Research Article

Biodiversity and spatial distribution of medusae in the Magellan Region (Southern Patagonian Zone)

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ABSTRACT. Epipelagic medusae collected in the Magellan Region (Southern Patagonian Zone) during spring 2009 were analyzed. A total of 27 species of medusae were identified (25 hydromedusae and 2 scyphomedusae). Twelve medusae species were recorded for the first time in the Magellan region. Six dominant species were found: *Clytia simplex* (19.8%), *Rhopalonema funerarium* (16.2%), *Aurelia* sp. (15.9%), *Bougainvillia muscoides* (15.5%), *Proboscidactyla stellata* (8.9%), and *Obelia* spp. (6.0%). The horizontal distribution of all these species, except *Obelia* spp., showed the highest abundances to the south of 54°S, particularly in the Almirantazgo and Agostini fjords and in the Beagle Channel. Most of the dominant species were collected in shallow strata (0-50 m), with less saline waters (<30), except for *R. funerarium*, which was mainly collected above depths deeper than 25 m in more saline waters (30-33). These results confirm the success of several species in the colonization of the inland waters of the Southern Patagonian Zone.

Keywords: medusae, horizontal distribution, vertical distribution, Magellan Region, Southern Patagonian Zone, Chile.

Biodiversidad y distribución especial de las medusas en la región Magallánica (Zona Patagónica Austral)

RESUMEN. Se analizaron las medusas epipelágicas colectadas en la región Magallánica (Zona Patagónica Austral) durante la primavera de 2009. Se identificó un total of 27 especies of medusas (25 hidromedusas y 2 escifomedusas). Se registraron 12 especies de medusas por primera vez en la región Magallánica. Se determinaron 6 especies dominantes: *Clytia simplex* (19,8%), *Rhopalonema funerarium* (16,2%), *Aurelia* sp. (15,9%), *Bougainvillia muscoides* (15,5%), *Proboscidactyla stellata* (8,9%) and *Obelia* spp. (6,0%). La distribución horizontal de las especies dominantes, a excepción de *Obelia* spp., mostraron las mayores abundancias al sur de los 54°S, particularmente en los fiordos Almirantazgo y Agostini, y Canal Beagle. La mayoría de las especies dominantes se colectaron en la capa superficial (0-50 m), de menor salinidad (<30), excepto *R. funerarium* que se colectó principalmente bajo los 25 m de profundidad en aguas de mayor salinidad (30-33). Estos resultados confirman el éxito de varias especies de medusas en la colonización de las aguas interiores del extremo sur de la Patagonia chilena.

Palabras clave: medusas, distribución horizontal, distribución vertical, región Magallánica, Patagonia austral, Chile.

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INTRODUCTION

Over the last three decades, frequent jellyfish blooms have been recorded in the oceans, resulting from population increases of cnidarians and ctenophores (Mills, 2001; Purcell *et al.*, 2007; Brotz *et al.*, 2012).

The Subantarctic Waters (SAAW) of the Humboldt Current System (HCS) that bathe the Chilean coast have also been affected by these population increases and in several coastal areas of high biological productivity, such as Antofagasta, Valparaíso, and Concepción, high densities of gelatinous organisms (medusae and siphonophores) have occurred (Palma, 1994; Palma & Rosales, 1995; Palma & Apablaza, 2004; Pavez *et al.*, 2010). In summer periods, the medusae are very abundant, particularly in northern Chile (Iquique and Antofagasta), where the scyphomedusa *Chrysaora plocamia* have a high impact on

fisheries and tourism activities (Mianzan *et al.*, 2014) and show predatory behavior over *Engraulis ringens* eggs and copepods (Riascos, 2014). To date, 93 species of medusae have been registered along the Chilean coast (Oliveira *et al.*, *in press*).

In recent years, high densities of gelatinous cnidarians have been also registered in the Patagonian Fjord Ecosystems of southern Chile, sometimes having a negative impact on aquaculture activities, particularly salmon farming (Palma *et al.*, 2007a; Mianzan *et al.*, 2014). Moreover, cnidarian population increases over time were found in several fjords and channels, showing an increase of three orders of magnitude in the abundance of several species of siphonophores between the Penas Gulf (48°S) and the Trinidad Channel (50°10'S) (Palma *et al.*, 2014).

Biogeographically, the southern zone of Chile comprising the area between Puerto Montt (41°S) and Cape Horn (55°S), is subdivided by Viviani (1979) into three regions, where there have been several studies on jellyfish: a) the Northern Patagonian Zone, from Puerto Montt (41°S) to the Taitao Peninsula (46°-47°S) (Galea, 2007; Galea et al., 2007; Palma et al., 2007a, 2007b; Villenas et al., 2009; Bravo et al., 2011), b) the Central Patagonian Zone to the Magellan Strait (52°30'S) (Häussermann et al., 2009), and d) the Southern Patagonian Zone to Cape Horn (56°S) (Pagès & Orejas, 1999). The Southern Patagonian Zone (52°30'-56°S) or Magellan region is characterized by its geographical and oceanographic complexity. The most important geographical feature of this area is the Magellan Strait, where the bathymetry is irregular due to the presence of several micro basins located along its length of 550 km (Antezana et al., 1992; Valdenegro & Silva, 2003). The intrusion of subantarctic waters may be limited by physical barriers such as the shallow shelf (30-50 m) at the Atlantic entrance and the shallow sill (20-50 m) at the Pacific entrance (Guglielmo & Ianora, 1997; Valdenegro & Silva, 2003). On the Pacific coast, there are several oceanic channels (i.e., Cockburn, Ballenero, Beagle) which allow the entry into the interior zone of subantarctic waters of the Cape Horn Current. These oceanic waters mix with freshwater from precipitation, fluvial contributions and icemelt from the Darwin Mountain Range Glaciers, generating an interior estuary system.

In the Magellan region, the pattern of the general circulation has a two-layer structure: a surface layer (0-25 m) of estuarine waters ($6-7^{\circ}$ C, salinity 10-31, dissolved oxygen 6-7 mL L⁻¹) that flow towards the open ocean, and a subsurface layer (25 m to bottom) of subantarctic waters ($6-7^{\circ}$ C, salinity 31-34, dissolved oxygen 5-6 mL L⁻¹) that enter to the interior zone; these are separated by a "strong" halocline (Silva &

Valdenegro, 2003). This two-layer structure is a common pattern of all Patagonian channels and fjords, affecting the biodiversity and vertical distribution of zooplankton populations (Palma *et al.*, 2007a, 2011, 2014; Villenas *et al.*, 2009; Bravo *et al.*, 2011).

In the past two decades, the knowledge of zooplankton populations in the Magellan region has increased due to the work of Guglielmo & Ianora (1995, 1997), Pagès & Orejas (1999); Palma & Aravena (2001), among others. However, studies on jellyfish are limited exclusively to the work of Pagès & Orejas (1999), who identified 31 species of medusae in this area: 29 hydromedusae and 2 scyphomedusae. Consequently, the aim of the present study is to improve our knowledge of the biodiversity, abundance, geographical distribution and vertical distribution of jellyfish and their relation to oceanographic features in this region, where there is a confluence of water masses from the Pacific, Atlantic and Southern oceans, and where the latter is part of the Antarctic ecosystem.

MATERIALS AND METHODS

Oceanographic data and zooplankton samples were obtained at 40 oceanographic stations distributed throughout the Magellan Strait and in the adjacent channels and fjords (52°-56°S) during the CIMAR 16 Fiordos cruise which took place between 11th October and 19th November 2010 on board the R/V Abate Molina. All 40 stations were used to perform the analysis of medusae biodiversity and abundance. Of these, 22 stations were selected to construct two transects for the analysis of the oceanographic characteristics and vertical distribution of medusae: Transect 1: Magellan Strait-Almirantazgo Fjord (13 stations), and Transect 2: Balleneros-Beagle Channels (9 stations) (Fig. 1).

During the oceanographic cruise, temperature and conductivity profiles were recorded with a CTD Seabird model SBE 19. Water samples for dissolved oxygen were taken with a 12 L Niskin bottle Rosette, at standard depths (0, 2, 5, 10, 25, 50, 75, 100, 150 and 200 m) depending on the bottom depth. Dissolved oxygen samples were fixed and analyzed on board, in accordance with Carpenter (1965). Oxygen saturation values were computed in accordance with Weiss (1970). CTD salinity records were corrected using the results of bench Salinometer analysis of discrete samples collected in the water column during the CTD casting.

Zooplankton samples were collected by oblique tows at three strata: surface (0-25 m), middle (25-50 m) and deep (50-100 or 200 m, depending on the bottom depth), during day and night. The strata were selected considering the two-layer oceanographic structure cha-

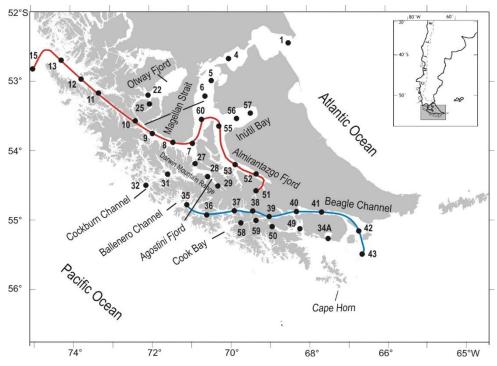


Figure 1. Geographical position of zooplankton sampling stations in the Magellan region (CIMAR 16 Fiordos cruise). Red line: Transect 1 (Magellan Strait-Almirantazgo Fjord), blue line: Transect 2 (Ballenero-Beagle Channels).

racterizing the interior region of the fjords and channels located in the Magellan region (Valdenegro & Silva, 2003). The sampling gear was a Tucker trawl net (1 m² mouth opening and 350 μ m mesh aperture), which included a three-net system fitted 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 buffered with sodium borate. All medusae were sorted, identified and counted from the original samples. The taxonomic identification of medusae species followed the work of Kramp (1961, 1965, 1968) and Bouillon (1999).

Zooplankton abundance was standardized to individuals per 1000 m⁻³ using the volume of water filtered by the nets. The average volume filtered for the different strata were 49.8 m³ (0-25 m), 54.5 m³ (25-50 m), 111.6 m³ (50-100 m) and 273.1 m³ (50-200 m). Only dominant species (>5% of the total collected specimens) were considered to describe horizontal and vertical distribution patterns.

For multivariate analysis, zooplankton abundance was transformed with fourth root. Analysis of Similarities (ANOSIM) was used to test whether any differences occurred between stations based on their faunal composition (Clarke & Green, 1988). The significance was set at P < 0.05. ANOSIM analyses were performed using the computer software package PRIMER 6.1.6 (Plymouth Routines in Multivariate Ecological Research) (Clarke & Warwick, 2001).

As the gradient length obtained in the Detrended Canonical Analysis (9.82 SD units) was higher than would be the case for a complete species turnover (3.0 SD units; Leps & Smilauer, 2003) unimodal ordination methods (Canonical Correlation Analysis, CCA, Ter Braak & Verdonschot, 1995) were used as non-linear responses were expected along such a gradient. The relationship between the distribution patterns of medusae abundance levels and oceanographic physical and chemical features over the sampling stations were explored using a CCA analysis. Prior to CCA analysis, environmental variables were square-root transformed whenever data were moderately skewed in distribution. The level of significance was set at P < 0.05. Initial analysis included abundance data for jellyfish species and 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 faunaenvironment relationships. The CCA analysis was performed using XLStat software (version 2011.4.04, Addinsoft).

RESULTS

Oceanographic characteristics

The surface layer (~50 m) temperatures in the Transect 1 (Magellan Strait-Almirantazgo Fjord), and in the Transect 2 (Ballenero-Beagle Channels) were low and around $6.5-7.5^{\circ}$ C, except at the western end of the

Magellan Strait, where the temperature was the highest (~8°C) and at the head of the Almirantazgo Fjord where the temperature was the lowest ($\sim 5.5^{\circ}$ C) (Figs. 2a-2b). The surface salinity layer in the Transect 1 presented its lowest values (<30) close to the western end of the Magellan Strait and at the head of the Almirantazgo Fjord and almost homogeneous salinities (30-31) at its center (Figs. 2c-2d). The highest surface salinity values (>32) were present at the Pacific end of this transect (Sta. 14-15). The Transect 2 showed its lowest surface layer salinity values (<31) at its western end and the highest at its eastern end (>32) (Fig. 2d). In both transects, below the surface layer the salinity increased steadily up to 33 at the western end and up to 30-32 at the eastern end. A halocline was present in the western side of both transects, and it was stronger in the Transect 1 (0.04 m^{-1}) than in the Transect 2 (0.02 m^{-1}). In the surface layer, dissolved oxygen concentrations in both transects, were almost homogeneous (>7 mL L^{-1}) and close to saturation values (i.e., 95-105%) (Figs. 2e-2f). Below this well oxygenated surface layer, the dissolved oxygen decreased slowly to concentrations less than 6.5 mL L⁻¹. At the head of Almirantazgo Fjord and at the western entrance of the Ballenero Channel, the dissolved oxygen concentrations diminished to less than 5.5 mL L^{-1} (<60% saturation).

Jellyfish species composition

A total of 27 species of jellyfish were identified: 25 hydromedusae and 2 scyphomedusae. Twelve jellyfish species (11 hydromedusae and 1 scyphomedusae) were recorded for the first time in the Magellan region (Table 1). The dominant species were *Clytia simplex* (19.8%), *Rhopalonema funerarium* (16.2%), *Aurelia* sp. (15.9%), *Bougainvillia muscoides* (15.5%), *Proboscidactyla stellata* (8.9%) and *Obelia* spp. (6.0%). In decreasing order, the most commonly occurring species were *C. simplex* (92.3%), *P. stellata* (84.6%), *B. muscoides* (82.1%), *Aurelia* sp. (76.9%) and *Obelia* spp. (71.8%).

Horizontal distribution patterns of jellyfish

The jellyfish were found in all sampled stations throughout the study area, and the total abundance ranged from 37 ind 1000 m⁻³ at Station 1 and 27,336 ind 1000 m⁻³ at Station 51, and the average was 2865 ± 4832 ind 1000 m⁻³. The highest abundance of medusae was found in interior waters, particularly in the Almirantazgo and Agostini fjords, and the Beagle Channel. In general, the pattern of horizontal distribution showed an increase of the abundance in a north-south gradient.

The most abundant species was *Clytia simplex*, which was widely distributed throughout the Magellan region; the horizontal pattern of distribution showed an

increase of abundance in the southern sector of the Magellan region, at south 54°S, mainly in the Almirantazgo Fjord where it reached 4972 ind 1000 m⁻³ at Sta. 53, and in the Beagle Channel (Fig. 3a). Rhopalonema funerarium is widely distributed throughout the study area, but it is scarcer at most stations, except in semi-closed areas such as Otway Sound and the Almirantazgo Fjord, where the densities were the highest, with a maximum of 15082 ind 1000 m⁻³ at Sta. 51 (Fig. 3b). The jellyfish of *Aurelia* sp. was widely distributed in the study area. Like C. simplex, the horizontal distribution showed an increase in abundance to the south of 54°S, where the highest densities occurred in the Beagle Channel and its surroundings, with a maximum of 4194 ind 1000 m⁻³ at Sta. 49 (Fig. 3c). Bougainvillia muscoides showed its highest densities in the central sector of the Magellan Strait (4700 ind 1000 m⁻³ Sta. 8), the Jerónimo Channel (1788 ind 1000 m⁻³ Sta. 25), and the Almirantazgo Fjord (2854 ind 1000 m⁻³ Sta. 51). Lower densities were registered in the eastern sector of the Magellan Strait and in the Transect 2 (Fig. 3d). Proboscidactyla stellata was widely distributed throughout the study area, except in the eastern sector of the Magellan Strait. Higher densities were registered at the head of the Almirantazgo Fjord (1498 ind 1000 m⁻³ at Sta. 51) and in the Beagle Channel (1476 ind 1000 m⁻³ at Sta. 41) (Fig. 3e). Finally, the species of genus Obelia, were found in lower densities in the Magellan region and only present two nucleus of greater abundance in the Jerónimo Channel (Sta. 22 and 25), with a maximum of 2057 ind 1000 m⁻³ at Sta. 25 (Fig. 3f).

Vertical distribution patterns of jellyfish

All dominant species did not show significant differences in their vertical patterns distribution in both transects (Table 2, P > 0.05) and were collected throughout the entire water column (Figs. 4-5). C. simplex was found mainly in the first 50 m, and only at stations 8, 7, 35, 39 and 51 was it found at depths of up to 200 m (Figs. 4a-4b). R. funerarium was collected only at 50% of stations; with greater frequency in Transect 1, where it was mainly found below 25 m (Figs. 4c-4d). Aurelia sp. was concentrated in the first 50 m, except for stations 8, 9, 39 and 52, where it reached depths of up to 200 m (Figs. 4e-4f). B. muscoides were found in both transects and throughout the water column (0-200 m). The highest densities were obtained in the first 50 m, with a preference for the surface layer (0-25 m), particularly in Transect 1 (Figs. 5a-5b). P. stellata showed a widely vertical distribution (Figs. 5c-5d). Finally, Obelia spp. showed a higher frequency in Transect 1 and was generally caught in the first 50 m, except at the western mouth of

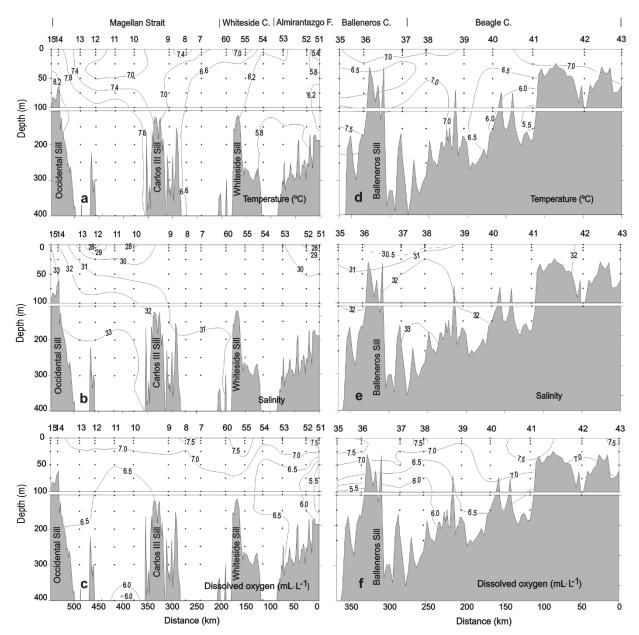


Figure 2. Vertical distribution of the oceanographic parameters in the Transect 1 (Magellan Strait-Almirantazgo Fjord) and Transect 2 (Ballenero-Beagle Channels) for spring 2010. a-b) temperature, c-d) salinity, e-f) dissolved oxygen. The station numbers are indicated in the top of each plot.

the Magellan Strait, where it was collected below depths of 50 m (Sta. 13) (Figs. 5e-5f).

Relationships between jellyfish species and oceanographic conditions

The relation between the station patterns of the most abundant medusae species (dominance >1%) and the environmental variables (temperature, salinity, dissolved oxygen and depth) are presented by the CCA triplot (Fig. 6). The Monte Carlo permutation test indicated a significant ordination diagram (F ratio = 3.43; P < 0.001) in which the two first axes explained 90.2% of the total variance (60.3% on the first axis and 29.9% on the second axis). Axis 1 was positively correlated with oxygen and negatively correlated with temperature and depth strata. This can be interpreted as a decrease in oxygen and an increase in temperature and depth strata, from right to left of the diagram (Fig. 6). The species associated with shallower strata, lower temperature and higher dissolved oxygen were *Bougainvillia muscus, Leuckartiara octona* and *B. macloviana* (Fig. 6). The majority of dominant species,

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Table 1. Summary of basic statistics for the medusae species. Total number of individuals, range of abundance, average per station, dominance and occurrence. Abundance is expressed as ind 1000 m⁻³. Bold letters indicate the dominant species and asterisks indicate the species registered for the first time in the Magellan region.

Species	Total number	Range of non-zero abundance	Average	Dominance (%)	Occurrence (%)
Hydromedusae					
Clytia simplex	22081	14-4972	566.2	19.76	92.3
Rhopalonema funerarium*	18051	5-15082	462.8	16.15	46.2
Bougainvillia muscoides*	17323	4-4701	444.2	15.50	82.1
Proboscidactyla stellata*	9963	13-1498	255.5	8.91	84.6
Obelia spp.	6746	3-2057	173.0	6.04	71.8
Bougainvillia macloviana	4376	3-2013	112.2	3.92	46.2
Proboscidactyla mutabilis	3494	5-887	89.6	3.13	64.1
Solmundella bitentaculata	3432	4-2765	88.0	3.07	30.8
Proboscidactyla ornata*	1728	9-438	44.3	1.55	53.8
Bougainvillia muscus*	1446	3-612	37.1	1.29	38.5
Leuckartiara octona	1085	3-377	27.8	0.97	53.8
Laodicea undulata*	943	4-412	24.2	0.84	20.5
Hydractinia borealis*	935	5-569	24.0	0.84	23.1
Laodicea pulchra	661	10-301	16.9	0.59	20.5
Euphysa aurata	605	3-108	15.5	0.54	48.7
Amphogona apicata	428	24-310	11.0	0.38	7.7
Halopsis ocellata	89	3-30	2.3	0.08	23.1
Hybocodon chilensis*	80	4-65	2.1	0.07	7.7
Rathkea formossisima	69	11-26	1.8	0.06	10.3
Coryne eximia*	59	8-29	1.5	0.05	10.3
Modeeria rotunda	46	1-46	1.2	0.04	2.6
Sminthea eurygaster*	26	10-16	0.7	0.02	5.1
Sarsia coccometra*	12	1-12	0.3	0.01	2.6
Non identified	74	4-41	1.9	0.07	10.3
Scyphomedusae					
Aurelia sp.	17722	9-4194	454.4	15.86	76.9
Chrysaora plocamia (ephyrae)*	228	4-60	7.1	0.25	28.2

Clytia simplex, Aurelia sp., Bougainvillia muscoides, Proboscidactyla stellata, P. ornata and P. mutabilis were located in the center of the diagram; therefore they are not associated to any stratum, temperature, salinity or dissolved oxygen, because they were found throughout the water column. In the deepest strata *Rhopalonema funerarium* and *Solmundella bitentaculata* were found associated to higher salinity and lower dissolved oxygen. The second axis explained a lower portion of the total variance and was mainly positively correlated with temperature.

DISCUSSION

The Chilean Southern Patagonian Zone is characterized by high oceanographic variability due to the influence of the Pacific, Atlantic and Southern oceans, whose more saline waters mix with freshwater (FW) from precipitation, fluvial contributions and ice-melt from the Darwin Mountain Range Glaciers, generating a large interior estuary system (Valdenegro & Silva, 2003; Silva & Palma, 2008). The Subantarctic Waters (SAAW), from the adjacent Pacific Ocean penetrates, into the different channels, fjords and micro-basins, through the western entrance of the Magellan Strait and several channels located along the western coastal border of this Patagonian area, giving the marine characteristics to the deeper layers. The SAAW from the adjacent Atlantic Ocean makes a lesser contribution to this estuary system due to the narrow and shallow eastern entrance of the Magellan Strait. As the SAAW spreads into the strait, channels and fjords, it mixes in different proportions with FW flowing ocean-ward (Valdenegro & Silva, 2003). Depending on the intensity of this mixing process, two types of water masses arise: a) waters with salinities between 31 and 33, known as Modified Subantarctic Water (MSAAW), and b) waters with salinities between 2 and 31, known as Estuarine Water (EW) (Sievers & Silva, 2008). The EW remains on the surface layer, but the MSAAW fills most of the subsurface and deeper layers

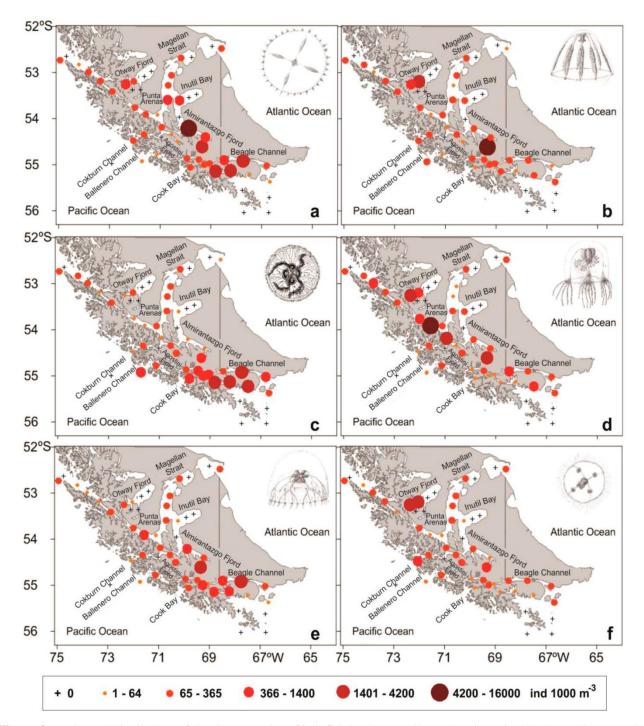
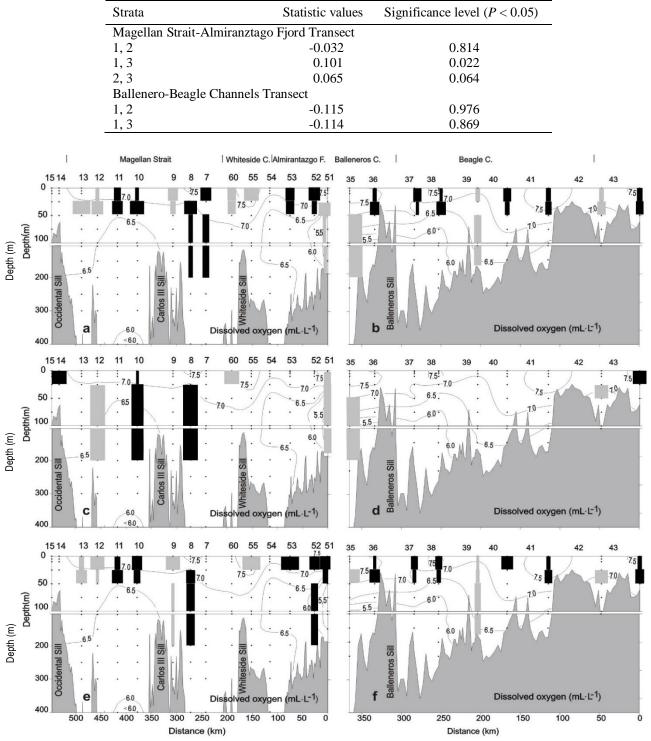


Figure 3. Horizontal distribution of dominant species of jellyfish in the Magellan region in spring 2010. a) *Clytia simplex*, b) *Rhopalonema funerarium*, c) *Aurelia* sp., d) *Bougainvillia muscoides*, e) *Proboscidactyla stellata*, f) *Obelia* spp.

of the Southern Patagonian micro-basins, while the SAAW (>33) fills only the western end of the Magellan Strait and the deep western part of the Beagle Channel (Figs. 2b, 2e). This general circulation pattern generates a two layer water column: a) a surface layer (0-50 m) with comparatively lower salinity but higher dissolved oxygen, and b) a deep layer (50 m-bottom) with com-

paratively higher salinity, but lower dissolved oxygen (Fig. 2). This circulation and vertical structure pattern are permanent features of this area, since they have been observed during other cruises performed in the region (Valdenegro & Silva, 2003; Palma & Silva 2004; Sievers & Silva 2008).

Table 2. Summary of basic statistics for species abundance (ind 1000 m⁻³) between the Transect 1 (Magellan Strait-Almirantazgo Fjord) and Transect 2 (Ballenero-Beagle Channels). Range of non-zero abundance, average per station, dominance and occurrence.



Abundance Scale : H = 100 %

Figure 4. Vertical distribution of jellyfish and dissolved oxygen in the Transect 1 (Magellan Strait-Almirantazgo Fjord) and Transect 2 (Ballenero-Beagle Channels) for spring 2010. a-b) *Clytia simplex*, c-d) *Rhopalonema funerarium*, e-f) *Aurelia* sp. Grey boxes: diurnal tows; black boxes: nocturnal tows. The station numbers are indicated in the top of each plot.

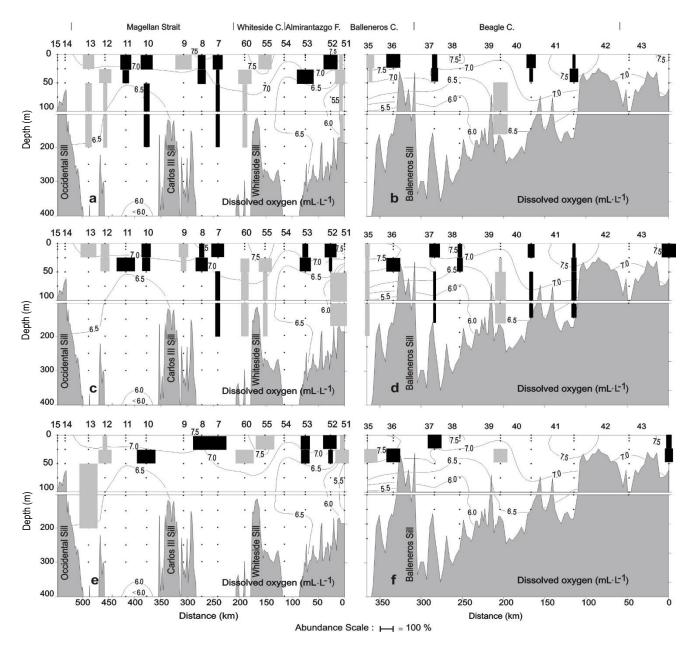


Figure 5. Vertical distribution of jellyfish and dissolved oxygen in the Transect 1 (Magellan Strait-Almirantazgo Fjord) and Transect 2 (Ballenero-Beagle Channels) for spring 2010. a-b) *Bougainvillia muscoides*, c-d) *Proboscidactyla stellata*, e-f) *Obelia* spp. Grey boxes: diurnal tows; black boxes: nocturnal tows. The station numbers are indicated in the top of each plot.

According to Guglielmo & Ianora (1995), in an environment with such high heterogeneity the specific adaptations of the plankton communities determine the richness of species diversity and dominance, as well as the energy flow within the community. In this sense, in semi-closed areas with higher vertical stability, such as the Otway, Almirantazgo and Agostini fjords, characterized by lower salinities in the upper layer (<30 at Almirantazgo Fjord and <31at Ballenero-Beagle Channels) due to permanent ice-melt from the adjacent Darwin Mountain Range Glaciers and subsurface penetration of more saline SAAW (>33), the highest phytoplankton concentrations (>1000 cell mL⁻¹; Avaria *et al.*, 1999), and the highest densities of the jellyfish dominant species (Fig. 3), have been registered in several station of this semi-closed area. This high trophic availability supports the highest values of zooplankton biomass registered in the same fjords, where Palma & Aravena (2001) have been recorded highest densities of eudoxids (siphonophore reproductive phase).

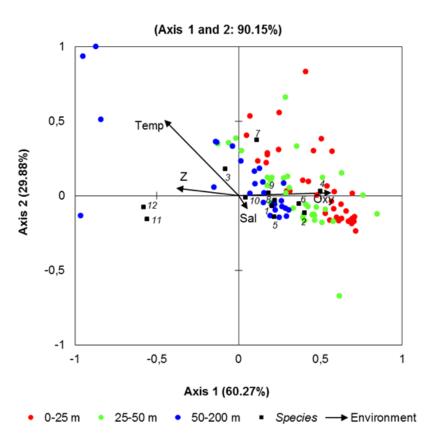


Figure 6. Canonical Correspondence Analysis (CCA) triplot based on data from spring 2010 showing scores of sampling stations by depth strata of the most abundant medusae species (dominance >1%) and oceanographic variables. 1: *Aurelia* sp., 2: *Bougainvillia macloviana*, 3: *B. muscoides*, 4: *B. muscus*, 5: *Clytia simplex*, 6: *Leuckartiara octona*, 7: *Obelia* spp., 8: *Proboscidactyla mutabilis*, 9: *P. ornata*, 10: *P. stellata*, 11: *Solmundella bitentaculata*, 12: *Rhopalonema funerarium*, Z: depth strata, Temp: temperature; Sal: salinity; Oxy: dissolved oxygen.

This association between the spring blooms of phytoplankton and the different components of zooplankton has also been reported for the same area by Mazzochi & Ianora (1991), who concluded that increases in phytoplankton are responsible for the increase in abundance and diversity of copepods in the Magellan region. Subsequently, Antezana (1999) and Hamamé & Antezana (1999) also found an association between phytoplankton blooms and the abundance of holo- and meroplanktonic larvae.

By contrast, the lowest densities of phytoplankton (Avaria *et al.*, 1999), zooplankton (Palma & Aravena, 1999) and jellyfish were registered in the areas with higher contribution of SAAW to the interior region through the western mouth of the Magellan Strait and the numerous oceanic channels (*i.e.* Cockburn, Ballenero and Beagle channels), which connect the adjacent Pacific with the interior waters.

The results obtained here show a level of species richness of jellyfish (27 species) very similar to that recorded previously for the same geographic area (29 species) (Pagès & Orejas, 1999). However, we have found an increase in jellyfish biodiversity, as we have identified 12 species not previously recorded in this area. This difference may explain why our sampling covered a wider geographical area than Pagès & Orejas (1999). Consequently, the number of jellyfish registered in the Magellan region has now increased to 41 species.

The medusae abundance levels indicate the presence of six dominant species, representing good repartition of habitat in the Magellan region. Of this group of jellyfish, the most abundant species was *Clytia simplex* (19.8%), which is very frequent and abundant in the Chilean Patagonian ecosystem from Puerto Montt to Cape Horn, mainly in the surface layer (0-50 m) (Galea, 2007; Palma *et al.*, 2007a, 2007b, 2011; Villenas *et al.*, 2009; Bravo *et al.*, 2011). In the Magellan region, *C. simplex* was found in areas with water temperatures associated to SAAMW, and its abun-

dance in low-salinity interior waters suggests a marked euryhaline nature. Pagès & Orejas (1999) show that *C. simplex* is one of the three most abundant species in the Magellan region. In southeastern Pacific Ocean, this species has a wide geographic distribution in the Humboldt Current System (HCS) where it is very common and frequent in coastal waters, mainly in upwelling areas, such as those of Antofagasta, Valparaíso and Concepción (Fagetti, 1973; Palma, 1994; Palma & Rosales, 1995; Pagès *et al.*, 2001; Palma & Apablaza, 2004; Apablaza & Palma, 2006; Pavez *et al.*, 2010).

Rhopalonema funerarium (16.2%) was collected for the first time in interior waters of Chilean Patagonia. In the HCS this species was recorded for the first time near the Juan Fernández Archipelago (Fagetti, 1973). *R. funerarium* is widely distributed in the Atlantic and Indian oceans, and more scattered in the Pacific Ocean (Kramp, 1965).

Aurelia sp. is one of the most widely distributed scyphozoan genera, ranging from 70°N and 55°S (Dawson & Martin, 2001); however, in the southern Pacific Ocean it is only recorded in inland waters of southern Chile (Pagès & Orejas, 1999; Häussermann *et al.*, 2009). Recently, Häussermann *et al.* (2009) identified the jellyfish and polyps of Aurelia sp. in different stations located in the Messier Channel at the Central Patagonian Zone (47°58'-49°08'S) and Pagès & Orejas (1999) did not found this jellyfish in the Magellan region. Therefore, it is very is important to highlight the abundance of the moon jelly Aurelia sp. (15.9%) in the same area.

Bougainvillia muscoides (15.5%) has been collected mainly in the Chilean Patagonian interior waters (Galea, 2007; Galea *et al.*, 2007; Palma *et al.*, 2007a, 2007b, 2011; Bravo *et al.*, 2011). In the Magellan region, this species was not collected by Pagès & Orejas (1999), and this therefore constitutes the first record in this region. In other marine regions *B. muscoides* has been recorded in Northwestern Europe, North Pacific, Gulf of Siam, Bismarck Sea and New Zealand (Bouillon, 1995).

Proboscidactyla stellata (8.9%) has mainly been collected in inland waters of the Chilean Patagonian ecosystem (Galea, 2007; Galea *et al.*, 2007; Palma *et al.*, 2007a, 2007b, 2011; Bravo *et al.*, 2011). In the HCS, *P. stellata* was recorded only off Antofagasta (23°S) by Palma & Apablaza (2004). In the Magellan region, this species were not collected by Pagès & Orejas (1999), therefore the numerous individuals collected in this study constitute the first record in this southern region. *P. stellata* has been recorded from the North Atlantic Ocean, Southeast Atlantic, Indian and Pacific oceans (Kramp, 1961, 1968; Bouillon, 1999).

Finally, Obelia spp. (8.5%) was also found in areas with water temperatures associated with SAAMW, and its abundance in low-salinity interior waters suggests a marked euryhaline nature. In the Chilean Patagonian Ecosystem it is widely distributed from Puerto Montt to Cape Horn, mainly in the surface layer (0-50 m) (Galea, 2007; Palma et al., 2007a, 2007b, 2011; Villenas et al., 2009; Bravo et al., 2011). In the Magellan region, Pagès & Orejas (1999) showed that C. simplex and Obelia spp. were two of the most abundant species and these authors show that the specimens of Obelia spp. that were collected probably correspond to O. geniculata or O. bidentata. In the southeastern Pacific Ocean, Obelia spp. is widely distributed in the HCS as C. simplex, mainly in coastal waters in upwelling areas, such as those of Antofagasta, Valparaíso and Concepción (Fagetti, 1973; Palma, 1994; Palma & Rosales, 1995; Pagès et al., 2001; Palma & Apablaza, 2004; Apablaza & Palma, 2006; Pavez et al., 2010). Jellyfish of the Obelia genus are very frequent, abundant and widespread medusae. Bouillon & Boero (2000) recognized five species of Obelia distributed throughout the world (O. bidentata, O, geniculata, O. dichotoma, O. fimbriata, O. longissima); however, the medusae of this genus are all very similar in morphology, such that connection with their hydroid stage is almost impossible and often unreliable.

In general, most of the non-dominant medusae species occurred in low quantities, which is very common in zooplankton communities. Dominance by a few and highly aggregated species is considered typical of zooplankton communities, and it is also a common characteristic in the inland waters of the Chilean Patagonia (Guglielmo & Ianora, 1995, 1997; Palma & Silva, 2004). Most jellyfish species identified in the Magellan region are common in the Chilean Patagonian ecosystem, which spans slightly more than 1000 km in a straight line from Puerto Montt (41°30'S) to Cape Horn (*ca.* 56°S) (Galea, 2007; Palma *et al.*, 2007a, 2007b, 2011; Villenas *et al.*, 2009; Bravo *et al.*, 2011).

The vertical patterns distribution of the dominant species: *Clytia simplex, Aurelia* sp., *Bougainvillia muscoides, Proboscidactyla stellata,* showed that their presence and higher abundance occurred throughout the water column in association with all strata. CCA plots showed that these species were located in the center of the diagram, indicating that a relatively large proportion of station-to-station variances in the abundance of these species were associated with the different conditions represented by the environmental variables measured. *Obelia* spp., another dominant species, was collected mainly in the upper layer (0-50 m), was negatively correlated with depth and salinity, and positively correlated with dissolved oxygen.

Rhopalonema funerarium, also a dominant species, was positively correlated with depth strata and temperature, and negatively with salinity and dissolved oxygen (Fig. 6).

Finally, in general, we found the highest abundance of jellyfish in some semi-closed areas of lower temperature and salinity, *i.e.*, the Almirantazgo and Agostini fjords (Valdenegro & Silva, 2003), where the majority of dominant species showed high population densities, such as *Clytia simplex*, *R. funerarium*, *B. muscoides* and *Obelia* spp. (Fig. 3). This suggests that these areas can be considered important in the reproduction and retention of organisms, because they have high phytoplankton productivity (Avaria *et al.*, 1999), which favors food availability (copepods, and larvae) for these gelatinous carnivores. Palma & Aravena (2001) also found high concentrations of eudoxids (reproductive phase) of siphonophores in the same areas.

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REFERENCES

- Antezana, T. 1999. Plankton of souththern Chilean fjords: trends and linkages. In: W.E. Arntz & C. Ríos (eds.). Magellan-Antarctic: ecosystems that drifted apart. Sci. Mar., 63(Suppl. 1): 69-80.
- Antezana, T., L. Guglielmo & E. Ghirardelli. 1992. Microbasins within the Strait of Magellan affecting zooplankton distribution. In: V.A. Gallardo, O. Ferretti & H. Moyano (eds.). Oceanografia in Antartide. ENEA, Italy-Centro EULA Chile, Ediciones Documentas, Santiago, pp. 453-458.
- 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.

- Avaria, S., C. Cáceres, P. Castillo & P. Muñoz. 1999. Distribución del microfitoplancton marino en la zona estrecho de Magallanes-Cabo de Hornos, Chile, en la primavera de 1998 (Crucero Cimar 3 Fiordos). Cienc. Tecnol. Mar, 26(2): 79-96.
- Bouillon, J. 1995. Hydromedusae of the New Zealand Oceanographic Institute (Hydrozoa, Cnidaria). N.Z. J. Zool., 22: 223-238.
- Bouillon, J. 1999. Hydromedusae. In: D. Boltovskoy (ed.). South Atlantic Zooplankton. Backhuys Publishers, Leiden, 1: 385-465.
- Bouillon, J. & F. Boero. 2000. Synopsis of the families and genera of the Hydromedusae of the world, with a list of the worldwide species. Thalas. Salentina, 24: 47-296.
- Bravo, V., S. Palma & N. Silva. 2011. Seasonal and vertical distributional patterns of medusae in Aysén region, southern Chile. Lat. Am. J. Aquat. Res., 39(2): 359-377.
- Brotz, L., W.W.L. Cheung, K. Kleisner, E. Pakhomov & D. Pauly. 2012. Increasing jellyfish populations: trends in Large Marine Ecosystems. Hydrobiologia, 690(1): 3-20.
- Carpenter, J. 1965. The Chesapeake Bay Institute Technique for the Winkler dissolved oxygen method. Limnol. Oceanogr., 10: 141-143.
- Clarke, K.R. & R.H. Green. 1988. Statistical design and analysis for a 'biological effects' study. Mar. Ecol. Prog. Ser., 46: 213-226.
- Clarke, K.R. & R.M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. Primer-E, Plymouth Marine Laboratory, Plymouth, 176 pp.
- Dawson, M.N. & L.E. Martin. 2001. Geographic variation and ecological adaptation in *Aurelia* (Scyphozoa: Semaeostomeae): some implications from molecular phylogenetics. Hydrobiologia, 451: 259-273.
- Fagetti, E. 1973. Medusas de aguas chilenas. Rev. Biol. Mar., Valparaíso, 15(1): 31-75.
- Galea, H.R. 2007. Hydroids and hydromedusae (Cnidaria: Hydrozoa) from the fjords region of southern Chile. Zootaxa, 1597: 1-116.
- Galea, H.R., V. Häussermann & G. Försterra. 2007. Hydrozoa, fjord Comau, Chile. Check List, 3(2): 151-167.
- Guglielmo, L. & A. Ianora (eds.). 1995. Atlas on marine zooplankton. Straits of Magellan. Copepods. Springer-Verlag, Berlin, 279 pp.
- Guglielmo, L. & A. Ianora (eds.). 1995. Atlas on marine zooplankton. Straits of Magellan. Amphipods,

Euphausiids, Mysids, Ostracods and Chaetognaths. Springer-Verlag, Berlin, 275 pp

- Hamamé, M. & T. Antezana. 1999. Chlorophyll and zooplankton in micro basins along the Straits of the Magellan-Beagle Channel passage. In: W.E. Arntz & C. Ríos (eds.). Magellan-Antarctic: ecosystems that drifted apart. Sci. Mar., 63(Suppl. 1): 35-42.
- Häussermann, V., M.N. Dawson & G. Försterra. 2009. First record of the moon jellyfish, *Aurelia* for Chile. Spixiana, 32: 3-7.
- Kramp, P.L. 1961. Synopsis of the medusae of the world. J. Mar. Biol. Ass. U.K., 40: 1-469.
- Kramp, P.L. 1965. The Hydromedusae of the Pacific and Indian Oceans. Dana Rep., 63: 1-162.
- Kramp, P.L. 1968. The Hydromedusae of the Pacific and Indian Oceans. Sections II and III. Dana Rep., 72: 1-200.
- Leps, J. & P. Smilauer. 2003. Multivariate analysis of ecological data using CANOCO. Cambridge University Press, Cambridge, 269 pp.
- Mazzocchi, M.G. & I. Ianora. 1991. A faunistic study of the copepods assemblages in the Straits of Magellan. Bol. Oceanol. Teor. Appl., 9(Spec. Issue 2-3): 163-177.
- Mianzan, H.W., J. Quiñones, S. Palma, A. Schiariti, E.M. Acha, K.L. Robinson & W.M. Graham. 2014. *Chrysaora plocamia*: a poorly understood jellyfish from South American waters. In: K.A. Pitt & C.H. Lucas (eds.). Jellyfish blooms. Springer, Dordrecht, pp. 219-236.
- Mills, C. 2001. Jellyfish blooms: are populations increasing globally response to changing ocean conditions? Hydrobiology, 451: 55-68.
- Oliveira, O.M.P., E.M. Araujo, P. Ayón, C.M. Cedeño-Posso, A.A. Cepeda, P. Córdova, H.R. Galea, G.N. Genzano, M.A. Haddad, H.W. Mianzan, A.E. Migotto, L.S. Miranda, T.P. Miranda, A.C. Morandini, R.M. Nagata, K.B. Nascimento, M. Nogueira Jr., S. Palma, J. Quiñones, C.S. Rodriguez, F. Scarabino, A. Schiariti, V.B. Tronolone & A.C. Marques. 2014. Census of Cnidaria (Medusozoa) and Ctenophora from South American marine waters. Zootaxa (in press).
- Pagès, F. & C. Orejas. 1999. Medusae, siphonophores and ctenophores of the Magellan region. Sci. Mar., 63(Suppl.): 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. Composición y distribución del macroplancton gelatinoso recolectado frente a la costa

central de Chile. Rev. Biol. Mar., Valparaíso, 29(1): 23-45.

- Palma, S. & P. Apablaza. 2004. Abundancia estacional y distribución vertical del zooplancton gelatinoso carnívoro en un área de surgencia en el norte del Sistema de la Corriente de Humboldt. Invest. Mar., Valparaíso, 32(1): 49-70.
- Palma, S. & G. Aravena. 2001. Distribución de quetognatos, eufáusidos y sifonóforos en la región magallánica. Cienc. Tecnol. Mar, 24: 47-59.
- Palma, S. & S. Rosales. 1995. Composición, abundancia y distribución estacional del macroplancton de la bahía de Valparaíso. Invest. Mar., Valparaíso, 23: 49-66.
- 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. Hydromedusae (Cnidaria) of the Chilean southern channels (from Corcovado Gulf to 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): 71-82.
- Palma, S., M.C. Retamal, N. Silva & C. Silva. 2014. Siphonophores spatial and vertical distribution and its relation with oceanographic conditions in Patagonian fjords, southern Chile. Sci. Mar., 78(3): 339-351.
- 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): 60-71.
- Pavez, M.A., M.E. Landaeta, L.R. Castro & W. Schneider. 2010. Distribution of carnivorous gelatinous zooplankton in the upwelling zone of central Chile (austral spring 2001). J. Plankton Res., 32(7): 1051-1065.
- Purcell, J.E., S. Uye & W.T. Lo. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar. Ecol. Prog. Ser., 350: 153-174.
- Riascos, J.M., V. Villegas & A.S. Pacheco. 2014. Diet composition of the large scyphozoan jellyfish *Chrysaora plocamia* in a highly productive upwelling center of northern Chile. Mar. Biol. Res., 10(8): 791-798.
- Sievers, H. & N. Silva. 2008. Water masses and circulation in austral Chilean channels and fjords. In: N. Silva & S. Palma (eds.). Progress in the oceanographic knowledge of Chilean interior waters, from Puerto Montt to Cape Horn. Comité Oceanográfico

Nacional-Pontificia Universidad Católica de Valparaíso, Valparaíso, pp. 53-58.

- Silva, N. & S. Palma (eds.). 2008. Progress in the oceanographic knowledge of Chilean interior waters, from Puerto Montt to Cap Horn. Comité Oceanográfico Nacional - Pontificia Universidad Católica de Valparaíso, Valparaíso, 161 pp.
- Ter Braak, C.J.F. & P.F.M. Verdonschot. 1995. Canonical correspondence-analysis and related multivariate methods in aquatic ecology. Aquat. Sci., 57: 255-289.
- Valdenegro, A. & N. Silva. 2003. Caracterización física y química de la zona de canales y fiordos australes de Chile entre el estrecho de Magallanes y cabo de Hornos (Cimar 3 Fiordo). Cienc. Tecnol. Mar, 26(2): 19-60.

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- Villenas, F., D. Soto & S. Palma. 2009. 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.
- Viviani, C. 1979. Ecografía del litoral chileno. Stud. Neotrop. Fauna Environ., 14: 65-123.
- Weiss, R. 1970. The solubility of nitrogen, oxygen and argon in water and sea water. Deep-Sea Res., 17: 721-735.