S). This ecosystem is ~1600 km long and covers a total area of 240,000 km² (Palma & Silva, 2004).

Throughout the large Patagonian region, plankton communities are affected by high spatial heterogeneity due to strong seasonal, latitudinal and vertical variations in oceanographic conditions (Sievers *et al.*, 2002; Silva & Calvete, 2002; Palma & Silva, 2004). These variations affect the composition, abundance and distribution of planktonic cnidarians (Palma *et al.*, 2007a, b, 2014a, b; Villenas *et al.*, 2009). Conspicuous zooplankton species previously reported (e.g. *Muggiaea atlantica*, *Lensia conoidea*, *Clytia simplex*, *Euphausia vallentini*, *Sagitta tasmanica*) have successfully adapted to an estuarine habitat, that is characterized by low levels of diversity, specific richness and abundance in comparison to the highly productive waters of the Humboldt Current System (Palma, 1994; Palma & Rosales, 1995; Palma & Apablaza, 2004; Pavez *et al.*, 2010).

The area between the Gulf of Penas and the Strait of Magellan experiences permanent inflow of Sub-Antarctic waters from the Pacific Ocean to the interior of the Patagonian Fjord Ecosystem, penetrating mainly through the Trinidad and Concepcion Channels and the Nelson and Magellan Straits. This more saline seawater mixes with the colder fresh water from rivers, coastal runoff, rainfall and glacial snowmelt (from the mountains and snowstorms), leading to a two-layer structure in the water system (Sievers & Silva, 2008). This leads to higher values of vertical stratification, associated with a strong pycnocline in the interior of the fjords and channels and lower stratification values in coastal waters close to the ocean (Bustos *et al.*, 2011).

However, the sector between the Trinidad Channel (50°10'S) and the mouth of the Strait of Magellan (52°45'S) has remained poorly studied. The first studies of zooplankton were obtained during the RV 'Hero' Expedition (1972–1973), reporting some species of copepods, euphausiids and chaetognaths (Arcos, 1974, 1976; Ahumada, 1976; Antezana, 1976). Later, during the CIMAR-2 Fjord Cruise (spring of 1996), the analysis was focused particularly on siphonophores, chaetognaths, cladocera and euphausiids (Palma *et al.*, 1999; Rosenberg & Palma, 2003). A total of nine siphonophore species were identified, of which *Muggiaea atlantica* and *Lensia conoidea* were dominant (Palma *et al.*, 1999). Both species are found widely distributed through the Patagonian

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Fjord Ecosystem, with the highest numbers of *M. atlantica* showing a positive correlation with temperatures associated with the adjacent Pacific Ocean waters and a preferentially surface bathymetric distribution (0–50 m). The highest number of *L. conoidea* show a positive correlation with salinity and density, and a deeper bathymetric distribution (>50 m) (Palma *et al.*, 1999, 2011).

The objective of the present study is to characterize the composition, abundance, horizontal and vertical distributions of the siphonophore community and to test the hypothesis that the strong environmental gradient found in this ecosystem shapes the abundances and community composition of siphonophores in this poorly known area.

MATERIALS AND METHODS

During the marine research cruises in remote areas (CIMAR-15), carried out aboard the RV ‘Vidal Gormaz’, 28 oceanographic stations were set up in the fjords and channels between the Trinidad Channel (50°06’S) and the mouth of the Strait of Magellan (52°45’S) between 11 October and 10 November 2009 (Figure 1). Of those stations, 13 were selected to build a north-south oceanographic cross-section close to the western edge of the Southern Ice Fields (Figure 1, blue line).

At each station temperature and salinity were recorded with a CTD Seabird SB-19, from the surface up to a depth of 500 m or to 10 m from the ocean floor (depending on the depth of the station). Discrete water samples were also taken using a rosette fitted with 24 Niskin bottles to determine dissolved oxygen concentration at standard depths (0, 2, 5, 10, 25, 50, 75 and 100 m) by the Winkler method as modified by Carpenter (1965).

Zooplankton samples were collected by oblique tows at three depth strata: surface (0–25 m), middle (25–50 m) and deep (50–100 or 200 m, depending on the bottom depth); using a Tucker trawl net (1 m² mouth opening and 350 µm mesh aperture) and a digital flowmeter to estimate the volume filtered by each net. Zooplankton samples were fixed immediately after collection and preserved in 5% formalin buffered with sodium borate.

The siphonophores were sorted and the nectophores (asexual polygastric stage) and eudoxids (sexual eudoxid stage) were identified and counted. The taxonomic identification followed the work of Totton (1965) and Pugh (1999). The abundances of Calyptophorae were estimated considering the highest number of anterior and posterior nectophores (asexual polygastric stage), and bracts and entire eudoxids (sexual eudoxid stage). *Pyrostephos vanhoeffeni* was the only species of the Physonectae collected, and its abundance was estimated by considering one individual to have 20 pairs of nectophores per colony (Totton, 1965). Data of polygastric and eudoxid stages were considered separately for *Muggiaea atlantica* and *Lensia conoidea*. Zooplankton abundance was standardized to individuals per 1000 m³.

Two indices commonly used to describe the siphonophore community (Palma *et al.*, 2007a, b, 2011, 2014a, b) are dominance (DO), calculated as the percentage of each species over the total individuals collected and frequency of occurrence (FO), which is the percentage of the presence of each species over the total number of stations sampled. Only the dominant species (DO > 5% of the total collected specimens)

were considered to describe the horizontal and vertical distribution patterns.

Temperature, salinity and dissolved oxygen concentration were used to determine the oceanographic characteristics of the study zone. However, as these variables are measured at different depths than zooplankton samples, the weighted means of the environmental variables were calculated for the zooplankton samples range, following:

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

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.

The siphonophore community structure was characterized using non-metric multi-dimensional scaling (nMDS) (Clarke & Warwick, 1994). The abundance data were transformed by the fourth root to reduce the contribution of the most abundant species and increase the contribution of rarer species. In order to test for significant differences among discrete groups coming from the nMDS analysis, the ANOSIM procedure was used (Clarke & Warwick, 1994). The association of the community structure with the environmental variables was achieved using canonical correspondence analysis (CCA) (Ter Braak, 1986). This analysis involved searching for correlations between species abundance and the environmental data considering species unimodal responses. In order to find the most parsimonious model (highest inertia explained by only significant explanatory variables) a forward stepwise model selection was performed using permutation tests. For the canonical correspondence analysis and for the permutations test the functions *cca* and *ordisep*, respectively, from the ‘vegan’ package were used (Oksanen *et al.*, 2015).

The association between environmental variables and each dominant species (DO > 5%) was evaluated through regression analysis. Due to the nature of species data (i.e. count numbers) and to avoid data transformation, generalized linear models (GLMs) with a binomial negative error family distribution and a log ‘link’ function were fitted using the *glm.nb* function from the ‘MASS’ package (Venables & Ripley, 2002). The volume sampled (log-transformed) was used as an offset inside the GLMs because of its high variability between stations (data not shown; Guerrero *et al.*, 2013). The optimal model was achieved using a backward selection procedure until all explanatory variables were significant (Zuur *et al.*, 2009). To avoid collinearity (i.e. significant correlation among environmental variables), a pairwise comparison between each explanatory variable was carried out using the Spearman rank correlation coefficient (ρ). When the coefficient value was higher than 0.6, the less (biologically) important variable was removed from the analysis (Zuur *et al.*, 2010). All the statistical tests used were conducted in the free programming language R, version 3.2.1 (R Core Team, 2015).

The vertical distribution of the dominant species was analysed along a longitudinal north-south transect composed of 13 stations located between the Peel Fjord (Station 73) and the south end of the Smyth Channel (Station 61) (Figure 1). The vertical transect for temperature, salinity and dissolved

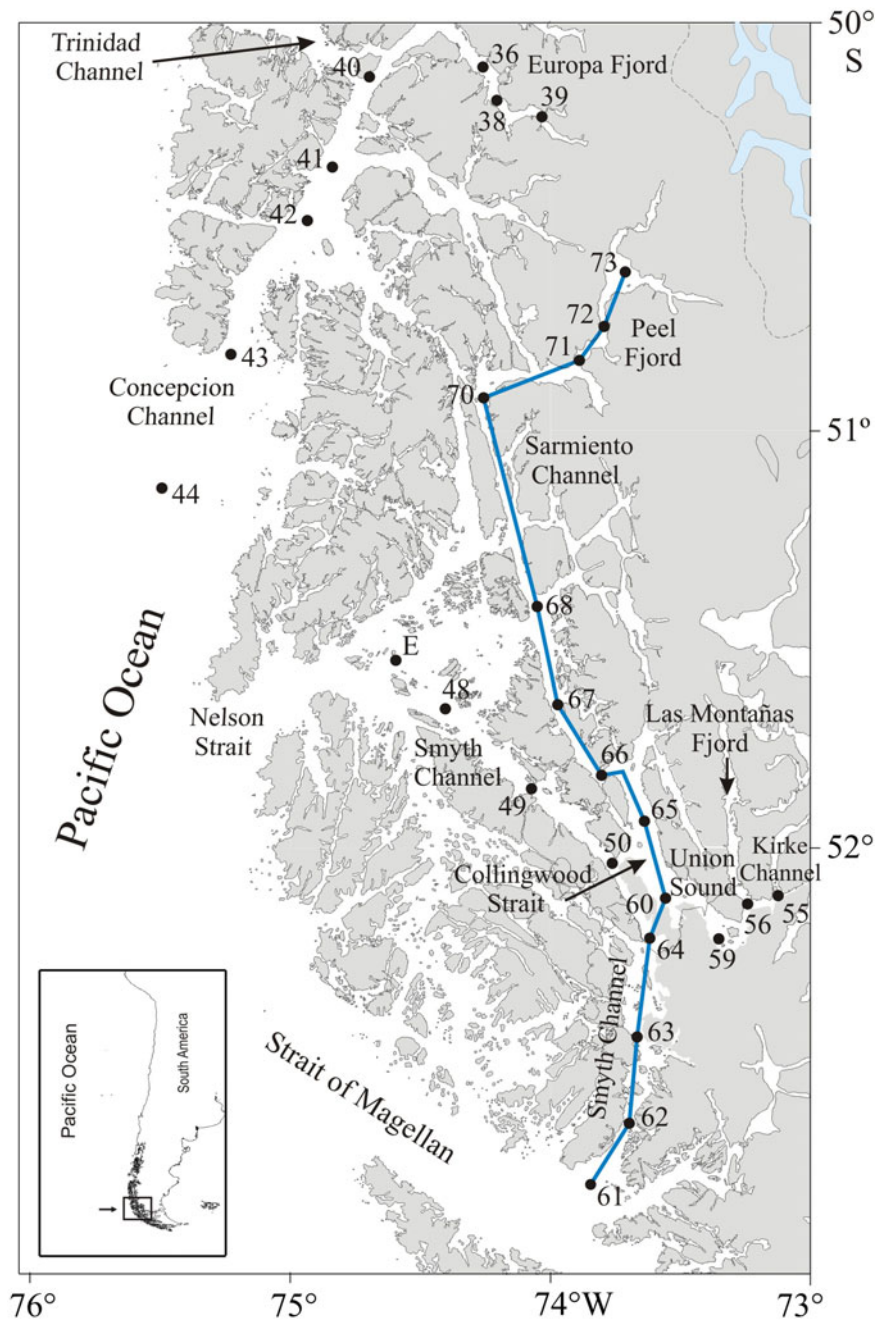


Fig. 1. Geographic position of sampling stations between the Trinidad Channel and Magellan Strait (CIMAR 15 Fiordos cruise). The blue line indicates the longitudinal north-south transect.

oxygen was built using a Kriging function with linear interpolation in the software package Surfer 8.0.

Finally, the inter-annual abundance of the siphonophores (polygastric stage) collected during the cruises CIMAR 2 Fiordos (C2F, 15 October to 4 November 1996; Palma *et al.*, 1999) and CIMAR 15 Fiordos (C15F, 11 October to 10 November 2009) was compared using only those stations with the same geographic location. To quantify significant differences in average siphonophore abundance between the two datasets, GLMs similar to those used for the environmental association were fitted (i.e. GLM with a negative binomial error family distribution and a log link function). It is important to highlight that both cruises were done during the same

months of the year (October–November), and in the cruise C2F we used Bongo nets and in the cruise C15F we used Tacker Trawls nets, but in both cruises we compared the standardized values of abundance of polygastric phase (i.e. nectophores).

RESULTS

Hydrography

The longitudinal transect from Peel Fjord to Smith Channel presented an inverted thermal vertical distribution with the

lower temperatures (5–7°C) in the surface layer (0–50 m) (Figure 2A). A weak inverted thermocline ($\approx -0.08^\circ\text{C m}^{-1}$) centred around 35 m was present around Peel Fjord (Stations 72–73; Figure 2A). The salinity showed a stratified low saline (26–32) surface layer, with high dissolved oxygen content (6–8 ml l⁻¹) (Figure 2B, C). The halocline ($\approx 0.15 \text{ m}^{-1}$) was centred at about 35 m depth, in the Collingwood–Smyth Fjords junction (Stations 63–66; Figure 2B). The deep layer (50 m to bottom) was less stratified, warmer (8–9°C), more saline (32–33) and less oxygenated (3–6 ml l⁻¹), than the surface layer (Figure 2A–C).

Siphonophore species composition

A total of 10 species of siphonophores (polygastric and eudoxid stages), nine calyphorans and one physonect were identified. *Agalma elegans* was recorded for the first time in the Patagonian Fjord Ecosystem (PFE), and *Rosacea plicata* and *Sphaeronectes fragilis* were recorded for the first time in this geographic area. Disregarding the eudoxid stages, four dominant species (DO > 5%) were found with very similar abundance percentages: *Lensia conoidea* (26.3%), *Dimophyes arctica* (24.6%), *Lensia meteori* (22.2%) and *Muggiaea atlantica* (20.7%). The other species accounted for only 6.2% of the total. For the eudoxid stage, the highest densities were found for *L. conoidea* (57.2%) and *D. arctica* (40.1%) (Table 1).

Horizontal distribution patterns of siphonophores

The abundances of siphonophores ranged between 11 ind. 1000 m⁻³ in the Concepcion Channel (Station 41) and 3080 ind. 1000 m⁻³ in the Collingwood Strait (Station 65), with an average per station of 65.7 ind. 1000 m⁻³. The highest densities were found in the Collingwood Strait (Stations 65 and 66) and the lowest densities were found in the Concepcion Channel (Stations 41 and 42).

Lensia conoidea was the most abundant species and showed the greatest geographic coverage (FO = 79%). Its non-zero range of abundance (NZRA) fluctuated between 5 and 865 ind. 1000 m⁻³ in Concepcion (Station 41) and the Sarmiento Channel (Station 68), respectively (Table 1). The highest densities were found in the Smyth and Sarmiento Channels and the lowest densities (even reached zero) in oceanic waters and areas close to the head of the fjords (e.g. Europa, Peel and Las Montañas Fjords) (Figure 3A). *Dimophyes arctica* (DO = 24.6%) was found only in interior waters and its NZRA varied from 18 to 806 ind. 1000 m⁻³ around Europa (Station 36) and the Peel Estuary (Station 72), respectively (Table 1). The highest densities were found in the Peel Fjord, and the Smyth and Kirke Channels (Figure 3B). Similar to *D. arctica*, *L. meteori* (DO = 22.2%) was present only in interior waters south of 51°S, with low abundances and a minimum of 4 and a maximum of 2085 ind. 1000 m⁻³ in the Smyth Channel (Station 48) and Collingwood Strait (Station 65), respectively. Besides this, *L. meteori* was mainly present in Station 65, where 50% of the total siphonophores were collected (Figure 3C). Finally, despite having the lowest abundance among the dominant species, *M. atlantica* (DO = 20.7%) had the highest geographic coverage with a high frequency of occurrence (FO = 93%). Its NZRA fluctuated between 6 and 756 ind. 1000 m⁻³ in the

Concepcion (Station 43) and Smyth Channels (Station 50) (Figure 3D), respectively. Among the occasional species (DO < 5%), *P. vanhoeffeni* showed high geographic coverage through the study zone (FO = 61%).

The eudoxids of *L. conoidea* (DO = 57.2%) and *D. arctica* (DO = 40.1%) were always more numerous than the polygastric stages, with average densities seven and four times higher than their respective polygastric stages, respectively. These eudoxids followed the same abundance patterns as the polygastric stage, though the highest abundances were found in the fjords (Figure 4A, B). In the case of *L. conoidea*, the highest accumulations of eudoxids (>4900 ind. 1000 m⁻³) were found in the Europa Fjord (Stations 36 and 38, Figure 4A), while for *D. arctica*, the highest accumulations (>1100 ind. 1000 m⁻³) were found in the Peel Fjord (Stations 70–74, Figure 4B).

Community structure of siphonophores

The nMDS community association analysis (0.13 stress) grouped the oceanographic stations in three areas with contrasting community structures. The first group (Group 1) contained 22 stations associated to estuarine waters located in the fjords (Europa, Peel and Las Montañas) and along the channels (Sarmiento and the Smyth Channel (except Station 61) and was characterized by low values of temperature, salinity and high vertical stratification. Group 2 represented stations associated to the high exchange between estuarine and oceanic waters. It was comprised of three stations, two located in the northern part of the Concepcion Channel (Stations 41 and 42) and one in the southern end of the Smyth Channel (Station 61). Finally Group 3 had only two stations and clearly associated to oceanic waters (Stations 43 and 44) (Figure 5). The stations of Groups 2 and 3 were characterized by higher values of temperature and salinity, and lower vertical stratification, because they represented well mixed waters, but at the same time with low siphonophore abundance. The pairwise tests of ANOSIM analysis showed high dissimilarity due to the differences in oceanographic conditions in the three groups (Group 1, 2: $R = 0.856$; Group 1, 3: $R = 0.936$, and Group 2, 3: $R = 1$; $P < 0.001$; Table 2).

Environmental associations

The environmental variables for which multiple comparisons showed a Spearman rank correlation coefficient (ρ) lower than 0.6 (e.g. Temperature, Salinity, Dissolved Oxygen) were kept to run the statistical models of species–environmental association (online Figure S1).

Temperature and dissolved oxygen played a significant role in the deviance (univariate) and inertia (multivariate) data (Tables 3 & 4). The dominant species (DO > 5%) showed a positive and significant response to temperature with a non-linear response (except for the case of *M. atlantica*) (i.e. significant quadratic term in GLMs; Table 2; Figure 6). On the other hand, the siphonophores species (except *L. meteori*) related negatively to dissolved oxygen (Table 2, Figure 6). From the multivariate perspective, the most parsimonious model explained a total inertia of 51.4%, where the first axis (CCA x-axis) explained more inertia than the second (CCA y-axis) axis, 29.9 and 21.5%, respectively. From the triplot analysis (scaling 2), the negative association between dissolved oxygen and the dominant species was also evident (Figure 7).

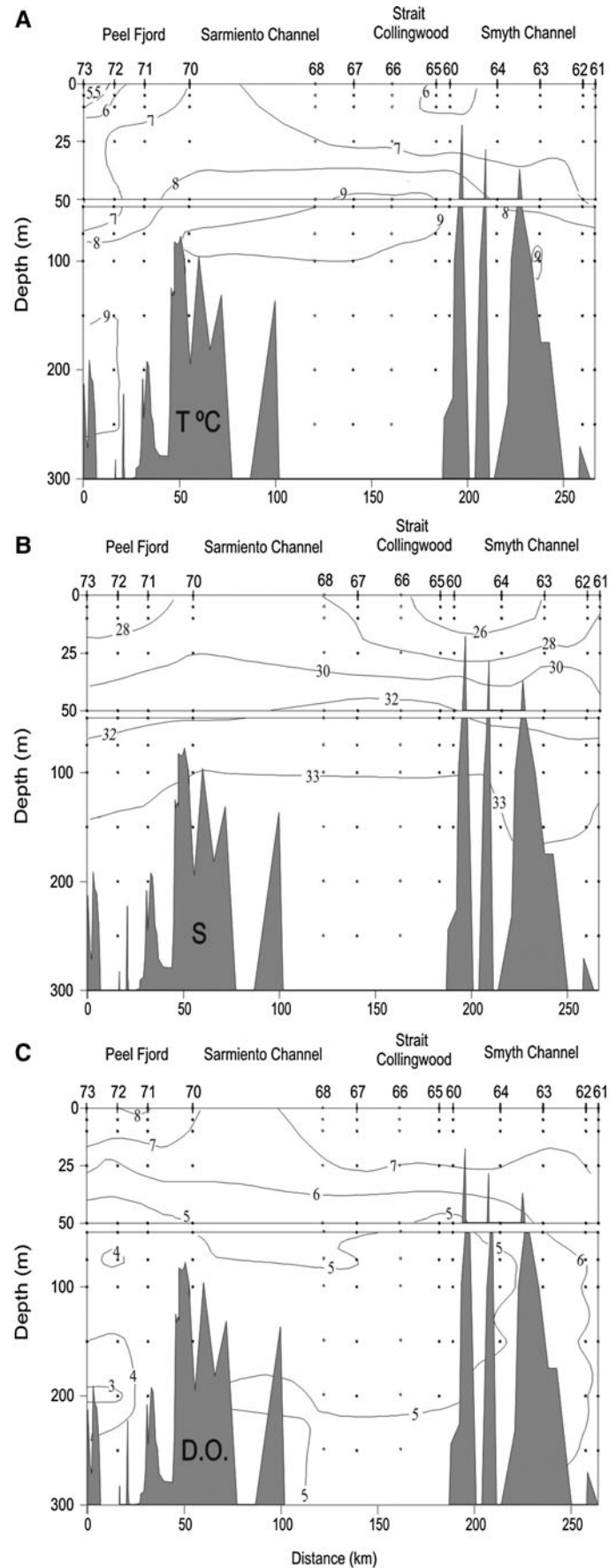


Fig. 2. Vertical distribution of (A) temperature, (B) salinity and (C) dissolved oxygen in the longitudinal north-south transect between Trinidad Channel and Magellan Strait in spring 2009.

Table 1. Summary of basic statistics for polygastric (po) and eudoxids (eu) stages of siphonophores. Total number of individuals, range of non-zero abundances, average per station, dominance and occurrence were calculated for polygastric and eudoxid stages separately. Abundances are expressed as ind. 1000 m⁻³.

Species	Life stage	Total number	Range of non-zero abundances	Average abundance	Dominance (%)	Occurrence (%)
<i>Lensia conoidea</i> *	Po	4833	5–865	172.6	26.3	79
	Eu	24,952	12–632	891.2	57.2	88
<i>Dimophyes arctica</i> *	Po	4525	18–806	161.6	24.6	68
	Eu	17,827	14–3536	636.7	40.9	85
<i>Lensia meteori</i> *	Po	4089	4–2085	146.1	22.2	64
<i>Muggiaea atlantica</i> *	Po	3803	6–756	135.8	20.7	93
	Eu	749	10–243	26.7	1.7	73
<i>Pyrostephos vanhoeffeni</i>	Ne	797	1–327	28.5	4.3	61
<i>Sphaeronectes koellikeri</i>	Po	155	5–64	5.3	0.8	17
<i>Eudoxoides spiralis</i>	Po	126	17–82	4.5	0.7	11
	Eu	94	10–73	3.4	0.2	35
<i>Rosacea plicata</i>	Po	41	1–41	1.4	0.2	4
<i>Sphaeronectes fragilis</i>	Po	27	1–27	1.0	0.1	4
<i>Agalma elegans</i>	Ne	10	1–10	0.4	0.1	4

Asterisk indicates the dominant species. Ne, nectophores.

A remarkably positive association with dissolved oxygen was evident for the group of non-dominant species (*S. fragilis*, *S. koellikeri*, *E. spiralis* and *A. elegans*; Figure 7).

Vertical distribution in the north–south transect

The vertical distribution of the dominant species (only polygastric stage) showed different patterns along the north–south transect (Figure 1, blue line). *Muggiaea atlantica* had a frequency of occurrence (FO) of 100% along the transect and showed deeper populations along the north–south gradient (Figure 8D). In the Peel Fjord it was collected mainly in the surface layer (0–25 m), in the Sarmiento Channel it was found mainly in the middle layer (25–50 m), and along the Smyth Channel it was collected mainly in the deep layer (>50 m), particularly at the most southern stations close to the Pacific. In the Peel Fjord, *L. conoidea* (FO = 92.3%) showed a uniform vertical distribution pattern, while in the Sarmiento and Smyth Channels it was collected mainly in the deep layer (50–200 m) (Figure 8A). *Dimophyes arctica* (FO = 84.6%) behaved similarly to *M. atlantica*, as it also moved deeper along the north–south gradient (Figure 8B). In the Peel Fjord it was found mostly in the surface layer, in the Sarmiento Channel in the middle layer and the deep layer, also moving deeper towards the stations with more oceanic characteristics (Figure 8B). In the Peel Fjord, *L. meteori* (FO = 84.6%) was found mainly in the surface and middle layers (0–50 m), while in the Sarmiento and Smyth Channels it was mainly collected in the deep layer (Figure 8C).

Inter-annual comparison between the abundance of siphonophores in springs of 1996 and 2009

Comparisons of weighted temperature, salinity and dissolved oxygen data between C2F and C15F (Figure 9) showed that salinity and dissolved oxygen do not show inter-annual differences. Nevertheless, surface temperature does not completely follow this pattern, since for C15F the surface layer (0–25 m) was significantly colder than for C2F ($\approx 1^\circ\text{C}$; Figure 9).

A total of seven siphonophore species were identified in the spring of 1996 and 10 in the spring of 2009. The dominant species for both periods were *Lensia conoidea* (DO = 52.2 and 26.8%), *L. meteori* (DO = 7.4 and 24.2%), *Muggiaea atlantica* (DO = 35.4 and 21.1%) and *Dimophyes arctica* (DO = 22.5 and 3.8% (not dominant)) in the springs of 1996 and 2009, respectively (Table 5).

In spring 1996, the abundance values fluctuated between 5 and 2413 ind. 1000 m⁻³, with the highest densities located in the northern part of the Sarmiento Channel. In the spring of 2009, the abundance varied between 10 and 4386 ind. 1000 m⁻³, with the highest densities recorded in the Collingwood Strait, south of the Sarmiento Channel (Table 4). The higher average abundance in 2009 (626.8 ind. 1000 m⁻³) compared with 1996 (177.7 ind. 1000 m⁻³) was strongly significant ($Z = 3.93$, $P < 0.01$, Table 6).

The mean abundance of *L. conoidea* in 2009 was 1.8 times higher than in 1996 (169 vs 93 ind. 1000 m⁻³), though this difference was not significant ($Z = 1.12$; $P = 0.26$). This species was absent from the collections at stations with greater influence from oceanic waters and in the Kirke Channel. In both periods, the highest densities were recorded in the Europa and Peel Fjords, and in the Sarmiento and Smyth Channels. *Lensia meteori* was significantly more abundant in 2009 than in 1996 (11.6 times; 24.2 vs 7.4 ind. 1000 m⁻³) ($Z = 3.46$; $P < 0.01$). Its geographic distribution in 1996 showed low coverage, while in 2009 its abundance increased south of 51°S , particularly in the Collingwood Strait. *Dimophyes arctica* was 21 times more abundant in 2009 than in 1996 (22.5 vs 3.8 ind. 1000 m⁻³) ($Z = 5.33$; $P < 0.01$). Its geographic distribution was very similar to that of *L. meteori*, though its high abundance was found in the Peel Fjord and Sarmiento and Smyth channels. It was particularly absent from stations with greater influence from oceanic waters. Finally, *M. atlantica* was the second most dominant species in 1996, while in 2009 it showed the lowest abundance of the dominant species. Although its geographic distribution was similar for both periods, its geographic coverage was much higher in 2009 (FO = 67 vs 93%). Its mean abundance was 2.1 times higher in 2009 ($Z = 1.46$; $P < 0.01$), particularly in association with the Sarmiento and Smyth channels (Figure 3). Other (non-dominant) species that showed

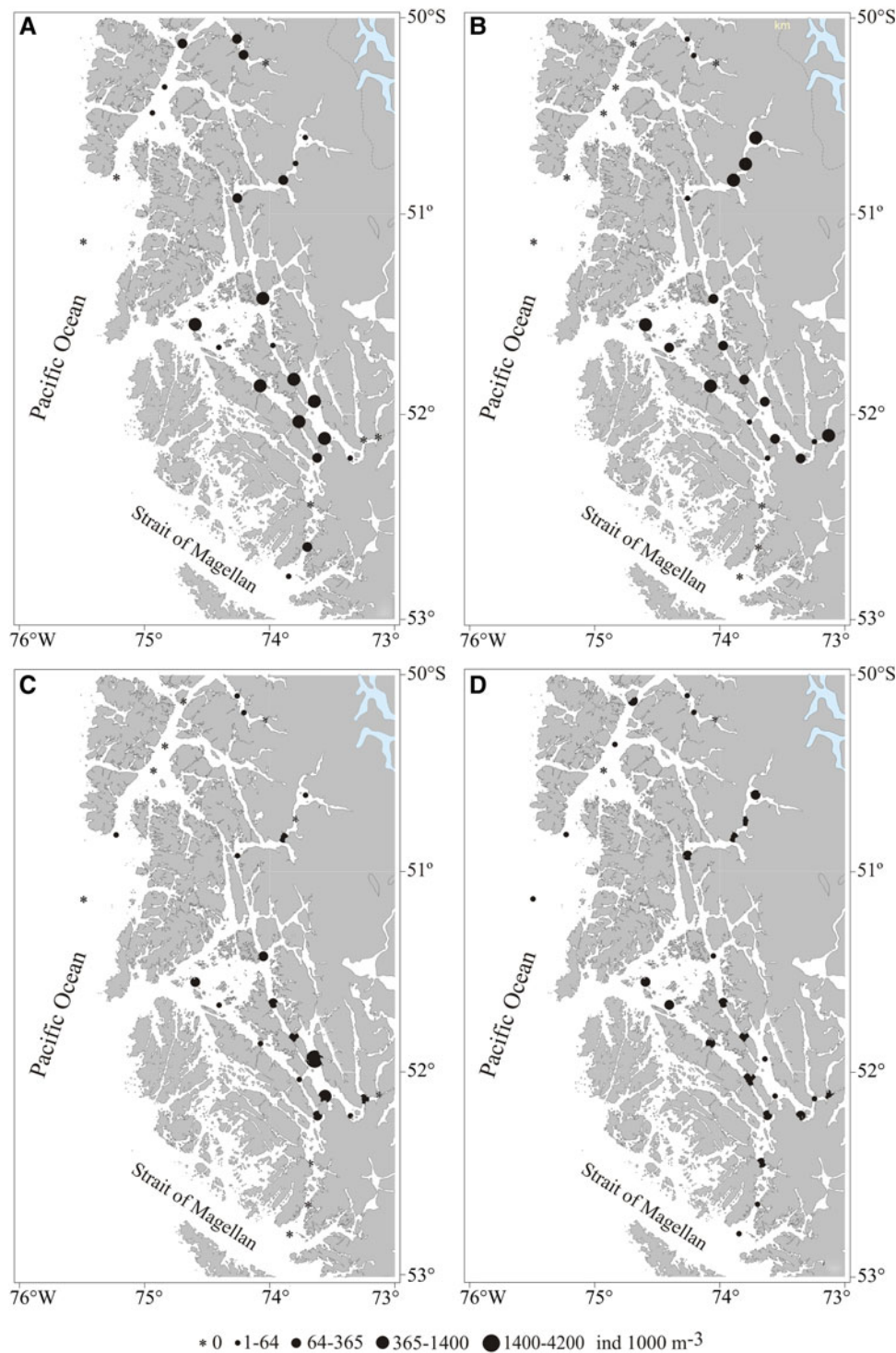


Fig. 3. Horizontal distribution of polygastric stages during spring 2009. (A) *Lensia conoidea*; (B) *Dimophyes arctica*; (C) *Lensia meteori* and (D) *Muggiaea atlantica*.

significant increases from 1996 to 2009 were *Pyrostephos vanhoeffeni* ($Z = 5.39$; $P < 0.01$) and *Eudoxoides spiralis* ($Z = 6.32$; $P < 0.01$) (Table 6).

DISCUSSION

Agalma elegans was recorded for the first time in the Patagonian Fjord Ecosystem (PFE). *Rosacea plicata* and

Sphaeronectes fragilis were recorded for the first time in this geographic area ($50^{\circ}10' - 52^{\circ}45'S$), but these species have been recorded previously in other areas of the PFE (Palma & Silva, 2004; Palma *et al.*, 2007a, 2011, 2014a; Villenas *et al.*, 2009). The highest siphonophore densities were found in estuarine waters, where all the dominant species were recorded (i.e. *Lensia conoidea*, *Dimophyes arctica*, *L. meteori* and *Muggiaea atlantica*). The lowest densities were found in the exterior zone influenced by the adjacent Pacific Ocean

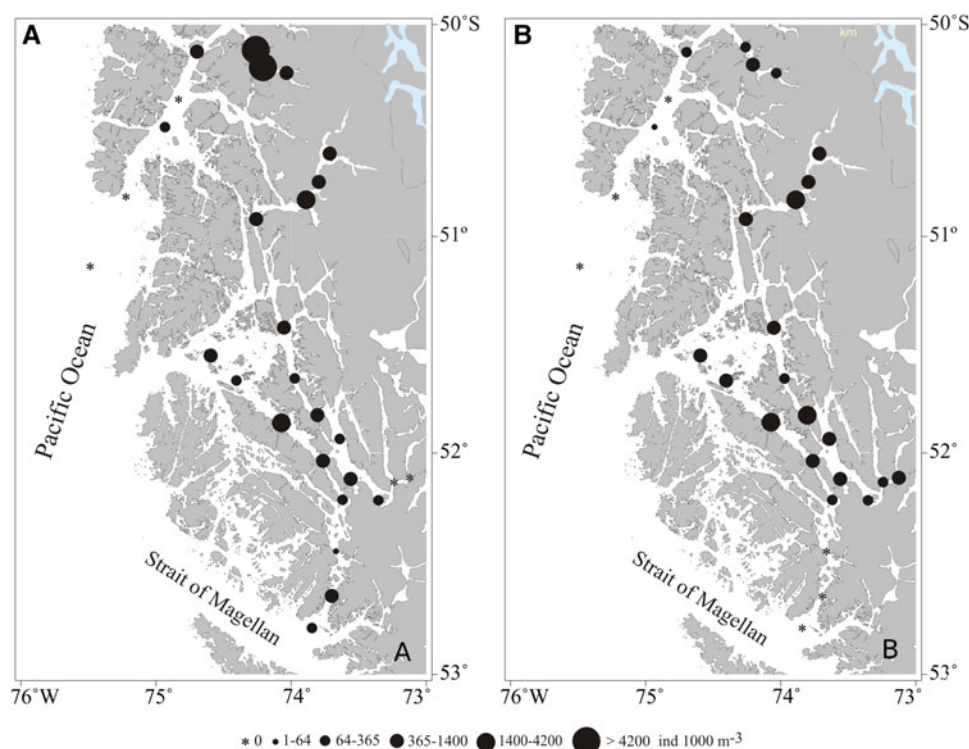


Fig. 4. Horizontal distribution of eudoxid stages during spring 2009; (A) *Lensia conoidea* and (B) *Dimophyes arctica*.

and characterized by the presence of occasional species (i.e. *Sphaeronectes fragilis*, *Agalma elegans*, *Sphaeronectes koellikeri* and *Eudoxoides spiralis*). The vertical distribution patterns of the dominant species showed that *M. atlantica* was distributed shallower (0–50 m) than *L. conoidea*, *D. arctica* and *L. meteori*, which were collected mostly in the deeper layer (below 50 m).

Siphonophore community composition and horizontal distribution

The community structure of the siphonophores between the Trinidad Channel and the Strait of Magellan had only been studied in the spring (October–November) of 1996 during the CIMAR-2 Fiordos cruise (Palma *et al.*, 1999). In general, this area is characterized by low values of species richness with 7 and 10 species for the springs of 1996 (Palma *et al.*, 1999) and 2009 (this study). These low species richness values confirm the results obtained for different zooplankton groups in the Patagonian Fjord Ecosystem (Puerto Montt to Cape Horn) in comparison to the waters of the Humboldt Current System (Palma, 2008). Most of the species identified are frequent in the PFE (Palma & Silva, 2004; Palma *et al.*, 2011, 2014a) and are common in Antarctic waters (i.e. *Dimophyes arctica*, *Pyrostephos vanhoeffeni*) and in Sub-Antarctic waters (*Agalma elegans*, *Eudoxoides spiralis*, *Lensia conoidea*, *L. meteori*, *Muggiaea atlantica*, *Rosacea plicata*, *Sphaeronectes fragilis* and *S. koellikeri*), respectively.

The three occasional species (*A. elegans*, *R. plicata* and *S. fragilis*) constitute new records for the study zone. Some nectophores of *A. elegans* were collected in some stations, becoming the first record for the PFE. However *R. plicata* and *S. fragilis* has been collected in other areas of the PFE, as a Chiloe Interior Sea and Magellanic Region (Pagès & Orejas, 1999; Palma & Silva, 2004; Palma *et al.*, 2007a). Some colonies of the Antarctic physonect *P. vanhoeffeni*, though not abundant, are widely distributed in the study area, showing increased geographic coverage compared with the spring of 1996, when it was collected exclusively in low temperature and low salinity estuarine waters (Palma *et al.*, 1999). An

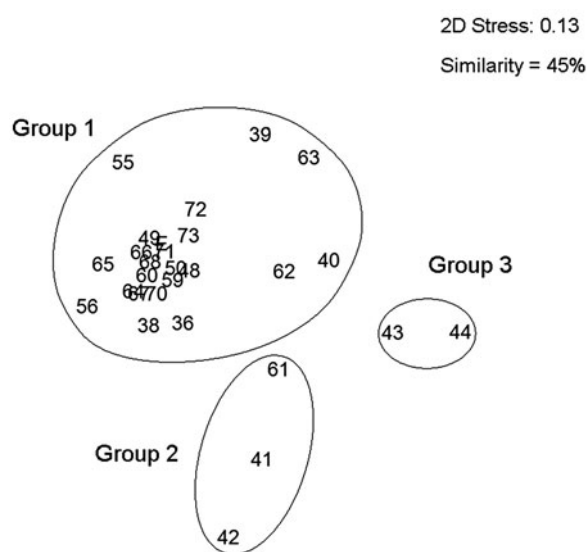


Fig. 5. Non-metric multidimensional scaling (nMDS) based on Bray–Curtis similarity index of the total siphonophore species collected. Group 1: species of estuarine waters; Group 2: species with oceanic influence; and Group 3: species of oceanic waters (spring 2009). Stress: 0.13.

Table 2. Results of the ANOSIM using the pairwise tests.

Group	R statistic	Significance level (%)	Possible permutations	Actual permutations	Number \geq observed
1, 2	0.856	0.1	2300	999	0
1, 3	0.936	0.4	276	276	1
2, 3	1	10	10	10	1

Table 3. Summary statistics of the generalized linear models (GLM) for each dominant species of Siphonophorae.

	<i>Dimophyes arctica</i>	<i>Lensia conoidea</i>	<i>Lensia meteori</i>	<i>Muggiaea atlantica</i>
Environmental variables	Z	Z	Z	Z
T/T^2	3.69**/−4.01**	1.43*/2.09*	−2.39*/3.40**	3.31**/ns
Salinity/salinity ²	Ns/ns	Ns/ns	Ns/ns	−3.94**/ns
DIO/DIO ²	5.66**/−6.83**	4.42**/−4.78**	ns/ns	8.78**/−9.15**
Total depth	2.44**	Ns	−2.24*	Ns
Explained deviance (%)	44.72	36.28	40.69	32.91

Values of the statistical test (Z-test from a binomial negative error family distribution and a log 'link'), explained deviance and significance are shown. T, temperature; DIO, dissolved oxygen.

* $P < 0.05$; ** $P < 0.01$; ns, non-significant.

incidental occurrence of this species was recorded off Valparaíso (33°S; Palma, 1986).

Lensia conoidea was the dominant species, showing wide geographic coverage over the study area, with maximum abundance values in estuarine waters (Sarmiento and Smyth Channels) and absence from most of the oceanic stations. The eudoxid stages were collected at the same stations as the polygastric stages, but the highest aggregations of individuals were recorded in the Europa Fjord. This species is very common and frequent in the PFE (Palma *et al.*, 1999, 2007a, 2011, 2014a; Palma & Silva, 2004). However, in the HCS it has been recorded only once in the bay of Valparaíso (Palma, 1973). This species is common and abundant in the great oceans, especially in the California and Benguela currents, and in the Mediterranean Sea, spanning broad depth distributions from the surface down to the pelagic zone (Alvariño, 1971; Pugh, 1984, 1999; Kirkpatrick & Pugh, 1984). It has been recorded also in other fjord ecosystems like Korsfjord Fjord in Norway (Hosia & Båmsted, 2008).

Dimophyes arctica was the second most dominant species and it was collected mainly in estuarine waters (Peel Fjord and Sarmiento and Smyth channels), i.e. water with low temperature ($<6^{\circ}\text{C}$) and salinity (<30). The eudoxid stages were collected at the same stations as the polygastric stages, but the highest aggregations of eudoxids were recorded in the Peel Fjord. Its abundance is very low with an irregular distribution in the PFE and its abundance increasing from Puerto Montt to

Cape Horn (Palma & Silva, 2004; Palma, 2008). This species is common in epipelagic Antarctic and Sub-Antarctic waters transported by the West Wind Drift Current that enters the PFE (Palma & Silva, 2004). *Dimophyes arctica* is a cosmopolitan species, inhabiting the great oceans and the Antarctic, Arctic, the Mediterranean Sea and boreal fjords (Alvariño, 1971; Hosia *et al.*, 2008). In boreal and austral latitudes it is more abundant in epipelagic waters than in tropical and temperate waters, where it is more common in meso- and bathypelagic waters (Pugh, 1984).

Lensia meteori was found at low density at most stations located in estuarine waters, with a maximum value in the Sarmiento Channel (Station 65) and absence from all oceanic stations. In Chilean waters it has been collected exclusively in the PFE, between Penas Gulf (50°S) and the Strait of Magellan (53°S) (Palma *et al.*, 1999, and this study). This species inhabits temperate regions in the three great oceans and in the Mediterranean Sea and has a broad vertical distribution extending down to depths of 800 m (Alvariño, 1971; Bouillon *et al.*, 2004).

Despite having the lowest abundance among the dominant species, *M. atlantica* showed high frequency of occurrence (FO = 90%) throughout the study zone. However, there is a notable lack of eudoxids collected in comparison to the number of nectophores (eudoxids:nectophores = 1:5), because in the Patagonian Fjord Ecosystem (PFE) we registered high densities of eudoxids in the same period, in spring 2008 between the Gulf of Penas (47°S) to Trinidad Channel (50°10'S) with superficial temperatures $<9^{\circ}\text{C}$ (Palma *et al.*, 2014a). Beside this, in the south extreme of PFE, in the Magellan Region (52–56°S), the highest densities of eudoxids of *M. atlantica* occur in the Almirantazgo Sound, where the superficial temperature is $<7^{\circ}\text{C}$ (Palma & Aravena, 2001; Valdenegro & Silva, 2003). In this sense, recently Blackett *et al.* (2015) found that the populations of *M. atlantica* appear to have a temperature threshold of 10°C for the eudoxid production in the western English Channel. This ratio is generally the inverse in spring among dominant species, as observed with *L. conoidea* and *D. arctica* in the

Table 4. Results of the permutation test for the canonical correspondence analysis (51.4% of explained inertia) for the siphonophorae community.

Canonical correspondence analysis	F	P
Global analysis	4.02	<0.01
Temperature	6.0	<0.01
Dissolved oxygen	4.2	<0.01
Salinity	1.8	0.12

Values of the statistical test (F-value) and significance (P) for the global test and for each explanatory variable are shown.

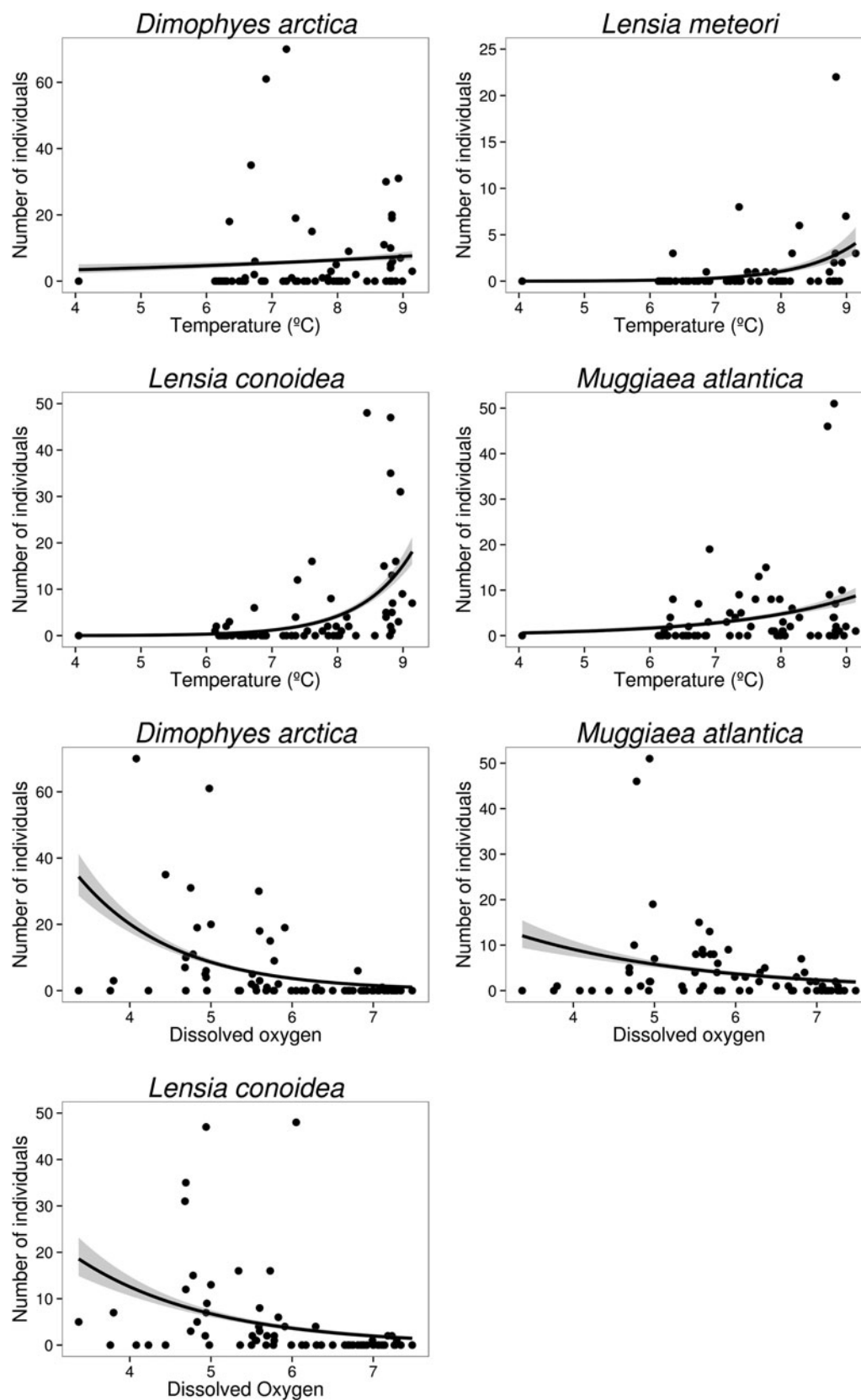


Fig. 6. Relationships of dominant siphonophore species with significant environmental variables from the generalized linear models (GLM).

present study, and as shown by other results obtained in the PFE (Palma & Silva, 2004; Palma *et al.*, 2007a, 2014a). *Muggiaea atlantica* is eurythermal and euryhaline, and is

widespread in both the adjacent oceanic waters of the Pacific Ocean (SAAW) and in the FPE (MSAAW and EW) throughout the study area. This species is the most common

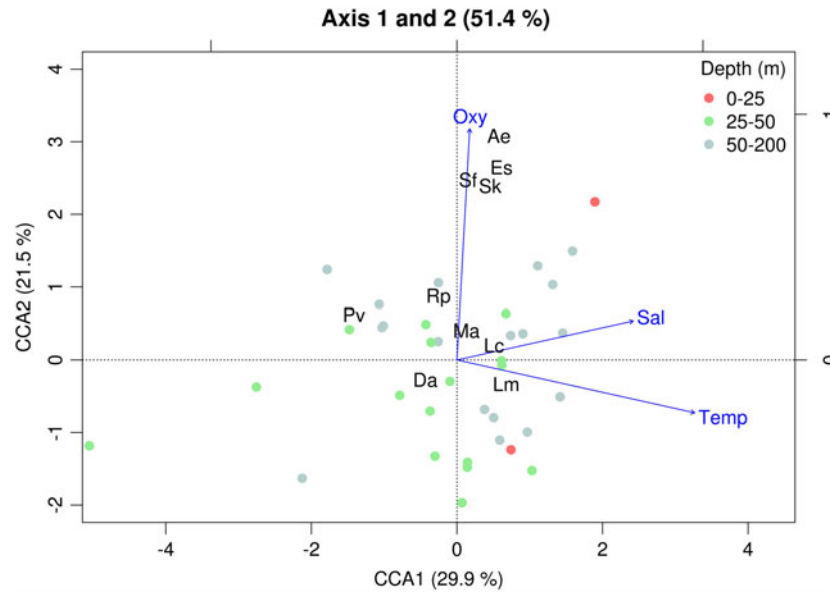


Fig. 7. Canonical Correspondence Analysis triplot (scaling 2) based on data from spring 2009 showing the distribution of sampling stations (points, $N = 40$) by depth strata, siphonophore species (black labels, $N = 10$) and environmental variables (blue arrows). The total explained inertia (51.4%), and partial explained inertia per axis is also shown. Lc: *Lensia conoidea*; Da: *Dimophyes arctica*; Lm: *Lensia meteori*; Ma: *Muggiaea atlantica*; Pv: *Pyrosophos vanhoeffeni*; Sk: *Sphaeronectes koellikeri*; Sf: *Sphaeronectes fragilis*; Rp: *Rosacea plicata*; Es: *Eudoxoides spiralis*; Ae: *Agalma elegans*. Temp: temperature; Sal: salinity; Oxy: dissolved oxygen.

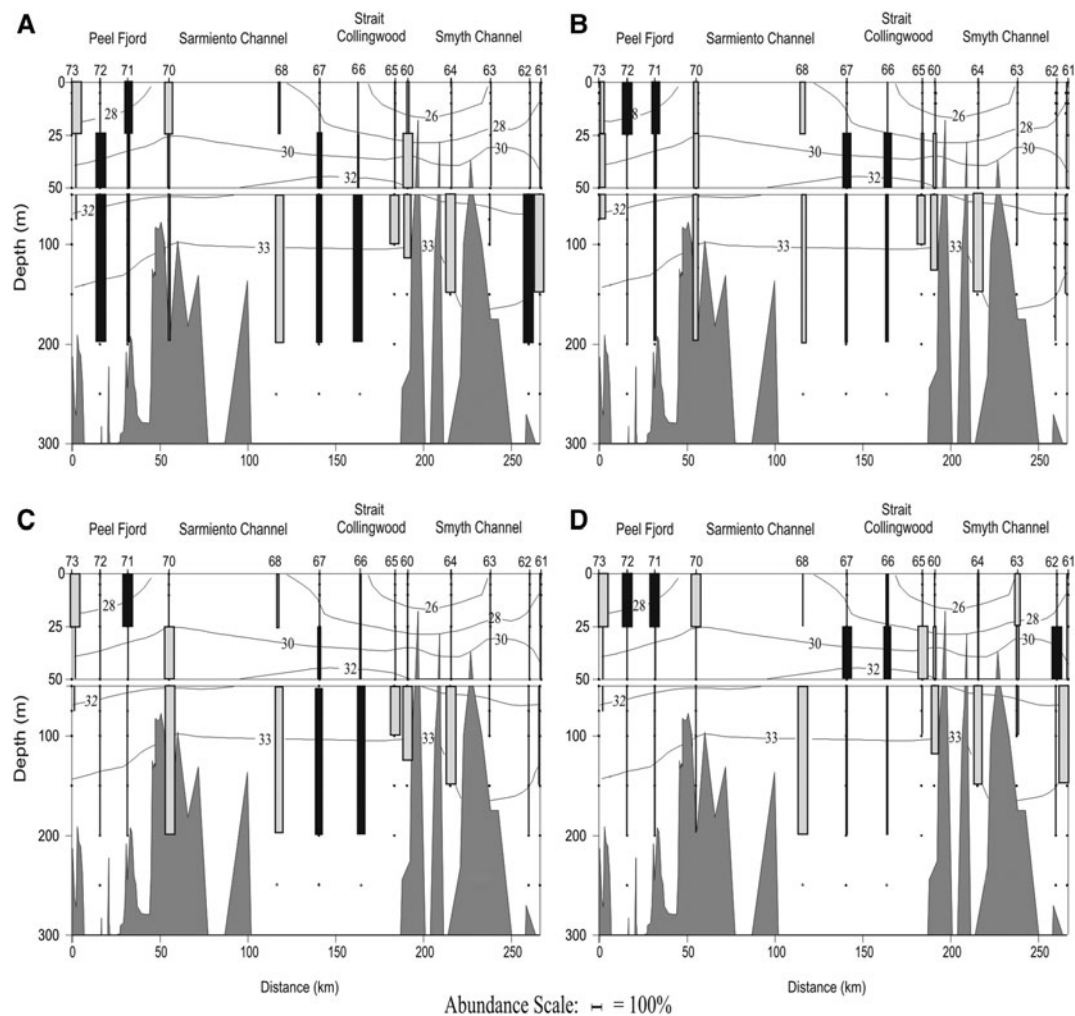


Fig. 8. Vertical distribution of dominant species: (A) *Lensia conoidea*; (B) *Dimophyes arctica*; (C) *Lensia meteori*; and (D) *Muggiaea atlantica* in a longitudinal north-south transect between Trinidad Channel and Magellan Strait in spring 2009. Grey boxes: diurnal tows, black boxes: nocturnal tows.

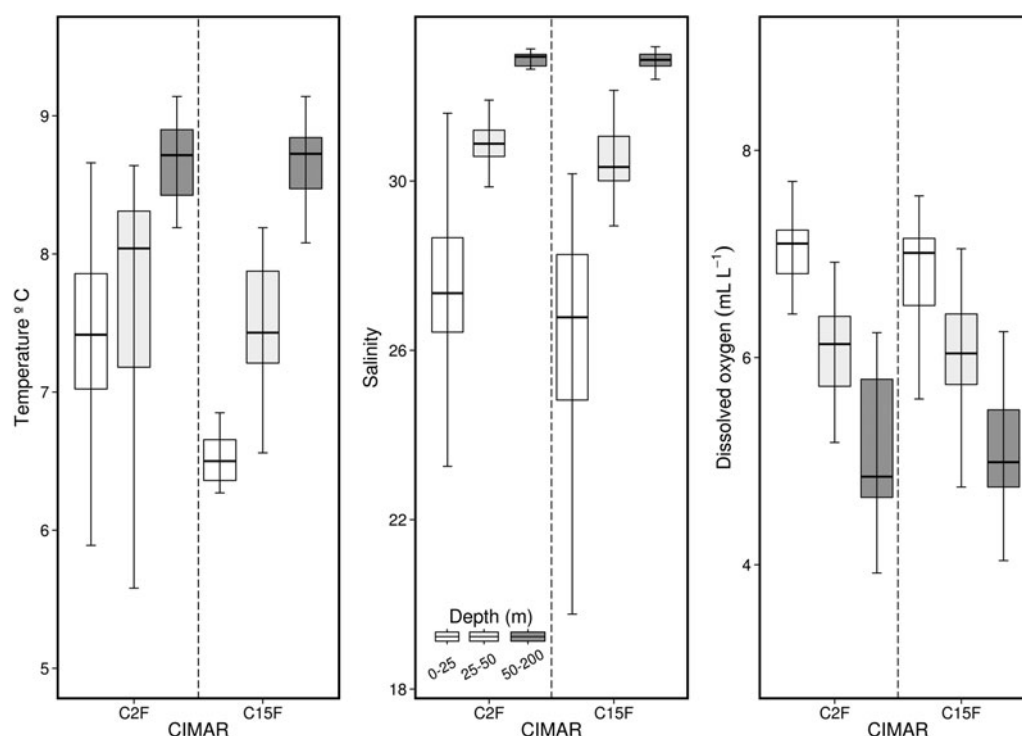


Fig. 9. Comparison of temperature, salinity and dissolved oxygen among different depths for both spring seasons (Cruises CIMAR 2–15 Fiordos).

and frequent siphonophore in the HCS (Palma, 1973, 1994; Palma & Rosales, 1995; Palma & Apablaza, 2004; Pavez *et al.*, 2010) and in the PFE (Palma & Silva, 2004; Palma *et al.*, 2007a, 2011, 2014a; Palma, 2008; Villenas *et al.*, 2009). *Muggiaea atlantica* is a neritic species inhabiting warm and temperate regions in the great oceans and in the Mediterranean Sea (Alvariño, 1971; Bouillon *et al.*, 2004).

With regard to the reproductive process of *L. conoidea* and *D. arctica*, the highest eudoxid densities were recorded in the interior of the fjords. The highest aggregations of eudoxids of *L. conoidea* were recorded in the Europa Fjord, while for *D. arctica* this occurred in the Peel Fjord. This would mean better division of the area and its resources, leading to greater reproductive success. In the PFE, it has been seen that the fjords appear to be favourable to reproduction,

displaying high concentrations of phytoplankton that would give higher food availability in such areas (Palma *et al.*, 2014a, b).

Environmental associations and vertical distribution

The nMDS and ANOSIM analysis, for the community structure, recognized three major groups of sampling stations (Figure 5). Group 1 was characterized by the abundance of those dominant species (*D. arctica*, *L. conoidea*, *L. meteori* and *M. atlantica*). Of these species, *D. arctica* and *L. conoidea* presented the highest abundances in the estuarine waters. These species are widely distributed through the PFE,

Table 5. Summary of statistics for the nectophores collected between springs 1996 and 2009. Total number of individuals, range of non-zero abundances, average per station, dominance and occurrence are shown. Abundances are expressed as ind. 1000 m⁻³.

Species	Total number of individuals		Range of non-zero abundances		Dominance (%)		Occurrence (%)	
	1996	2009	1996	2009	1996	2009	1996	2009
<i>Lensia conoidea</i> *	2413	4386	92.8	168.7	52.2	26.8	74	78
<i>Lensia meteori</i> *	341	3961	13.1	152.4	7.4	24.2	48	63
<i>Dimophyes arctica</i> *	175	3675	6.7	141.4	3.8	22.5	59	67
<i>Muggiaea atlantica</i> *	1635	3454	62.9	132.9	35.4	21.1	67	93
<i>Sphaeronectes koellikeri</i>	10	155	0.4	6.0	0.2	0.9	7	22
<i>Pyrostephos vanhoeffeni</i>	5	527	0.2	20.3	0.1	3.2	11	59
<i>Eudoxoides spiralis</i>	40	126	1.5	4.8	0.9	0.8	11	15
<i>Agalma elegans</i>	0	10	0.0	0.4	0.0	0.1	0	7
<i>Rosacea plicata</i>	0	41	0.0	1.6	0.0	0.2	0	7
<i>Sphaeronectes fragilis</i>	0	27	0.0	1.0	0.0	0.2	0	7

Asterisks indicate the dominant species of siphonophores in both spring seasons.

Table 6. Summary statistics of the generalized linear models (GLM) for the comparisons of average abundance between years 1996 and 2009.

Species	Abundance		Z	P
	1996	2009		
<i>Lensia conoidea</i> ^a	92.8	168.7	1.12	0.26
<i>Lensia meteori</i> ^a	13.1	152.4	3.46	<0.01
<i>Dimophyes arctica</i> ^a	6.7	141.4	5.33	<0.01
<i>Muggiaea atlantica</i> ^a	62.9	132.9	1.46	<0.01
<i>Sphaeronectes koellikeri</i>	0.4	6.0	1.76	0.078
<i>Pyrostephos vanhoeffeni</i>	0.2	20.3	5.39	<0.01
<i>Eudoxoides spiralis</i>	1.5	4.8	6.32	<0.01
<i>Agalma elegans</i>	0.0	0.4	0.06	0.99
<i>Rosacea plicata</i>	0.0	1.6	–	–
<i>Sphaeronectes fragilis</i>	0.0	1.0	–	–
Total abundance	177.7	626.8	3.93	<0.01

– Species not registered in spring 1996.

Values of the statistical test (Z-test from a negative binomial distribution with a link = 'log') and significance are shown.

^aDominant species, bold font: significant differences between years.

particularly *M. atlantica* and *L. conoidea* (Palma & Silva, 2004; Palma *et al.*, 2007a, 2011, 2014a; Villenas *et al.*, 2009). Group 2 was characterized by *M. atlantica* and *L. conoidea* but in low densities and Group 3 was characterized by the presence of occasional species (*S. fragilis*, *A. elegans*, *S. koellikeri* and *E. spiralis*) which are also occasional inhabitants of the PFE (Palma & Silva, 2004; Palma *et al.*, 2007a, 2011, 2014a; Villenas *et al.*, 2009). Of these occasional species, only *S. koellikeri* is abundant along the Chilean coast, where it is found in association with *M. atlantica* (Palma, 1994; Palma & Rosales, 1995; Pavez *et al.*, 2010).

Both the univariate and multivariate analysis showed a positive association with temperature and a negative association with dissolved oxygen. The positive association with temperature has been previously demonstrated for *M. atlantica* (Palma *et al.*, 1999; Palma & Silva, 2004). The negative association with dissolved oxygen for *L. conoidea* (Palma & Silva, 2004) was attributed to the presence of Equatorial Sub Superficial Waters (ESSW), demonstrating that even when those species are present in a wide range of environmental conditions, their maximum abundances are restricted to particular conditions.

Muggiaea atlantica presented broad vertical distribution throughout the study zone, though the highest concentrations of nectophores occurred in the surface and middle layers (Figure 8D). This layer (0–50 m) is associated with EW and has higher vertical stability in the water column, low temperature and salinity, and high values of dissolved oxygen. Its lower limit is determined by a strong halocline located at that depth which separates the EW from the deeper water (below 30 m), known as Modified Sub-Antarctic Water (MSAAW). The polygastric stages of *L. conoidea*, *D. arctica* and *L. meteori* were preferentially distributed in deeper waters (below 50 m). They were found in the surface layer in the Peel Fjord, but moved deeper from the Sarmiento Channel until south of the Smyth Channel, with the exception of Stations 61–63, where *D. arctica* and *L. meteori* were in fact absent (Figure 8A–C). These species were associated with the predominantly MSAAW in the deeper layer (depths of 50–200 m), characterized by quasi-homogeneous conditions for temperature, salinity and dissolved oxygen. These results

confirm the bathymetric distribution of the siphonophore species in other geographic areas of the PFE (Palma *et al.*, 2007a, 2011, 2014a). The two-layer marine circulation identified in the study zone is also an important trait throughout the PFE, affecting the vertical distribution of not only siphonophores but also other planktonic cnidarians, such as hydro-medusae (Palma *et al.*, 2007b, 2014b; Villenas *et al.*, 2009; Bravo *et al.*, 2011). Thus our results allow us to successfully prove the hypothesis that even with the eurythermic and euryhaline siphonophore species (i.e. *M. atlantica*, *L. conoidea*) the strong oceanographic gradients found in the study area shape the community structure and determine species-specific responses (Figures 6 & 7).

Interannual comparison between the abundance of siphonophores in springs of 1996 and 2009

The comparative results for this sector of the Patagonian Fjord Ecosystem (50°06'–52°45'S) from 1996 to 2009 show a 3.5-fold increase in the abundance of siphonophores. This rise in recent years has also been observed in other studies on planktonic cnidarians (medusa and siphonophores) in other sectors of the PFE (Villenas *et al.*, 2009; Bravo *et al.*, 2011; Palma *et al.*, 2011, 2014a, b), although Brotz *et al.* (2012) showed a decrease in jellyfish in the Humboldt Current LME. There are several studies that show increases in gelatinous organisms in recent decades in several oceanic coastal areas. This has been attributed to different anthropogenic stress factors, such as widespread ocean temperature increases, overfishing and habitat alteration (e.g. aquaculture facilities) (Brodeur *et al.*, 1999, 2002; Mills, 2001; Purcell *et al.*, 2007; Duarte *et al.*, 2013; but see Condon *et al.*, 2013). In this way, the PFE is not away from these anthropogenic stress factors, mostly affected by the aquaculture activities (reviewed in Mianzan *et al.*, 2014).

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315416001302>.

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REFERENCES

- Ahumada A. (1976) Nota sobre los quetognatos capturados en la Expedición Hero 72-4. Segunda etapa. *Boletín de la Sociedad de Biología de Concepción* 50, 27–34.
- Alvaríño A. (1971) Siphonophores of the Pacific with a review of the world distribution. *Bulletin of the Scripps Institution of Oceanography* 6, 1–432.
- Antezana T. (1976) Diversidad y equilibrio ecológico en comunidades pelágicas. In Orrego F. (ed.) *Preservación del Medio Ambiente Marino*. Santiago: Instituto de Estudios Internacionales, Universidad de Chile, pp. 40–54.
- Arcos D. (1974) Los copépodos calanoideos colectados en la región Magallánica por la Expedición Hero 72-4b. *Boletín de la Sociedad de Biología de Concepción* 47, 215–225.
- Arcos D. (1976) Los copépodos calanoideos de la región Magallánica. Expedición Hero 72-4. *Revista de la Comisión Permanente del Pacífico Sur* 5, 85–100.
- Blackett M., Lucas C.H., Harmer R.A. and Licandro P. (2015) Population ecology of *Muggiaea atlantica* (Cnidaria, Siphonophora) in the Western English Channel. *Marine Ecology Progress Series* 535, 129–144.
- Bouillon J., Medel M.D., Pagès F., Gili J.M., Boero F. and Gravili C. (2004) Fauna of the Mediterranean Sea. *Scientia Marina* 68(Suppl. 2), 5–438.
- Bravo V., Palma S. and Silva N. (2011) Seasonal and vertical distributional patterns of medusae in Aysén region, southern Chile. *Latin American Journal of Aquatic Research* 39, 359–377.
- Brodeur R., Sugisaki H. and Hunt G. (2002) Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology Progress Series* 233, 9–103.
- Brodeur R.D., Mills C.E., Overland J.E., Walters G.E. and Schumacher J.D. (1999) Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. *Fisheries Oceanography* 8, 296–306.
- Brotz L., Cheung W.W.L., Kleisner K., Pakhomov E. and Pauly D. (2012) Increasing jellyfish populations: trends in Large Marine Ecosystems. *Hydrobiologia* 690, 3–20.
- Bustos C.A., Landaeta M.F. and Balbontín F. (2011) Ichthyoplankton spatial distribution and its relation with water column stratification in fjords of southern Chile (46°48'–50°09'S) in austral spring 1996 and 2008. *Continental Shelf Research* 31, 293–303.
- Carpenter J. (1965) The Chesapeake Bay Institute Technique for the Winkler dissolved oxygen method. *Limnology and Oceanography* 10, 141–143.
- Clarke K.R. and Warwick R.M. (1994) *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth: Plymouth Marine Laboratory, 144 pp.
- Condon R.H., Duarte C.M., Pitt K.A., Robinson K.L., Lucas C.H., Sutherland K.H., Mianzan H.W., Borgeberg M., Purcell J.E., Decker M.B., Uye S., Madin L.P., Brodeur R.D., Haddock S.H.D., Malej A., Parry G.D., Eriksen E., Quiñones J., Acha M., Harvey M., Arthur J.M. and Graham W.M. (2013) Recurrent jellyfish blooms are a consequence of global oscillations. *Proceedings of the National Academy of Sciences USA* 110, 1000–1005.
- Duarte C.M., Pitt K.A., Lucas C.H., Purcell J.E., Uye S., Robinson K., Brotz L., Decker M.B., Sutherland K.R., Malej A., Madin L., Mianzan H., Gili J.-M., Fuentes V., Atienza D., Pagés F., Breitburg D., Malek J., Graham W.M. and Condon R.H. (2013) Is global ocean sprawl a cause of jellyfish blooms? *Frontiers in Ecology and the Environment* 11, 91–97.
- Guerrero E., Gili J.-M., Rodríguez C., Araujo E.M., Canepa A., Calbet A., Genzano G., Mianzan H.W. and González R.A. (2013) Biodiversity and distribution patterns of planktonic cnidarians in San Matías Gulf, Patagonia, Argentina. *Marine Ecology* 34, 71–82.
- Hosia A. and Båmstedt U. (2008) Seasonal abundance and vertical distribution of siphonophores in western Norwegian fjords. *Journal of Plankton Research* 30, 951–962.
- Hosia A., Stemmann L. and Youngbluth M. (2008) Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses. *Deep-Sea Research Part II: Topical Studies in Oceanography* 55, 106–118.
- Kirkpatrick P.A. and Pugh P.R. (1984) *Siphonophores and velellids. Synopses of the British Fauna (New Series)*. London: E.J. Brill Academic Publications, 154 pp.
- Mianzan H., Quiñones J., Palma S., Schiariti A., Acha E.M., Robinson K.L. and Graham W.M. (2014) *Chrysaora plocamia*: a poorly understood jellyfish from South American Waters. In Pitt, K.A. and Lucas, C.H. (eds), *Jellyfish blooms*. Dordrecht: Springer, pp. 219–236. http://doi.org/10.1007/978-94-007-7015-7_10.
- Mills C. (2001) Jellyfish blooms: are populations increasing globally response to changing ocean conditions? *Hydrobiology* 451, 55–68.
- Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Peter Solymos P., Henry M., Stevens H. and Wagner H. (2015) *Vegan: community ecology package*. R package version 2.3–0. <http://CRAN.R-project.org/package=vegan> (accessed 10 July 2015).
- Pagès F. and Orejas C. (1999) Medusae, siphonophores and ctenophores of the Magellan region. *Scientia Marina* 65, 51–57.
- Palma S. (1973) Contribución al estudio de los sifonóforos encontrados frente a la costa de Valparaíso. I. Taxonomía. *Investigaciones Marinas* 4, 17–88.
- Palma S. (1986) Sifonóforos fisonectes colectados frente a la costa de Valparaíso. *Investigaciones Marinas* 14, 69–78.
- Palma S. (1994) Composición y distribución del macroplankton gelatinoso recolectado frente a la costa central de Chile. *Revista de Biología Marina* 29, 23–45.
- Palma S. (2008) Zooplankton distribution and abundance in the austral Chilean channels and fjords. In Silva N. and Palma S. (eds) *Progress in the oceanographic knowledge of Chilean interior waters, from Puerto Montt to Cape Horn*. Valparaíso: Comité Oceanográfico Nacional-Pontificia Universidad Católica de Valparaíso, pp. 107–113.
- Palma S. and Apablaza P. (2004) Abundancia estacional y distribución vertical del zooplancton gelatinoso carnívoro en un área de surgencia en el norte del Sistema de la Corriente de Humboldt. *Investigaciones Marinas* 32, 49–70.
- Palma S., Apablaza P. and Silva N. (2007b) Hydromedusae (Cnidaria) of the Chilean southern channels (from the Corcovado Gulf to the Pulluche-Chacabuco Channels). *Scientia Marina* 71, 65–74.
- Palma S., Apablaza P. and Soto D. (2007a) Diversity and aggregation areas of planktonic cnidarians of the southern channels of Chile (Boca del Guafo to Pulluche Channel). *Investigaciones Marinas* 35, 71–82.
- Palma S. and Aravena G. (2001) Distribución de quetognatos, eufáusidos y sifonóforos en la región magallánica. *Ciencia y Tecnología Marina* 24, 47–59.
- Palma S., Córdova P., Silva N. and Silva C. (2014b) Biodiversity and spatial distribution of medusae in the Magellan Region (Southern Patagonian Zone). *Latin American Journal of Aquatic Research* 42, 1175–1188.

- Palma S., Retamal M.C., Silva N. and Silva C.** (2014a) Horizontal and vertical distributions of siphonophores in relation to oceanographic conditions in Chilean Patagonian fjords. *Scientia Marina* 78, 339–351.
- Palma S. and Rosales S.** (1995) Composición, abundancia y distribución estacional del macroplankton de la bahía de Valparaíso. *Investigaciones Marinas* 23, 49–66.
- Palma S. and Silva N.** (2004) Distribution of siphonophores, chaetognaths, euphausiids and oceanographic conditions in the fjords and channels of southern Chile. *Deep-Sea Research Part II: Topical Studies in Oceanography* 51, 513–535.
- Palma S., Silva N., Retamal M. and Castro L.** (2011) Seasonal and vertical distributional patterns of siphonophores and medusae in the Chiloé Interior Sea, Chile. *Continental Shelf Research* 31, 260–271.
- Palma S., Ulloa R. and Linacre L.** (1999) Sifonóforos, quetognatos y euphausiidos de los canales australes entre el Golfo de Penas y Estrecho de Magallanes. *Ciencia y Tecnología del Mar* 22, 111–142.
- Pavez M.A., Landaeta M.E., Castro L.R. and Schneider W.** (2010) Distribution of carnivorous gelatinous zooplankton in the upwelling zone of central Chile (austral spring 2001). *Journal of Plankton Research* 32, 1051–1065.
- Pugh P.R.** (1984) The diel migrations and distribution within a mesopelagic community in the North East Atlantic. 7 Siphonophores. *Progress in Oceanography* 13, 461–489.
- Pugh P.R.** (1999) Siphonophorae. In Boltovskoy D. (ed.) *South Atlantic Zooplankton*, Volume 1. Leiden: Backhuys Publishers, pp. 467–511.
- Purcell J.E., Uye S. and Lo W.T.** (2007) Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series* 350, 153–174.
- R Core Team** (2015) R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org/>
- Rosenberg P. and Palma S.** (2003) Cladóceros de los fiordos y canales patagónicos localizados entre el golfo de Penas y el estrecho de Magallanes. *Investigaciones Marinas* 30, 15–24.
- Sievers H.A., Calvete C. and Silva N.** (2002) Distribución de características físicas, masas de agua y circulación general para algunos canales australes entre el golfo de Penas y el estrecho de Magallanes (Crucero CIMAR Fiordo 2), Chile. *Ciencia y Tecnología del Mar* 25, 13–39.
- Sievers H.A. and Silva N.** (2008) Water masses and circulation in austral Chilean channels and fjords. In Silva N. and Palma S. (eds) *Progress in the oceanographic knowledge of Chilean interior waters, from Puerto Montt to Cape Horn*. Valparaíso: Comité Oceanográfico Nacional-Pontificia Universidad Católica de Valparaíso, pp. 53–58.
- Silva N. and Calvete C.** (2002) Características oceanográficas físicas y químicas de canales australes chilenos entre el golfo de Penas y el estrecho de Magallanes (Crucero CIMAR-Fiordo 2). *Ciencia y Tecnología del Mar* 25, 23–88.
- Ter Braak C.J.F.** (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67, 1167–1179.
- Totton A.** (1965) *A synopsis of Siphonophora*. London: British Museum of Natural History, 230 pp.
- Valdenegro A. and Silva N.** (2003) Caracterización oceanográfica física y química de la zona de canales y fiordos australes de Chile entre el Estrecho de Magallanes y Cabo de Hornos (CIMAR 3 Fiordos). *Ciencia y Tecnología del Mar* 26, 19–60.
- Venables W.N. and Ripley B.D.** (2002) *Modern applied statistics with S*. New York, NY: Springer.
- Villenas F., Soto D. and Palma S.** (2009) Cambios interanuales en la biomasa y biodiversidad de zooplancton gelatinoso en el sur de Chile (Primaveras 2004 y 2005). *Revista de Biología Marina y Oceanografía* 44, 309–324.
- Zuur A.F., Ieno E.N. and Elphick C.S.** (2010) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1, 3–14.
- and
- Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A. and Smith G.M.** (2009) *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.

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