Seasonal and vertical distributional patterns of siphonophores and medusae in the Chiloé Interior Sea, Chile

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ABSTRACT

The horizontal and vertical distribution of jellyfish was assessed in the Chiloé Inland sea, in the northern area of the Chilean Patagonia. A total of 41 species of cnidarians (8 siphonophores, 31 hydromedusae, 2 scyphomedusae) were collected. Eleven jellyfish species were recorded for the first time in the area. Species richness was higher in spring than in winter (37 vs. 25 species, respectively). Species such as *Muggiaea atlantica*, *Solmundella bitentaculata*, and *Clytia simplex* were extremely abundant in spring. The total abundance (408,157 ind 1000 m^{-3}) was 18 times higher in spring than in winter (22,406 ind 1000 m^{-3}).

The horizontal distribution of the most abundant species (four in winter, five in spring) showed decreasing abundances in the north–south direction in winter and spring. Peak abundances occurred in the northern microbasins (Reloncaví Fjord, Reloncaví and Ancud gulfs), where the water column stability, phytoplankton and zooplankton abundance were higher, compared with the southern microbasins (Corcovado Gulf, Boca del Guafo). During the spring higher jellyfish abundance season, the vertical distribution of the dominant species (except *M. atlantica*) showed peak values at mid-depth (30–50 m) and in the deepest sampled layer (50–200 m). This vertical distribution pattern reduced seaward transport in the shallowest layer through estuarine circulation and also limited mortality by predation in the more illuminated shallow layers. Thus, jellyfish were able to remain in the interior waters during the season of maximum biological production.

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1. Introduction

In recent decades, a notorious increase of gelatinous predator populations (cnidarians and ctenophores) has been observed in several marine ecosystems (Brodeur et al., 2002; Mills, 2001). These organisms are known to be voracious predators that may affect the web structure and dynamics of the pelagic community by consuming a wide variety of herbivorous zooplankters and fishes in early life stages and, on some occasions, by competing with the latter for food (Boltovskoy, 1999; Matsakis and Conover, 1991; Purcell, 1997). Jellyfish are also prey for a number of predators such as ctenophores, medusae, fishes, and turtles (Mills, 1995). However, studies on these gelatinous plankton groups have been scarce in some southern high-latitude areas due to an overall scarcity of oceanographic information on the region and difficult access that limits research, especially during periods of harsher environmental conditions. Interestingly, the pristine waters in some of these zones (e.g., the Chilean Patagonia) have

attracted new ventures in aquaculture activities in recent years. Information on the presence and seasonal variability of gelatinous zooplankton groups in these areas, which are also spawning and nursery areas for economically important demersal fishes, prior to and during the current massive development of human settlements and aquaculture farms is necessary to elucidate the role gelatinous organisms play in ecosystem functioning at different times of the year, especially considering the contrasting primary productivity observed between seasons.

The complex fjord and channel system in austral Chile extends from Reloncaví Fjord (41°31′S) to Cape Horn (55°S); these 84,000 km of coastline encompass the contours of more than 3300 islands (Silva and Palma, 2008). The area from the northern part of this region (Reloncaví Fjord) to Boca del Guafo passage (43°30′S) farther south, and from Chiloé Island (8350 km^2) eastward to the continent is known as the Chiloé Interior Sea. This area has a surface of around 15,800 km^2 and maximum depths reaching down to 480 m in Comau Fjord (Silva et al., 2009). Two microbasins exist in this interior sea: the northern one is made up of Reloncaví Fjord and Reloncaví and Ancud gulfs, and the southern one by Corcovado Gulf and Boca del Guafo. These microbasins are interconnected by narrow passages between

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islands, some of which constitute bathymetric constrictions and sills. One of the main constrictions is the Desertores passage (5 km wide, and 200 m maximum depth). The Chiloé Interior Sea exchanges waters with the adjacent Pacific Ocean through the narrow (4 km), shallow (50 m depth) Chacao Channel to the north and through the wide (66 km), deeper (150 m depth) Boca del Guafo passage to the south (Fig. 1).

The environmental conditions in the microbasins to the north and south of the Desertores Islands are different. The northern microbasin has a highly stratified water column due to a conspicuous low salinity layer at the surface (<30 m) resulting from rain, freshwater runoff, rivers, and melting ice. As this upper layer flows out of the Chiloé Interior Sea towards the ocean, it also exports a large fraction of the primary production that occurs in the interior sea. In turn, sea water enters the northern microbasin through a subsurface flow that is also capable of importing zooplankton organisms from the adjacent oceanic shelf waters (Palma and Silva, 2004). This two-layer estuarine system affects the taxonomic composition, horizontal and vertical plankton distribution, and diel vertical migration of different cnidarian species (Palma et al., 2007b). North of the Desertores Islands, chlorophyll-a and plankton production are high, phytoplankton blooms are recurrent (Iriarte et al., 2007), and reports indicate high biomass of copepods, euphausiids, and gelatinous plankton groups. South of these islands, in the southern microbasin, the vertical stratification is less pronounced and chlorophyll-a values are usually lower (Palma and Silva, 2004; Ramírez and Pizarro, 2005).

In the Chiloé Interior Sea ecosystem, gelatinous organisms constitute an important fraction of the plankton biomass in the shallower 200 m layer in spring (Palma and Rosales, 1997; Villenas et al., 2009a). No information is available on their taxonomic composition, abundance, or distribution in other seasons, when environmental conditions change drastically. In this study, we compare the composition, abundance, and distribution of jellyfish in winter with those in the springs of the same (2006) and previous years. This information constitutes a baseline for future comparisons, as environmental conditions are expected to vary, either due to the effect of anthropogenic impacts or to larger scale environmental changes.

2. Materials and methods

Oceanographic data and zooplankton samples were obtained from the CIMAR 12 Fiordos cruise carried out in winter (8–24 July) and spring (3–13 November) 2006 between Reloncaví Fjord (41°31′S) and Boca del Guafo (43°39′S). During each cruise, we analyzed a longitudinal transect that included 14 (winter) and 18 (spring) oceanographic stations (Fig. 1). The oceanographic data compiled included temperature, salinity, and dissolved oxygen measured with a Seabird 25 CTDO. Bathymetric information was obtained from the nautical charts of the hydrographic and oceanographic service of the Chilean navy (charts 7400, 7410, 7330, 7320, 7300).

Zooplankton samples were collected from three strata (surface: 0–25 m, middle: 25–50 m, and deep: 50–200 m, depending on bottom depth) through oblique tows with a Tucker trawl net (300 μm mesh; 1 m² mouth opening) equipped with a flowmeter. Depth strata were selected considering the two-layer hydrographic structure that characterizes the interior waters (Silva et al., 1997, 1998). The zooplankton samples were preserved immediately on board in 5% buffered formaldehyde.
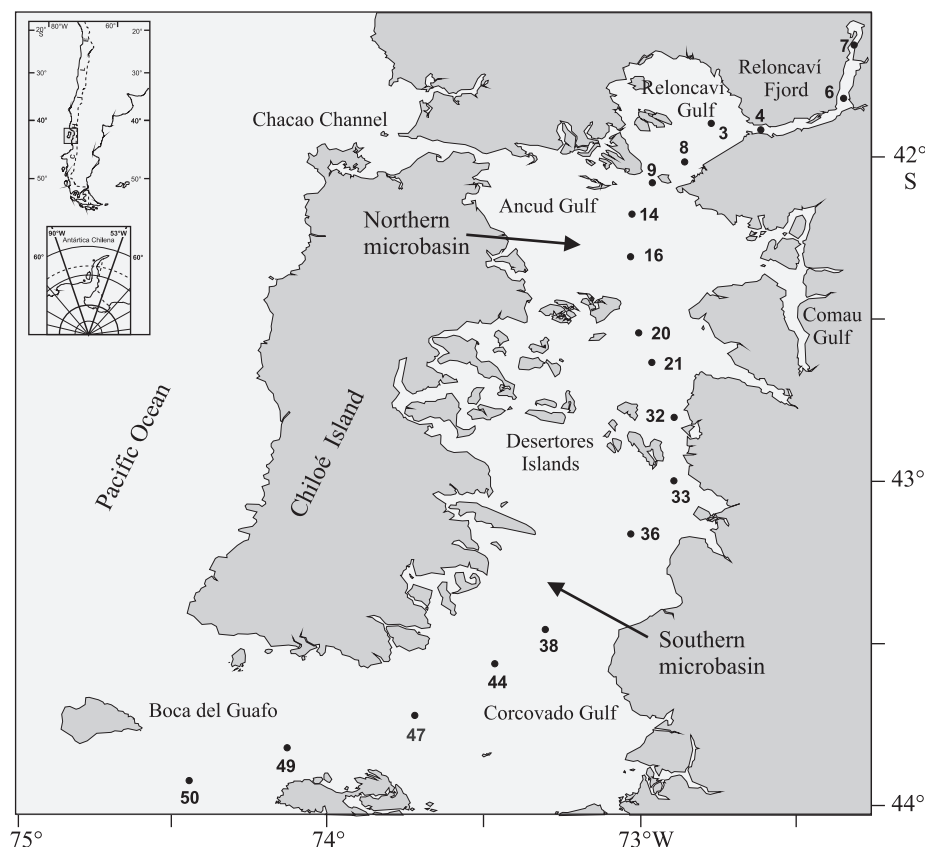

Fig. 1. Study area and locations of sampling stations in a longitudinal section between Reloncaví Fjord and Boca del Guafo (CIMAR 12 Fiordos cruise).

All siphonophores and medusae from the 39 samples were sorted, identified, and counted. The Calycophorae abundance was estimated considering the highest number of anterior and posterior nectophores. The only Physonectae recorded was *Pyrostephos vanhoeffeni*. Since no pneumatophores were found, we estimated their abundance considering the number of nectophores collected in the samples, with a maximum of 10 per colony (Totton, 1965). Calculations of total abundance (ind 1000 m^3) over all stations, mean abundance per station, and frequency of occurrence in the samples included all zooplankton net tows performed. The vertical distribution was expressed as the percentage of organisms in each layer over the total organisms collected at a single station. Vertical distributions were then presented along with the salinity data, as this is the hydrographic characteristic that varies most in the vertical plane of the interior waters.

The weighted mean depth (WMD) of the vertical distribution of dominant species was calculated according to Pearre (1973):

$$WMD = \frac{\Sigma n_i d_i}{\Sigma n_i}$$

where d is the median depth of stratum i and n_i the number of specimens collected in that stratum.

3. Results

3.1. Hydrological seasonal fluctuations

3.1.1. Winter cruise

The water column of Reloncaví Fjord was highly stratified, with lower temperatures (8–10 °C) and salinities (3–32 psu), but higher dissolved oxygen (5–8 mL L^{-1}) in the surface layer (0–25 m) (Fig. 2A). The deep layer was warmer, more saline, and less oxygenated (11.0–11.3 °C; 32.0–32.6 psu; 3–5 mL L^{-1}). The Reloncaví and Ancud gulfs were also stratified, but less so than Reloncaví Fjord. Their surface layer was cooler (10.5–11.3 °C) and less saline (32.0–32.5 psu), but showed higher dissolved oxygen (5–6 mL L^{-1}), whereas the deep layer was warmer, more saline, and less oxygenated (11.0–11.5 °C; 32.0–32.6 psu; 4–5 mL L^{-1}) (Fig. 2A).

Around the Desertores Islands and in Corcovado Gulf, the whole water column was quasi-homogeneous in temperature (~10.5 °C), salinity (~32.5 psu), and dissolved oxygen (~6 mL L^{-1}) (Fig. 2A).

3.1.2. Spring cruise

The water column of Reloncaví Fjord was again stratified, with higher temperatures (11–13 °C) and dissolved oxygen (5–8 mL L^{-1})
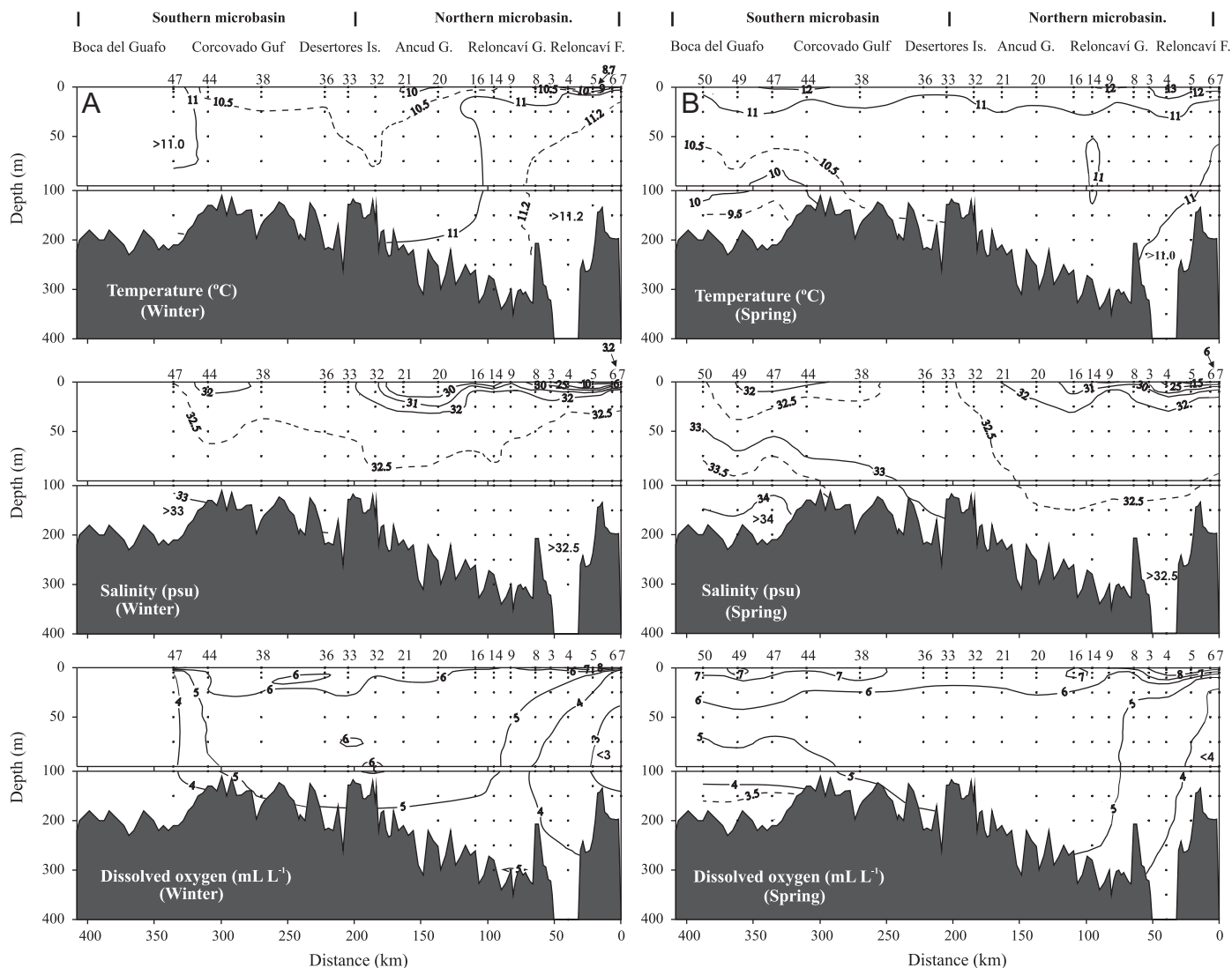

Fig. 2. Vertical distribution of temperature, salinity and dissolved oxygen in a longitudinal section between Reloncaví Fjord and Boca del Guafo: (A) winter 2006 and (B) spring 2006.

Table 1
Stations mean, total abundance, percentage and frequency of cnidarians collected in the study area.

Species	Stations mean (ind 1000 m^{-3})	Winter			Stations mean (ind 1000 m^{-3})	Spring		
		Total abundance (ind 1000 m^{-3})	Percentage (%)	Frequency (%)		Total abundance (ind 1000 m^{-3})	Percentage (%)	Frequency (%)
Siphonophora								
Abylopsis tetragona*	1.3	17	0.3	31	–	–	–	–
Dimophyes arctica*	–	–	–	–	5.6	101	0.0	22
Lensia conoidea*	8.9	116	1.9	38	47.0	846	0.3	56
Muggiaea atlantica*	431.3	5607	93.7	92	14210.2	255783	97.3	100
Pyrostephos vanhoeffeni*	3.4	44	0.7	46	174.9	3148	1.2	89
Sphaeronectes gracilis*	6.6	86	1.4	46	123.2	2218	0.8	78
Sphaeronectes fragilis*	8.2	107	1.8	46	37.1	667	0.3	50
Sphaeronectes irregularis	0.4	5	0.1	8	–	–	–	–
Total		5982				262763		
Hydromedusae								
Aequorea coerulescens	–	–	–	–	1.5	28	0.0	11
Aequorea globosa	-	–	–	-	2.5	45	0.0	22
Amphinema rugosum*	–	–	–	–	3.3	59	0.0	28
Amphogona apicata*	30.3	393	2.4	23	1215.3	21875	14.2	94
Bougainvillia macloviana	–	–	–	–	1.8	32	0.0	22
Bougainvillia muscoides*	805.1	10467	63.7	100	624.7	11245	7.3	100
Bougainvillia pyramidata*	–	–	–	–	357.0	6426	4.7	72
Clytia simplex*	1.3	17	0.1	15	2224.7	40044	25.9	100
Coryne eximia*	1.5	20	0.1	15	11.2	201	0.1	61
Cunina peregrina*	25.4	331	2.0	31	363.7	6546	4.5	44
Ectopleura dumortieri*	17.3	225	1.4	31	39.6	713	0.5	61
Euphysa aurata*	150.0	1951	11.9	62	203.3	3659	2.5	78
Halopsis ocellata*	–	–	–	–	47.4	854	0.6	56
Heterotiara minor*	–	–	–	–	53.5	963	0.6	83
Hydocodon chilensis*	1.3	17	0.1	23	54.7	984	0.6	83
Hydocodon unicus*	1.7	22	0.1	23	7.2	130	0.1	44
Hydractinia borealis*	156.9	2039	12.4	77	199.7	3594	2.1	94
Hydractinia minima	20.4	265	1.6	23	–	–	–	–
Hydractinia tenuis*	13.2	172	1.0	23	2.6	46	0.0	22
Laodicea undulata	–	–	–	–	212.7	3828	2.6	61
Laodicea pulchra	–	–	–	–	66.9	1203	0.8	67
Leuckartiara octona*	0.8	10	0.1	8	69.1	1244	0.9	100
Liriope tetraphylla	10.0	130	0.8	23	0.5	8	0.0	6
Modeeria rotunda*	0.3	3	0.0	8	17.1	308	0.2	83
Obelia spp.*	–	–	–	–	224.6	4042	2.8	78
Phialella quadrata*	–	–	–	–	32.4	584	0.4	44
Proboscidactyla mutabilis	–	–	–	–	13.4	242	0.2	39
Proboscidactyla ornata*	0.7	9	0.1	8	191.9	3455	2.4	56
Proboscidactyla stellata*	3.0	39	0.2	23	39.4	709	0.5	83
Solmundella bitentaculata*	0.5	7	0.0	15	2303.6	41464	28.5	100
Rophalonema velatum*	0.1	2	0.0	8	–	–	–	–
Total		16425				145296		
Scyphomedusae								
Chrysaora plocamia	–	–	–	–	5.2	93	94.9	28
Nausithoe rubra	–	–	–	–	0.3	5	5.1	6
Total						98		

Asterisk indicates the species recorded previously in the same area by Palma and Rosales (1997), Galea (2007), Galea et al. (2007) and Villenas et al. (2009a).
–: species not found.

and lower salinities (3–32 psu) in the surface layer (0–25 m) (Fig. 2B). The deep layer was colder, more saline, and less oxygenated (11.0–11.3 °C; 32.0–32.6 psu; 3–5 mL L^{-1}). The Reloncaví and Ancud gulfs were also stratified, but less so than Reloncaví Fjord, with a warmer surface layer (10.5–11.3 °C), higher dissolved oxygen (6–7 mL L^{-1}), and lower salinities (32.0–32.5 psu); the deep layer was colder, more saline, and less oxygenated (10.5–11.0 °C; 32.0–32.7 psu; 5–6 mL L^{-1}) (Fig. 2B).

Around the Desertores Islands and at Corcovado Gulf, the whole water column was quasi-homogeneous in temperature (10.5–11.0 °C), salinity (32.5–33.0 psu), and dissolved oxygen (5–6 mL L^{-1}). Boca del Guafo was less stratified than Reloncaví Fjord, with a warmer surface layer (11.0–12.0 °C), higher dissolved oxygen (6–7 mL L^{-1}), and lower salinities (32.0 to 32.5 psu); the deep layer was colder, more saline, and

less oxygenated (10.5–11.0 °C; 32.5–34.0 psu; 3–6 mL L^{-1}) (Fig. 2B).

3.2. Seasonal jellyfish distribution patterns

We identified 41 species of gelatinous organisms: eight siphonophores, 31 hydromedusae, and two scyphomedusae. A total of 11 cnidarian species were recorded for the first time in the study area (Table 1). Of all the species, 54% were recorded in both winter and spring; the rest were collected in just one of the two seasons. The species richness increased from 27 species in winter to 37 in spring. Although the number of species in winter was lower than in spring, diversity was only slightly higher in winter than in spring (Shannon–Weaver Index: 2.27 bits vs. 2.35 bits),

due principally to the peak abundances of the dominant species (*Muggiaea atlantica*, *Solmundella bitentaculata*, *Clytia simplex*, and *Amphogona apicata*). The total abundance was nearly 18 times greater in spring (408,157 ind 1000 m^{-3}) than in winter (22,406 ind 1000 m^{-3}). No association was found between winter and spring abundances of the most common species (Kendall Tau=0.214; P=0.274). Five species made up 92.78% of the total winter abundance. Meanwhile, in spring, 80.63% of the total abundance was accounted for by only three species. The abundances of two of these (*S. bitentaculata* and *C. simplex*) dropped below 1% in winter.

3.2.1. Winter cruise

Density values were low and highly variable, fluctuating between 45 and 8589 ind1000 m^{-3} at Sta. 20 and 7, respectively, with an average of 1772 ind1000 m^{-3}. In winter, the siphonophores (27%) were less abundant than the hydromedusae (73%), with averages of 459 and 1263 ind 1000 m^{-3}, respectively.

M. atlantica was the most abundant (94%) and frequent (92%) siphonophore, peaking at Sta. 14 in Ancud Gulf with a maximum of 1616 ind 1000 m^{-3} and an average of 431 ind 1000 m^{-3}. The greatest densities occurred in Seno Reloncaví and Ancud Gulf (northern microbasin) and decreased heavily towards Boca del Guafo (Fig. 3A).

In this period, the dominant hydromedusae were *Bougainvillia muscoides* (63.7%), *Hydractinia borealis* (12.2%), and *Euphysa aurata* (11.9%), with respective frequencies of 100%, 77%, and 62%. The geographic distribution pattern of *B. muscoides* was very similar to that of *M. atlantica*, although the density of the former was high in Reloncaví Fjord and low towards Boca del Guafo (Figs. 3A and 3B). On the other hand, the distribution of *H. borealis* and *E. aurata* was restricted mainly to the northern microbasin, with greater densities in Reloncaví Fjord, where the peaks were located, particularly of *E. aurata* (Figs. 3C and 3D).

3.2.2. Spring cruise

In spring, we observed a significant increment in species richness and jellyfish abundances. The density values were elevated and highly variable, ranging from 3721 to 78,581 ind1000 m^{-3} at Sta. 4 and 20, respectively, with an average density of 23,189 ind1000 m^{-3}. Unlike the wintertime situation, hydromedusae (37%) were less abundant than siphonophores (63%) in spring, with respective averages of 8591 and 14,598 ind1000 m^{-3}.

In spring, the predominance of *M. atlantica* (97.3%) was much greater than in winter and its abundance was extremely high, surpassing 4000 ind·1000 m^{-3} at all stations (Fig. 4A) and peaking at 45,954 ind 1000 m^{-3} at Sta. 20 in Ancud Gulf.

In spring, we found four dominant medusa species: *S. bitentaculata* (28.5%), *C. simplex* (25.9%), *A. apicata* (11.7%), and *B. muscoides* (7.3%). All had frequencies exceeding 94%, indicating extensive geographic coverage in the study area. *S. bitentaculata* and *A. apicata* presented the greatest concentrations in the northern microbasin, declining heavily towards the Corcovado Gulf and the Boca del Guafo, particularly *A. apicata*. The spatial distribution patterns of *C. simplex* and *B. muscoides*, however, were highly similar to that of *M. atlantica*, with high density cores at some stations in the northern microbasin (Figs. 4A–4E).

3.3. Vertical jellyfish distribution patterns

3.3.1. Winter cruise

The vertical distribution of the siphonophore *M. atlantica* deepened from north to south along the transect. In Reloncaví Fjord, specimens were concentrated in the first 25 m; in Reloncaví

and Ancud gulfs, they were found in the first 50 m; and south of the Desertores Islands, they were distributed beneath 50 m depth (Sta. 33–44) (Fig. 5A).

Of the hydromedusae, *B. muscoides* was located mostly under 50 m depth in the study area, except at some night stations where a greater density of individuals was found in the first 50 m. *H. borealis* was located principally in the first 50 m in Reloncaví fjord and Seno Reloncaví, but below 50 m depth in Ancud Gulf, except at the night stations. Finally, the vertical distribution pattern of *Euphysa aurata* was very similar to that of *H. borealis*: both species were collected nearly exclusively in the northern microbasin, where they also showed a deepening along the north–south gradient (Fig. 5A).

The weighted mean depth (WMD) of the dominant species changed in winter, with average values of around 30–35 m for each species. The greatest variation (37 m) was found for *E. aurata* (*M. atlantica*: 55–83 m, *B. muscoides*: 51–80 m, *E. aurata*: 50–87 m, *H. borealis*: 54–81 m).

3.3.2. Spring cruise

In spring, *M. atlantica* was distributed homogeneously in the water column regardless of the time of sampling. As in winter, we observed a deeper distribution at stations in the southern microbasin, with the greatest abundances found below 50 m, especially in the Boca del Guafo (Fig. 5B).

In general, *S. bitentaculata* preferred depths below 25 m at all stations. This species was found at greater depths (> 50 m) in Reloncaví Fjord and Gulf, between 25 and 50 m in the gulfs of Ancud and Corcovado, and then deepened again (> 50 m) in the Boca del Guafo (Fig. 5B).

C. simplex presented no defined vertical distribution pattern, but made use of a large part of the water column (Fig. 5B). *A. apicata* was scant in the surface layer (0–25 m), especially to the south of Corcovado Gulf and Boca del Guafo. In the north sector (Reloncaví Fjord and Gulf, part of Ancud Gulf), this species was distributed at greater depths (> 50 m) than in Corcovado Gulf (Fig. 5B).

Like *C. simplex*, *B. muscoides* presented a wide vertical distribution but revealed no defined pattern along the north–south gradient (Fig. 5B). Nonetheless, their largely overlapping distributions in the water column led us to believe that these two species must have highly similar ecological requirements (Fig. 5B).

The calculation of the WDM for spring showed no differences in the diurnal–nocturnal vertical distribution of any of the dominant species.

4. Discussion

4.1. Oceanographic characteristics

During the winter cruise, the vertical distribution of the physical and chemical variables in the area from Ancud Gulf to Reloncaví Fjord (Sta. 3 to 8) showed a highly stratified vertical structure consisting of two layers: a surface layer (20–30 m) with more variable temperatures and salinity and a deeper (> 30 m), quasi homothermal and homohaline layer. Around the Desertores Islands and in the north sector of Corcovado Gulf, the vertical structure was quasi-homogeneous, whereas in the south sector of Corcovado Gulf and Boca del Guafo, the water column was stratified, albeit less intensely than in the north zone.

The surface layer presented strong differences between the two seasons. In winter, the temperatures in Reloncaví Fjord were lower at the surface (< 10 °C) and higher at depth (~11 °C). In spring, on the other hand, the opposite occurred: temperatures
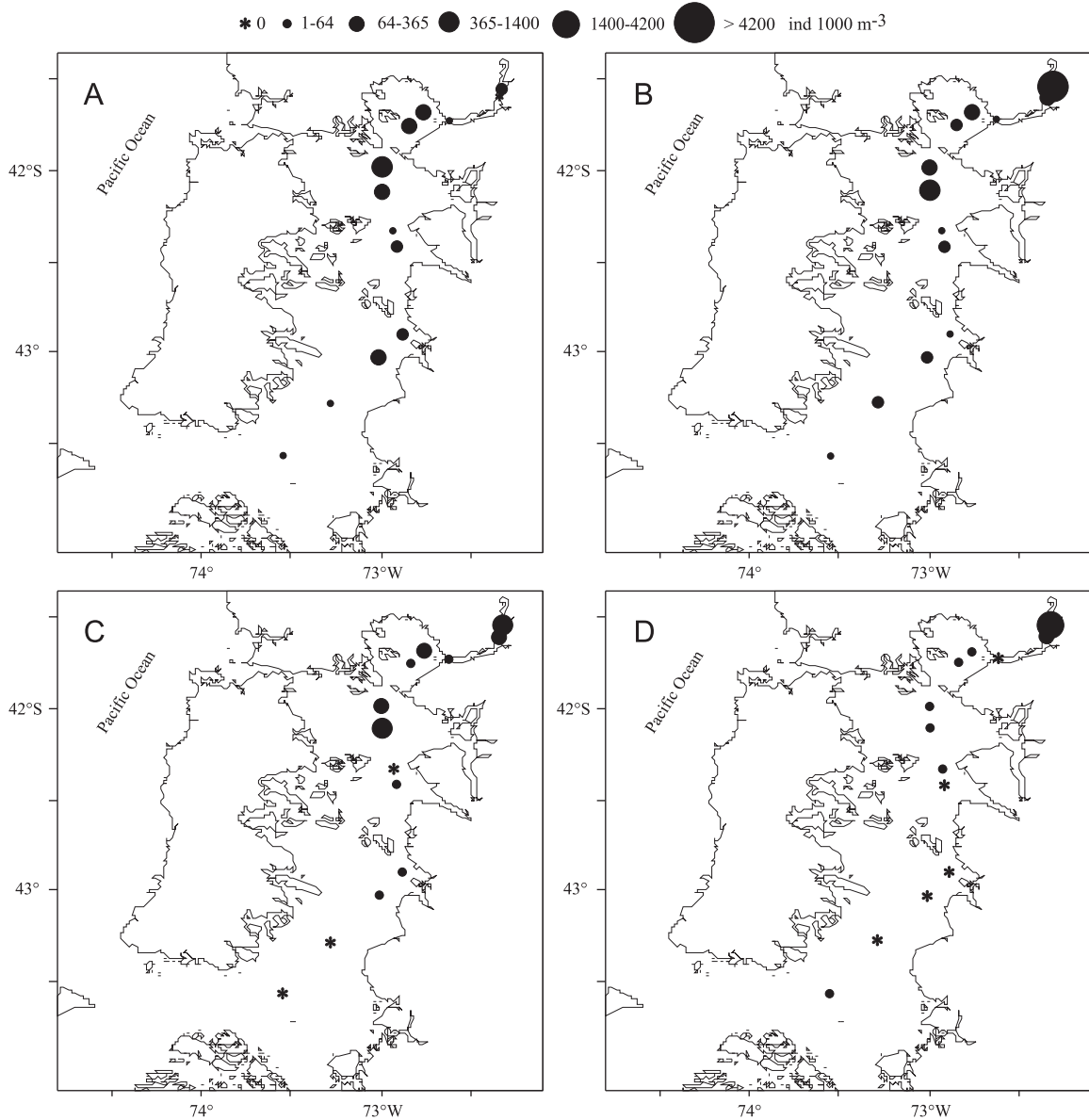
Fig. 3. Spatial distribution of dominant species in a longitudinal section between Reloncaví Fjord and Boca del Guafo (winter 2006): (A) *Muggiaea atlantica*, (B) *Bougainvillia muscoides*, (C) *Hydractinia borealis*, and (D) *Euphysa aurata*.

were higher at the surface ($>13\ °C$) and lower at depth ($\sim 11\ °C$) (Figs. 2A and 2B). This reversal was due to increased solar radiation and contributions of continental waters, which are cooler in winter and warmer in spring. The vertical structure of the deep layer (>30 m) was similar to that of winter.

In both seasons, salinities in the surface layer of Seno Reloncaví and Reloncaví Fjord remained lower (<20 psu) than at depth (>32 psu). This favored a stable vertical density structure that kept the colder surface water from sinking. The same situation has been observed at the heads of other austral Chilean fjords (e.g., Aysén and Cupquelán) that receive fluvial contributions (Silva et al., 1997).

Dissolved oxygen in the surface layer of Reloncaví Fjord and Seno Reloncaví was higher in spring ($>7\ mL\ L^{-1}$) than in winter ($>6\ mL\ L^{-1}$). In both seasons, dissolved oxygen dropped below $4\ mL\ L^{-1}$ beneath the surface layer, around 100 m (Figs. 2A and 2B), due to consumption caused by the degradation of autochthonous and allochthonous particulate organic matter

coming from the surface layer (Silva, 2008). As found at the head of Reloncaví Fjord, low dissolved oxygen concentrations have been recorded in Aysén Fjord and the Puyuguapi, Quitralco, and Cupquelán channels, all of which receive fluvial contributions carrying particulate organic matter (Silva et al., 1997).

The temperature, salinity, and dissolved oxygen of the water column around Desertores Islands presented a quasi-homogeneous vertical structure in both seasons (Figs. 2A and 2B). This structure is caused by the presence of the island group, which gives rise to various sills and constrictions/passages that generate increased turbulence, favoring vertical mixing and, therefore, the quasi-homogeneous vertical distribution of the analyzed variables.

In both seasons, Corcovado Gulf and Boca del Guafo presented a stratified vertical structure, although this was more defined in spring. This area is more exposed to the oceanic influence through Boca del Guafo, dampening the effect of freshwater. In the Ancud Gulf–Seno Reloncaví–Reloncaví Fjord region, a strong, two-layer,
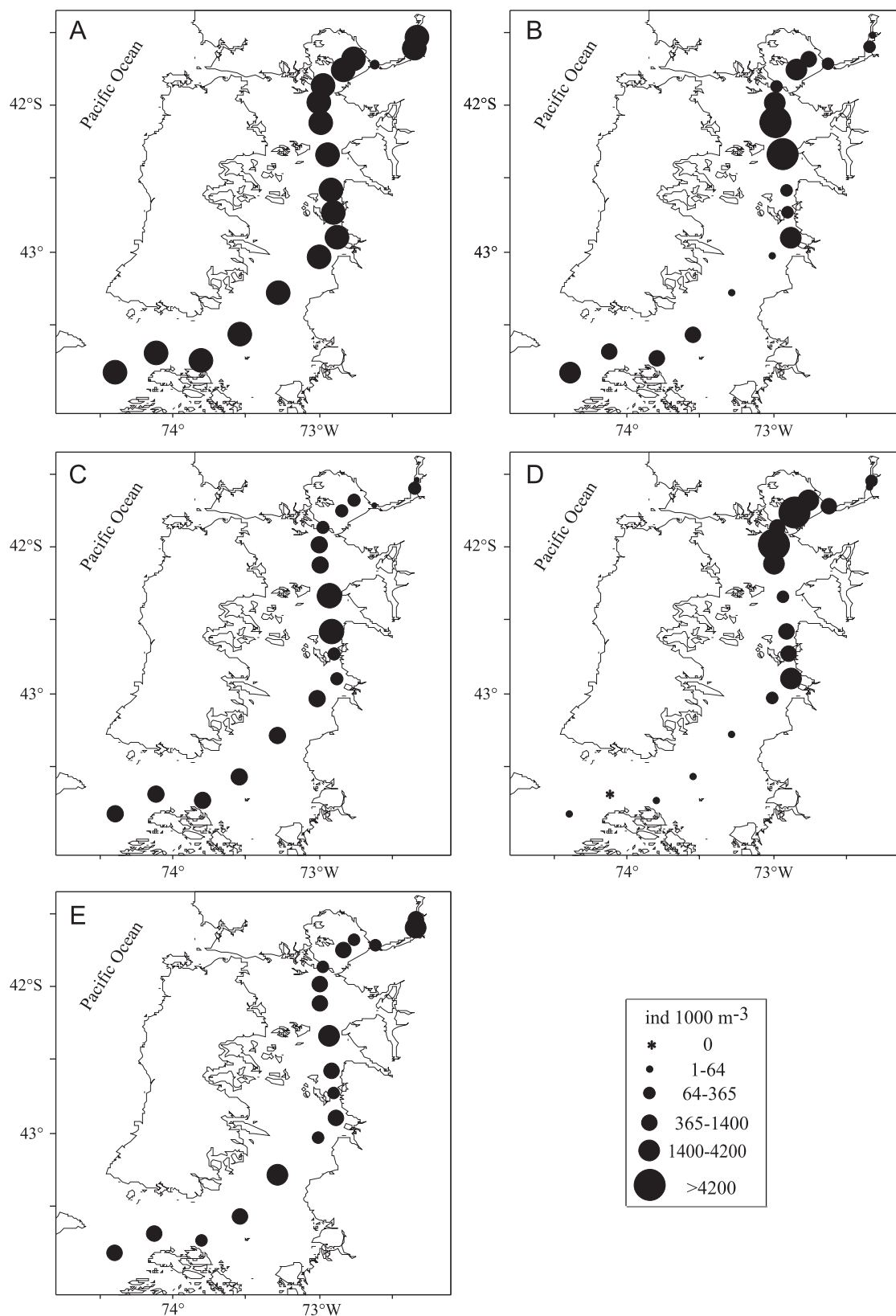
Fig. 4. Spatial distribution of dominant species in a longitudinal section between Reloncaví Fjord and Boca del Guafo (spring 2006): (A) *Muggiaea atlantica*, (B) *Solmundella bitentaculata*, (C) *Clytia simplex*, (D) *Amphogona apicata*, and (E) *Bougainvillia muscoides*.

highly stratified estuarine system occurs due to the proximity of continental fluvial contributions. Boca del Guafo receives equatorial subsurface waters coming from Peru. These deep waters enter the area from the upper shelf of the adjacent coastal zone and have low temperatures ($< 9\,^{\circ}$C) and dissolved oxygen ($< 4\,\mathrm{mL\,L^{-1}}$) and high salinity (> 34 psu) (Silva et al., 2009).
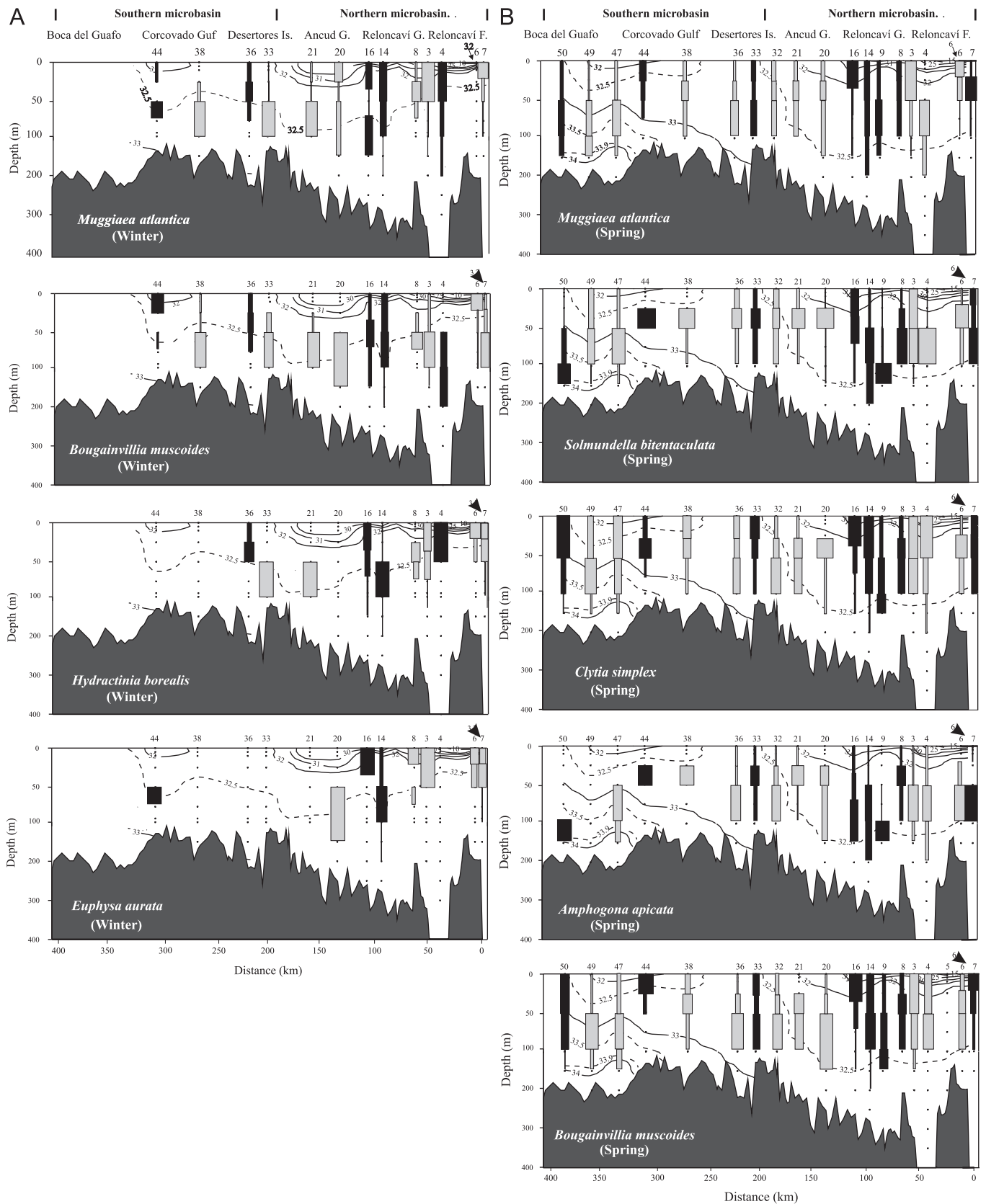
Fig. 5. Vertical distribution of dominant species in a longitudinal section between Reloncaví Fjord and Boca del Guafo: (A) winter 2006, and (B) spring 2006. Grey columns: diurnal hauls, black columns: nocturnal hauls.

4.2. Jellyfish species composition

Thirty of the 41 jellyfish species identified (73%) had been registered previously between Reloncaví Fjord and Boca del Guafo (Galea, 2007; Galea et al., 2007; Palma and Rosales, 1997; Villenas et al., 2009a). The addition of 11 new records for this vast interior zone (1 siphonophore, 8 hydromedusae, 2 scyphomedusae) (Table 1) significantly increments the richness of gelatinous species in this geographical area. Of these, the hydromedusa *Hydractinia minima* and the scyphomedusa *Nausithoe rubra* constituted new records of cnidarians in Chilean waters.

Despite the lower salinity in the surface layer (0–25 m) of the interior waters, especially in Reloncaví Fjord (4–32 psu), and with the exception of *Hydractinia borealis*, most of the dominant species (*Muggiaea atlantica*, *Amphogona apicata*, *Bougainvillia muscoides*, *Clytia simplex*, *Euphysa aurata*, *Solmundella bitentaculata*) are also common and abundant in the epipelagic subantarctic waters of the Humboldt Current System (HCS) (Fagetti, 1973; Kramp, 1966; Palma and Rosales, 1995; Palma and Silva, 2006; Ulloa et al., 2000).

The HCS is characterized by high biological productivity (Daneri et al., 2000). In spring and summer, when coastal upwelling events are more frequent and intense, thick aggregations of jellyfish take advantage of the elevated trophic availability. High densities of *M. atlantica*, *S. gracilis*, *Bassia bassensis*, *Aglaura hemistoma*, *Obelia* spp., and *S. bitentaculata* have been reported during the upwelling season in northern Chile off Antofagasta (Apablaza and Palma, 2006; Pagès et al., 2001; Palma and Apablaza, 2004). Likewise, in central Chile off Valparaíso, high densities of *M. atlantica*, *Sphaeronectes gracilis*, *Obelia* spp., *Clytia* spp., *A. hemistoma*, *Euphysa aurata*, *Ectopleura dumortieri*, *Liriope tetraphylla*, *Phialella quadrata*, and *S. bitentaculata* have also been recorded (Palma, 1994; Palma and Rosales, 1995; Palma and Silva, 2006; Ulloa et al., 2000).

The subantarctic species that enter through Boca del Guafo have euryhaline characteristics that allow them to adapt to estuarine water with low surface salinity, as is found in Reloncaví Fjord (Figs. 2A and 2B), where dense aggregations of gelatinous organisms have been observed in winter (Fig. 3) and spring (Fig. 4). These aggregations have been reported in several marine areas, where they are associated with density gradients, which are especially pronounced in fjords and estuaries (Graham et al., 2001). Nevertheless, although the remaining species caught in the interior waters (~30 species, Table 1) occur frequently in the HCS and sometimes at high densities (e.g., *Euphysa aurata*, *Leukartiara octona*, *Liriope tetraphylla*, *Obelia* spp., *Ropalonema velatum*) (Palma, 1994; Palma and Rosales, 1995), they have not been able to prosper or establish resident populations in interior waters, probably due to the low salinities typical of the superficial estuarine water and subantarctic modified water, which characterize the Chiloé Interior Sea (Sievers and Silva, 2008).

4.3. Seasonal distribution patterns of cnidarians

Of the 41 species registered, 54% were collected in both seasons, indicating important seasonal changes in species composition and abundance. These changes have two causes. The first is the reproductive cycle of the siphonophores and hydromedusae. In interior waters, this cycle occurs mainly in spring and summer. The intense period of asexual production is reflected in a high proliferation of organisms, particularly eudoxias of siphonophores (Palma and Aravena, 2001; Palma et al., 2007b). The second cause is trophic availability, which increases in spring as the main prey of the jellyfish follow the cycle of primary productivity (with peaks in spring and summer) (Iriarte

et al., 2007). In fact, for this same area and time of year, González et al. (2010) estimated values of integrated chlorophyll-*a* concentrations (0–25 m) that were two orders of magnitude higher in spring (52–447 mg Chl-*a* m^{-2}) than in winter (1–18 mg Chl-*a* m^{-2}).

The jellyfish were much more abundant in spring than in winter (ca. 18 times); this was more pronounced in siphonophores (44 times) than in hydromedusae (9.4 times) (Table 1).

In both seasons, we observed decreasing abundances along the north–south gradient, with greater densities in the northern microbasin (Reloncaví Fjord and Reloncaví and Ancud gulfs) and lower densities in the southern microbasin (Corcovado Gulf and Boca del Guafo). This latitudinal variation was related to the oceanographic characteristics of the water column in both basins. In the northern microbasin, the water column was more stable due to the steady contribution of continental freshwater that generated an intense halocline ($\sim$1.2 psu m^{-1}). On the other hand, in the southern microbasin, saltier, subantarctic water entered through Boca del Guafo, mixing with the estuarine water and giving rise to a less intense halocline ($\sim$0.02 psu m^{-1}), resulting in lower vertical stability in this microbasin (Silva et al., 1998). Such latitudinal variation (greater richness in the northern microbasin) has also been observed in the distribution of integrated chlorophyll-*a* (Ramírez and Pizarro, 2005), zooplanktonic biomass, and gelatinous biomass (Palma and Silva, 2004; Villenas et al., 2009a). This same latitudinal pattern was found in winter, suggesting that it could be permanent over time in this area. Consequently, the high seasonal and vertical oceanographic variability are likely to be determinant factors for species richness and the seasonal and vertical distribution patterns of southern Chile's planktonic community, as Guglielmo and Ianora (1995) suggested for the Magallanes Region.

Of the dominant species, *M. atlantica* was the most abundant siphonophore in both seasons, with a heavy increment in the population in spring, when environmental conditions are more favorable. *M. atlantica* is an eurythermal and euryhaline species that widely dominates the siphonophore community throughout the austral fjord and channel region stretching from Reloncaví Fjord to Cape Horn (Pagès and Orejas, 1999; Palma and Silva, 2004; Palma et al., 2007b; Villenas et al., 2009a, 2009b). In this vast area, the amount of eudoxias in spring can be two to six times greater than that of the nectophores (Palma and Aravena, 2001; Palma et al., 2007b). Moreover, this species is a common component in several coastal upwelling areas: the HCS off the Chilean coast (Pagès et al., 2001; Palma and Apablaza, 2004; Palma and Rosales, 1995; Palma and Silva, 2006; Ulloa et al., 2000), Benguela Current (Pagès and Gili, 1992), Agulhas Current (Thibault-Botha et al., 2004), and other upwelling areas elsewhere (Nogueira and Oliveira, 1991).

Of the remaining siphonophore species, *Dimophyes arctica*, *Lensia conoidea*, and *Pyrostephos vanhoeffeni* are frequent but not very abundant in the austral fjord and channel region (Pagès and Orejas, 1999; Palma and Silva, 2004; Palma et al., 2007b; Villenas et al., 2009a) and are found occasionally in the epipelagic waters of the HCS (Palma, 1986; Palma and Rosales, 1995).

The hydromedusae presented high species diversity (31 species) due to the springtime appearance of numerous meroplanktonic species whose contribution produces significant changes in the composition and spatial-temporal distribution. Compared to the siphonophores, the hydromedusae have been studied less in the estuarine ecosystems of fjords and channels. In fact, 26% of the species identified constitute new records for this area, significantly increasing the diversity of these conspicuous organisms between Reloncaví Fjord and Boca del Guafo. As with the siphonophores, we also identified an ensemble of species, to date, recorded exclusively in the interior waters: *Anphinema*

rugosum, *Bougainvillia macloviana*, *B. muscoides*, *B. pyramidata*, *Halopsis ocellata*, *Heterotiara minor*, *Hybocodon chilensis*, *H. unicus*, *Hydractinia borealis*, *H. tenuis* (=*H. minuta*), *Laodicea pulchra*, and *Modeeria rotunda* (Galea, 2007; Galea et al., 2007; Pagès and Orejas, 1999; Palma et al., 2007a, b; Villenas et al., 2009a).

In this area, occasional records exist of the polyp stages of *Clytia gigantea*, *C. hemispherica*, *C. noliformis*, and *Obelia dichotoma*; these were collected during the Lund University Chile Expedition (1948–1949) (Leloup, 1974). Later, Galea (2007) and Galea et al. (2007) identified the polyp and medusa stages collected in the Comau Fjord (42°10′S) and at some sites to the south of Penas Gulf (50–52°S), where they also found the planktonic stages of the dominant hydromedusae registered in our study (*A. apicata*, *B. muscoides*, *C. simplex*, *E. aurata*, *S. bitentaculata*). Those authors noted the abundances of *C. simplex* and *S. bitentaculata*, but indicated scant or null polyp stages. Given the limited polyp records, we were unable to relate the life cycle with the seasonal distribution of the dominant jellyfish in the study area.

The seasonal distribution and abundance of jellyfish are largely regulated by the factors that control their larval production (Boero et al., 2002, 2008). Temperature, food abundance, salinity, and the light/dark ratio affect the release of medusae from the hydroids (Arai, 1992). Therefore, several gelatinous species, including meroplanktonic hydromedusae and diphyid siphonophores, have rapid asexual reproductive processes and their populations respond rapidly to favorable environmental conditions (Alldredge, 1984). In the interior waters of southern Chile, high trophic availability has been determined in spring, when zooplanktonic biomass values are high (chitinous and gelatinous fractions) (Palma and Silva, 2004; Villenas et al., 2009a). Copepods constitute the main contribution to the biomass and, at the same time, are the main preys of the gelatinous carnivores (Purcell, 1997). This follows the seasonal high productivity cycles, in which spring maxima can be two orders of magnitude greater than those of winter, as González et al. (2010) found for the same geographic area and seasons.

When comparing the results obtained for this work (spring 2006) with those from the springs of 2004 and 2005 (Villenas et al., 2009a, 2009b), also carried out in November between Reloncaví Fjord and Boca del Guafo, we find relatively similar average densities for siphonophore species in all three years (Table 2), with high densities of *M. atlantica* recorded in 2005 and 2006. On the contrary, the results for the jellyfish show a sustained increase in abundance, particularly in 2006. Table 2 presents some 20 species whose average densities in 2006 exceeded those recorded in the springs of 2004 and 2005 by 100% and, in some cases (e.g., *A. apicata*, *C. simplex*, and *S. bitentaculata*), by much more. Moreover, we determined a heavy increment in the species diversity over time (19, 20, and 30 species in 2004, 2005, and 2006, respectively) (Table 2). Overall, jellyfish abundances have increase in recent years in different parts of the world. Said increments have been attributed to a variety of factors such as global warming, unspecified anthropogenic perturbation, or the removal of top predators from trophic networks (Boero et al., 2008; Brodeur et al., 2002; Mills, 1995, 2001). Nonetheless, the oceanographic evidence from our study zone does not allow us to confirm any of these possibilities, hindering our ability to draw concrete conclusions on this matter.

Similar seasonal fluctuations have also been observed in the interior waters of the Scandinavian fjords for some common species found in both hemispheres; the siphonophores *D. arctica* and *L. conoidea* are frequently present in Norwegian fjords, where summertime increments have been recorded for the hydromedusae *Bougainvillia muscoides*, *Euphysa aurata*, and *Obelia* spp. (Hosia and Bamstedt, 2007). As observed at high latitudes, the medusae of

Table 2
Mean abundance (ind 1000 m^{-3}) in the springs 2004 to 2006 between Reloncaví Fjord and Boca del Guafo.

Species	Spring		
	2004	2005	2006
Siphonophora			
Dimophyes arctica	–	–	6
Lensia conoidea	9	116	47
Muggiaea atlantica	2857	17127	14210
Pyrostephos vanhoeffeni	162	139	175
Sphaeronectes gracilis	108	75	123
Sphaeronectes fragilis	0	8	37
Hydromedusae			
Aequorea coerulescens	–	–	2
Aequorea globosa	–	–	3
Amphinema rugosum	–	3	3
Amphogona apicata	223	4	1215
Bougainvillia macloviana	–	–	2
Bougainvillia muscoides	137	52	625
Bougainvillia pyramidata	0	100	357
Clytia simplex	412	196	2225
Coryne eximia	–	–	11
Cunina peregrina	45	118	364
Ectopleura dumortieri	10	8	40
Euphysa aurata	9	–	203
Halopsis ocellata	4	16	47
Heterotiara minor	–	–	54
Hydocodon chilensis	1	17	55
Hydocodon unicus	5	12	7
Hydractinia borealis	35	14	200
Hydractinia minima	20	265	–
Hydractinia tenuis	343	5	3
Laodicea undulate	–	–	213
Laodicea pulchra	–	–	67
Leuckartiaria octona	29	14	69
Liriope tetraphylla	–	–	1
Modeeria rotunda	–	7	17
Obelia spp.	44	101	225
Phialella quadrata	–	–	32
Proboscidactyla mutabilis	–	–	13
Proboscidactyla ornata	32	6	192
Proboscidactyla stellata	5	1	39
Solmundella bitentaculata	530	271	2304
Rophalonema velatum	4	8	–
Scyphomedusae			
Chrysaora plocamia	–	–	5
Nausithoe rubra	–	–	0

Data of springs 2004 and 2005 Villenas et al. (2009a), and data of spring 2006 (present study).
–: species not found.

different species appear in a more or less predictable succession in the zooplanktonic community (Ballard and Myers, 2000; Hosia and Bamstedt, 2007).

In general, our results show that most of the species collected are common inhabitants of the austral Chilean fjord and channel ecosystems (Palma, 2008; Palma and Silva, 2004; Palma et al., 2007a, 2007b; Villenas et al., 2009a), where the predominant oceanographic conditions are low temperatures and sharp salinity gradients in the surface layer (0–25 m) due to the mixing of oceanic waters with interior waters coming from melting in the mountains and fluvial contributions. The community of planktonic cnidarians in the interior waters consists of characteristic species from circumpolar Subantarctic waters (i.e., *Muggiaea atlantica*, *Lensia conoidea*, *Sphaeronectes gracilis*, *Amphogona apicata*, *Clytia simplex*, *Hydractinia borealis*, *H. tenuis*, *Euphysa aurata*) and Antarctic waters (i.e., *Dimophyes arctica*, *Pyrostephos vanhoeffeni*, *Halopsis ocellata*). These species can extend their range of distribution to the north of the polar front and are distributed at greater depths towards lower latitudes

(Ulloa et al., 2000). Occasionally, these species have been caught in surface waters (< 100 m) associated with coastal upwelling events off the coast of Valparaíso (33°S) (Palma, 1986; Palma and Rosales, 1995).

Samples were taken up to 200 m depth, the maximum depth of Corcovado Gulf, but mesopelagic species such as *Physophora hydrostatica*, *Vogtia pentacantha*, and *V. serrata* were not found in the deeper interior waters of Ancud Gulf, Seno Reloncaví, and Reloncaví Fjord, although they have been found on the shelf adjacent to Boca del Guafo (Palma and Rosales, 1997). The absence of mesopelagic gelatinous species in interior waters could be due to the shallow sills in Chacao Channel and Boca del Guafo (50 and 150 m minimum depth, respectively), which are the two passes that communicate the waters of the adjacent Pacific with those of the interior zone. These shallow sills hinder the penetration of the equatorial subsurface and antarctic intermediate water masses coming from the adjacent Pacific (Silva et al., 1997, 1998). Consequently, the entrance of the mesopelagic species that inhabit these waters is also blocked. The deeper northern microbasin (Reloncaví and Ancud gulfs; > 200 m depth; Figs. 2A and 2B) is filled by subantarctic water that enters through the two shallow passes mentioned earlier, where it mixes with the low salinity interior water.

4.4. Vertical distribution patterns of jellyfish

In general, the bathymetric distribution of the dominant species observed in both seasons of the year showed that most of the dominant species tended to be distributed in the middle (0–30 m) and deep (> 50 m) strata and at even greater depths in Corcovado Gulf, where higher salinity waters predominate. Nictimeral displacements were only observed in winter for the dominant species due to area's lower trophic availability in this season. The vertical displacements, therefore, might be part of a behavior tending to increase the jellyfish chances finding food. On the other hand, in spring, when biological productivity is high (González et al., 2010), the species tended to remain within the same stratum of the water column. By maintaining a same depth of residence throughout the day, therefore, they increase their chances of finding food throughout the day and also reduce the loss of population by advective transport towards the open ocean in the low salinity surface layer. This behavior, even more, might decreases mortality rates since the possibility of being preyed on is higher in the better-lit surface layer, as Gorsky et al. (2000) suggested for the Norwegian fjords. In the same study area (Reloncaví Fjord to Boca del Guafo), Villenas et al. (2009b) indicated that the deepest distribution tends to favor reproductive processes, as observed in *Sagitta tasmanica*, where specimens with eggs are located at greater depths than those without eggs.

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