Horizontal and vertical distributions of siphonophores in relation to oceanographic conditions in Chilean Patagonian fjords

Sergio Palma [1], María Cristina Retamal [1,2], Nelson Silva [1], Claudio Silva [1]

[1] Escuela de Ciencias del Mar, Pontificia Universidad Católica de Valparaíso, P.O. Box 1020, Valparaíso, Chile.
E-mail: spalma@ucv.cl
[2] Servicio Hidrográfico y Oceanográfico de la Armada, P.O. Box 324, Valparaíso, Chile.

Summary: Siphonophores collected in Chilean Patagonian fjords, between the Gulf of Penas and the Trinidad Channel in 2008 were analysed. A total of 12 species were recorded, of which *Muggiaea bargmannae, Lensia subtilis, Praya dubia* and *Sphaeronectes fragilis* were identified for the first time in this sector of the Patagonian fjords. *M. bargmannae* represents a new record for the southeastern Pacific. The most abundant species were *Muggiaea atlantica* (78.6%), *Lensia conoidea* (8.7%) and *Dimophyes arctica* (8.5%). *M. atlantica,* the dominant species, showed high densities in both oceanic and interior waters. *L. conoidea* and *D. arctica*, on the other hand, were principally collected in interior waters. *M. atlantica* was collected in less saline (<30), more oxygenated (6-7 mL L^{-1}) shallow strata (0-50 m), while *L. conoidea* and *D. arctica* were collected below 50 m depth in more saline (30-33) and less oxygenated (4-6 mL L^{-1}) waters. The eudoxids of these species followed the same horizontal and vertical distribution patterns as their polygastric stages. These results confirm the success of *M. atlantica* in the colonization of all the southern fjords and document an increase with respect to the results obtained for the same geographical area in the spring of 1996. They also allowed us to infer that salinity and dissolved oxygen vertical gradients play an important role in determining the depth distribution patterns of these species.

Keywords: siphonophores; gelatinous zooplankton; horizontal distribution; vertical distribution; Chilean Patagonian fjords.

Distribución horizontal y vertical de los sifonóforos en relación con las condiciones oceanográficas en fiordos patagónicos chilenos

Resumen: Se analizaron los sifonóforos muestreados en fiordos patagónicos chilenos, entre el golfo de Penas y canal Trinidad en primavera de 2008. Se identificó un total de 12 especies, de las cuales *Muggiaea bargmannae, Lensia subtilis, Praya dubia* y *Sphaeronectes fragilis* fueron registrados por primera vez en este sector de fiordos patagónicos. *M. bargmannae* constituye un nuevo registro de sifonóforos en el Pacífico suroriental. Las especies más abundantes fueron *Muggiaea atlantica* (78.6%), *Lensia conoidea* (8.7%) y *Dimophyes arctica* (8.5%). *M. atlantica,* la especie dominante, mostró altas densidades tanto en aguas oceánicas como interiores. Por otra parte, *L. conoidea* y *D. arctica* se colectaron principalmente en aguas interiores. Las eudoxias de estas especies siguieron los mismos patrones de distribución horizontal que sus fases poligástricas. *M. atlantica* se encontró en aguas menos salinas (<30) y más oxigenadas (6-7 mL L^{-1}) en el estrato superficial (0-50 m), mientras que *L. conoidea* y *D. arctica* se colectaron bajo los 50 m de profundidad en aguas más salinas (30-33) y menos oxigenadas (4-6 mL L^{-1}). Estos resultados confirman el éxito de *M. atlantica* en la colonización de todos los fiordos australes y su incremento respecto a resultados obtenidos en la misma área geográfica en primavera de 1996.

Palabras clave: sifonóforos; zooplancton gelatinoso; distribución horizontal; distribución vertical; fiordos patagónicos chilenos.

INTRODUCTION

A steady increase in gelatinous predator populations in marine ecosystems has been observed in recent years, and this has promoted studies on gelatinous macroplankton due to their significance in determining marine ecosystem structure (Mills 2001, Brodeur et al. 2002, Purcell et al. 2007). Such predators include the siphonophores, a widespread and abundant group that are found in coastal and oceanic waters and play a critical ecological role as competitors and predators of other zooplankters, particularly micro-crustaceans and marine invertebrate and vertebrate larval stages (Mackie et al. 1987, Pugh 1999). Siphonophores have a polymorphic colony structure, with a life cycle allowing them to produce high quantities of the sexual stage (eudoxids in the Calycophorae), thus generating large population densities during some periods of the year, particularly in highly productive biological areas (Pugh 1999, Palma and Apablaza 2004, Thibault-Botha et al. 2004, Pavez et al. 2010).

Siphonophore communities have been studied in diverse geographical areas bathed by the Humboldt Current System in Chilean coastal waters, particularly in coastal areas of upwelling such as Antofagasta, Valparaíso and Concepción, where common species (e.g. *Muggiaea atlantica* and *Sphaeronectes koellikeri*) can reach high population densities during spring and summer (Palma 1994, Palma and Rosales 1995, Pagès et al. 2001, Palma and Apablaza 2004, Apablaza and Palma 2006, Pavez et al. 2010). *M. atlantica* also commonly inhabits Chilean Patagonian fjords and channels and is a dominant species in this southern region (Palma and Silva 2004, Villenas et al. 2009, Palma et al. 2007a, 2011).

The Chilean Patagonian fjords form one of the most extensive estuarine areas in the world, extending from the Reloncaví fjord (41°20'S) to Cape Horn (55°58'S) and including areas of complex geomorphology and oceanography. They are approximately 1600 km long and cover a total area of 240000 km^2 (Palma and Silva 2004). This ecosystem involves a two-layer estuarine circulation system: a surface layer (from the surface to 20-30 m depth) of Estuarine Water (EW) flowing towards the adjacent ocean, with low salinity due to freshwater discharge, high annual precipitation and coastal runoff; and a deeper layer (20-30 m to the bottom), which is more saline, colder and of higher density as a result of the inward flow of the Subantarctic Water (SAAW). A strong halocline develops between the two layers and, therefore, a pycnocline forms at 20-30 m depth, thus generating a highly stratified system (Silva and Calvete 2002).

The ecosystem of the interior waters, located between the Reloncaví Fjord and the Elefantes Gulf (46°30'S), has been intensively studied during the last two decades because of activities associated with marine transportation, tourism, fisheries and aquaculture (Buschmann et al. 2006, Silva and Palma 2008). Thus, numerous oceanographic and biological studies have been carried out in this zone (Silva and Palma 2008), including studies on siphonophores and jellyfish with results showing that the two-layer hydrographic structure may affect not only the species composition but also the vertical distribution of the zooplankton in interior waters (Palma et al. 2007a, 2007b, 2011, Villenas et al. 2009, Bravo et al. 2011).

In contrast, the fjord ecosystem located between the Gulf of Penas (47°S) and Cape Horn has received little attention. In this vast area, the sector covering the Gulf of Penas and the Trinidad Channel (50°10'S) has been barely studied and published works on zooplankton are restricted to reports on siphonophores, chaetognaths, euphausiids and cladocerans (Palma et al. 1999, Rosenberg and Palma 2003), ichthyoplankton (Bustos et al. 2011) and decapod crustacean larvae (Mujica and Medina 2000). This southern area receives Subantarctic Water input from the adjacent Pacific, entering through the Gulf of Penas (0-150 m) to the north, the Ladrillero Gulf (0-50 m) in the centre and the Trinidad Gulf (0-70 m) to the south. These highly saline subantarctic waters merge with freshwater from rivers, such as the Baker (870 m^3 s^{-1}) and Pascua (574 m^3 s^{-1}) Rivers and melt water from the Southern Ice Field, thus forming EW flowing seawards in the upper 25-30 m depth stratum (Silva and Calvete 2002, Calvete and Sobarzo 2011).

This work analyses the effect of water column stratification on the spatial distribution of the polygastric and eudoxid stages of siphonophores in the central Patagonian fjords of southern Chile (47°-50°10'S).

MATERIALS AND METHODS

A total of 40 oceanographic stations were occupied during the CIMAR 14 Fiordos cruise performed between 25 October and 24 November 2008, and these were distributed between the Gulf of Penas (47°S) and the Trinidad Channel (50°10'S) (Fig. 1). Only the sampling stations situated along two longitudinal transects were considered in the vertical distribution analysis. The oceanic transect (OT, 10 stations) comprised the Gulf of Penas and the Fallos, Ladrillero, Picton and Trinidad Channels, and included the stations with the highest adjacent oceanic water input. The estuarine transect (ET, 9 stations), on the other hand, involved the Gulf of Penas and the Messier, Paso del Indio and Wide Channels and the stations with the highest EW input (Fig. 1).

A CTDO Sea-Bird model SBE 25 was used at each station to record the oceanographic variables of temperature, salinity and dissolved oxygen content in the water column. Salinity and dissolved oxygen records were corrected using the results from instrumental (salinometer) and chemical (Winkler) analyses of discrete samples collected in the water column during the CTDO casting.

Zooplankton samples were obtained by oblique tows in three strata: surface (0-25 m at 40 stations), middle (25-50 m at 40 stations) and deep (50-200 m or 50 m-near bottom, depending on bottom depth at 28 stations), during day and night. The strata were selected considering the two-layer oceanographic structure characterizing the interior region of the fjords and channels (Silva and Calvete 2002). The sampling gear was a Tucker trawl net (1-m^2 mouth opening and 350-
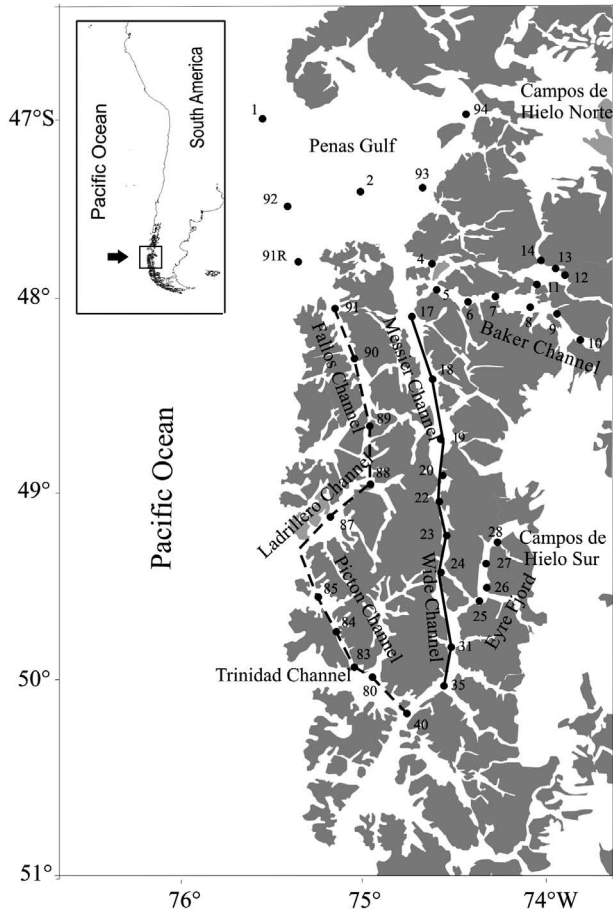
Fig. 1. – Geographic positions of sampling stations between Penas Gulf and Trinidad Channel (CIMAR 14 Fiordos cruise). Dashed line, oceanic transect (OT); solid line, estuarine transect (ET).

µm mesh aperture), which included a two-net system provided with a digital flowmeter in order to estimate the volume filtered by each net. Zooplankton samples were fixed immediately after collection and preserved in 5% formalin-seawater buffered with sodium borate.

A total of 108 vertically stratified samples were examined. The siphonophores were sorted from the original samples, and the nectophores (asexual polygastric stage) and eudoxids (sexual eudoxid stage) were identified and counted. The abundances of Calycophorae were estimated considering the highest number of anterior or posterior nectophores. *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). The taxonomic identification of siphonophore species followed the works of Totton (1965) and Pugh (1999). Polygastric and eudoxid stages for the whole column were converted for every stage to density (ind 1000 m^{-3}), using the volume of water filtered by the nets. Only the dominant species (>5% of the total of individuals) were considered when characterizing the horizontal and vertical distribution patterns. Vertical distributions, using the normalized data, were expressed according to the percentage of individuals in each stratum compared to the total number of individuals collected from the entire water column; and dif-

ferences in the vertical distributions in depth strata at sampling stations were tested by a Kruskal-Wallis test. The relationship between the distribution patterns of siphonophore abundances and oceanographic physical and chemical features over the sampling stations were explored using a canonical correspondence analysis (CCA; Ter Braak and Verdonschot 1995). The level of significance was set at p<0.05. Initial analysis included abundance data for 11 dominant faunal and 4 environmental variables (depth strata, temperature, salinity and dissolved oxygen). The Monte Carlo permutation test (with 999 unrestricted permutations) was used to determine the significance of fauna-environment relationships. The CCA analysis was performed using XLStat software (version 2011.4.04, Addinsoft).

RESULTS

Hydrographic characteristics

The surface temperatures in the Baker Fjord (not shown) were almost uniform from its mouth to its head (~9°C); in the Eyre Fjord (not shown), however, they decreased from its mouth (~8°C) to its head (~7°C). The water column was almost homothermal (~8°C) below 50 m in both fjords, while the whole water column was almost homothermal in the oceanic and longitudinal transects. Surface temperatures for the interior channels were around 8°C-9°C and around 9°C-10°C for the external channels (Fig. 2A and D). The highest surface temperature values were observed in the Gulf of Penas, at the northern extreme of both longitudinal transects. The lowest surface temperature values in the ET were observed near the middle of Angostura Inglesa and in the OT, at the southernmost end of the Concepción Channel. Below 200 m the temperature of the deep layer was almost homothermal in every single micro basin (~8°C).

The surface salinity in the Baker and Eyre Fjords decreased from their mouths to their heads (28 to 2 and 26 to 24, respectively). Both fjords had a highly stratified low salinity (20-33) surface layer (~50 m), giving rise to strong haloclines above 50 m (Fig. 2B and E). The water column below 50 m was almost homogeneous, with salinities around 33-34 in the Baker Fjord and 32-33 in the Eyre Fjord. In the ET transect, the lowest surface salinity values occurred near Angostura Inglesa (<24), Wide Channel (<20), in the OT transect and in the Fallos-Ladrillero channels (<26). A highly stratified low salinity (20-33) surface layer (~50 m) occurred in both transects, giving rise to strong haloclines. The depth of the bottom of the halocline generally coincided with the 32 salinity isopleth, which was at around 50 m depth. Below this highly stratified surface layer (i.e. >50 m), the water column was saltier (32-34) and almost homogeneous.

Dissolved oxygen concentration in the Baker and Eyre Fjords was almost homogeneous in the surface layer (~0-10 m) from mouth to head (~7 mL L^{-1}). Below this well-oxygenated surface layer, dissolved oxygen decreased to around 3 mL L^{-1} in the Baker Fjord and to around 4 mL L^{-1} in the Eyre Fjord. In both longitudinal
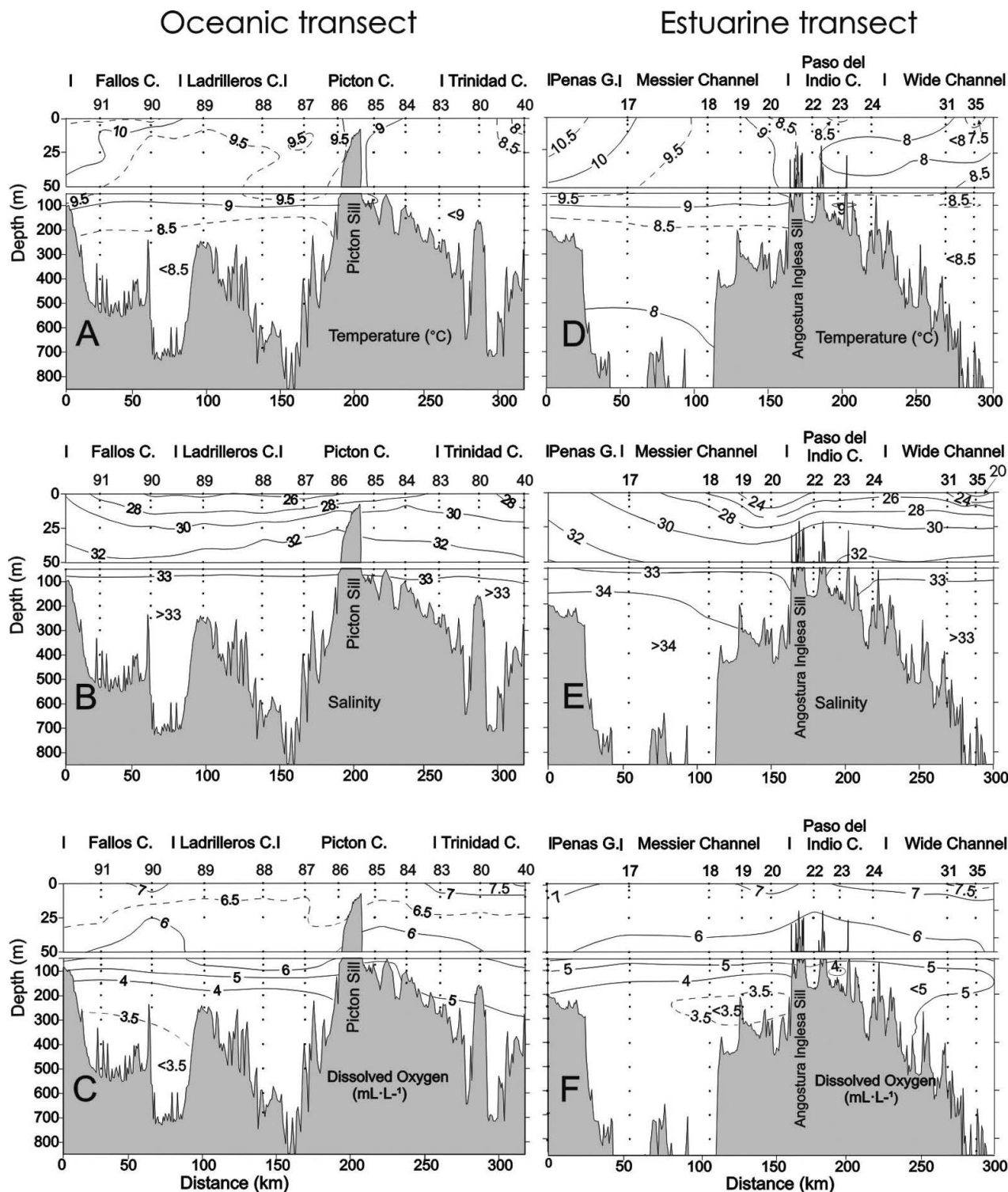
Oceanic transect

Estuarine transect

Fig. 2. – Vertical distribution of temperature (A), salinity (B) and dissolved oxygen (C) in the longitudinal oceanic transect (OT) and temperature (D), salinity (E) and dissolved oxygen (F) in the longitudinal estuarine transect (ET) between Penas Gulf and Trinidad Channel in spring 2008.

transects (Fig. 2C and F) the surface layer (~0-50 m) had a nearly homogeneous high dissolved oxygen content (>6 mL L^{-1}). Below this layer, the dissolved oxygen decreased rapidly to 4 mL L^{-1} at around 100 m. In the deep layer of both transects the dissolved oxygen concentrations decreased below 3.5 mL L^{-1} in the northern micro basin and below 5 mL L^{-1} in the southern micro basin.

Specific composition

A total of 12 species of siphonophores (polygastric and eudoxid stages), 11 calycophorans and one physonect were identified. The total number of collected organisms, abundance ranges, average abundance, dominance and occurrence data are shown in

Table 1. – Summary of basic statistics for polygastric (po) and eudoxid or sexual (eu) stages of siphonophores. Total number of individuals, range of abundances, average per station, dominance and occurrence. Abundances are expressed as ind 1000 m^{-3}. Ne, nectophores; Sg, stem group.

Species	Life stage	Total number	Range of non-zero abundances	Average abundance	Dominance (%)	Occurrence (%)
Muggiaea atlantica	Po	124752	14-38174	3118.8	78.62	100
	Eu	95078	10-50136	2376.9	63.44	88
Lensia conoidea	Po	13854	6-3500	346.3	8.73	88
	Eu	13631	4-3707	340.8	9.10	83
Dimophyes arctica	Po	13428	13-2685	335.7	8.46	90
	Eu	36685	18-6455	917.1	24.48	93
Pyrostephos vanhoeffeni	Ne	2882	1-427	72.0	1.82	70
Lensia meteori	Po	1535	3-419	38.4	0.97	58
Sphaeronectes koellikeri	Po	847	3-289	21.2	0.53	25
Sphaeronectes fragilis	Po	627	4-228	15.7	0.40	25
Lensia subtilis	Po	391	13-186	9.8	0.25	10
Eudoxoides spiralis	Po	320	6-107	8.0	0.20	20
	Eu	4466	10-2202	111.7	2.98	48
Muggiaea bargmannae	Po	21	1-21	0.5	0.01	3
Chelophyes appendiculata	Po	13	1-13	0.3	0.01	3
Praya dubia	Sg	2	1-1	0	0	5

Table 2. – Summary of basic statistics for polygastric stage abundances (ind 1000 m^{-3}) between the oceanic and estuarine transects. Range of non-zero abundances, average abundance per station, dominance and occurrence.

Species	Oceanic Transect				Estuarine Transect			
	Range of non-zero abundances	Average per station	Dominance (%)	Occurrence (%)	Range of non-zero abundances	Average per station	Dominance (%)	Occurrence (%)
Muggiaea atlantica	8-2132	992.0	47.0	100	436-38174	7567.4	90.7	100
Lensia conoidea	5-3499	685.4	32.5	100	17-995	402.0	4.8	100
Dimophyes arctica	53-1611	337.3	16.0	100	58-661	222.3	2.7	90
Pyrostephos vanhoeffeni	3-218	43.2	2.0	60	3-404	86.5	1.0	80
Sphaeronectes fragilis	8-227	37.1	1.8	30	3-162	19.8	0.2	30
Lensia meteori	8-38	11.6	0.5	60	6-75	17.6	0.2	50
Sphaeronectes koellikeri	5-8	2.0	0.1	30	16-241	28.6	0.3	30

Table 1. The calycophorans *Muggiaea bargmannae, Lensia subtilis, Praya dubia* and *Sphaeronectes fragilis* are recorded for the first time in this central Chilean Patagonian area (47-50°S). The presence of four nectophores of *M. bargmannae* in the Picton Channel (Sta. 88) represents the first record of this species in Chilean waters. *L. subtilis* and *S. fragilis* were collected from several stations; meanwhile, *P. dubia* was only represented by two stem groups collected in the Baker Fjord (stations 4 and 6). The dominant gelatinous species in terms of relative abundances were *Muggiaea atlantica* (78.6% of the total number of polygastric stages), *Lensia conoidea* (8.7%) and *Dimophyes arctica* (8.5%), while the remaining species were only found occasionally (Table 1). In decreasing order, the most commonly occurring species were *M. atlantica* (100% of stations), *D. arctica* (90% of stations) and *L. conoidea* (88% of stations).

Horizontal distribution

The abundances of siphonophores ranged between 35 and 39140 ind 1000 m^{-3} in the Picton and Messier channels (stations 87 and 22, respectively). *M. atlantica* occurred with a minimum abundance of 14 ind 1000 m^{-3} (station 14) in the Baker Channel, and a maximum of 38174 ind 1000 m^{-3} (station 22) in the Messier Channel (Fig. 3A). The highest densities were found in the Gulf of Penas (oceanic waters), the Messier Channel and the Eyre Fjord (interior waters). Intermediate densities were obtained

in the oceanic channels (Fallos, Ladrillero, Picton and Trinidad) and the lowest density was found in the Baker Channel, where the salinity fluctuated between 5 and 33 in the upper 100 m. *Lensia conoidea* and *Dimophyes arctica* showed a very similar spatial distribution, with maxima in the Eyre Fjord and at some stations in the Messier and Trinidad channels (Fig. 3B-C). The most significant difference between the two species was found in the Gulf of Penas, where *L. conoidea* was almost absent, and *D. arctica* was collected at most stations, being concentrated at the mouth of the gulf.

The eudoxids of *M. atlantica, L. conoidea* and *D. arctica* were always more numerous than the polygastric stages. These eudoxids followed the same patterns of geographic distribution as the polygastric stages. Eudoxids of *M. atlantica* also exhibited abundance maxima in the Gulf of Penas and Messier Channel (Fig. 3D). Maximum concentrations of the eudoxids of *L. conoidea* were found in the Trinidad Channel and of *D. arctica* in this same channel and in the Eyre Fjord (Fig. 3E-F). It is worth mentioning that in the Gulf of Penas, where highly saline waters (ASAA) predominated, only *M. atlantica* eudoxids were abundant, with both *L. conoidea* and *D. arctica* being extremely rare.

The abundance of polygastric stages of *M. atlantica* (Table 2) exhibited significant differences between the two transects (p<0.05), with a higher dominance in the ET (90.7%) than in the OT (47.0%). This difference in abundance was also observed for rarer species,
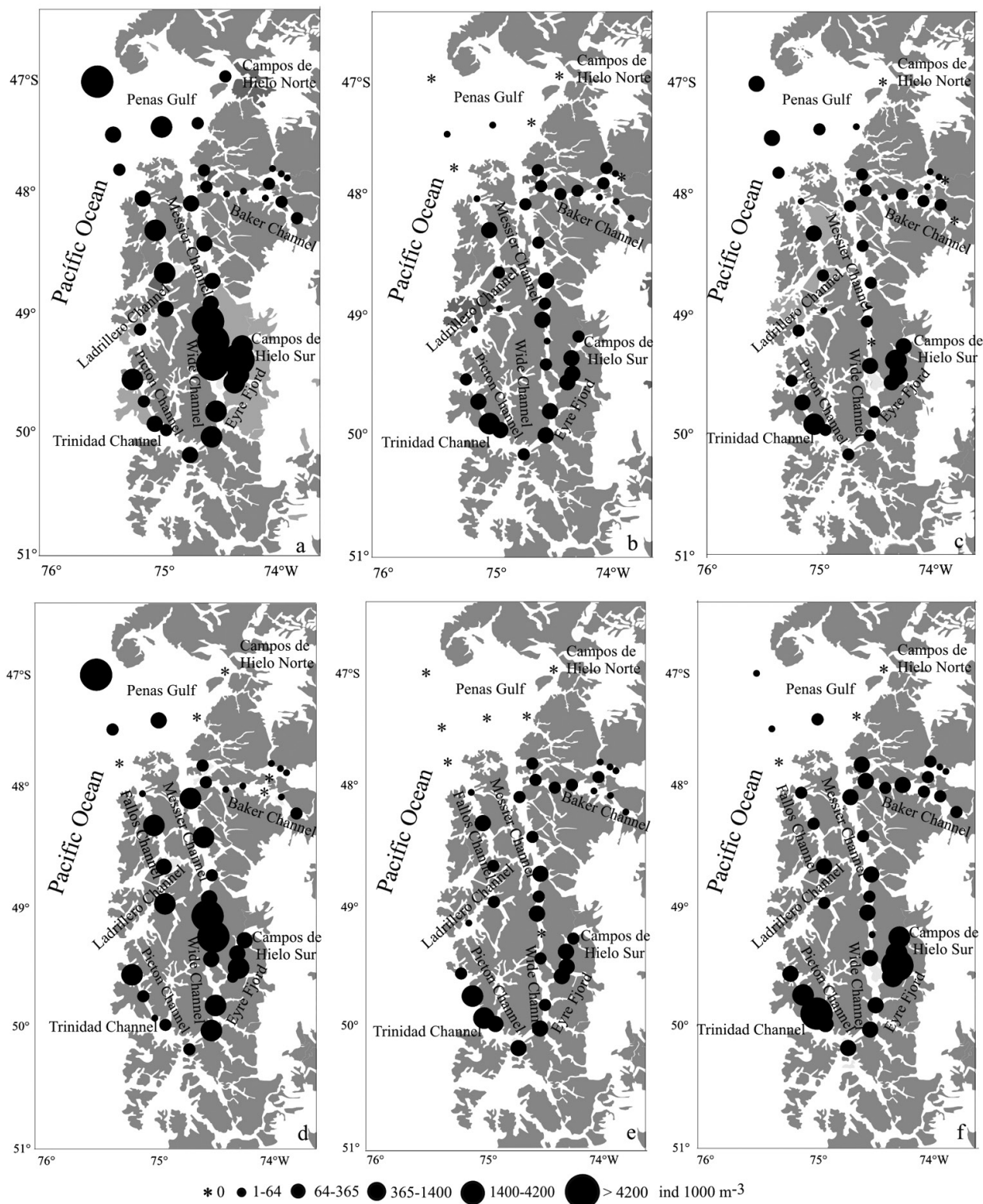
Fig. 3. – Spatial distribution in spring 2008 of polygastric stages of *Muggiaea atlantica* (A), *Lensia conoidea* (B), *Dimophyes arctica* (C), and eudoxids of *M. atlantica* (D), *L. conoidea* (E) and *D. arctica* (F).

such as *Pyrostephos vanhoeffeni, Lensia meteori* and *Sphaeronectes koellikeri* (Table 2). *Lensia conoidea* and *D. arctica* also showed significant differences in abundance between the two transects (p<0.05); however, their maxima occurred in the OT, with dominance values of 32.5% and 16%, respectively—a trend also apparent in *S. fragilis* (Table 2).

Vertical distribution in OTs and ETs

The dominant species showed two kinds of vertical distribution patterns. *Muggiaea atlantica* was found throughout the water column, the highest densities always being found in the upper 50 m, except at station 2 in the Gulf of Penas, where the greatest numbers were found be-
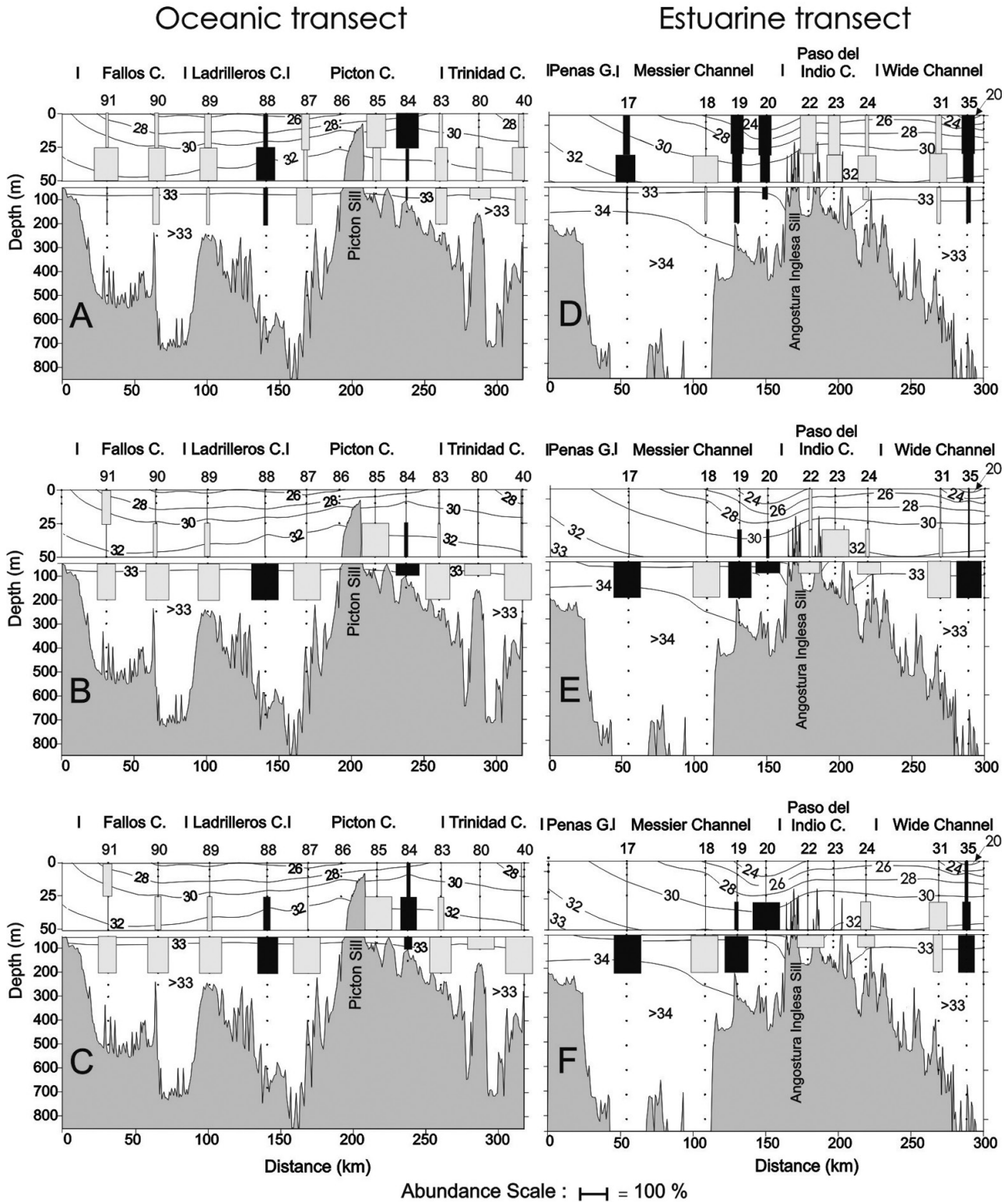
Fig. 4. – Vertical distribution in spring 2008, of polygastric stages in terms of relative abundances at each station (boxes) and salinity (isolines), in the longitudinal oceanic transect (OT) and estuarine transect (ET). A-B, *Muggiaea atlantica*; C-D, *Lensia conoidea*; E-F, *Dimophyes arctica*. Grey boxes, diurnal tows; black boxes, nocturnal tows.

low 50 m (Fig. 4A-B). On the other hand, *Lensia conoidea* and *Dimophyes arctica* were more abundant at greater depths, below 50 m at most stations (Fig. 4C and F). There were non-significant differences between the vertical distributions of polygastric and eudoxid stages of *M.*

atlantica between the two transects (Kruskal-Wallis test, $p > 0.05$, Table 3). In contrast, significant differences were obtained between the vertical distributions of polygastric and eudoxid stages for both *L. conoidea* and *D. arctica* in both transects (Kruskal-Wallis test, $p < 0.05$, Table 3).

Table 3. – Kruskal-Wallis test for differences in abundances of polygastric and eudoxid stages of the dominant species between the three depth strata in both the oceanic and estuarine transects. Significant values are indicated in bold (p<0.05).

| | Oceanic transect | | Estuarine transect | |
	Polygastric stage	Eudoxid stage	Polygastric stage	Eudoxid stage
Muggiaea atlantica	0.2653	0.8466	0.3845	0.2398
Lensia conoidea	**0.0089**	**0.0318**	**0.0021**	**0.0026**
Dimophyes arctica	**0.0002**	**0.0227**	**0.00007**	**0.00003**

Relationships between siphonophores and oceanographic conditions

The relationships between siphonophore abundances and oceanographic variables are presented in a CCA triplot (Fig. 5). The Monte Carlo permutation test indicated significance in the ordination diagram (F_{ratio}=2.83, p<0.001), in which the first two axes explained 98.9% of the total variance (83.8% in the first axis and 15.1% in the second axis). Axis one was positively correlated with depth strata and salinity, and negatively correlated with dissolved oxygen and temperature. This indicated an increase in salinity and depth strata from left to right in the diagram (Fig. 5), mainly evidenced at the deepest sampling stations (50-200 m). The species coupling with these environmental conditions in the deepest stratum were *Muggiaea bargmannae, Lensia conoidea, L. meteori, L. subtilis, Pyrostephos vanhoeffeni, Sphaeronectes koellikeri* and *Dimophyes arctica* (Fig. 5). On the other hand, the species associated with the shallower stratum, lower salin-

ity and higher oxygen were *Chelophyes appendiculata* and *Eudoxoides spiralis*. At the centre of the diagram, *Muggiaea atlantica* is located as a dominant species which is not associated with any particular depth stratum, because it was found throughout the water column. The second axis explained a lower fraction of the total variance and was mainly negatively correlated with temperature, indicating an increase in this environmental variable in the shallower strata.

DISCUSSION

Hydrographic characteristics

During the CIMAR 14 Fiordos cruise, the temperature was nearly homogeneous over the whole water column along both longitudinal transects, which was not the case for salinity, leading to a highly stratified water column (Fig. 2B and E). Therefore, the vertical density structure is governed by the salinity distribution. The vertical distribution of salinity was character-
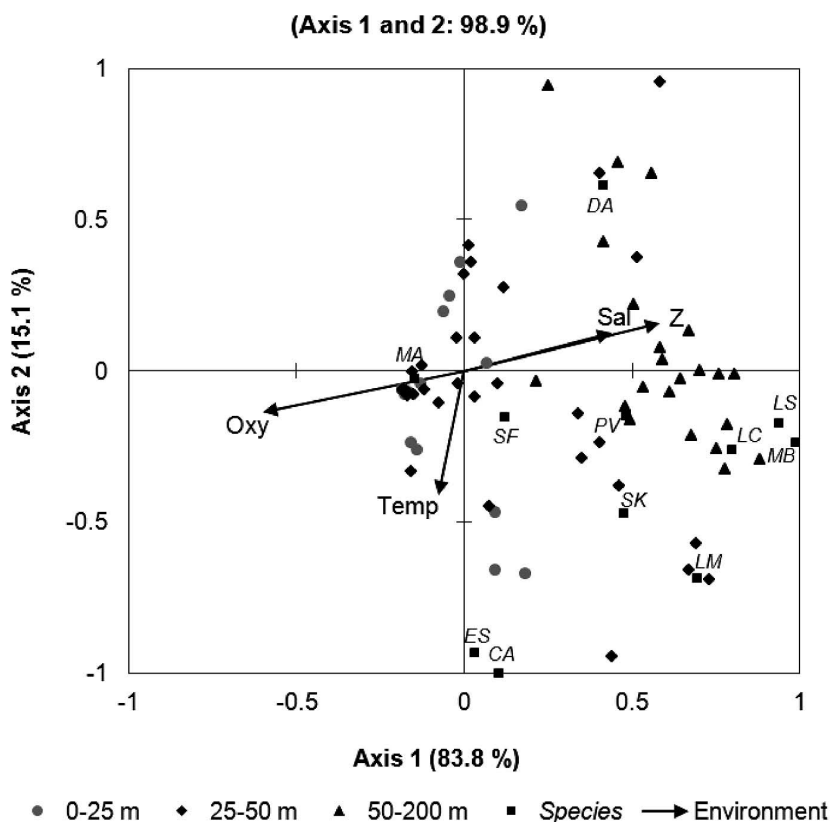

(Axis 1 and 2: 98.9 %)

Fig. 5. – Canonical correspondence analysis triplot based on data from spring 2008 showing scores of sampling sites by depth strata, the 11 most abundant siphonophore species and oceanographic variables. MA, *Muggiaea atlantica*; LC, *Lensia conoidea*; DA, *Dimophyes arctica*; PV, *Pyrostephos vanhoeffeni*; LM, *Lensia meteori*; SK, *Sphaeronectes koellikeri*; SF, *Sphaeronectes fragilis*; LS, *Lensia subtilis*; ES, *Eudoxoides spiralis*; MB, *Muggiaea bargmannae*; CA, *Chelophyes appendiculata*; Z, depth strata; Temp, temperature; Sal, salinity; Oxy, dissolved oxygen.

ized by two layers: a surface layer (0 to ~30-50 m), and a deeper layer (30-50 m to the bottom) including a strong vertical salinity gradient and therefore a pycnocline. The vertical stratification was less intense at both the northern and southern oceanic ends and more intense at the centre of the transects (Fig. 2B and E), where the freshwater input from continental rivers and glacial melting is greater (Silva and Calvete 2002, Sievers et al. 2002). The freshwater input in the ET and at the heads of Baker and Eyre fjords is greater, due to the input from continental rivers, rain and melting water. This explains the lower salinities (20-32) in the surface layer of the ET, compared with the low salinities (26-32) along the OT, which receives mainly rainwater input. Below the highly stratified surface layer, a marine, saltier (33-34) deep layer is present (~50 m to the bottom), and is less variable and almost homohaline (Fig. 2B and E).

The surface layers (0-50 m) of the Baker and Eyre Fjords and along both longitudinal transects were well oxygenated, generally above 6 mL L^{-1} (>90% saturation; Fig. 2C and F), due to photosynthetic processes (Aracena et al. 2011) and ocean-atmosphere oxygen exchange. Beneath the highly oxygenated surface layer, dissolved oxygen concentrations dropped below 4 mL L^{-1} (<50% saturation), presumably due to consumption caused by the degradation of autochthonous and allochthonous particulate organic matter coming from the surface layer and river discharge (Silva 2008). Similar low dissolved oxygen concentrations (3-4 mL L^{-1}) have been recorded previously in the area (Silva and Calvete 2002).

Subantarctic Water (SAAW) from the adjacent Pacific Ocean penetrates into the region through the Gulf of Penas and Trinidad Strait, giving the marine characteristics to the deeper layers. As the SAAW spreads into the channels and fjords, it mixes with freshwater (FW) in different proportions (Sievers and Silva 2008). The water formed of salinities between 31 and 33 is known as Modified Subantarctic Water (MSAAW) or if fresher (2-31) it is known as Estuarine Water (EW). The EW remains in the surface layer and the MSAAW fills the subsurface and deeper layers of the interior fjords.

Siphonophore community composition and horizontal distribution

Results from spring 2008 were similar to those of spring 1996 (Palma et al. 1999), with 8 out of the 12 presently identified species overlapping (Table 4). The nine rare species that were recorded, representing 4.2% of the total number of siphonophores caught, were collected in estuarine interior waters and included some species found widely in oceanic waters, such as *Eudoxoides spiralis, Chelophyes appendiculata, Lensia subtilis* and *Praya dubia* (Totton 1965, Pugh 1999). However, it is supposed that the extreme oceanographic characteristics of these interior waters would be detrimental for the maintenance of reproducing populations. In general, all the identified species were epipelagic species, including some species abundant in Antarctic waters, such as *Dimophyes arctica, Muggiaea bargmannae* and *Pyrostephos vanhoeffeni* (Pagès et al. 1994, Pugh et al. 1997), and some species from warm and temperate oceanic waters (the remaining species), which may enter through the Gulf of Penas and the Ladrillero and Trinidad Channels. Their shallow sills (Ladrillero and Trinidad ~50 m, and Penas ~150 m) would prevent the entrance of mesopelagic species into interior waters.

M. bargmannae is a bipolar species mainly collected in boreal waters (Totton 1965, Pugh 1999). This finding represents the first record for Chilean waters, thus increasing the biodiversity of siphonophores known from the southeastern Pacific. The number of siphonophore species reported in the southern fjords ecosystem has therefore increased from the 14 previously recorded species (Palma and Silva 2004, Palma et al. 2007a, 2011, Villenas et al. 2009) to 17 species. However, the southern Chilean Patagonian fjords exhibit a lower diversity of siphonophores than the Humboldt Current System, where 54 species have been recorded (Palma 1977, 1994, Palma and Rosales 1995, Pagès et al. 2001, Palma and Apablaza 2004, Apablaza and Palma 2006, Pavez et al. 2010), and than the global ocean, where almost 190 species have been recorded (Pugh 1999, Boltovskoy et al. 2005). In any event, the

Table 4. – Summary of basic statistics for polygastric stages of siphonophores between the springs of 1996 (CIMAR 2 Fiordos cruise) and 2008 (CIMAR 14 Fiordos cruise). Total number of individuals, range of abundances, average abundance per station, standard deviation (SD), dominance (D) and occurrence (O). Abundances are expressed as number of individuals per 1000 m^{-3}. Ne, nectophores.

Species	Spring 1996						Spring 2008					
	Total	Range of non-zero abundances	Average per station	SD	D (%)	O (%)	Total	Range of non-zero abundances	Average per station	SD	D (%)	O (%)
Muggiaea atlantica	11476	3-3613	337.5	706.4	67.51	88.2	120761	14-38174	3551.8	7599.6	79.82	100.0
Lensia conoidea	5104	4-1547	150.1	301.6	30.02	79.4	12813	6-3500	376.8	627.7	8.47	88.2
Dimophyes arctica	168	3-47	4.9	8.9	0.99	44.1	11675	13-2685	343.4	551.7	7.72	88,2
Pyrostephos vanhoeffeni (ne)	3	1-1	0.1	0.0	0.02	8.8	2459	1-427	72.3	115.0	1.63	73.5
Lensia meteori	166	3-57	4.9	13.5	0.98	23.5	1486	4-419	43.7	95.6	0.98	58.8
Sphaeronectes koellikeri	47	6-25	1.4	4.6	0.28	11.8	786	5-289	23.1	68.8	0.52	23.5
Eudoxoides spiralis	29	8-21	0.9	3.8	0.17	5.9	267	9-107	7.8	21.8	0.18	17.6
Chelophyes appendiculata	6	1-6	0.2	1.0	0.04	2.9	13	2-13	0.4	2.3	0.01	2.9
Abylopsis tetragona	18	1-3	0.5	1.1	0.11	17.7	0	0	0	0	0	0
Sphaeronectes fragilis	0	0	0	0	0	0	627	4-228	18.5	50.6	0.41	29.4
Lensia subtilis	0	0	0	0	0	0	391	13-186	11.5	41.3	0.26	11.7
Muggiaea bargmannae	0	0	0	0	0	0	21	2-21	0.6	3.6	0.01	2.9
Praya dubia	0	0	0	0	0	0	9	1-1	0,3	1.2	0.01	5.9
Total	170175						151288					

low diversity detected in Chilean fjords and channels has also been reported for Norwegian fjords (Båmstedt 1988, Hosia and Båmstedt 2007).

The high abundance of *Muggiaea atlantica* was particularly noteworthy. It is a eurythermic and euryhaline species, widely distributed in both the adjacent oceanic SAAW and the interior MSAAW and EW throughout the study area. Both polygastric and eudoxid stages abundances were highest in the ET, particularly in the Wide Channel and Eyre Fjord (Table 2). We hypothesize that the high tolerance of *M. atlantica* to the temperature and salinity gradients favours its reproductive success in interior waters, where it is the dominant siphonophore species in the fjords of southern Chile (Pagès and Orejas 1999, Palma et al. 1999, 2007a, 2011, Palma and Aravena 2001, Villenas et al. 2009). *M. atlantica* is common in neritic zones and represents the predominant siphonophore along the coast of Chile, where it forms dense coastal aggregations in spring and summer (Palma 1977, 1994, Palma and Rosales 1995, Ulloa et al. 2000, Palma and Apablaza 2004, Apablaza and Palma 2006). *M. atlantica* occurs widely in coastal and shelf waters from warm and temperate regions in the Pacific, Atlantic and Indian Oceans, and the Mediterranean Sea (Alvariño 1971). It is also very frequent in areas of high productivity such as upwelling ecosystems like the Benguela Current (Pagès and Gili 1992) and the Humboldt Current (Palma and Rosales 1995, Palma and Silva 2004, Pavez et al. 2010).

Lensia conoidea and *Dimophyes arctica* occurred at much lower densities than *M. atlantica*, and their highest densities were found in the OT (Table 2), where SAAW waters were dominant. Only some polygastric stages of *L. conoidea* were collected in the Gulf of Penas and eudoxids were not found there at all (Fig. 3E). On the other hand, a larger abundance of the polygastric stages of *D. arctica* occurred, although eudoxids were extremely scarce. The spatial distribution of eudoxids for both species was shifted towards MSAAW and EW with lower temperatures (<6°C) and salinities (<30) (Silva and Calvete 2002), a situation even clearer in the Eyre Fjord, where the highest densities of eudoxids were found (Fig. 3F).

L. conoidea is common and abundant in the great oceans, particularly in the California and Benguela currents, and in the Mediterranean Sea (Alvariño 1971), spanning a broad depth distribution from the surface down to the bathypelagic zone (Pagès and Gili 1992). *D. arctica* is a cosmopolitan species with a bipolar distribution, inhabiting the great oceans as well as the Antarctic, Arctic, and Mediterranean Sea (Alvariño 1971). 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 (Pagès and Gili 1992).

It is interesting to note that the dominant siphonophores (*M. atlantica, Lensia conoidea* and *Dimophyes arctica*) found in these Patagonian fjords have also been found in fjords in the northern hemisphere, such as the Norwegian fjords Fanasfjord, Korsfjord and Hardangerfjord (Bakke and Sands 1977; Pagès et al. 1996). Though *M. atlantica* has been found sporadically, it appeared in large numbers during the warmer than average year of 2002 in Fanafjord (Fossa et al. 2003), which had received high salinity waters from the Atlantic Ocean (Hosia and Bamsted 2007, 2008). In the Korsfjord Fjord, an abundance of polygastric stages of both *Lensia conoidea* and *Dimophyes arctica* has been found throughout the year, with the maximum abundance being reached in spring (late May to early June) (Hosia and Bamsted 2008).

Vertical distribution

The presence of a strong pycnocline at around 50 m depth, separating the EW from the MSAAW, had an important effect on the vertical distribution of *M. atlantica*, concentrating the polygastric and eudoxid populations in the upper 50 m, where the more stable, oxygenated, low-salinity layer of the water column occurred (Fig. 4A-B). *L. conoidea* and *D. arctica*, on the other hand, for which the polygastric and eudoxid populations also coexisted, were distributed in deeper waters (below 50 m) where quasi-homogeneous conditions for temperature, salinity and dissolved oxygen occurred (Fig. 4C and F). The results of a Kruskal-Wallis test indicated that these species had a significantly different depth distribution, being deeper (>50 m) in both OTs and ETs (p<0.05; Table 3). The difference in the use of the water column suggests that *M. atlantica* has different ecological requirements to *L. conoidea* and *D. arctica.* The diel vertical distribution of this species could not be studied, because day and nighttime samplings were never performed at the same stations.

The vertical distribution pattern of some dominant siphonophore species (*Lensia conoidea, Dimophyes arctica* and *Pyrostephos vanhoeffeni*) was such that their presence and higher abundances were associated with the deeper (50-200 m) stratum: CCA plots showed a clear separation between the shallower (0-25 m and 25-50 m) and deeper strata. The CCA indicated that a relatively large proportion of among-site variances in the abundance of these three species among the sampling stations were positively correlated with depth strata and salinity, and negatively with dissolved oxygen and temperature. This is an expected association, because as depth increases so does the salinity, and the temperature and dissolved oxygen concentration decrease (Fig. 2). The oceanographic conditions in the deeper stratum where three species were most abundant are characteristic of the MSAAW water masses. The CCA also demonstrated that *M. atlantica*, the most dominant species, was mainly associated with high dissolved oxygen and low salinity in surface layers. However, the low correlation also indicates that *M. atlantica* can be distributed throughout the water column (Palma et al. 2011). The canonical analysis also indicated that *L. subtilis* and *M. bargmannae* abundances were correlated with the deeper stratum with high salinity and low dissolved oxygen concentrations. *E. spiralis* and *C. appendiculata* were found in shallow and warm waters, probably associated with the influence of oceanic waters. Rare species such as *L. meteori* and *S. koellikeri* were

correlated with the deeper stratum with higher salinity and temperatures.

Comparison between the results obtained in spring 1996 and 2008

Species richness in spring 1996 was 75% of that found in spring 2008 (see Palma et al. 1999), with *Muggiaea bargmannae, Lensia subtilis, Praya dubia* and *Sphaeronectes fragilis* being found for the first time in this area (9 and 12 species in 1996 and 2008, respectively). The average abundance per station for siphonophores was almost one order of magnitude higher in 2008 (Table 4). This trend was observed for most species, except for *L. conoidea*, whose average abundance per station was only 2-3 times higher in 2008. The most significant increases were observed in *M. atlantica* and *D. arctica* (Table 4). Moreover, *D. arctica*, which was a very rare species comprising less than 1% of the total number of siphonophores in spring 1996, comprised 7.7% of the total number of siphonophores in spring 2008, with a wide geographic distribution of both polygastric and eudoxid stages in the same area (Fig. 3C-F).

The results obtained in the spring of 1996 indicated that the community of siphonophores was mainly dominated by *M. atlantica* (67.51%) and *L. conoidea* (30.02%), while *D. arctica* (0.99%) was almost absent. However, in spring 2008, a high dominance of *M. atlantica* (80.37%) compared with *L. conoidea* (8.53%) and *D. arctica* (7.77%) was evident (Table 4). The large increase in the relative abundance of *M. atlantica* observed in different areas of the southern Chilean fjords ecosystem (Palma et al. 2007a, 2011, Villenas et al. 2009) confirms its high adaptability to areas of low water temperature and salinity, where the highest densities of its eudoxid phase were concentrated (Fig. 3D). In fact, in spring 1996 the highest densities were found in ocean channels (OT, Fallos and Ladrillero Channels), while in spring 2008 a peak of abundance was found in EWs with lower temperature and salinity (ET, Messier Channel and Eyre Fjord). This species has become the dominant species in the Chilean fjords ecosystem, where it has achieved considerable reproductive success.

This increase in abundance cannot be explained on the basis of inter-annual differences in the abiotic variables analysed, as temperature, salinity and dissolved oxygen concentration values recorded in spring 2008 were similar to those recorded in spring 1996 by Silva and Calvete (2002). The increase may be the result of the different sampling gear used. In November 1996, integrated oblique tows (0-200 m) were carried out using bongo nets (0.28-m^2 mouth opening and 350-μm mesh size),while in November 2008 the oblique tows were performed at three depth levels (0-200 m) using Tucker trawl nets with a much larger mouth opening (1 m^2, 350-μm mesh size). The capture results were standardised according to the volumes filtered by each net (ind 1000 m^{-3}) but, according to Pepin and Shears (1997), the large sample volume of the Tucker trawl relative to the bongo nets can result in significantly

higher estimates of species diversity for fish eggs and larvae but not for crustaceans or medusae. Therefore, the differences may actually be due to a higher abundance of gelatinous organisms in interior waters, especially for *M. atlantica*, a situation also observed in other areas of the interior water region in southern Chile (Palma et al. 2007a, 2011, Villenas et al. 2009).

FINAL REMARKS

A total of 12 species were recorded, of which *Muggiaea bargmannae, Lensia subtilis, Praya dubia* and *Sphaeronectes fragilis* were identified for the first time in the central Patagonian fjords. *M. bargmannae* represents a new record for the southeastern Pacific. The most common and abundant species in Chilean Central Patagonian fjords were *Muggiaea atlantica* (78.6% of total), *Lensia conoidea* (8.7%) and *Dimophyes arctica* (8.5%). *M. atlantica,* the dominant species, was present at high relative abundances in EW (ET, 90.7%), while *L. conoidea* and *D. arctica* were principally collected in oceanic waters (OT, 32.5% and 16.0%, respectively) (Table 2). The eudoxids of these species followed the same horizontal distribution patterns as their polygastric stages. These distributions allowed us to hypothesize that salinity and dissolved oxygen vertical gradients play an important role in determining the depth distribution patterns of some of the siphonophore species. This is in agreement with results reported for many species of gelatinous zooplankton from the northern hemisphere, which are distributed in different water column strata of varying thickness, also reflecting the physical/chemical structure of the water column (i.e. Graham et al. 2001, Raskoff et al. 2005).

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