Research Article

Seasonal and vertical distribution of medusae in Aysén region, southern Chile

Viviana Bravo[1,2], Sergio Palma[1] & Nelson Silva[1]
[1]Escuela de Ciencias del Mar, Pontificia Universidad Católica de Valparaíso
P.O. Box 1020, Valparaíso, Chile
[2]Departamento de Oceanografía, Universidad de Concepción
P.O. Box 160-C, Concepción, Chile

ABSTRACT. Medusae collected in winter and spring 2007 were analyzed in a longitudinal transect made between the Boca de Guafo and Elefantes Fjord, southern Chile. A total of 30 species were identified, Hydromedusae (29) and Scyphozoa (1), where *Bougainvillia macloviana, Hybocodon chilensis, Hydractinia tenuis, Laodicea pulcra, L. undulada, Modeeria rotunda* and *Chrysaora plocamia* represent new records for the area. A significant increase in the jellyfish abundance was higher in spring than in winter (fourteen times higher), with 68% of common species in both seasons. The specific diversity was slightly higher in winter (3.4 bits) than spring (3.2 bits), the species richness instead was higher in spring than in winter, with a mean of 5 and 12 species, respectively. The vertical distribution showed the presence of surface (*H. borealis*), deep (*A. apicata, C. peregrina* and *R. velatum*) and wide bathymetric distribution (*B. muscoides* and *B. muscus*) species. Results from the area were compared with previous results (2002-2003) thus proving that most species identified are common in southern Chilean fjords and channels.

Keywords: Cnidaria, hydromedusae, scyphozoa, seasonal distribution, vertical distribution, southern Chile.

Distribución estacional y vertical de medusas en la región de Aysén, sur de Chile

RESUMEN. Se analizaron las medusas colectadas en invierno y primavera de 2007, en una transecta longitudinal efectuada entre la boca del Guafo y fiordo Elefantes, sur de Chile. Se identificó un total de 30 especies, Hydromedusae (29) y Scyphozoa (1), de las cuales *Bougainvillia macloviana, Hybocodon chilensis, Hydractinia tenuis, Laodicea pulcra, L. undulada, Modeeria rotunda* y *Chrysaora plocamia* constituyen nuevos registros para esta área. Se determinó un fuerte incremento en la abundancia de medusas en primavera respecto a invierno y (14 veces mayor), con un 68% de especies comunes en ambas estaciones. La diversidad específica fue levemente mayor en invierno (3.4 bits) que primavera (3.2 bits), en cambio la riqueza de especies fue mayor en primavera que en invierno, con una media de 5 y 12 especies, respectivamente. La distribución vertical mostró en ambas estaciones la presencia de especies superficiales (*H. borealis*), profundas (*A. apicata, C. peregrina* y *R. velatum*) y de amplia distribución batimétrica (*B. muscoides* y *B. muscus*). Los resultados obtenidos en esta área se compararon con resultados obtenidos anteriormente (años 2002 y 2003) y se confirmó que la mayoría de las especies identificadas son comunes en fiordos y canales australes de Chile.

Palabras clave: Cnidaria, hidromedusas, escifozoos, distribución estacional, distribución vertical, sur de Chile.

Corresponding author: Sergio Palma (spalma@ucv.cl)

INTRODUCTION

An increasing concern on the explosive proliferation of gelatinous organisms in diverse marine areas has been observed during the last years, given their significant role in the organization of the coastal ecosystems and impact on human activities (Mills, 2001; Brodeur *et al*., 2002). Jellyfish are among the most conspicuous gelatinous organisms, which are very primitive though highly diverse planktonic group. Some groups, as Lepto- and Anthomedusae have metagenic life cycles with benthic stages, alternating sexual and asexual reproductive processes that may lead to seasonally jellyfish blooms in coastal waters (Palma & Rosales, 1995; Palma & Apablaza, 2006; Purcell *et al*., 2007). Such blooms are mainly promoted by temperature and food availability fluctuations, factors that play a predominant role in the

composition and abundance of zooplankton in the oceans (Parsons & Lalli, 2002; Kehayias, 2004). These blooms may cause a seasonal dominance of the zooplanktonic biomass by the gelatinous organisms in a given geographical area (Mianzán & Guerrero, 2000; Genzano et al., 2008; Miglietta et al., 2008).

Medusae are important planktonic predators that fed on copepods, invertebrate larvae, and fish larvae (Purcell, 1985, 1997). Due to their predatory nature, food competition, parasite transmission, distribution and seasonal abundance, jellyfishes may have economic implications, as they may compete for food with commercial fish and/or cause negative impacts on fish farming activities.

Economic activities have been developed in inner waters of southern Chile since mid 80s, which are associated to tourism, maritime transport and aquaculture. The latter has particularly shown a significant growth in the regions of Chiloé (41º31'-43º39'S) and Aysén (43º39'-46º29'S), due to the intensive cage culture of salmon species, which have occasionally been affected by mortalities involving jellyfish proliferations, as observed between February-June 2002 (S. Palma, unpublished).

The phylum Cnidaria has been widely studied in the Chiloé region (Galea, 2007; Galea et al., 2007; Palma et al., 2007a, 2007b, 2011; Villenas et al., 2009a), which is characterized by high biological production reflected on high values of chlorophyll-a (González et al., 2011) and zooplanktonic biomass, mainly supported by copepods, euphausiids and carnivorous jellyfish (Palma & Silva, 2004). In this area, strong seasonal fluctuations have been established in jellyfish abundance in winter and spring, observing 33 species with a summer dominance of *Amphogona apicata, Bougainvillia muscoides, Clytia simplex, Cunina peregrina, Hydractinia tenuis, Obelia* spp. and *Solmundella bitentaculata* (Villenas et al., 2009a; Palma et al., 2011). In Aysén region, the available data exclusively involve spring and indicate the presence of 31 species, with a dominance of *Amphogona apicata, Clytia simplex, Lizzia blondina* (= *Hydractinia minuta*), *Proboscidactyla ornata* and *Solmundella bitentaculata* (Palma et al., 2007a, 2007b). These regions are separated by the Boca de Guafo (43º39'S), which corresponds to the main water exchange route between the Pacific Ocean and the inner water ecosystem.

Aysén shows peculiar oceanographic charac-teristics influenced by the Meninea constriction-sill which, due to its shallow depth (50-60 m), gives origin to the formation of two microbasins with different oceanographic characteristics. On one hand, the northern microbasin is about 250 m deep, and

communicates with the adjacent Pacific through the Boca de Guafo, where more saline waters penetrate and mix with less saline waters coming from precipitations, rivers, and glacial contributions (Palma & Silva, 2004; Palma et al., 2007a, 2007b; Silva & Palma, 2008). This constant exchange has allowed the entry of oceanic planktonic species that have successfully colonized the inner waters (Palma, 2008). On the other hand, the southern microbasin appears more shallow, with a mean depth of 150 m, and is semi-isolated from the oceanic influence as a result of the "dam" effect exerted by the Meninea constriction-sill that plays a fundamental role over circulation, residence period and physical and chemical characteristics of both microbasins (Silva et al., 1997, 1998).

Considering the relevance attained by cnidarians in the marine ecosystems and their seasonal abundance fluctuations associated to environmental factors, this study aims to analyse (i) the spatial and temporal variability of jellyfish in winter and spring 2007 in order to establish the spatial/temporal variability of such organisms and (ii) the comparison of the results obtained for spring 2007 with 2002-2003 springs in the same area.

MATERIALS AND METHODS

The CIMAR 13 Fiordos cruise was carried out between the Boca de Guafo (43º46´S) and Elefantes Fjord (46º29´S) (Fig. 1), where two oceanographic campaigns were undertaken, one in winter (July 23-August 7, 2007) and the other in spring (October 29-November 14, 2007). During each campaign, a northern-southern longitudinal transect was assessed, allocating 23 oceanographic stations. However, due to meteorological problems during the winter campaign, only 19 stations were sampled.

A CTDO Sea-Bird model SBE 25 was used at each station to record the oceanographic variables (temperature, salinity and dissolved oxygen content) in the water column, which were used to develop vertical profiles for the oceanographic characterization of the studied area. Salinity and dissolved oxygen records were corrected using the results from the chemical analysis of discrete samples collected in the water column during the CTDO casting.

Zooplankton samples were obtained through oblique tows at three different depth strata: superficial (0-25 m), medium (25-50 m) and deep (50 to a maximum of 200 m, depending on the bottom depth), using a 350 μm mesh sieve Tucker trawl net, provided with flowmeters to estimate the filtered water
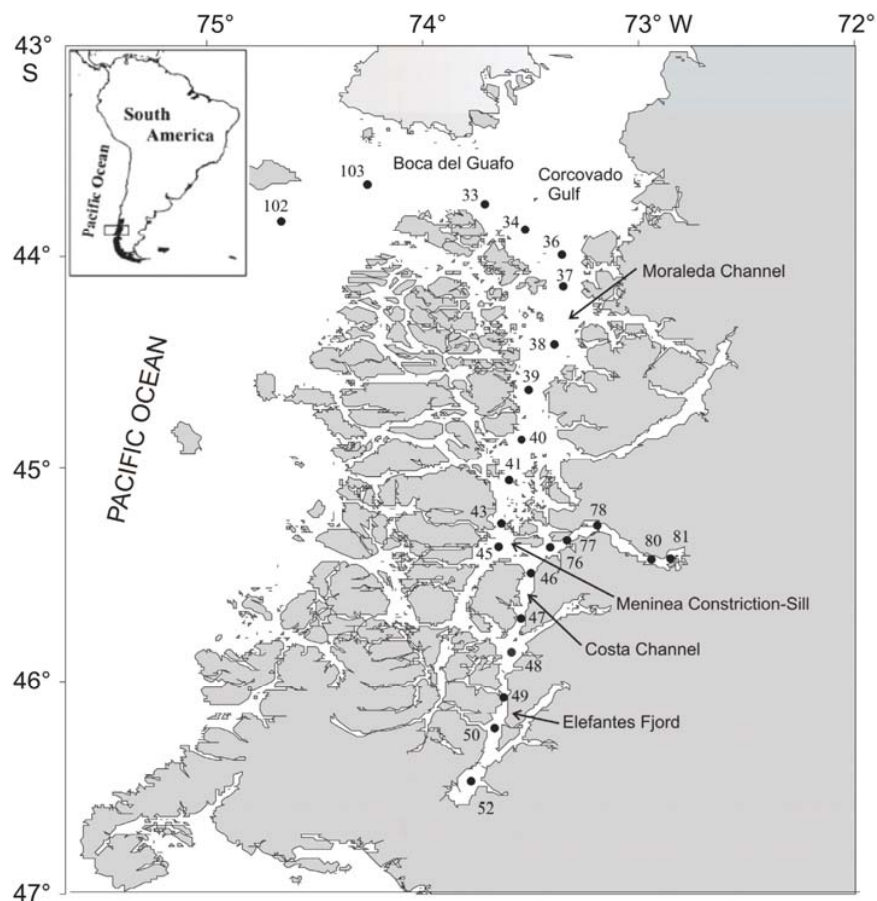
Figure 1. Location of the oceanographic stations during the Cruise CIMAR 13 Fiordos.
Figura 1. Localización de las estaciones oceanográficas durante el Crucero CIMAR 13 Fiordos.

volume. These strata were chosen considering the oceanographic features of two layers characterizing the inner region of fjords and channels (Silva *et al*., 1997, 1998). The zooplankton samples were fixed immediately after collection and preserved in 5% neutral formaldehyde in seawater buffered with borax.

Jellyfishes were sorted, identified and counted from a total of 53 zooplankton samples collected in winter and 64 samples collected in spring. Taxonomic identifications were done using specialised bibliographies (mainly Kramp, 1959, 1968; Bouillon, 1999). The specific abundance was expressed in individuals per 1000 m^3 (ind 1000 m^{-3}), based on the water volume filtered through the net. Seasonal and vertical patterns were determined considering only the dominant species (> 5% of the specimen total) in winter and spring. The vertical distribution was expressed according to the specimen percentage collected per stratum with respect to the total of specimens in the water column and its graphical representation was associated to the salinity values,

which is the parameter with higher vertical variability in inner waters (Palma *et al*., 2007). The specific richness index, which is the number of species in a community and the Shannon-Wiever diversity index, was used for the community analysis (Pielou, 1977). The establishment of areas with higher fauna affinity was done through the Bray-Curtis similarity analysis (Bloom, 1981), standardizing the relative abundance data by the expression log (x+1). Finally, the relationship between the dominant species abundance and the oceanographic parameters was analyzed using the Pearson correlation analysis.

RESULTS

Environmental conditions
Winter cruise

The Moraleda Channel and Boca del Guafo water columns (Fig. 2a) were almost homothermal, with temperatures around 9°C. Salinity showed a highly

stratified low saline (29-33 psu) surface layer (0-25 m), but with a nearly homogeneous high oxygen content (> 6 mL L^{-1}), whereas the deep layer (25 m to bottom) was less stratified than the surface one, being more saline (32-34 psu) and less oxygenated (3-5 mL L^{-1}).

At the Costa Channel (Fig. 2a), a vertical stratification was present, with a surface layer with low temperature (> 9.5°C) and salinity (25-29 psu), thus giving rise to a strong halocline. The deep layer was comparatively slightly warmer (> 9.5ºC) and more saline (29-32 psu). The oxygen content in the whole water column was nearly homogeneous (≈ 6 mL L^{-1}). At the Elefantes Fjord (Fig. 2a), the water column was almost vertically mixed, with low temperatures (≈ 8 °C) and salinities (22-28 psu, depending on the station location) and high dissolved oxygen content (≈ 6 mL L^{-1}). Aysén Fjord surface layer was highly stratified, with a shallow inverted thermocline and a normal halocline, both stronger at its head (Fig. 2a). In this fjord, the surface layer was cool (7-9°C) and less saline (10-29 psu), but with a high dissolved oxygen content (6-9 mL L^{-1}). The deep layer was comparatively warmer (9-11ºC), more saline (29-31 psu), and less oxygenated (2-5 mL L^{-1}).

Spring cruise

The water columns of both Moraleda Channel and Boca del Guafo (Fig. 2b) were slightly homothermal, with temperatures around 9-10°C. The salinity, showed a highly stratified low saline (28-32 psu) surface layer, but with a nearly homogenoeus high oxygen content (> 6 mL L^{-1}), whereas the deep layer, was less stratified than the surface one, being more saline (29-34 psu) and less oxygenated (4-6 mL L^{-1}).

At the Costa Channel (Fig. 2b), a vertical stratification occurred, with a surface layer with low temperatures (> 9.5 °C), salinities (27-31 psu), and high dissolved oxygen (> 6 mL L^{-1}). The deep layer was comparatively cooler (< 9.5 ºC) and more saline (29-31 psu). The oxygen content in the whole water column was nearly homogeneous (≈ 6 mL L^{-1}). At the Elefantes Fjord (Fig. 2b), the water column was almost vertically homogeneous, with low temperatures (≈ 9°C) and salinities (22-28 psu, depending on the station location), and high dissolved oxygen (≈ 6 mL L^{-1}). Aysén Fjord surface layer was highly stratified (Fig. 2b), with a strong shallow halocline (10-29 psu). In this fjord, the surface layer was also almost homothermal (≈ 9°C), with high dissolved oxygen (6-7 mL L^{-1}). The deep layer was comparatively warmer (9-10ºC), more saline (29-31 psu), and less oxygenated (2-5 mL L^{-1}).

Seasonal faunistic composition and distribution patterns

In all, thirty medusa species (21 in winter and 30 in spring) were identified in the studied area (Table 1). Sixty seven percent of the species were collected during both periods, with a larger richness of species in spring. Jellyfish abundance significantly varied between winter and spring, being higher on the latter season. The hydromedusae *Bougainvillia macloviana, Hybocodon chilensis, Hydractinia tenuis, Laodicea pulcra, L. undulata, Modeeria rotunda* and the scyphomedusa *Chrysaora plocamia* were recorded for the first time for this geographical area. During spring, ephirae probably of *C. plocamia*, were collected at 26% on the analyzed oceanographic stations.

Winter cruise

The jellyfish number during winter ranged between 17 and 1630 ind 1000 m^{-3}, with an average of 442 ind 1000 m^{-3}. The highest densities were recorded in the central area of the Moraleda Channel and Aysén Fjord. Dominant species were *Bougainvillia muscus* (29.7%), *B. muscoides* (28.8%), *Cunina peregrina* (7.5%), *Amphogona apicata* (6.8%), *Hydractinia borealis* (6.1%) and *Rhopalonema velatum* (5.4%). The highest occurrence of frequency percentages (> 70%) included *B. muscoides* (84%), *B. muscus* (74%) and *C. peregrina* (74%) (Table 1).

Bougainvillia muscus (= *B. pyramidata*) was the most abundant and more frequent species (an average of 138 ind 1000 m^{-3}) although it was not observed in both transect ends (Fig. 3a). The highest densities were recorded in the central area of the Moraleda Channel and close to the Aysén Fjord, reaching a maximum at station 45 (464 ind 1000 m^{-3}). The other species belonging to the same genus, *B. muscoides*, showed a mean of 134 ind 1000 m^{-3} and was the most common species during winter. The higher densities were obtained in the same areas as for *B. muscus*, with a maximum of 605 ind 1000 m^{-3} close to the head of Aysén Fjord (Fig. 3b). Among the remaining species, *C. peregrina* was the only species found at both ends of the transect; additionally, *A. apicata, H. borealis* and *R. velatum* showed a more reduced geographical distribution and none was collected at the Elefantes Fjord, especially *A. apicata*, whose populations were mainly concentrated at the Aysén Fjord, an area where all species showed the highest densities (Figs. 3c-3f).

Spring cruise

Abundance in spring ranged between 68 and 35,616 ind 1000 m^{-3} at stations 49 and 80, respectively, with an average of 3,667 ind 1000 m^{-3}. The highest densities were recorded in the north of Moraleda
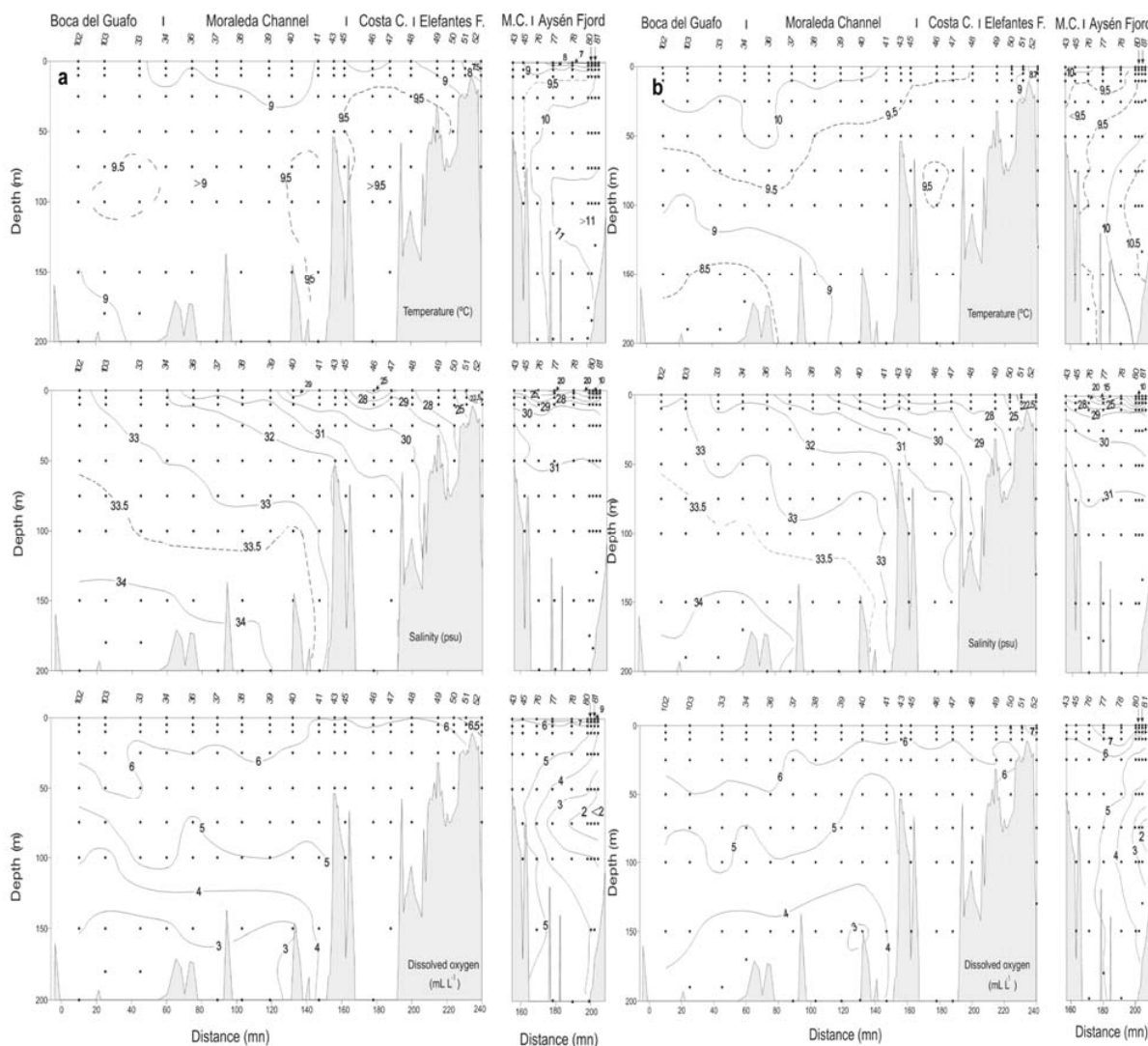
Figure 2. Vertical distribution of temperature, salinity and dissolved oxygen between Boca del Guafo to Elefantes Fjord. a) Winter 2007, b) Spring 2007.

Figura 2. Distribución vertical de temperatura, salinidad y oxígeno disuelto entre Boca del Guafo y fiordo Elefantes. a) invierno 2007, b) primavera 2007.

Channel, at Aysén Fjord and the head of the Elefantes Fjord. The dominant species were *B. muscoides* (34.1%), *Proboscidactyla ornata* (17.5%), *Clytia simplex* (10.8%), *A. apicata* (7.2%) and *P. stellata* (7.2%). Except for *A. apicata* (39%), which was not collected at the stations located at the Boca de Guafo and Moraleda Channel, all the remaining species showed high occurrence frequency percentages: *P. ornata* (100%), *C. simplex* (100%), *P. stellata* (100%) and *B. muscoides* (96%) (Table 1).

B. muscoides was the only dominant species during both seasons, being extremely abundant in spring, reaching a mean of 1,602 ind 1000 m^{-3} and a

maximum of 24,365 ind 1000 m^{-3} (Stat. 80) near the head of the Aysén Fjord (Fig. 4a).

Proboscidactyla ornata showed a high frequency and abundance, with a mean of 974.6 ind 1000 m^{-3} and maximums close to the head of both Aysén and Elefantes fjords (Fig. 4b). *Clytia simplex* presented a wide geographical distribution, with mean densities of 601.0 ind 1000 m^{-3} and two nuclei of high concentration at the Corcovado Gulf and Elefantes Fjord (Fig. 4c). *Amphogona apicata,* with a mean density of 401.8 ind 1000 m^{-3}, was found with low frequency and abundance at all oceanographic stations, except close to the head of Aysén Fjord,

Table 1. Total abundance, mean abundance, percentage of abundance and frequency of occurrence of species collected between the Boca del Guafo and Elefantes Fjord. The asterisk (*) indicates the first records for this area.

Tabla 1. Abundancia total, abundancia promedio, porcentaje de abundancia y frecuencia de ocurrencia de las especies colectadas entre la Boca del Guafo y fiordo Elefantes. El asterisco (*) indica las especies registradas por primera vez en esta área.

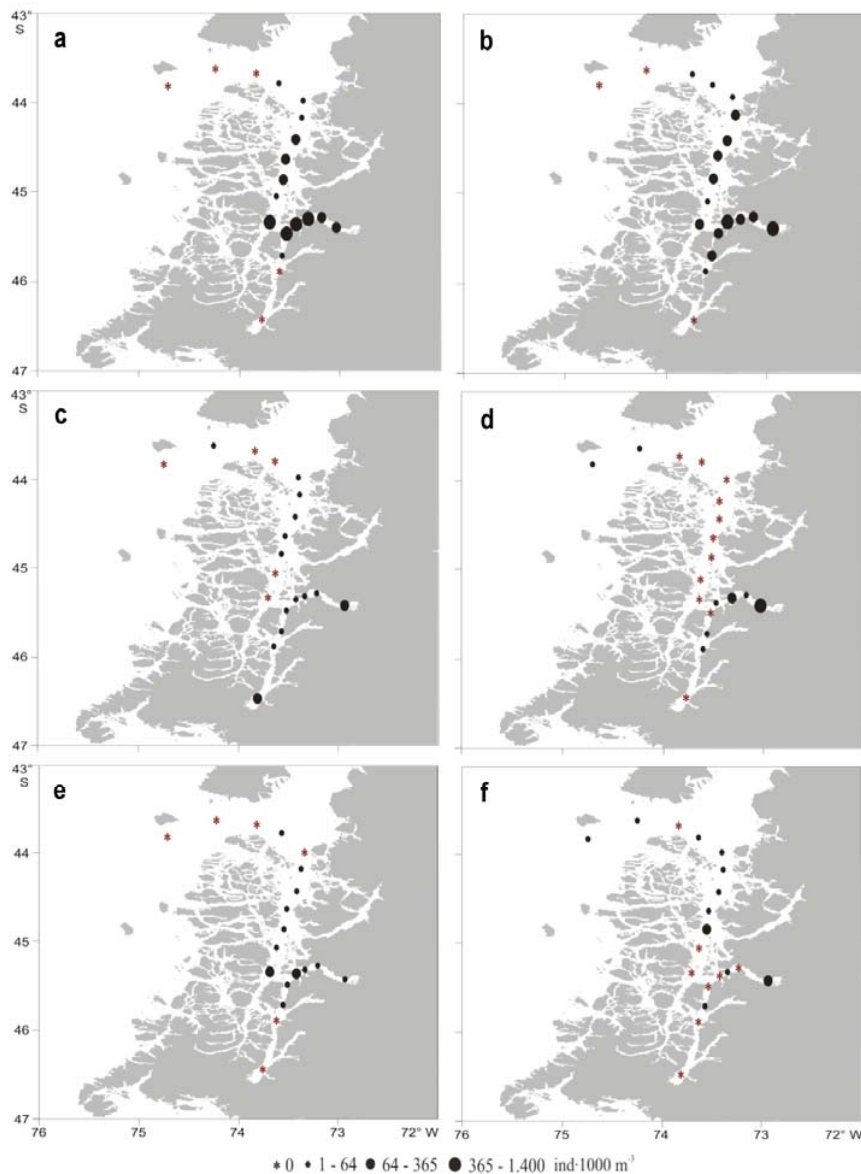| Species	Winter				Spring			
	Total abundance (ind 1000 m⁻³)	Mean abundance (ind 1000 m⁻³)	Percentage (%)	Frequency (%)	Total abundance (ind 1000 m⁻³)	Mean abundance (ind 1000 m⁻³)	Percentage (%)	Frequency (%)
Hydromedusae								
Amphinema rugosum	-	-	-	-	221	9.6	0.2	35
Amphogona apicata	602	31.7	6.8	42	9242	401.8	7.2	39
Bougainvillia macloviana*	-	-	-	-	170	7.4	0.1	17
Bougainvillia muscoides	2551	134.3	28.8	84	43752	1902.3	34.1	96
Bougainvillia muscus	2628	138.3	29.7	74	4893	212.7	3.8	65
Bougainvillia sp.	193	10.1	2.2	53	1792	78.0	1.3	26
Clytia simplex	68	3.6	0.8	32	13824	601.0	10.8	100
Coryne eximia	207	10.9	2.3	58	1235	55.6	1.0	65
Cunina peregrina	661	34.8	7.5	74	2658	115.6	2.1	30
Ectopleura dumortieri	-	-	-	-	739	32.1	0.6	52
Euphysa aurata	121	6.4	1.4	37	671	29.2	0.5	39
Gossea brachymera	-	-	-	-	10	0.4	0.0	4
Halopsis ocellata	-	-	-	-	715	31.1	0.6	26
Heterotiara sp.	12	0.6	0.1	11	566	24.6	0.4	4
Hybocodon chilensis*	53	2.8	0.6	32	577	25.1	0.4	52
Hydractinia borealis	539	28.4	6.1	68	4755	206.7	3.7	100
Hydractinia tenuis*	198	10.4	2.2	47	1663	72.3	1.3	78
Laodicea pulcra*	-	-	-	-	22	0.9	0.0	13
Laodicea undulada*	-	-	-	-	153	6.6	0.1	17
Leuckartiaria octona	127	6.7	1.4	58	1750	76.1	1.4	78
Modeeria rotunda*	-	-	-	-	848	36.8	0.7	61
Obelia spp.	-	-	-	-	953	41.5	0.7	61
Proboscidactyla ornata	91	4.8	1.0	42	22415	974.6	17.5	100
Proboscidactyla stellata	17	0.9	0.2	16	9217	400.8	7.2	100
Rophalonema velatum	475	25.0	5.4	58	192	8.3	0.2	26
Sarsia coccometra	4	0.2	0.1	5	569	24.7	0.4	65
Solmundella bitentaculata	278	14.6	3.1	32	1536	66.8	1.2	30
Total	8652				125604			
Scyphomedusae								
Chrysaora plocamia*	-	-	-	-	758	32.9	0.6	52
Ephyrae	21	1.1	0.2	16	185	8.0	0.1	26

Figure 3. Winter distribution of dominant species. a) *Bougainvillia muscus*, b) *B. muscoides*, c) *Cunina peregrina*, d) *Amphogona apicata*, e) *Hydractinia borealis*, f) *Rhopalonema velatum*.

Figura 3. Distribución invernal de las especies dominantes. a) *Bougainvillia muscus,* b) *B. muscoides,* c) *Cunina peregrina,* d) *Amphogona apicata,* e) *Hydractinia borealis,* f) *Rhopalonema velatum.*

where the highest concentrations were recorded (Fig. 4d). Finally, *P. stellata* showed a high occurrence frequency, with mean densities slightly inferior to *A. apicata* (400.8 ind 1000 m^{-3}), with maximums near the heads of Aysén Fjord and Elefantes Fjord (Fig. 4e).

Similarity analysis

Based on the Bray-Curtis similarity analysis, two groups of stations were distinguished in winter (Fig. 5a): a) the group A, involving most of the stations located at the Corcovado Gulf, Moraleda channels and Aysén Fjord, which are characterised by high densities of *B. muscus* and *B. muscoides,* and high frequencies of *A. apicata, H. borealis* and *R. velatum*; and b) the group B, formed exclusively by the stations located at the Costa Channel and Elefantes Fjord, which were characterised by the presence of *C. peregrina* and the absence of many species that were only distributed until the Maninea Constriction-sill.
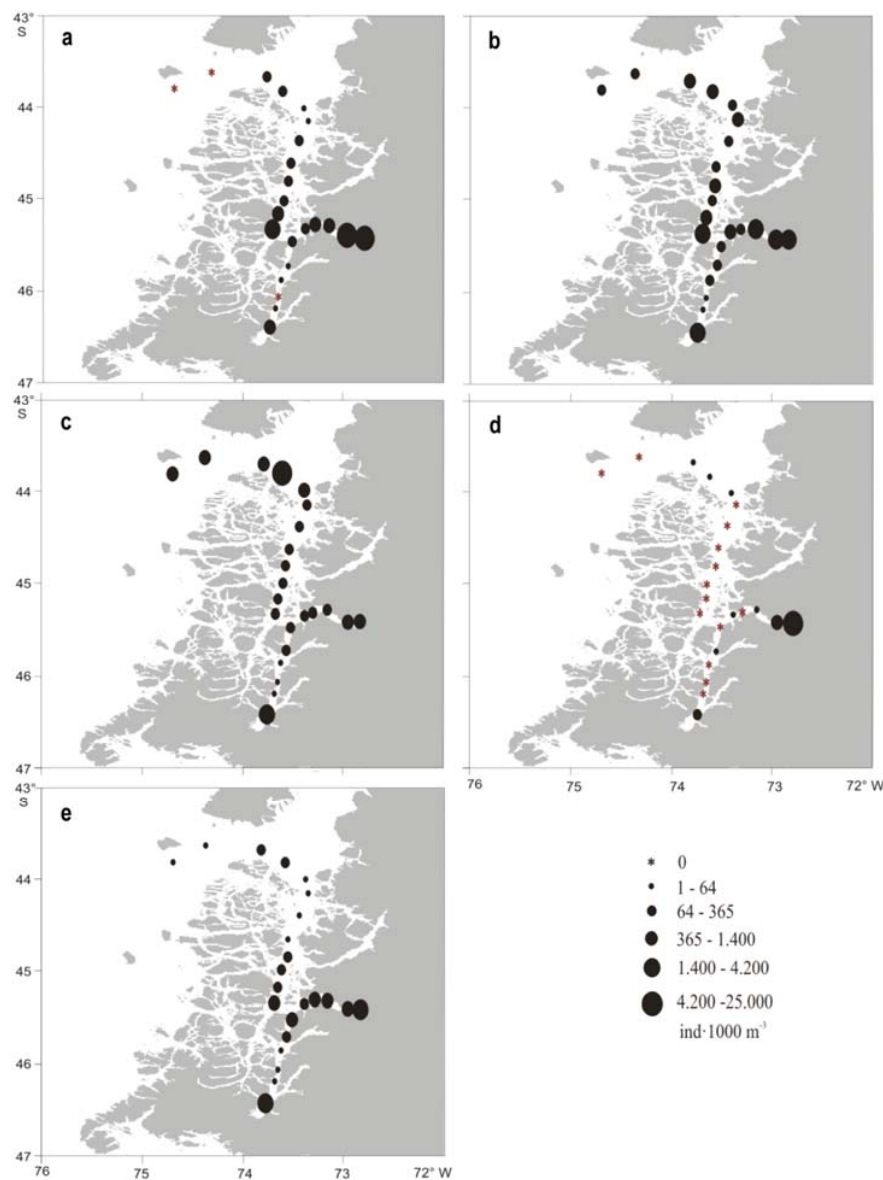
Figure 4. Spring distribution of dominant species. a) *Bougainvillia muscoides*, b) *Proboscidactyla ornata*, c) *Clytia simplex,* d) *Amphogona apicata,* e) *P. stellata.*

Figura 4. Distribución primaveral de las especies dominantes. a) *Bougainvillia muscoides*, b) *Proboscidactyla ornata*, c) *Clytia simplex,* d) *Amphogona apicata,* e) *P. stellata.*

Like for the winter, during the spring, two groups of stations were also distinguished (Fig. 5b): a) the group A, formed by most stations located at the Corcovado Gulf, Moraleda Channel and Aysén Fjord, where high densities of all dominant species were established (*A. apicata, B. muscoides, C. simplex*, *P. ornata, P. stellata*); and b) the group B, comprising the stations located at the Elefantes Fjord, where minimums of abundance for all dominant species were recorded.

Species richness and diversity

The species richness in winter ranged between 1 and 7 species per station, with an average of 5 species. The highest values were recorded at the Moraleda Channel and Aysén Fjord, while the lowest occurred at the Boca de Guafo, Costa Channel and Elefantes Fjord (Fig. 6a). Conversely, spring showed a higher species richness, ranging from 5 to 17 species per station, with an average of 12. The highest values were recorded at
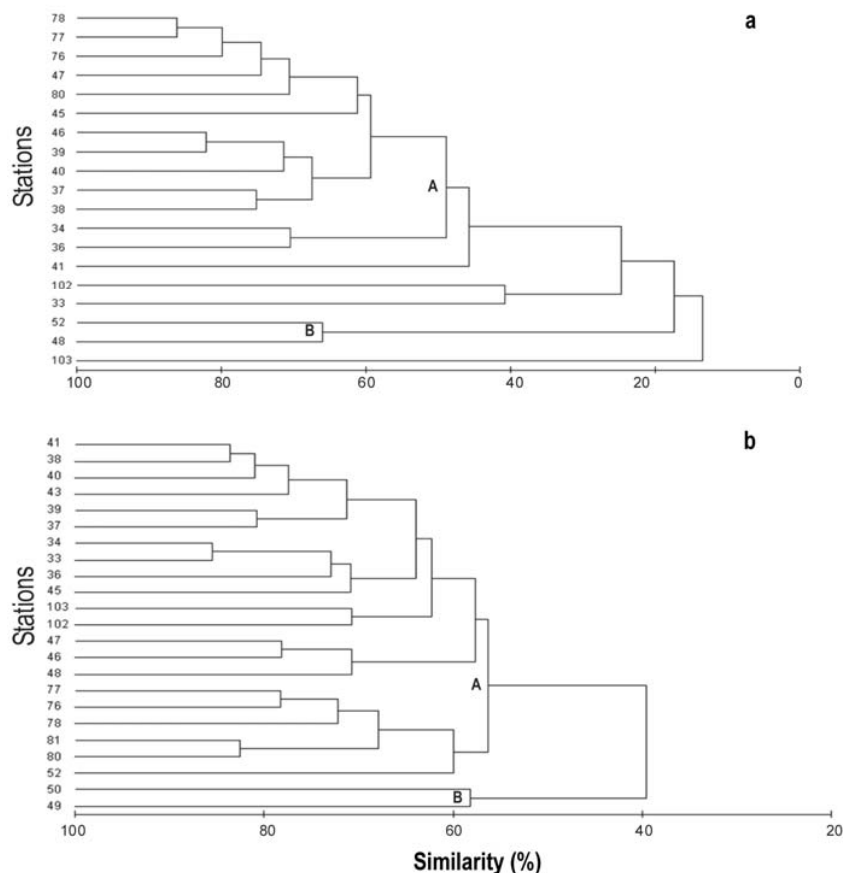
Figure 5. Similarity dendrograms based on Bray-Curtis Index between the sampling stations. a) Winter, b) Spring.

Figura 5. Dendrogramas de similitud basados en el índice de similitud de Bray-Curtis entre las estaciones analizadas. a) invierno, b) primavera.

the Corcovado Gulf, southern area of the Moraleda Channel, Aysén and Elefantes fjords.

The Shannon-Weaver specific diversity rate showed the values ranged between 0.2 and 3.4 bits during winter, with maximums at the Corcovado Gulf and Moraleda Channel (Fig. 6b). In spring, however, these values ranged between 0.9 and 3.2 bits, with a main maximum at the Boca de Guafo, followed by high values at the Costa Channel and Elefantes Fjord.

Correlation coefficient

The results of the Pearson correlation index ($P < 0.05$) showed that the abundance of *A. apicata, B. muscoides, C. peregrina* and *R. velatum* was positively correlated with temperature. The abundance of *A. apicata, C. peregrina* and *R. velatum* was, however, negatively correlated with the concentration of the disolved oxygen (Table 2). During summer, the Pearson index ($P < 0.05$) showed, in general, a limited correlation between species and oceanographic

parameters. Only the abundance of *P. ornata* was observed to show a negative correlation with the temperature, and the abundance of *A. apicata* showed a negative correlation with the dissolved oxygen (Table 2).

Vertical distribution

Winter Cruise

In general, the vertical distribution showed that the dominant species were mainly distributed under 25 m deep during the winter (Fig. 7). The most superficial species was *H. borealis*, which was generally found in the first 50 m, with a higher abundance at the 25-50 m stratum. *C. peregrina, A. apicata,* and *R. velatum* were collected at greater depth, with abundance maximums at the 50-100 m stratum. Meanwhile, the species of the genus *Bougainvillia, B. muscus* and *B. muscoides* showed a wider vertical distribution between the surface and 100 m of depth, with the highest specimen percentage above 25 m.
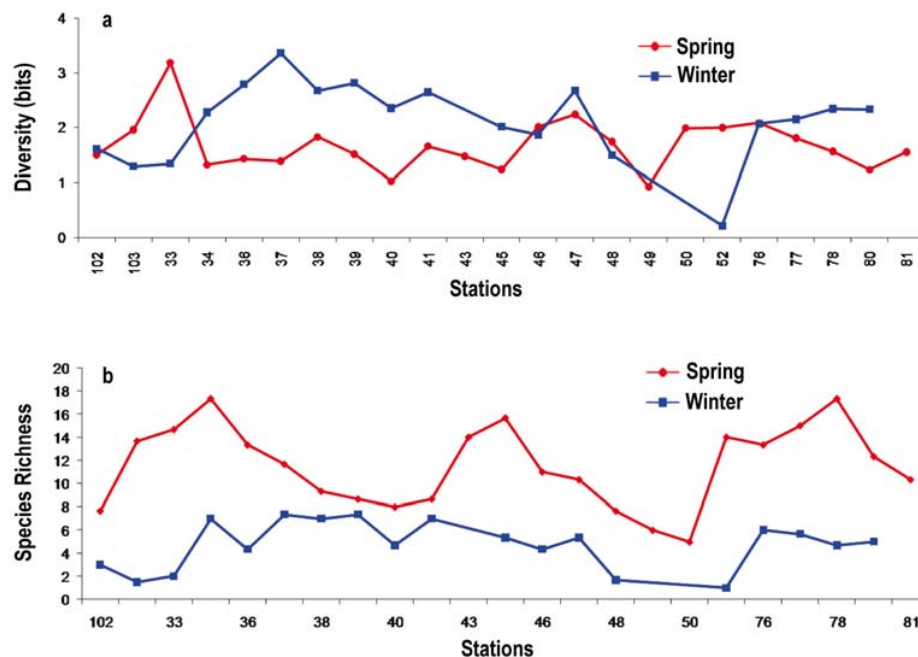
Figure 6. a) Species diversity, b) richness species during the CIMAR 13 Fjords Cruise.

Figura 6. a) Diversidad específica, b) riqueza de especies durante el Crucero CIMAR 13 Fiordos.

Table 2. Pearson correlation values between the abundance of dominant species and the oceanographic variables in winter cruise. Significant values are indicated in bold ($P < 0.05$).

Tabla 2. Valores correlación de Pearson entre la abundancia de las especies dominantes y las variables oceanográficas en el crucero de invierno. Los valores significativos se indican en negrita ($P < 0,05$).

	Temperature	Salinity	D. oxygen	*A. apicata*	*B. muscoides*	*B. muscus*	*C. peregrina*	*H. borealis*	*R. velatum*
Temperature	1.00								
Salinity	0.33	1.00							
Oxygen	**-0.91**	-0.20	1.00						
A. apicata	**0.56**	0.02	**-0.67**	1.00					
B. muscoides	0.29	-0.21	-0.28	0.23	1.00				
B. muscus	0.16	-0.20	-0.09	-0.09	**0.62**	1.00			
C. peregrina	0.28	-0.24	-0.46	**0.82**	0.12	-0.16	1.00		
H. borealis	0.16	-0.18	-0.15	-0.03	**0.68**	**0.73**	-0.12	1.00	
R. velatum	0.27	0.22	-0.37	**0.60**	0.17	-0.07	**0.56**	-0.19	1.00

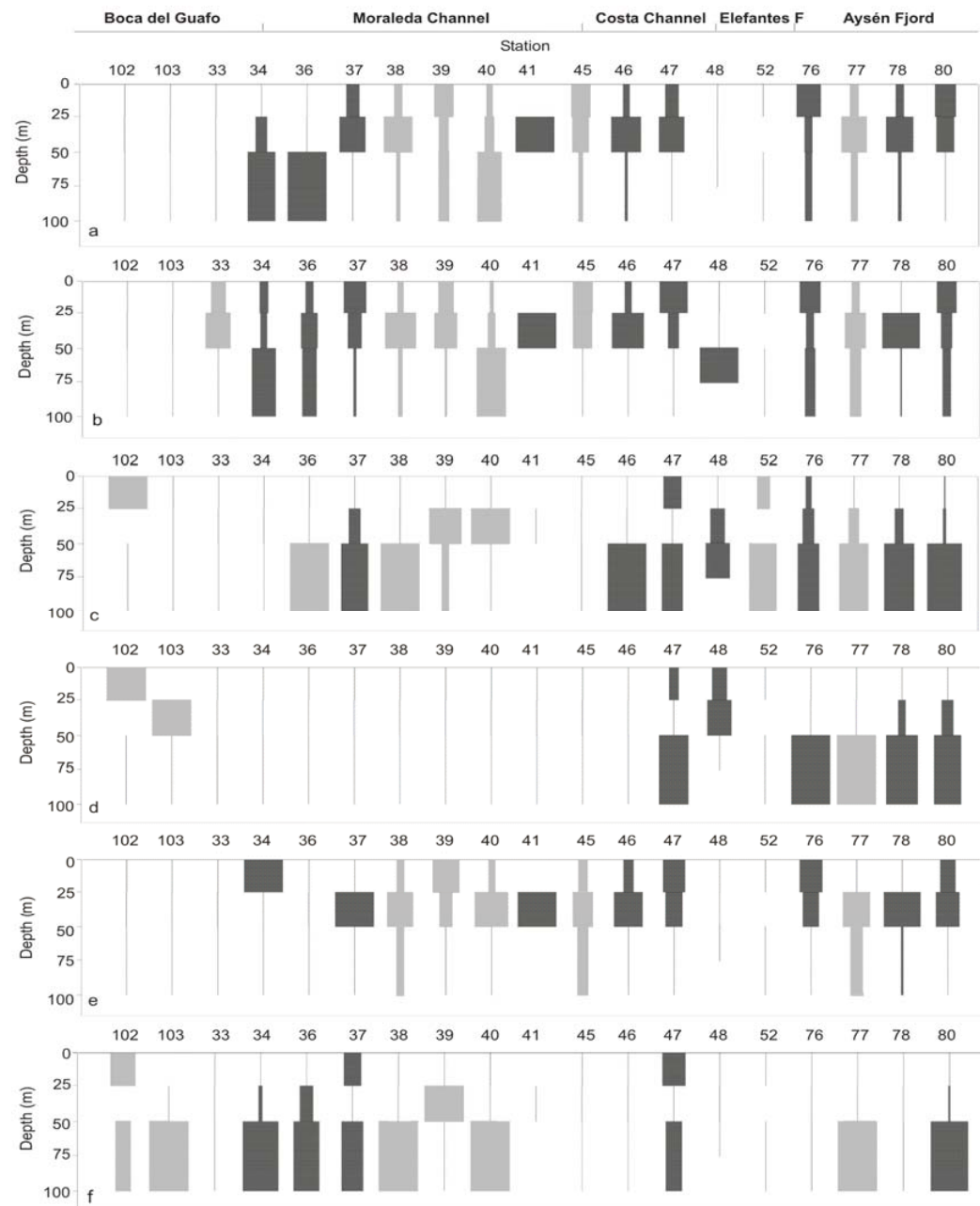|	Temperature	Salinity	D. oxygen
A. apicata	0.01	0.44	0.99
B. muscoides	0.02	0.94	0.98
B. muscus	0.13	0.93	0.75
C. peregrina	0.02	0.95	0.99
H. borealis	0.14	0.9	0.85
R. velatum	0.03	0.94	0.9

Figure 7. Vertical distribution of dominant species in winter. a) *Bougainvillia muscus*, b) *B. muscoides*, c) *Cunina peregrina*, d) *Amphogona apicata,* e) *Hydractinia borealis*, f) *Rhopalonema velatum.* Grey columns: diurnal tows, black colums: nocturnal tows.

Figura 7. Distribución vertical de las especies dominantes en invierno. a) *Bougainvillia muscus*, b) *B. muscoides*, c) *Cunina peregrina*, d) *Amphogona apicata,* e) *Hydractinia borealis*, f) *Rhopalonema velatum.* Columnas en gris: muestreos diurnos, columnas en negro: muestreos nocturnos.

Spring Cruise

Only *Amphogona apicata* was collected under 50 m, both in spring and winter (Fig. 8), while the other dominant species (*B. muscoides, Clytia simplex, P. or-* *nata* and *P. stellata*) showed a wide bathymetric distribution (0-100 m). In the latter group, only *C. simplex* showed a continuous distribution in the water column (0-100 m) in the longitudinal transect. Addi-
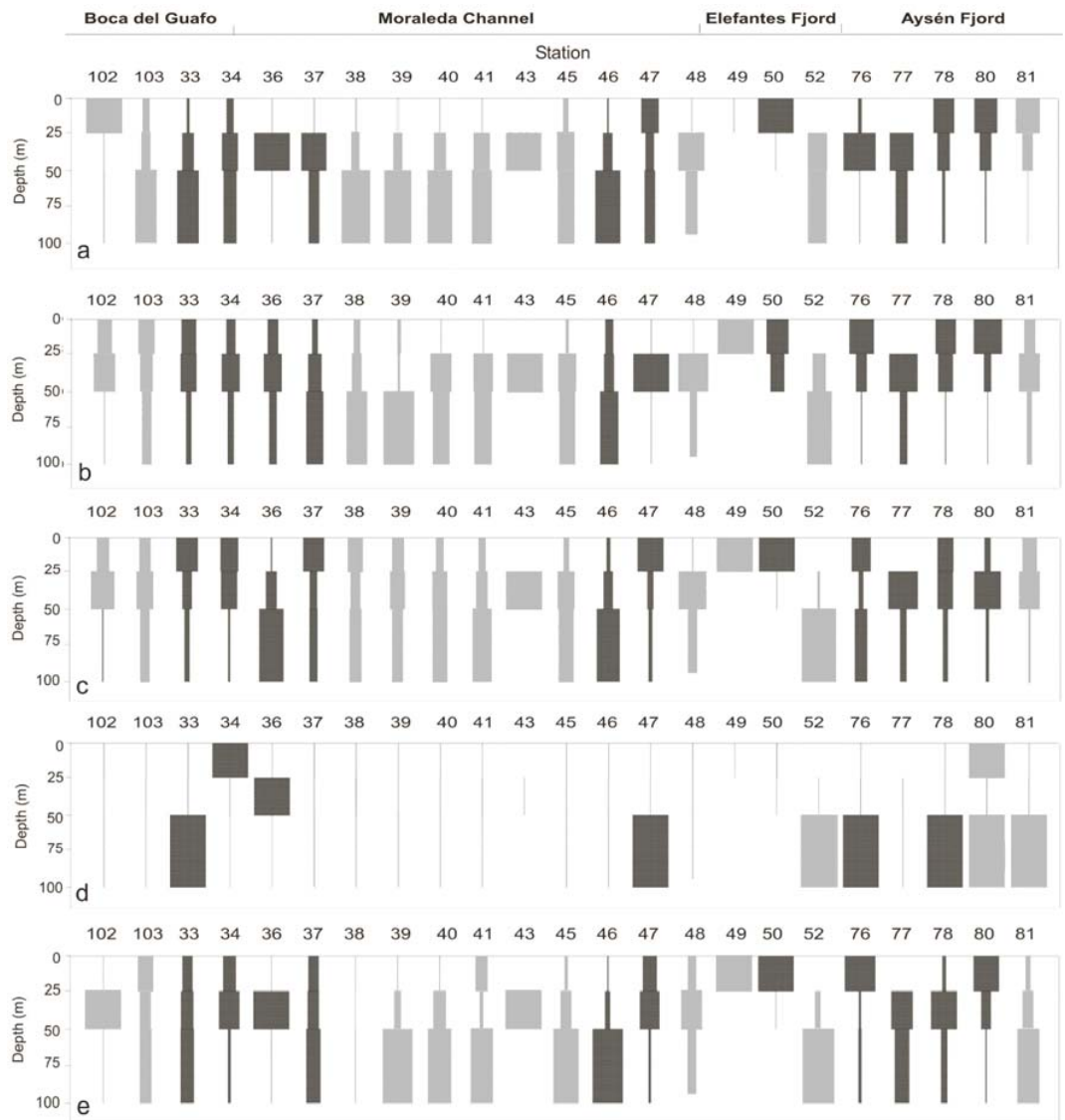
Figure 8. Vertical distribution of dominant species in spring. a) *Bougainvillia muscoides*, b) *Proboscidactyla ornata*, c) *Clytia simplex*, d) *Amphogona apicata,* e) *P. stellata.* Grey columns: diurnal tows, black columns: nocturnal tows.

Figura 8. Distribución vertical de las especies dominantes primaveral. a) *Bougainvillia muscoides*, b) *Proboscidactyla ornata*, c) *Clytia simplex*, d) *Amphogona apicata,* e) *P. stellata.* Columnas en gris: muestreos diurnos, columnas en negro: muestreos nocturnos.

tionally, *B. muscoides, P. ornata* and *P. stellata* were absent and collected at low densities in the surface stratum (0-25 m) along the Moraleda Channel.

DISCUSSION

Environmental conditions

During winter and spring cruises, the vertical distribution of salinity, which govern the density

structure in the study area, showed a stratified distribution consisting of two layers: a surface layer (≈ 25 m), more variable in temperature and salinity, and therefore in density, frequently presenting thermo-clines and/or haloclines, and a deep layer (from *ca*. 25 m to the bottom), less variable, being occasionally almost homothermal and/or homohaline (Fig. 2). The intensity of this vertical stratification showed a latitudinal gradient, being less intense at the Boca del

Guafo, where the oceanic influence is higher, and more intense at the Aysén and Elefantes fjords, where the freshwater input from continental rivers and glacier melting are more relevant (Palma & Silva 2004; Calvete & Sobarzo, 2011) .

Seasonally, the water column temperature showed minor seasonal differences (< 1°C) between both seasons, with the exception of Aysén Fjord surface layer, where this difference increased up to almost 3°C. The Aysén Fjord winter cooler surface water, due to the input of winter coldest river fresh water, gave origin to an inverted thermocline, which was not observed during spring, as the surface water was warmer (Fig. 2), but not enough to form a normal thermocline. This variation of the temperature corresponds to a normal seasonal fluctuation pattern for the Aysén Fjord, as established by Silva *et al.* (1997).

In both seasonal cruises, surface layer salinities of Moraleda-Costa Channels and Elefantes-Aysén fjords, remained lower than at the bottom layer (Fig. 2), giving origin to a surface strong halocline, and consequently to a very stable water column. Even though the study area shows seasonal differences in river water input (Calvete & Sobarzo, 2011), being higher inspring than in winter, the water column salinity did not show significant differences between cruises, which were generally low (≈ 1 psu; Fig. 2). A possible explanation for this lack of differences may be associated to a similar river flow during the days preceding the sampling.

The water column stratification was lower at the Boca del Guafo than at the Moraleda-Aysén-Costa channels, where the surface/bottom salinity differences in the former were low (≈ 1 psu v/s 3-20 psu; Fig. 2). At the stations 50 to 52 in the Elefantes Fjord, an almost vertical homogeneous structure was present (Fig. 2), giving origin to a much less stable water column, compared with the rest of the study area. These differences are a characteristic oceano-graphic pattern of the Aysén area, since it has been observed in most of the cruises performed in this area (Silva *et al.*, 1997; Calvete & Sobarzo, 2011).

Dissolved oxygen in the surface layer of Boca del Guafo-Moraleda Channel was well oxygenated and with similar contents in both cruises (> 6 mL L^{-1}). Beneath the surface layer, around 100 m, the dissolved oxygen dropped below 4 mL L^{-1} (Fig. 2), due to consumption caused by the degradation of autoch-thonous and allochthonous particulate organic matter coming from the surface layer (Silva, 2008). Low oxygen concentrations (2-4 mL L^{-1}) have been recorded at mid depth close to the head of Aysén Fjord (≈ 75-150 m; Fig. 2). Similar low dissolved

oxygen content has been also recorded in Reloncaví, Puyuguapi, Quitralco, and Cupquelán fjords, all of which, as in Aysén Fjord, receive fluvial contributions carrying particulate organic matter (Silva *et al.*, 1997; Silva & Guzmán, 2006).

Two oceanic water masses were detected adjacent to the Chiloé zone, between the surface and 300 m depth: Subantarctic Water (SAAW) above 150 m, and remnants of Equatorial Subsurface Water (ESSW) between 150 and 300 m.

Both of these water masses penetrate into the region mainly through the Boca del Guafo, the SAAW through the surface and the ESSW through the subsurface layer, spreading as far as the bathymetry of the gulfs and channels allows them. As the SAAW penetrates, it mixes with the fresh water (FW) in different proportions, according to the contributions from rivers, glaciers, coastal runoff, pluviosity, and the distance or proximity of the FW sources (Sievers & Silva, 2008). The water resulting from this process, having salinities between 31 and 33 psu, is known as Modified Subantarctic Water (MSAAW) and the lower-salinity water to as Estuarine Water (EW). The ESSW enters by the subsurface (below 150 m), but its displacement to the inland region is limited by the submarine topography and, when it reaches the Menina constriction-sill (50-60 m high), it does not allow the ESSW to go further south into the Aysén-Elefantes fjords (Fig. 2), thus impeding the passage of ESSW with low dissolved oxygen content towards the southern microbasins.

Jellyfish species composition

Thirty jellyfish species were recorded at the Aysén region, which involves the area between the Boca del Guafo and the Elefantes Fjord, a quantity very similar (30 species) to that recorded in the same area in spring 2002 and 2003 (Table 4; Palma *et al.*, 2007a, 2007b). Seven out of the total species identified correspond to new records for the study area (*Bougainvillia macloviana, Hybocodon chilensis, Hydractinia tenuis, Laodicea pulcra, L. undulata, Modeeria rotunda* and *Chrysaora plocamia*) (Table 1). It is worth noting the presence of *C. plocamia* from this group of species, which showed a marked increase in the ephyrae (probably of *C. plocamia*) and adult quantities (Table 1). This species is currently more frequently found in inner waters and sometimes, as in February-June 2002, it has represented a negative effect on salmon cage farming in Chiloé (S. Palma, unpublished).

Jellyfish fauna of the inner waters is made up by common species of the ecosystems of the southern channels and fjords between Puerto Montt and the

Cape Horn (genera *Bougainvillia, Hybocodon, Hydractinia* and *Proboscidactyla*) (Pagès & Orejas, 1999; Galea, 2006, 2007; Galea *et al.,* 2007; Palma *et al.*, 2007a, 2007b, 2011; Villenas *et al.,* 2009a), as well as diverse common species in subantarctic waters from the Humboldt Current System (genera *Amphogona, Clytia, Coryne, Ectopleura, Obelia, Rhopalonema, Sarsia* and *Solmundella*) (Fagetti, 1973; Palma, 1994; Palma & Rosales, 1995; Palma & Apablaza, 2004), which have penetrated and settled with more or less success in the inner zone of the Chilean Patagonia fjords, and where some of them prove quite frequent and abundant (Table 4). Some subantarctic species have successfully populated inner waters, adapting to a highly stratified environment, with a low salinity (3-32 psu), surface layer (≈ 25 m), generally avoided by many species that spread in the deep, more homogeneous and saline (32-34 psu) layer, as shown by the vertical distribution patterns in both seasons (Figs. 7 and 8).

Seasonal distributions patterns of jellyfish

A high seasonal difference in the jellyfish abundance was determined, which was 14 times higher in spring with respect to winter (Table 1). Sixty four species were common for both seasons, which entails a significant change in the seasonal specific composition. A latitudinal increase in the abundance was detected in winter, from Boca del Guafo up to the Aysén Fjord, where the abundance maximums were recorded. Such latitudinal variation may be associated to the constant entrance of SAAW that mixes with the EW, causing less vertical stability in the water column of the northern sector (Boca del Guafo, Corcovado Gulf and northern area of the Moraleda Channel) (Silva & Guzmán, 2006), and a higher stability in the southern zone (Aysén and Elefantes fjords), where the continental freshwater input is higher. In spring, however, no geographical distribution pattern was observed, as there is a generalized abundance in the whole study area probably due to a higher trophic availability as a result of the elevated biological productivity caused by a larger solar radiation and temperature increase typical of the beginning of the summer period (González *et al.*, 2011), which promotes jellyfish reproduction and proliferation in the study area.

In all oceans, it has been observed that seasonal fluctuations of temperature play a fundamental role in the zooplankton composition and abundance, promoting the proliferation of various species, particularly juvenile stages (Parsons & Lalli, 2002; Kehayias, 2004). These seasonal changes are quite marked for jellyfishes due to their reproductive cycles, which mainly occur in spring and summer, when the asexual reproduction is influenced to a greater extent by temperature increases (Palma, 1994; Palma & Rosales, 1995; Bouillon, 1999). In fact, the Pearson analysis showed significant positive correlations (*P* > 0.5) between the abundance of some dominant species and the temperature values (Table 2). These abundance fluctuations have also been ascribed to the trophic availability and inter-specific competence in highly productive systems (Edwards & Richardson, 2004). Studies on inner waters have shown a high biological productivity in inner waters during spring, especially in the Moraleda Channel, reflected in high primary productivity values and zooplanktonic biomass (Palma & Silva, 2004; González *et al.*, 2011). Besides, it has also been suggested the simultaneous occurrence of two or more species in the community reflects some degree of consistency in the ecological, environmental or biological requirements with a tendency to form more or less compact groups according to their requirement similarities (Lie *et al.*, 1983; Gasca *et al.*, 1996). This is also observed in this zone, where a positive association among various dominant species sharing their spatial and vertical distribution was seen, such as the species belonging to genera *Bougainvillia* and *Proboscidactyla* (Figs. 4 and 8). Among the most abundant species, only *Bougainvillia muscoides* and *Amphogona apicata* showed dominance in both seasons. *B. muscoides* was highly abundant, with high dominance percentages in winter (28.84%) and spring (34.14%), a period where its abundance was highly superior to that observed in winter (Table 1). This species was gathered at the stations remote from the influence of the SAAW, and presented its maximums at the Aysén Fjord, under 50 m thus avoiding the low salinity EW superficial layer. Such distribution pattern of *B. muscoides* supports results obtained in the same geographical area (Palma *et al.*, 2007a, 2007b), as well as in all the southern ecosystem of inner waters (Pagès & Orejas, 1999; Villenas *et al.*, 2009a; Palma *et al.*, 2011).

In both seasons *A. apicata* showed a limited frequency as it was generally absent in areas with higher temperature and salinity, and the maximums were recorded at the Aysén Fjord (Figs. 3 and 4). Its presence in this area confirms its wide distribution in the northern ecosystem of interior waters (Palma *et al.,* 2007a, 2007b; 2011; Villenas *et al.*, 2009a). This is a common species in tropical and subtropical waters in all oceans (Segura-Puertas, 1984), and has a wide distribution in the northern area of the Humboldt Current System (HCS) (Pagès *et al.*, 2001; Palma & Apablaza, 2004; Apablaza & Palma, 2006).

It may be pointed out that except the other dominant species collected in both winter and spring, the presence of *Bougainvillia muscus, Cunina peregrina, Hydractinia borealis, Rhopalonema velatum, Clytia simplex, Proboscidactyla ornata* and *P. stellata* confirms the results previously obtained for this geographical area (Palma *et al.,* 2007a, 2007b), as well as those obtained for the northern sector (Reloncavi Fjord to Boca del Guafo) (Villenas *et al.*, 2009a; Palma *et al.*, 2011). It is worth noting about this group that most of the species are common to inner waters, except for *R. velatum* which is quite uncommon, although widely spread in HCS oceanic and Cape Horn current subantarctic waters (Kramp, 1966; Fagetti, 1973; Pagès & Orejas, 1999; Pagès *et al.*, 2001; Palma & Apablaza, 2004).

Diversity values were slightly superior in winter, although the species richness was higher (58%) in spring. Such obvious contradiction may be explained by the strong increase of almost all jellyfish species during spring (> 14 times), which results in a disguising of the diversity values, as the Shannon-Wiever index includes the specific abundance, which was extremely high for *Bougainvillia muscoides, Proboscidactyla ornata, P. stellata* and *Clytia simplex*. The higher diversity values during both seasons (> 3.2 bits) was recorded at the Moraleda Channel, which receives a regular supply of SAAW from the adjacent Pacific, thus promoting the entry of oceanic species

not common in interior waters, thus increasing their diversity, confirming the results by Palma & Rosales (1997) and Palma *et al.* (2007a). The lower diversity (< 1 bits) and specific richness values were recorded at the Elefantes Fjord, where the low salinity, temperature and stratification conditions prevailed, which affected not only the abundance, but also the diversity and species richness (Fig. 6).

In general, it has been shown that the vertical distribution of jellyfishes in all the analyzed area showed a preference for deeper strata (> 25 m), thus avoiding the superficial and more stable layer of EW, though low in salinity, that characterizes the superficial stratum (0-25 m). The latter was especially obvious for those species typical of HCS oceanic subantarctic waters (*A. apicata, C. peregrina, R. velatum*; Figs. 7 and 8), which were distributed at greater depths (> 50 m). The deeper distribution of *A. apicata* is consistent with the negative association observed in winter and the dissolved oxygen concentration (r = -0.67; Table 2), especially at the Aysén Fjord, where its abundance maximums were observed in winter and spring. A positive association among species from the same genus was observed at depth, such as *Bougainvillia muscoides* and *B. muscus* (r = 0.62; Table 2), *Proboscidactyla ornata* and *P. stellata* (r = 0.69; Table 3), which coexisted in the water column in winter and spring, respectively. Furthermore, it has been pointed out that *P. stellata* is

Table 3. Pearson correlation values between the abundance of dominant species and the oceanographic variables in spring cruise. Significant values are indicated in bold (*P* < 0.05).

Tabla 3. Resultados del análisis de correlación de Pearson entre la abundancia de las especies dominantes y las variables oceanográficas en el crucero de primavera. Los valores significativos se indican en negrita (*P* < 0,05).

	D. oxygen	Salinity	Temperatura	*A. apicata*	*B. muscoides*	*C.simplex*	*P. ornata*	*P. stellata*
Oxygen	1.00							
Salinity	-0.,44	1.00						
Temperature	0.03	0.33	1.00					
A. apicata	-0.48	0.03	0.10	1.00				
B. muscoide:	0.10	-0.46	-0.22	-0.01	1.00			
C. simplex	0.22	0.00	0.14	-0.04	0.09	1.00		
P. ornata	0.22	**-0.55**	-0.15	-0.01	**0.57**	0.32	1.00	
P. stellata	-0.15	-0.42	-0.13	**0.55**	0.39	0.27	**0.69**	1.00

	Temperature	Salinity	D. oxygen
A. apicata	0,21	0,41	1,00
B. muscoides	0,96	1,00	1,00
C. simplex	0,13	0,50	0,04
P. ornata	0,88	1,00	0,04
P. stellata	0,84	1,00	0,87

Table 4. Mean abundance (ind 1000 m^{-3}) in the springs 2002, 2003 and 2007 and winter 2007 between Boca del Guafo and Elefantes Fjord. Data for springs 2002 (Palma *et al*., 2007a), 2003 (Palma *et al*., 2007b) and 2007 (present study). (-): Species not registered.

Tabla 4. Abundancia media (ind 1000 m^{-3}) en las primaveras 2002, 2003 y 2007 e invierno 2007 entre Boca del Guafo y fiordo Elefantes. Datos de primavera 2002 (Palma *et al*., 2007a), 2003 (Palma *et al.*, 2007b) y 2007 (presente estudio). (-): Especies no registradas.

	Spring	Spring	Spring	Winter
Species	2002	2003	2007	2007
Hydromedusae				
Aglaura hemistoma	1.5	-	-	-
Amphinema rugosum	2.2	-	9.6	-
Amphogona apicata	413.9	440.9	401.8	31.7
Bougainvillia macloviana	-	-	7.4	-
Bougainvillia muscoides	-	107.9	1902.3	134.3
Bougainvillia muscus	-	1.92	212.7	138.3
Bougainvillia sp.	60.9	80.9	-	-
Calycopsis sp.	-	0.4	-	-
Clytia simplex	882.1	699.2	601.0	3.6
Coryne eximia	1.3	2.8	55.6	10.9
Cunina peregrina	2.9	1.1	115.66	34.8
Cunina sp.	-	4.4	-	-
Dipurena ophiogaster	0.2	-	-	-
Ectopleura dumortieri	0.4	63.7	32.1	-
Euphysa aurata	23.7	178.2	29.2	6.4
Gossea brachymera	-	4.0	0.4	-
Halopsis ocellata	13.3	17.4	31.1	-
Heterotiara minor	0.3	-	24.6	0.6
Hydocodon chilensis	-	90.0	25.1	2.8
Hydractinia borealis	7.3	163.5	206.7	28.4
Hydractinia tenuis	-	-	72.3	10.4
Laodicea pulchra	-	-	0.9	-
Laodicea undulata	-	-	6.6	-
Leuckartiaria octona	14.4	21.7	76.1	6.7
Liriope tetraphylla	10.0	55.2	-	-
Lizzia blondina	7.9	26.0	-	-
Modeeria rotunda	-	-	36.8	-
Obelia spp.	135.0	20.1	41.5	-
Phialella quadrata	26.3	14.0	26.0	0.2
Proboscidactyla mutabilis	3.1	6.5	72.2	0.9
Proboscidactyla ornata	56.2	527.4	974.6	4.8
Proboscidactyla stellata	10.0	195.9	400.8	0.9
Proboscidactyla sp.	-	39.2	-	-
Rophalonema velatum	27.6	20.9	8.3	25.0
Sarsia coccometra	-	4.8	24.7	0.2
Solmundella bitentaculata	611.3	380.8	66.8	14.6
Scyphomedusae				
Chrysaora plocamia	-	-	32.9	-
Ephyrae	-	-	8.0	1.1

an euryhaline species common in cold waters of the Irish coast where, during the year, concentrates under 20 m depth (Ballard & Myers, 1997). It has been observed in some planktonic species that the bathymetric distribu-tion tends to favour the reproductive processes of some species (i.e. *Sagitta tasmanica*) (Villenas *et al.,* 2009b), as it may also represent a strategy to reduce the mortality rates, thus decreasing predation and loss by planktonic species advection (Gorsky *et al*., 2000).

ACKNOWLEDGEMENTS

REFERENCES

Apablaza, P. & S. Palma. 2006. Efecto de la zona de mínimo oxígeno sobre la migración vertical de zooplancton gelatinoso en la bahía de Mejillones. Invest. Mar., Valparaíso, 34(2): 81-95.

Ballard, L. & A. Myers. 1997. Vertical distribution, morphology and diet of *Proboscidactyla stellata* (Cnidaria): Limnomedusae) in Lough Hyne Marine Reserve, Co. Cork, Ireland. J. Mar. Biol. Assoc. U.K., 77: 999-1009.

Ballard, L. & A. Myers. 2000. Observations on the seasonal occurrence and abundance of gelatinous zooplankton in Lough Hyne, Co. Cork, South-West Ireland. Biol. Environ. Proc. Roy. Ir. Acad. B, 100: 75-83.

Bloom, S.A. 1981. Similarity indices in community studies: potential pitfall. Mar. Ecol. Prog. Ser., 5: 125-128.

Bouillon, F. 1999. Hydromedusae. In: D. Boltovskoy (ed.). South Atlantic zooplankton. Backhuys Publishers, Leiden, pp. 385-465.

Brodeur, R., H. Sugisaki & G. Hunt Jr. 2002. Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. Mar. Ecol. Prog. Ser., 233: 89-103.

Calvete, C. & M. Sobarzo 2011. Quantification of the surface brackish water layer and frontal zones in southern Chilean fjords between Boca del Guafo (43°30′S) and Estero Elefantes (46°30′S). Cont. Shelf Res., 31: 162-171.

Edwards, M. & A.J. Richardson. 2004. The impact of climate change on the phenology of the plankton community and trophic mismatch. Nature, 430(7002): 881-884.

Fagetti, E. 1973. Medusas de aguas chilenas. Rev. Biol. Mar., Valparaíso, 15(1): 31-75.

Galea, H.R. 2006. Rediscovery and redescription of *Hybocodon chilensis* Hartlaub, 1995 (Cnidaria: Hydrozoa) from Comau Fjord, southern Chile. Zootaxa, 1258: 57-68.

Galea, H.R. 2007. Hydroids and hydromedusae (Cnidaria: Hydrozoa) from the fjords region of southern Chile. Zootaxa, 1579: 1-116.

Galea, H.R., V. Häussermann & G. Forsterra. 2007. Hydrozoa, fjord Comau, Chile. Check List, 3(2): 159-167.

Gasca, R., J.N. Alvarez-Cadena & E. Suárez-Morales. 1996. Chaetognath assemblages in the Mexican Caribbean Sea (1991). Caribb. Mar. Stud., 5: 41-50.

Genzano, G., H. Mianzan, L. Díaz-Briz & C. Rodríguez. 2008. On the occurrence of *Obelia* medusa blooms and empirical evidence of unusual massive accumulations of *Obelia* and *Amphisbetia* hydroids on the Argentina shoreline. Lat. Am. J. Aquat. Res., 36(2): 301-307.

González, H., L. Castro, G. Daneri, J.L. Iriarte, N. Silva, C.A. Vargas, R. Giesecke & N. Sánchez. 2011. Seasonal plankton variability in Chilean Patagonian fjords: Carbon flor through the pelagic web of Aysén Fjord and plankton dynamics in the Moraleda Channel basin. Cont. Shelf Res., 31: 225-243.

Gorsky, G., P.R. Flood, M. Youngbluth, M. Picheral & J.M. Grisoni. 2000. Zooplankton distribution in four western Norwegian fjords. Estuar. Coast. Shelf Sci., 50, 129-135.

Kehayias, G. 2004. Spatial and temporal abundance distribution of chaetognaths in eastern Mediterranean pelagic waters. Bull. Mar. Sci., 74(2): 253-270.

Kramp, P.L. 1952. Medusae collected by the Lund University Chile Expedition 1948-49. Rep. Lunds Univ., Arsskr., 47(7): 1-19.

Kramp, P.L. 1959. The Hydromedusae of the Atlantic Ocean and adjacent waters. Dana Rep., 46: 1-283.

Kramp, P.L. 1966. A collection of Medusae from the coast of Chile. Vidensk. Meddr. Dansk. Naturh. Foren., 129: 1-38

Kramp, P.L. 1968. The Hydromedusae of the Pacific and Indian Oceans. Sections II and III. Dana Rep., 72: 1-200.

Ludwig, J.A. & J.F. Reynolds. 1988. Statistical ecology. John Wiley & Sons, Nueva York, 337 pp.

Lie, U., T. Magnesen, B. Tunberg & D. Aksnes. 1983. Preliminary studies on the vertical distribution of size-fractions in the zooplankton community in Lindaspollene, western Norway. Sarsia 68: 65-80.

Matsakis, S. & R. J. Conover. 1991. Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. Can. J. Fish. Aquat. Sci., 48: 1.419-1.430.

Mianzan, H.W. & R.A. Guerrero. 2000. Environmental patterns and biomass distribution of gelatinous macrozooplankton. Three study cases in the South-western Atlantic Ocean. Sci. Mar., 64(1): 215-224.

Miglietta, M.P., M. Rossi & R. Collins. 2008. Hydromedusae blooms and upwelling events in the bay of Panama, Tropical East Pacific. J. Plankton Res., 30(7): 783-793.

Mills, C. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiology, 451: 55-68.

Pagès, F. & C. Orejas. 1999. Medusae, siphonophores and ctenophores of the Magellan region. Sci. Mar., 63 (Suppl. 1): 51-57.

Pagès, F., H. González, M. Ramón, M. Sobarzo & J.M. Gili. 2001. Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System and potential predatory impact by *Bassia bassensis* (Siphonophora: Calycophorae). Mar. Ecol. Prog. Ser., 210: 13-24.

Palma, S. 1994. Distribución del macroplancton gelatinoso en un área de desove de peces frente a la costa central de Chile (32°-33°S). Rev. Biol. Mar., 29(1): 23-45.

Palma, S. & P. Apablaza. 2004. Abundancia estacional y distribución vertical del zooplancton gelatinoso carnívoro en una área de surgencia en el norte del sistema de la Corriente Humboldt. Invest. Mar. Valparaíso, 32(1): 49-70.

Palma, S. & S. Rosales. 1995. Composición, distribución y abundancia estacional del macroplancton de la bahía de Valparaíso. Invest. Mar., Valparaíso, 23: 43-66.

Palma, S. & S. Rosales. 1997. Sifonóforos epipelágicos de los canales australes de Chile (41°30'-46°40'S). Cienc.Tecnol. Mar, 20: 125-146.

Palma, S. & N. Silva. 2004. Distribution of siphonophores, chaetognaths and euphausiids and oceanographic conditions in the fjords and channels of southern Chile. Deep-Sea Res. II, 51(6-9): 513-535.

Palma, S., P. Apablaza & N. Silva. 2007a. Hydromedu-sae (Cnidaria) of the Chilean southern channels (from the Corcovado Gulf to the Pulluche-Chacabuco Channels). Sci. Mar., 71 (1): 65-74.

Palma, S., P. Apablaza & D. Soto. 2007b. Diversity and aggregation areas of planktonic cnidarians of the southern channels of Chile (Boca del Guafo to Pulluche Channel). Invest. Mar., Valparaíso, 35(2): 71-87.

Palma, S., N. Silva, M.C. Retamal & L. Castro. 2011. Seasonal and vertical distributional patterns of siphonophores and medusae in the Chiloé Interior Sea, Chile. Cont. Shelf Res., 31(3-4): 260-271.

Parsons, T.R. & C.M. Lalli. 2002. Jellyfish populations explosions: revisiting a hypothesis of possible causes. La Mer, 40: 111-121

Pielou, E. 1977. Mathematical ecology. John Wiley & Sons, New York, 378 pp.

Purcell, J.E. 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bull. Mar. Sci., 37(2): 739-755.

Purcell, J.E. 1997. Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates, and effects on prey populations. Ann. Inst. Océanogr., 73(2), 125-137.

Segura-Puertas, L. 1984. Morfología, sistemática y zoogeografía de las medusas (Cnidaria, Hydrozoa y Schyphozoa) del Pacifico Tropical Oriental. Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Publicación especial, 320 pp.

Sievers, H. & N. Silva. 2008. Water masses and circulation in austral Chilean channels and fjords. In: N. Silva & S. Palma (eds.). Progress in the oceano-graphic knowledge of Chilean inner waters, from Puerto Montt to Cape Horn. Comité Oceanográfico Nacional-Pontificia Universidad Católica de Valpa-raíso, Valparaíso, pp. 58-53.

Silva, N. 2008. Dissolved oxygen, pH, and nutrients in the austral Chilean channels and fjords. In: N. Silva & S. Palma (eds.). Progress in the oceanographic knowledge of Chilean inner waters, from Puerto Montt to Cape Horn. Comité Oceanográfico Nacio-nal-Pontificia Universidad Católica de Valparaíso, Valparaíso, pp. 37-43.

Silva, N. & D. Guzmán. 2006. Condiciones oceanográ-ficas físicas y químicas, entre Boca del Guafo y fiordo Aysén (Crucero CIMAR 7 Fiordos). Cienc. Tecnol. Mar, 29: 25-44.

Silva, N., C. Calvete & H. Sievers. 1997. Características oceanográficas físicas, químicas y circulación general para algunos canales entre Puerto Montt y laguna San

Rafael, Chile (Crucero CIMAR Fiordo 1). Cienc. Tecnol. Mar, 20: 23-106.

Silva, N., C. Calvete & H. Sievers. 1998. Masas de agua y circulación general para algunos canales australes entre Puerto Montt y Laguna San Rafael (Crucero Cimar-Fiordo 1). Cienc. Tecnol. Mar, 21: 17-48.

Villenas, F., D. Soto & S. Palma. 2009a. Cambios interanuales en la biomasa y biodiversidad de zooplancton gelatinoso en aguas interiores de Chiloé, sur de Chile (primaveras 2004 y 2005). Rev. Biol. Mar. Oceanogr., 44(2): 309-324.

Villenas, F., S. Palma & D. Soto. 2009b. Chaetognath spatial distribution and how egg-carrying affects the vertical distribution of *Sagitta tasmanica* off southern Chile. Sci. Mar., 73(1), 29-38.