Cordiales saludos

Sergio

Distribution of siphonophores, chaetognaths, euphausiids and oceanographic conditions in the fjords and channels of southern Chile

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Abstract

Interior waters of the fjords and channels of southern Chile (41.5°S–56°S) receive inputs of Subantarctic Water, Equatorial Subsuperficial Water and Western Pacific Subsurface Water from the adjacent Pacific Ocean by means of numerous connecting channels that lead inward from the ocean margin. These waters become mixed in the interior zone with freshwater from precipitation, river flow, and meltwater from cordilleran glaciers. A two-layered positive estuarine circulation becomes established, with a superficial layer having a net movement towards the adjacent ocean, and a deep layer with net movement towards the fjords. The biomass of the interior waters is composed principally of planktonic crustaceans (copepods and euphausiids), chaetognaths, and gelatinous carnivores. In a southerly direction, decreases are observed in biomass, in relative abundance, and in species diversity of siphonophores, chaetognaths, and euphausiids. Only a few species have been able to adapt successfully to the extreme oceanographic conditions typical of the region, reflected in dominant monospecific populations such as *Muggiaea atlantica*, *Sagitta tasmanica*, and *Euphausia vallentini*. The zooplankton fauna of interior waters, characterized by its low degree of specific richness, is made up of a mixture of species typical of Subantarctic Water (*Sagitta tasmanica*, *S. decipiens*, *Euphausia lucens*, *Nematoscelis megalops*, *Thysanoessa gregaria*), antarctic water (*Pyrosthephos vanhoeffeni*, *Dimophyes arctica*, *Sagitta marri*, *S. gazellae*, *Eukrohnia hamata*, *E. bathyantarctica*, *Euphausia vallentini*), temperate and warm epipelagic waters (*Eudoxoides spiralis*, *Lensia conoidea*, *Chelophyes appendiculata*, *Muggiaea atlantica*, *Sphaeronectes gracilis*, *S. fragilis*, *Abylopsis tetragona*, *Sagitta enflata*), and mesopelagic water (*Physophora hydrostatica*, *Stylocheiron maximum*, *Vogtia pentacantha*, *V. serrata*).

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1. Introduction

Chile's austral region from 41°20′S to 55°58′S includes one of the planet's most complex system of fjords and channels, which, along with similar estuarine systems of Scandinavia, Iceland,

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Greenland, British Columbia, and Alaska, form some of the largest estuarine areas in the world (Cameron and Pritchard, 1963). In Chile, this ecosystem has a length of over 1600 km, and a surface area of about 240,000 km², with a high degree of geomorphological and hydrographic complexity. These factors, plus the highly unstable climatic conditions, produce an ecosystem that can be considered structurally and functionally unique.

A series of oceanographic studies and expeditions have been carried out in the last three decades with the object of increasing knowledge of the oceanography and marine fauna of the channels of southern Chile. Most of these were carried out in the spring season. The first zooplankton studies were during the R/V "Hero" expedition of September–October 1972 and May–June 1973, results of which were primarily centered on copepods (Arcos, 1974, 1976; Marín and Antezana, 1985), euphausiids (Antezana, 1976), and chaetognaths (Ahumada, 1976). Several studies were subsequently published on copepods (Hirakawa, 1986, 1988) as part of a project related to the introduction of Pacific salmon into the Aysen Fjord and adjacent channels by the Japan International Cooperation Agency and the Chilean National Fisheries Service (1980–1983).

The R/V "OGS Explora" expedition to the Magellanic region was carried out in October–November 1989, the results of which also centered on copepods and chaetognaths (Ghirardelli et al., 1991; Mazzocchi and Ianora, 1991). This was followed in February–March 1991 by the "Cariboo" expedition, which produced a detailed study on the taxonomy and distributions of copepods, amphipods, euphausiids, mysids, ostracods, and chaetognaths in the Magallanes Strait (Guglielmo and Ianora, 1995, 1997). More recently, the "Victor Hensen" expedition of October–November 1994 analyzed the geographic distribution of medusae and siphonophores and the relation between planktonic organisms of the different Magellanic micro-basins (Antezana, 1999a; Defren-Janson et al., 1999; Pagès and Orejas, 1999).

The oceanographic characteristics of the interior waters of the southern fjords and channels suggest a permanent input of Subantarctic Water (SAAW)

through various channels located on the coastal border; this water has higher temperature and salinity than water of the interior zone. The oceanic water mixes in the interior zone with freshwater from precipitation, river runoff, and glacial meltwater, producing a positive estuarine circulation (Pickard, 1973; Panella et al., 1991; Silva et al., 1998; Antezana, 1999b; Valdenegro and Silva, 2003).

Studies carried out on the planktonic communities indicated that in spring the interior waters are highly fertile as reflected by high rates of phytoplankton growth (Avaria et al., 1999; Pizarro et al., 2000), which favor the abundance of planktonic herbivores and carnivores (Antezana, 1999a; Hamamè and Antezana, 1999; Palma and Aravena, 2001). This trophic availability is also effectively used by larval fishes and crustaceans (Balbontín and Bernal, 1997; Mujica and Medina, 1997, 2000; Bernal and Balbontín, 1999), which are found at high densities in some channels, particularly those with higher exchange with oceanic waters.

Planktonic crustaceans, particularly the copepods and the euphausiids, predominate in abundance in the fjords and channels, followed by the chaetognaths and gelatinous carnivores including medusae and siphonophores. The role of these carnivorous organisms is becoming more apparent, due to abundances that may cause significant impacts on the remaining zooplankters (Purcell, 1985; Alvariño, 1985; Pagès et al., 1996).

Since the 1980's the south of Chile has been increasingly become used for forestry, fishery, aquaculture, and tourist activity, particularly to the interior of Chiloé Island and the Aysén region. Over time these activities may cause alterations in the little-disturbed natural ecosystem of this region, as it has had minimal human population. For this reason the Cimar Fjord Program was initiated in 1995 in interior waters of southern Chile between Puerto Montt and Cape Horn in order to study the characteristics and processes related to the local oceanography, sedimentology, and pelagic and benthic community structure. These results also serve as baseline data for estimation of future effects of human activities in this region.

The present study analyzes the geographic distribution of zooplankton biomass and dominant species of siphonophores, chaetognaths, and euphausiids because of their abundance in this ecosystem, as well as the related oceanographic characteristics of the Chilean southern fjords and channels.

2. Materials and methods

The study area, between Puerto Montt (41°20'S) and Cape Horn (55°58'S), was divided into three zones as follows; (a) *Northern zone*: from Puerto Montt to the Taitao Peninsula (46°30'S), which is the only location where the continent extends to the west to reach the ocean, thus dividing the fjord-canal region into two main portions; (b) *Central Zone*: between the Taitao Peninsula and the Magallanes Strait (52°45'S) where glaciers exert their major influence due to the extent of the Southern Ice Fields which are actually a relict of the last glaciation; and (c) *Southern zone*: from the Magallanes Strait to Cape Horn (55°55'S).

Cruise data: Expeditions to the three zones were carried out as follows (Fig. 1):

(a) *Northern zone*: Cimar 1 Fjords, 18 October–10 November 1995, comprising 103 stations between Puerto Montt and San Rafael Lagoon (46°40'S).
(b) *Central zone*: Cimar 2 Fjords, 16 October–7 November 1996, comprising 71 stations between the Penas Gulf and the Magallanes Strait.
(c) *Southern zone*: Cimar 3 Fjords, 11–23 October 1998, comprising 46 stations between the Magallanes Strait and Cape Horn.

Temperature and salinity were measured at each oceanographic station using a Seabird 25® CTD, water samples were taken with a 24 Niskin Bottle Rosette, and dissolved oxygen was determined following Carpenter (1965).

Oblique zooplankton tows were made at 224 stations using 60-cm diameter Bongo nets equipped with flowmeters for determining the volume of water filtered. Plankton samples were collected over a 24 h period from near the bottom to the surface, from a maximum depth of 200 m. However, most of tows were made in depths shallower than 200 m, therefore the effect of vertical migration was considered negligable. The mean net towing speed was 20 m min^{-1}. The plankton nets on Cimar Cruises 1 and 2 had a net aperture of 350 μm. For Cimar 3 a net aperture of 200 μm was used to capture the small copepods for another project. All samples were preserved in borate-neutralized 5% formalin for subsequent laboratory analyses.

Estimations of zooplankton biomass were carried out using the volume displacement method and expressed as ml wet plankton per 1000 m^3 of seawater filtered by the net (ml 10^3 m^{-3}). To compare the zooplankton biomass and to minimize the effect of the gelatinous specimens, the displacement volume values were transformed in logarithm of dry weight using a transformation equation (Wiebe, 1988). All specimens of siphonophores, both asexual and sexual stages, (Cimar 1–3), and chaetognaths and euphausiids (Cimar 2 and 3) were identified and counted on all samples from the respective cruises.

The relative abundance of dominant species was standardized to number of individuals per 1000 m^3 of water filtered (ind 10^3 m^{-3}), for describing the general distribution pattern. For calycophoran siphonophores the numbers of anterior and posterior nectophores were counted, recording the highest number of both, while for the physonects one colonial individual was tallied for every 10 nectophores collected (Pugh, 1984).

3. Results and discussion

3.1. Oceanographic characteristics

The zone of fjords and channels is located where the West Wind Drift reaches the extreme southern coast of South America. This current transports Subantarctic Water (SAAW) having salinities between 33 and 34 psu and bifurcates north and south between 42° and 48°S. The branch that runs north forms the Humboldt Current, and the branch running south forms the Cape Horn
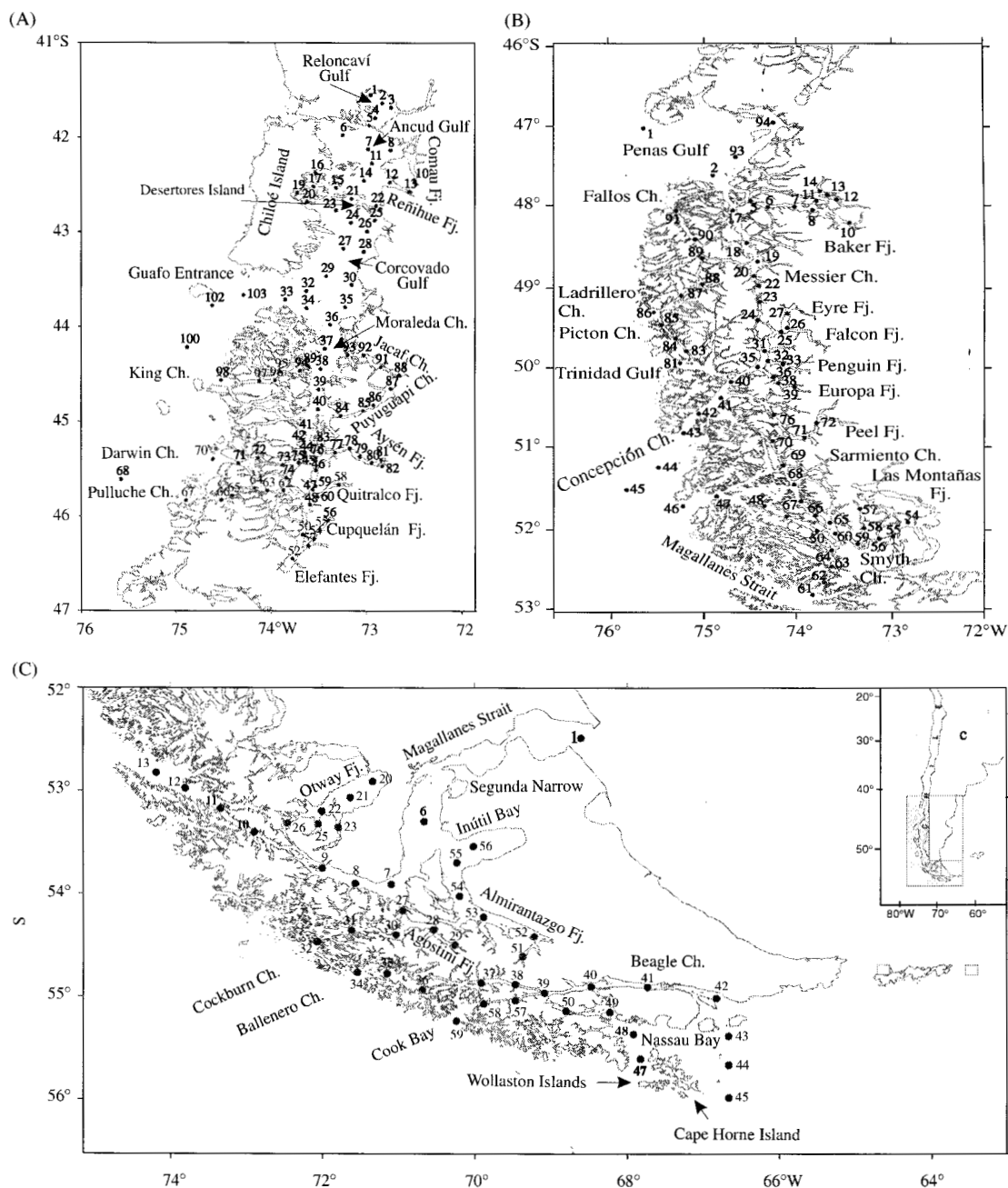
Fig. 1. Chilean Inlets Region, showing principal fjords, channels, sounds and gulfs. The Cimar Fiordo Cruise areas are indicated on a regional and global setting.

Current (Silva and Neshyba, 1979a). A portion of the surface SAAW (0–100 m) penetrates into the Chilean fjords and channels (Silva et al., 1998). Below the SAAW, at the subsurface level (100–

300 m) and up to 48°S lie remnants of the Equatorial Subsurface Water (ESSW) coming from off Peru (Silva and Neshyba, 1979b) and at the intermediate level (300–1200 m), the Antarctic

Intermediate Water (AAIW) (Silva and Neshyba, 1979a) (Table 1).

The inflow of SAAW and high rainfall (700–8000 mm yr^{-1}, MOP-DGA, 1987) in the fjord region produces a general estuarine circulation of the positive type. Freshwater input from rivers, coastal runoff, and thawing of local glaciers flows out at the surface, and mixes with seawater in subsurface layers (Silva et al., 1998; Sievers et al., 2002, Valdenegro and Silva, 2003).

The continental shelf adjacent to the coastal margin shoals to maximum depths that vary between 60 and 150 m, producing coastal sills that prevent oceanic waters deeper than 150 m from entering the inner fjords and channels, which are, on average, deeper. Although numerous channels connect directly with the sea, the most important sites of exchange of oceanic waters with the interior waters occur at the wider and deeper connections, including the Chacao Channel (41°50′S), Guafo Entrance (43°30′S), Penas Gulf (47°20′S), Trinidad Channel (50°S), Concepción Channel (51°S), Nelson Strait (51°50′S), Magallanes Strait (52°45′S), Cockburn Channel (54°30′S), and Ballenero Channel (54°50′S) (Silva et al., 1998; Antezana, 1999b; Sievers et al., 2002; Valdenegro and Silva, 2003).

The inner fiords and channels are in general deep, with maximum depths of 600 m at the Jacaf Channel (*Northern zone*), 1300 m in the Messier Channel (*Central zone*), and 1200 m in the Magallanes Strait (*Southern zone*) (Fig. 2).

In the *Northern zone* the SAAW from the oceanic zone moves to the interiors of the channels, passing over the coastal sill at the Guafo Entrance (≈ 150 m) and occupies the 0–150 m layer, mixing with freshwater, producing modified SAAW (MSAAW) with salinities from 32 to 33 psu, and Estuarine Waters (EW) with salinities ranging from 1 to 32 psu, depending on their proximity to sources of freshwater (Silva et al., 1998). The ESSW able to pass the coastal sill moves below 150 m and enters only where the bathymetry permits, flooding the deep zone of the Corcovado Gulf and the Moraleda, Jacaf, and Puyuguapi Channels. The sills of the Apiao and Desertores Islands to the north, and of Meninea Island to the south, block inflow of this water past these limits, thus producing two semi-isolated micro-basins (Fig. 2A and B). The estuarine circulation allows the ASAAW to flow over the sill of the Apiao and Desertores Islands, and it sinks on the far side due to its higher density, filling the semi-isolated micro-basins to the north (Fig. 2B). In contrast, due to the shoal nature of

Table 1

Water mass characteristics (temperature, salinity and dissolved oxygen) for oceanic water off the three study zones in the upper 1200 m depth

Water mass	Depth range (m)	Temperature range (°C)	Salinity range (psu)	Dissolved O$_2$ range (ml l^{-1})
Northern zone				
Subantarctic Water (SAAW)	0–150	9–13	34.0–34.3	5–8
Equatorial Subsurface Water (remnants) (ESSW)	150–300	6–9	34.0–34.3	2–4
Antarctic Intermediate Water (AAIW)	300–1200	4–7	34.0–34.1	4–6
Central zone				
SAAW	0–175	9–10	33.0–34.2	5–8
ESSW	175–300	6–9	34.0–34.1	3–4
AAIW	300–1200	4–7	34.0–34.1	4–6
Southern zone				
SAAW	0–200	7–9	33.0–34.2	5–6
AAIW	300–1,200	4–7	34.0–34.1	4–6

(A)

(B)

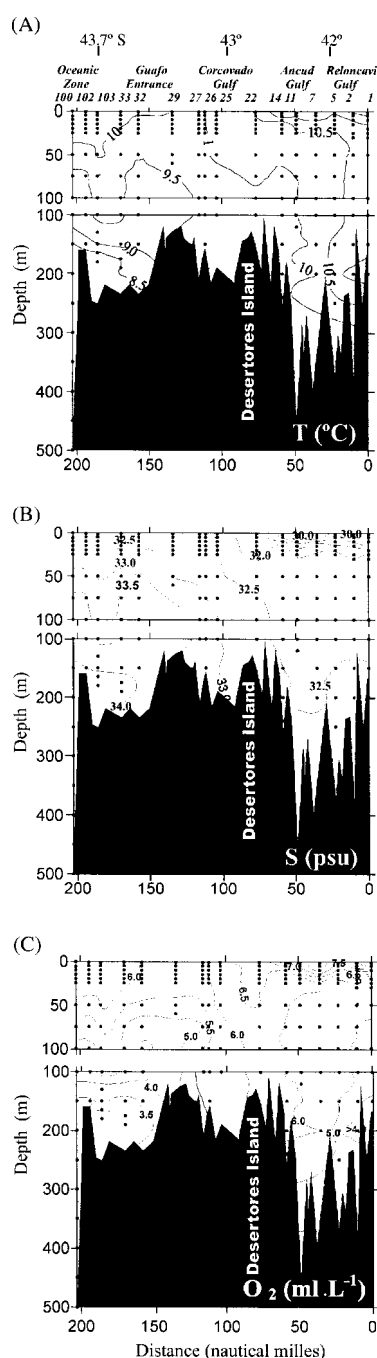(C)

Distance (nautical milles)

Fig. 2. Water masses in the (A) Oceanic Zone to Reloncavi Sound section, (B) Oceanic Zone to Elefantes Gulf section, (C): Penas Gulf to Oceanic Zone section and (D) Magellan Strait section.

Meninea Island sill, only EW is able to flow over the sill and sink on its the far side due to higher density, filling the semi-isolated micro-basins to the south (Fig. 2A). Therefore these north and south micro-basins are filled with relatively warm (9–11°C), less saline (30–32 psu) and more oxygenated waters (4–5 ml L^{-1}) (Figs. 3 and 4). Due to the bathymetry constraints, AESS is restricted to the deeper central part of the northern zone (Fig 2A and B).

The northern and southern micro-basins receive a greater input of freshwater due to the numerous sources of freshwater (rivers and glaciers). The water column shows a two layered structure, one from surface to about 30 m depth, with greater variability, higher temperature, lower salinity, and high dissolved oxygen, and a second more stable, cooler, deeper layer ($\approx$30–600 m), with higher salinity and less dissolved oxygen (Figs. 3 and 4). In winter, the river freshwater is cooler than in summer, producing thermal inversions in the surface layer near the heads of the fjords and channels (Silva et al., 1998). The micro-basin open to the ocean adjacent to or across the Guafo Entrance has a low import of freshwater and is thus vertically more homogeneous than the inner channels (Figs. 3 and 4).

In the *Central zone*, the sill at the constriction of English Narrows (<50 m depth) in the Messier Channel (49°S) divides this zone into two large and deep micro-basins (Fig. 2C), each of which includes various tributary fjords and channels (Sievers et al., 2002). The northern micro basin has a maximum depth of 1300 m and is colder (8.3–8.5 vs. 8.8–9.0°C), more saline (33.8–34.0 vs. 33.0–33.3 psu), and less oxygenated (3.2–5.0 vs. 4.0–6.0 ml l^{-1}) than the southern micro-basin which has a maximum depth of 800 m (Fig. 5).

Exchange between the ocean and the interior waters occurs primarily through the Penas Gulf in the northern micro basin, and in the southern micro-basin via the Concepcion Channel and Nelson Strait. SAAW first enters the northern micro-basin, passing the coastal sill in the Gulf of Penas ($\approx$ 150 m). In the Gulf and inner fjords and channels the SAAW mixes with freshwater from both local rivers and from the Southern Ice Fields, producing MSAAW and EW that remains in the
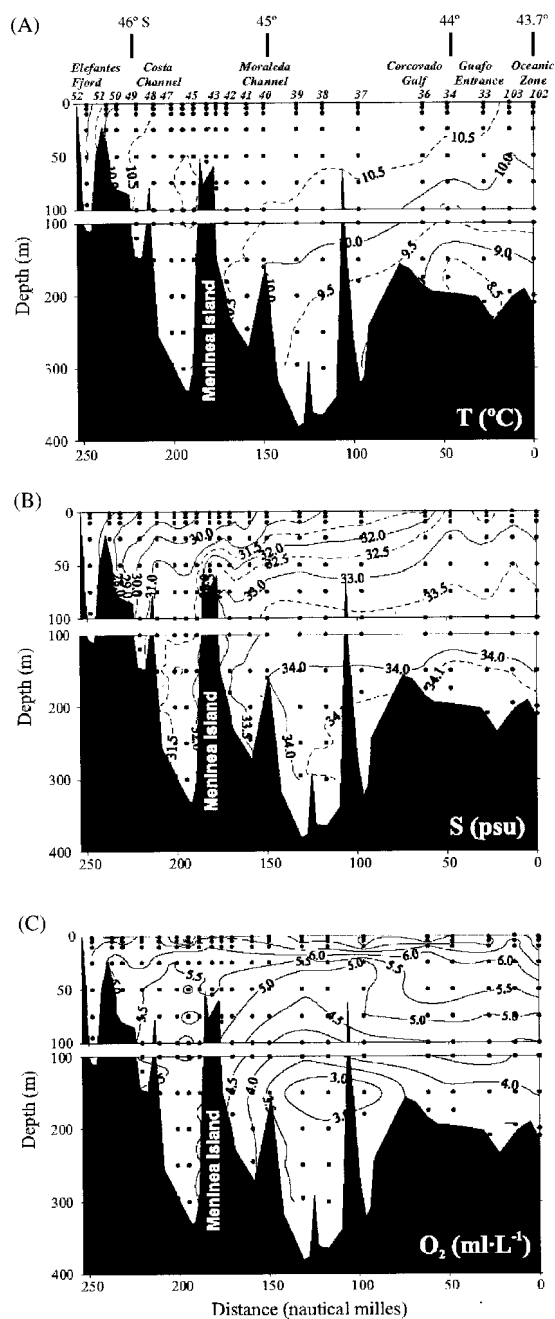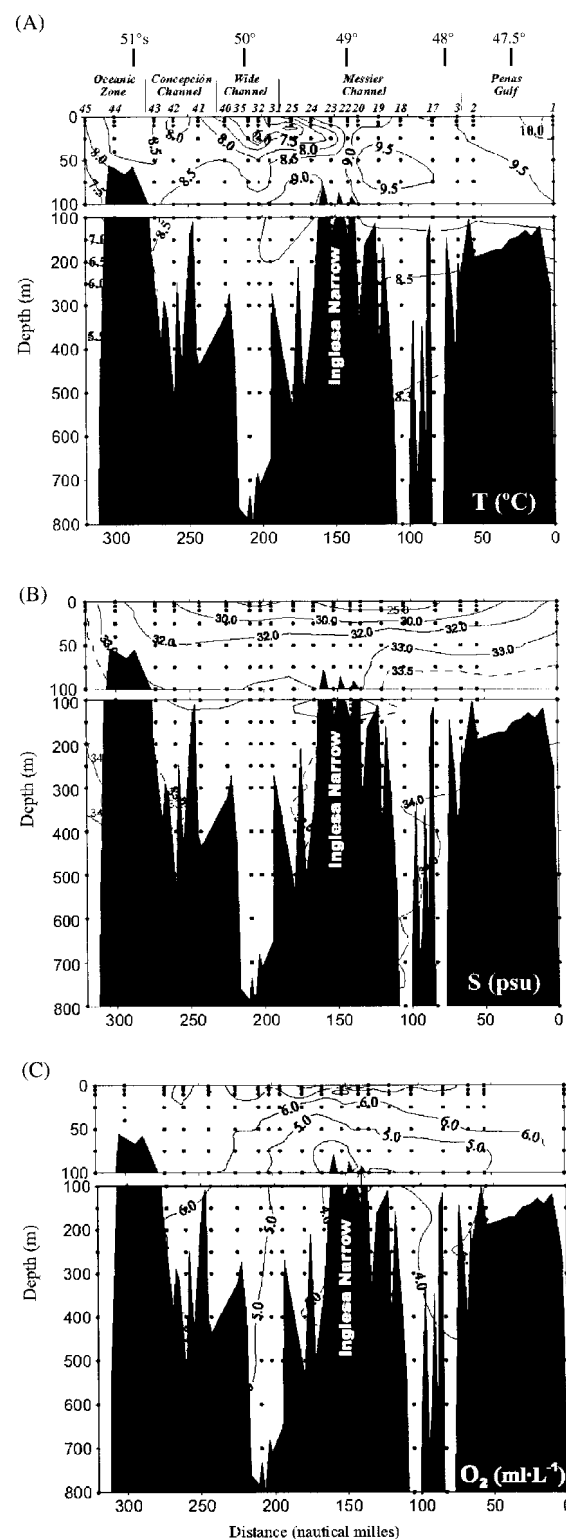
Fig. 3. Vertical distribution of (A) temperature, (B) salinity and (C) dissolved oxygen, in the Oceanic Zone to Reloncavi Sound section.

Fig. 4. Vertical distribution of (A) temperature, (B) salinity and (C) dissolved oxygen, in the Oceanic Zone to Elefantes Fjord section.
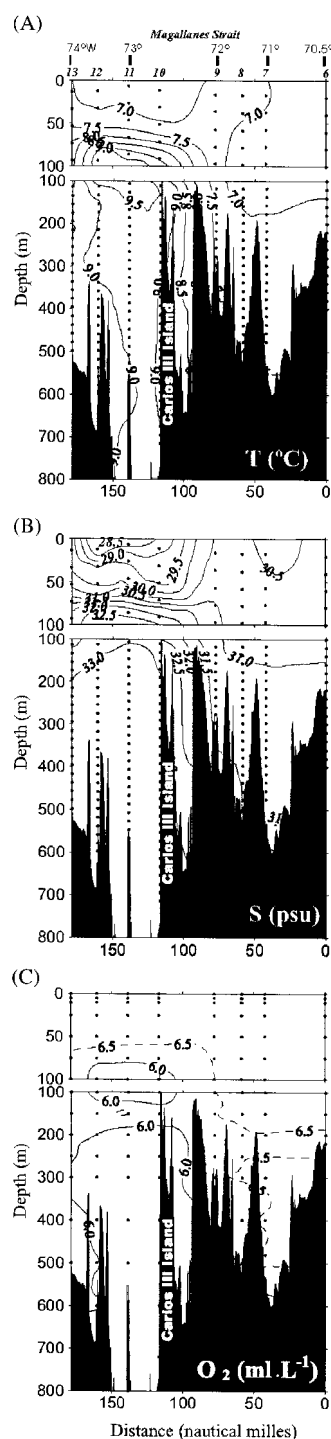
Fig. 5. Vertical distribution of (A) temperature, (B) salinity and (C) dissolved oxygen, in the Penas Gulf to Oceanic Zone section.

surface layer; meanwhile in the lower layer the SAAW sinks and fills the micro-basin below 75 m (Fig 2C). The remnants of the ESSW, located between 150 and 200 m depth in the oceanic zone, also flow over the Penas Gulf sill, sinking and filling part of the northern micro-basin, with salinities higher than 34 psu below 300 m (Fig. 2C).

In the southern extreme of the Central Zone, the coastal sills of the Concepción Channel and Nelson Strait are very shallow ($\approx$ 60–70 m) and only SAAW reaches the interior of the southern micro-basin. SAAW mixes with fresh water in the inner part of the region, producing MSAAW and EW, which remains in the surface layer, while the SAAW fills the deep part of the southern micro-basin, and has salinities greater than 33 psu below 100 m (Fig. 2C).

The water column distribution (Fig. 5) shows two layers, one surface ($\approx$ 0–50 m) with greater variability, higher temperature, lower salinity and better oxygenation, and a deeper layer ($\approx$ 50–1300 m) which is more stable, cooler, more saline and less oxygenated (Fig. 5). There are sectors, however, where there is vertical mixing throughout the water column, and others where cold fresh-water from the glaciers produces low temperatures in the surface layer causing thermal inversions at the fjords heads near the Southern Ice Field (Silva and Calvete, 2002).

In the *Southern zone*, the Otway Fjord acts as an isolated micro-basin with restricted interchange with the Magallanes Strait, due to the narrowing produced by the Jerónimo Channel. This fjord is filled with EW and shows a two-layer vertical stratification, one at the surface with salinities lower than 30 psu and an almost homogeneous deeper layer with salinities of about 30 psu (Valdenegro and Silva, 2003).

The sill caused by Carlos III Island (< 60 m) separates the Magallanes Strait into two deep micro-basins, one western, with a maximum depth of 1200 m, and another central with a maximum depth of 600 m (Panella et al., 1991; Antezana, 1999b; Valdenegro and Silva, 2003). In the eastern sector of the strait between the Segunda Narrow and the Argentine continental shelf there is a shallow plain (< 50 m) named the "eastern micro-basin" (Panella et al., 1991). This area, however,

does not have characteristics of a basin; it is flat and has no sills at its extremes. At the western entrance to the strait the sill is quite shallow ($\approx 60–70$ m), and only SAAW enters from the Pacific, mixing with the surface layer and fresh waters to produce Pacific MSAAW and EW. The deep portion of the western micro-basin is filled with SAAW. The central portion is filled with Pacific MSAAW and EW from the western micro-basin, which pass the narrows at Carlos III Island and then sink due to their greater density (Fig. 2D). The inflow of oceanic waters to the interior of the Magallanes Strait and other channels with deep, semi-isolated micro-basins permits their ventilation, maintaining concentrations of dissolved oxygen above $5 \, \text{ml}^{-1}$ (Fig. 6).

The western sector of the strait has low salinities in the surface layer (< 29 psu) because of the high precipitation in the region ($2000–8000 \, \text{mm yr}^{-1}$; MOP-DGA, 1987), plus the melting waters of the Darwin Mountain Range glaciers. In the central and eastern sectors, the salinity of the surface layer is greater (> 30 psu) due to the lower precipitation ($300–500$ mm), and absence of glaciers. The result is a stronger vertical stratification on the western micro-basin, with a two-layer structure; while in the central micro-basin the water column shows a tendency towards vertical homogeneity and over the eastern plain the water column is homogeneous (Fig. 6).

The Agostini and Almirantazgo Fjords receive fresh water from rains and glaciers of the Darwin Mountain Range, which produces stratification at their heads that decreases toward their mouths. Away from their heads, these fjords are filled with EW with salinities of about 29–31 psu (Valdenegro and Silva, 2003).

Cookburn Channel and Cook Bay are zones of major exchange with the adjacent Pacific. The coastal sill is about 75–100 m in depth and some SAAW and MSAAW penetrates to the inner deep channels (> 300 m), filling part of their micro-basins at the inner edge close to the sill. Both channels are filled with EW psu, but Cookburn shows a relatively homogeneous water column with salinities of about 31, while Cook Bay shows a stratified water column (salinities 30–33 psu) due to the fresh water input from the Darwin Mountain

Range glaciers and the SAAW overflow from the Pacific (Valdenegro and Silva, 2003). The Beagle Channel is very shallow (< 100 m) and contains EW at its inner extreme (31 psu) and ASAA at its mouth (33 psu), behaving as a vertically homogeneous estuary (Valdenegro and Silva, 2003).

3.2. North-South distribution of zooplankton biomass

The zooplankton biomass for this area was estimated in different years (1995, 1996, 1998), but for the same spring months (October and November). Therefore, the observed variations were considered to be independent of the annual cycle of zooplankton in this area.

Two areas of high abundance were found in the *Northern zone* where estuarine conditions are produced by higher freshwater inflow (Fig. 7A). One area was located between the Reloncavi Gulf and Desertores Islands (mean of 5.19), where a semi-isolated micro-basin was formed with high stability of the water column. The second area was located in the southern part of the Corcovado Gulf (mean of 4.92), with increases in biomass found in the Moraleda and Darwin Channels, and Aysén Fjord. Both areas were separated by a central sector with low biomass (mean of 4.60) in the Corcovado Gulf where the permanent inflow of SAAW across the Guafo Entrance and lower import of freshwater allow instability in the water column reflected by nearly homogeneous values of temperature, salinity, and dissolved oxygen (Figs. 3 and 4). Lowest biomass was found in the southern extreme of the Costa Channel, in Cupquelán and Elefantes Fjords, associated with estuarine waters which were cold, turbid, and of lower salinity, originating from the Northern Ice Fields Glacier.

The geographic distribution of biomass in the *Central zone* showed two main areas (Fig. 7B). A western area was bordered by the Messier Channel, oceanic channels, and the Penas Gulf, had the highest value (4.73), with an important abundance of decapod crustacean larvae in the Fallos, Picton, and Ladrillero Channels. The lowest biomass was recorded in the inner fjord area adjacent to the Southern Ice Fields (mean of 3.93) where EW
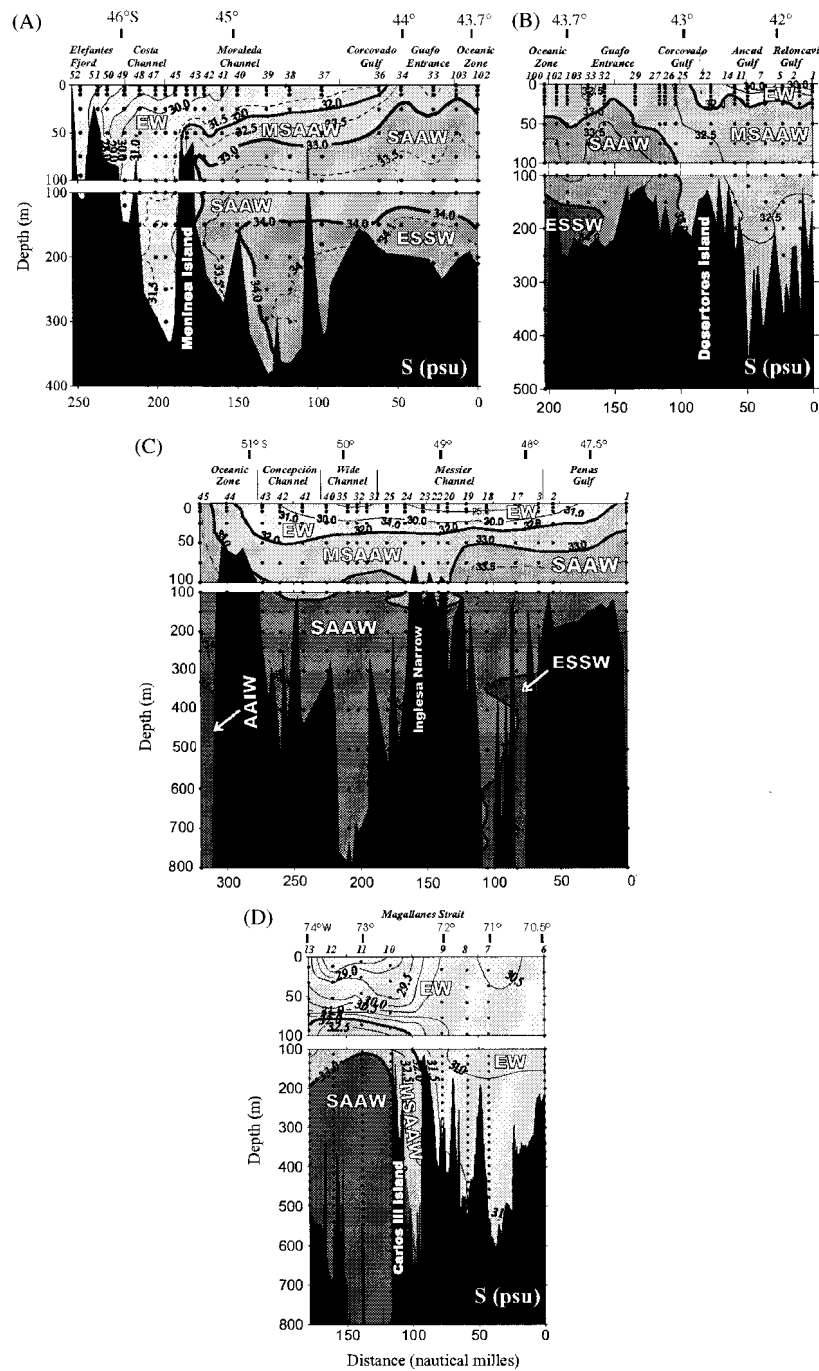
Fig. 6. Vertical distribution of (A) temperature, (B) salinity and (C): dissolved oxygen, in the Magellan Strait section.

prevailed, with low temperature and salinity (Figs. 5A and 5B), and greater turbidity due to glacial silt in suspension (Silva et al. 2002).

The biomass in the *Southern zone* showed the lowest values in the oceanic channels and the Magallanes Strait (mean of 4.18) (Fig. 7C).
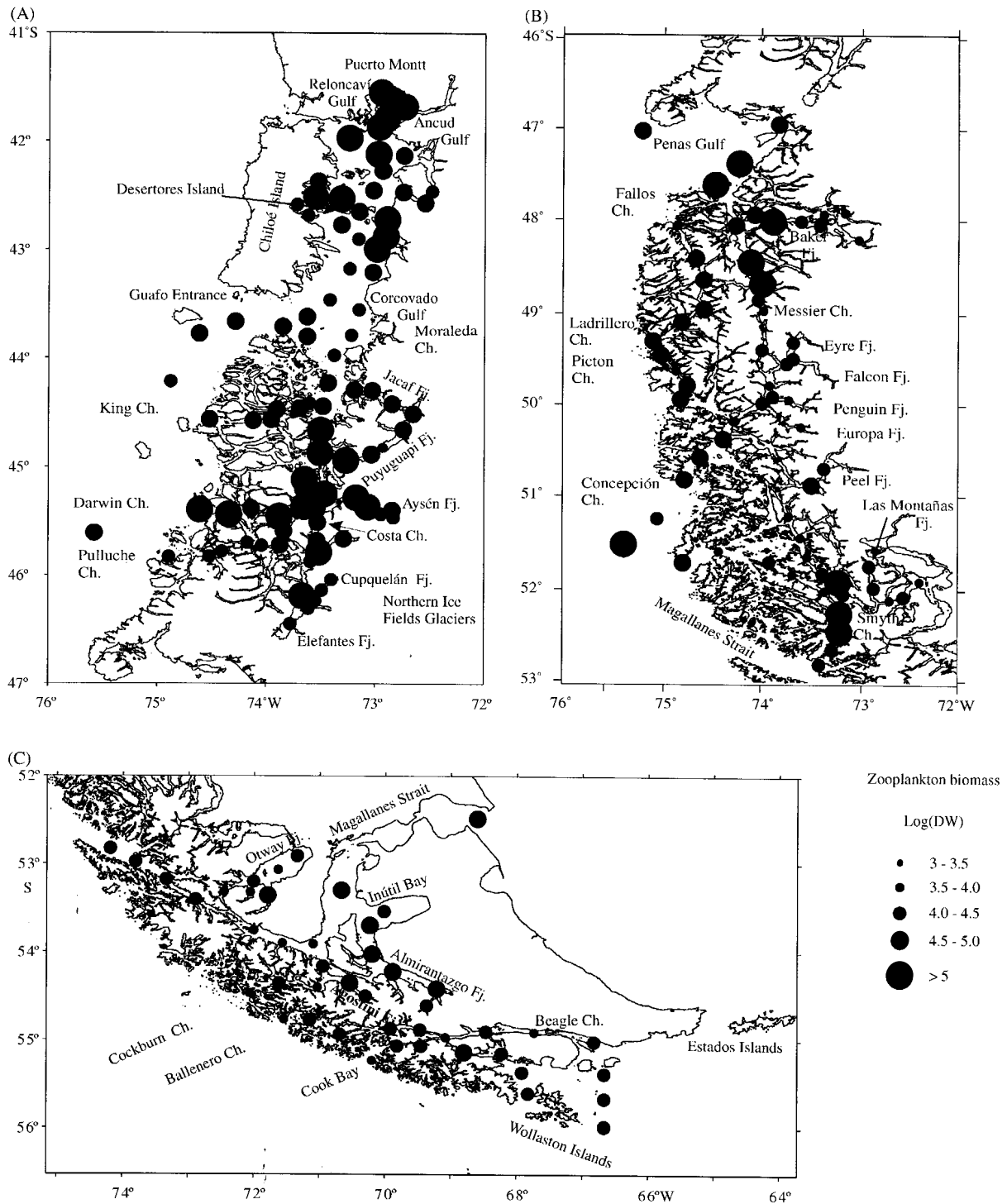
Fig. 7. Horizontal distribution of zooplankton biomass in the (A) Northern Zone, (B) Central Zone and (C) Southern Zone.

Table 2
Latitudinal distribution of zooplanktonic biomass in dry wigth (DW) in spring and total organic matter in surface sediments (%) in the Chilean southern fjords and channels

Zone	n	Zooplankton biomass (Log DW)		Total organic matter (%)		
		Median	Standard deviation	N	Median	Standard deviation
Northern Zone (NZ) 41°20′–46°40′S	103	4.80	0.43	74	5.33	3.29
Central Zone (CZ) 47°10′–52°45′S	71	4.31	0.61	65	4.28	2.83
Southern Zone (SZ) 52°45′–55°58′S	46	4.24	0.33	35	3.77	1.72
Kruskal–Wallis (H) Ho: NZ = CZ = SZ	207	$H = 48.11^* \chi^2 = 3.91$		174	$H = 4.40^* \chi^2 = 3.91$	
Kruskal–Wallis (H) Ho: NZ = CZ	207	$H = 25.34 \chi^2 = 2.18$		174	$H = 2.44 \chi^2 = 2.18$	
Kruskal–Wallis (H) Ho: NZ = SZ	207	$H = 42.91 \chi^2 = 2.18$		174	$H = 3.96 \chi^2 = 2.18$	
Kruskal–Wallis (H) Ho: CZ = SZ	207	$H = 0.67^* \chi^2 = 2.18$		174	$H = 0.031^* \chi^2 = 2.18$	

Asteriks indicates significant differences ($p < 0.15$).

In the Straits, the biomass was greater in the western section due to the greater abundance of epi- and mesopelagic organisms from the adjacent Pacific, and also to the greater stratification of this micro-basin. The stratification decreased in the central micro-basin (Fig. 6) and the biomass values were lower. The maximum biomass occured in the Otway, Almirantazgo, and Agostini Fjords (mean of 4.49) which was supported by the high concentrations of phytoplankton (Pizarro et al., 2000). In this area the water did not show high turbidity as in the Central Zone fjords. Various authors have remarked on the association between the proliferations of phytoplankton and population increases of copepods, and holo- and meroplanktonic larvae (Mazzocchi and Ianora, 1991; Antezana, 1999a; Hamamé and Antezana, 1999).

The results showed a decline in zooplankton biomass progressing southward in the study area (Table 2). According to the Kruskal–Wallis test, the biomass values for the Northern zone were significatively different than those for the Central and Southern Zones (Table 2). These differences are probably produced by the lesser extreme oceanographic conditions to the north, with higher temperatures and salinities, while at the south of Penas Gulf, many glaciers contribute water with lower temperature and salinity, and high silt content (light penetration < 20 cm), which affects the phytoplankton production.

The above agrees with the southward decline observed in total organic matter values (TOM) in the surface sediments (Table 2). According to the Kruskal–Wallis test, TOM values for the Northern zone were also significatively different of those for the Central and Southern Zones. Silva and Prego (2002) suggested that the organic matter in the sediments was primarily of marine origin. Therefore, TOM can be considered as a time integrator of the marine biomass production in water column of the area and hence as indicative of zooplankton biomass distribution.

3.3. Distribution of macroplankton in austral fjords and channels

The macrozooplanktonic communities of the austral region are exposed to a large degree of spatial heterogeneity related to strong temperature and salinity gradients that may be seasonal, vertical, and latitudinal, and are based on the hydrographic characteristics of the zone (Pickard, 1973; Silva et al., 1995, 1997, 1998; Sievers et al., 2002; Valdenegro and Silva, 2003). These gradients may be driven by annual variations in precipitation (MOP-DGA, 1987) and solar radiation, which affect the estuarine system of the region.

The high degree of temporal heterogeneity may be the main cause of a decrease in the species richness, as only 25 species have been identified among the taxa selected for this study, including 13 siphonophores, seven chaetognaths, and five euphausiids (Table 3). Most of the siphonophores and chaetognaths are recorded for the first time in these waters, therefore expanding their geographic distribution limits in the southeastern Pacific.

Table 3
Distribution of the total number (ind 1000 m^3) of siphonophores, chaetognaths and euphausiids and species percentage (%) in the Chilean southern fjords and channels

Species	Cimar 1 Fjord 41°20′–46°40′S	Cimar 2 Fjord 47°10′–52°45′S	Cimar 3 Fjord 52°45′–55°58′S
Siphonophores	**38462**	**23042**	**25379**
Physophora hydrostatica	0.06	—	—
Pyrostephos vanhoeffeni	10.65	0.05	0.61
Abylopsis tetragona	0.20	0.07	—
Chelophyes appendiculata	—	0.03	—
Dimophyes arctica	1.89	1.99	4.10
Eudoxoides spiralis	0.02	0.42	0.20
Lensia conoidea	40.66	35.38	36.01
Lensia meteori	—	2.24	—
Muggiaea atlantica	45.92	59.55	58.39
Sphaeronectes fragilis	0.53	—	0.03
Sphaeronectes gracilis	0.03	0.30	0.66
Vogtia pentacantha	0.02	—	—
Vogtia serrata	0.04	—	—
Chaetognaths	**w/I**	**71808**	**37820**
Sagitta decipiens	w/I	—	2.78
Sagitta enflata	w/I	2.37	—
Sagitta gazellae	w/I	2.55	0.20
Sagitta marri	w/I	19.71	—
Sagitta tasmanica	w/I	66.08	95.93
Eukrohnia bathyantarctica	w/I	0.11	—
Eukrohnia hamata	w/I	9.19	1.09
Euphausiids	**w/I**	**46335**	**18837**
Euphausia lucens	w/I	2.63	0.34
Euphausia vallentini	w/I	46.28	98.36
Nematoscelis megalops	w/I	45.61	0.63
Stylocheiron maximum	w/I	1.77	0.62
Thysanoessa gregaria	w/I	3.71	0.05

w/i-without information.

3.3.1. Siphonophores

The most abundant species were *Muggiaea atlantica* and *Lensia conoidea*. The former species had the broadest distribution, while the remaining species were scarce and some only occasional (Table 3). Collection of *Physophora hydrostatica*, *Vogtia pentacantha* and *V. serrata* represent the first records of these siphonophores in Chilean waters.

In the *Northern zone* the highest densities of *Muggiaea atlantica* were recorded in the Gulf of Ancud and at the heads of the Comau and Reñihue Fjords (Fig. 8A). The lowest densities of this species were recorded in the rest of this zone, except in the Jacaf and Puyuguapi Channels where

high densities were found. South of the Aysén Fjord this species was scarce or absent. *M. atlantica* was most abundant in the *Central zone* between 48° and 50°S, particularly in the middle reach of the Messier Channel, and in the Fallos and Picton Channels where a maximum of 3613 individuals were obtained per m^3. A major drop in abundance of this species was observed south of 50°S, particularly in the inner fjords (Fig. 8B). This species was caught only in the central area of the *Southern zone*, with maximum numbers in the Otway, Almirantazgo, and Agostini Fjords (Fig. 8C). In this zone *M. atlantica* was absent from almost all channels experiencing oceanic influence, except for the Cockburn Channel.
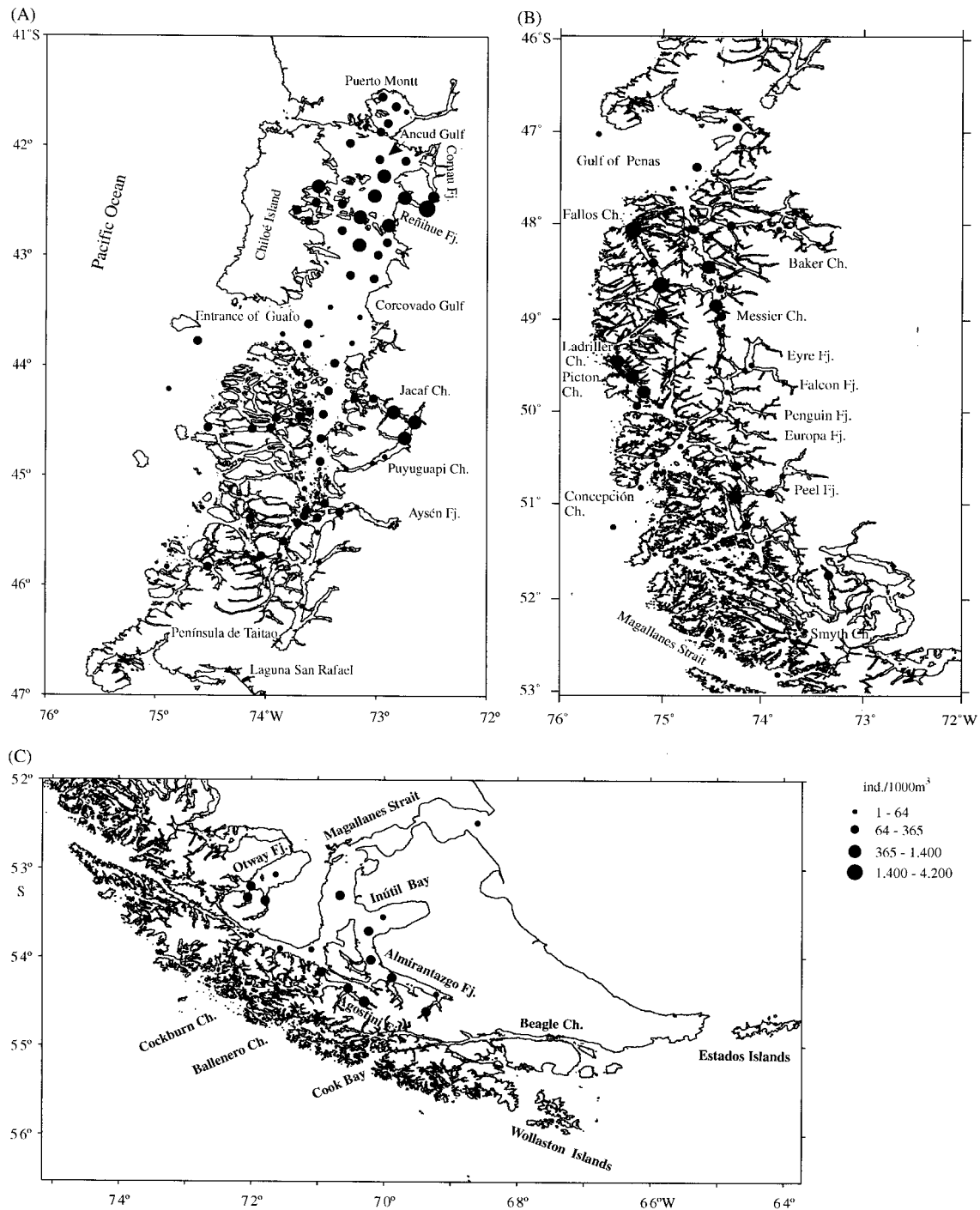
Fig. 8. Horizontal distribution of nectophores of *M. atlantica* in the (A) Northern Zone, (B) Central Zone and (C) Southern Zone.

With the exception of the *Southern zone, M. atlantica* had a broad distribution at oceanic stations and in the channels with major inputs of SAAW. Highest abundances were associated with waters with comparatively higher temperature and salinity values. This species is found along the entire coast of Chile, associated with the Humboldt Current System, reaching Cape Horn. In the central zone of Chile (32–33°S), dense aggregations of *M. atlantica* have been recorded in spring and summer (Palma, 1994; Palma and Rosales, 1995). Its broad distribution and occurrence in the austral channels south of 42°S (Palma and Rosales, 1997; Palma et al., 1999; Pagès and Orejas, 1999; Palma and Aravena, 2001) may be due to its euryhaline adaptation.

Lensia conoidea was distributed primarily in EW of low temperature and salinity, and was most abundant in the channels with the lowest concentration of dissolved oxygen like relict ESSW, which enters inner fjords such as the Jacaf and Puyuhuapi Fjords (Silva et al., 1998). In areas where EW predominated, abundance of this siphonophore exceeded that of *M. atlantica*. This species is also frequent in Scandinavian fjords where, along with *Dimophyes arctica*, it dominates superficial (0–25 m; Lie, 1967), subsuperficial layers (25–50 m; Hansen, 1951) or in the water column (0–100 m; Pagès et al., 1996). It is uncommon in southeastern Pacific waters but has been occasionally collected in the central zone off Chile (Ulloa et al., 2000a).

In the *Northern Zone, L. conoidea* was distributed north and south of the Corcovado Gulf, associated with EW, which apparently favors its development (Fig. 9A). Its maximum abundance was recorded in the Reloncaví Gulf, Jacaf and Puyuhuapi Fjords, and around Meninea Island. It was scarce or absent in the Corcovado Gulf and oceanic channels in which oceanic waters predominated. This species was broadly distributed in the *Central zone*, with top abundance reached in the Picton Channel (Fig. 9B). It was very common in the inner fjords, where it was often collected at the heads of fjords such as the Baker, Eyre, Penguin, Europa, and Peel, where oceanographic conditions are more extreme. In the *Southern zone*, this species was mostly absent, except in the areas

with higher exchange of SAAW, as in the western mouth of the Magallanes Strait and the Ballenero Channel (Fig. 9C).

3.3.2. Chaetognaths

The most abundant and frequent species was *Sagitta tasmanica* (66.1% and 95.9% in the *Central* and *Southern zones* respectively). Among the remaining species, *S. marri* was notable in the *Central zone* and *S. decipiens* in the *Southern zone*, while the other species were occasional in both zones (Table 3).

S. tasmanica formed dense concentrations throughout the *Central zone*, with maxima in oceanic waters of the Penas Gulf, and the Concepción, Fallos, and Ladrillero Channels (Fig. 10A). It was also abundant in the interior waters of fjords, with high concentrations recorded in Messier and Sarmiento Channels, and in Baker, Peel, and Las Montañas Fjords. This species was broadly distributed in the *Southern zone* at all stations, but maximum densities occurred in the Otway, Almirantazgo, and Agostini Fjords (Fig. 10B).

In the Patagonian sector *S. tasmanica* was most abundant in the oceanic channels, while in the Magellanic sector it was dominant within the inner fjords. It had previously been recorded from some Patagonian channels (Ahumada, 1976) and Magellanes Strait (Guglielmo and Ianora, 1997), where it was the most abundant chaetognath. This species is characteristic of SAAW (Alvariño, 1965) and has been collected at latitudes as low as 20°S in waters of the Humboldt Current System (Fagetti, 1972; Ulloa et al., 2000b, 2004).

In the *Central zone, S. marri* (19.7%) was broadly distributed in EW and in the inner fjords; high densities were recorded in some of these such as the Baker, Eyre, and Peel Fjords. It was caught on uncommon occasions in oceanic channels, as was the case at the Fallos Channel. In contrast, there was an important change in the species composition in the *Southern zone*, where the occurrence of *S. tasmanica* (95.9%) was followed by *S. decipiens* (2.8%), while *S. marri* was not collected. In spite of its low abundance, *S. decipiens* was broadly distributed throughout the entire Magellanic region.
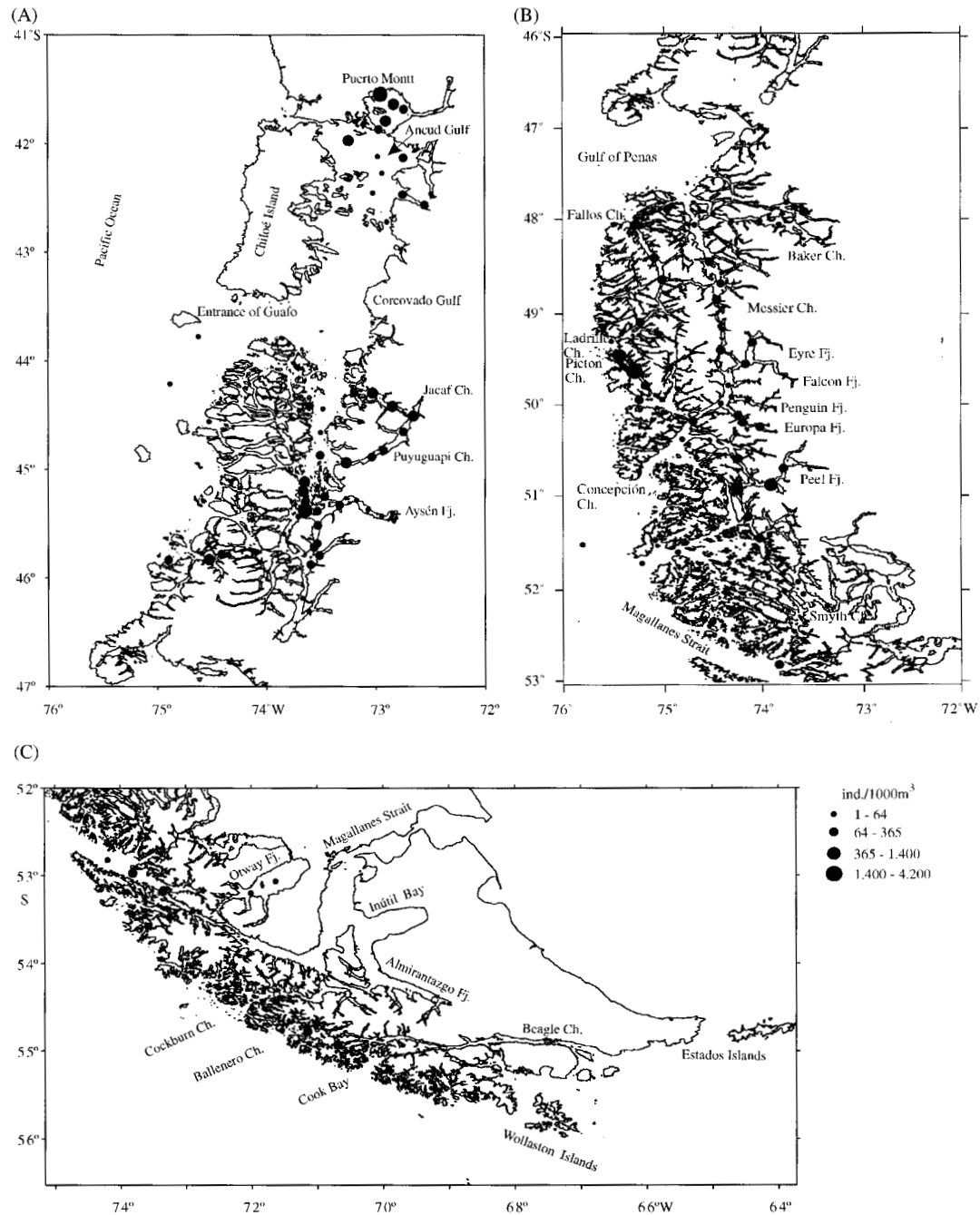
(A)

(B)
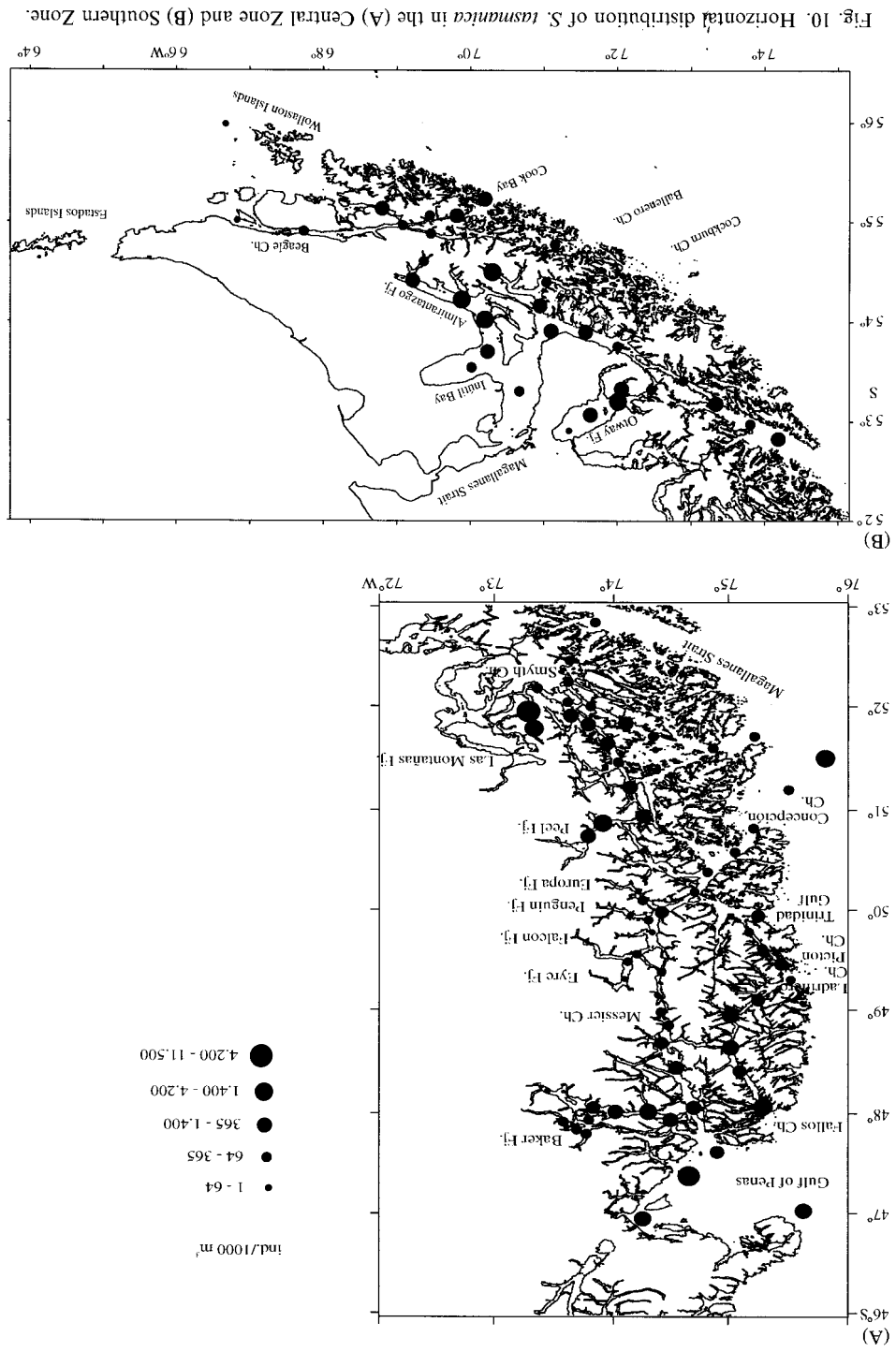
(C)

Fig. 9. Horizontal distribution of nectophores of *L. conoidea* in the (A) Northern Zone, (B) Central Zone and (C) Southern Zone.

3.3.3. Euphausiids

The dominant species in decreasing order of abundance were *Euphausia vallentini* and *Nema-* *toscelis megalops*. Of these, the former had the broader distribution in the austral region. The remaining species were occasional (Table 3).

Fig. 10. Horizontal distribution of *S. tasmanica* in the (A) Central Zone and (B) Southern Zone.

(B)

Wollaston Islands
Estados Islands
Cook Bay
Ballenero Ch.
Cockburn Ch.
Beagle Ch.
Almirantazgo Fj.
Inutil Bay
Otway Fj.
Magallanes Strait

(A)

Magallanes Strait
Smyth Ch.
Las Montañas Fj.
Concepción Ch.
Peel Fj.
Europa Fj.
Penguin Fj.
Trinidad Gulf
Falcon Fj.
Picton Ch.
Eyre Fj.
Ladrillero Ch.
Messier Ch.
Baker Fj.
Fallos Ch.
Gulf of Penas

ind./1000 m³

4.200 - 11.500
1.400 - 4.200
365 - 1.400
64 - 365
1 - 64

The occurrence of *E. vallentini* (46.3%) was similar to that of *N. megalops* (45.6%) in the *Central zone*. *E. vallentini* was irregularly distributed in this zone (Fig. 11A), and its high percentage of abundance was due to the occurrence of high aggregations recorded in the Penas Gulf and Picton Channel (>6800 ind $10^3\,\mathrm{m}^{-3}$). It was uncommon at the remaining stations, particularly in most fjords with the exception of Peel Fjord. Conversely, *N. megalops* had a much broader distribution than *E. vallentini*, but had a similar pattern of high densities in oceanic stations and in oceanic channels, with lower densities recorded in the fjords.

E. vallentini was the dominant species in the *Southern zone*, constituting 98% of the euphausiids. Its largest concentrations were observed in the eastern mouth of the Magallanes Strait, and within the Otway and Almirantazgo Fjords, with the latter showing in excess of $11,500$ ind.$10^3\,\mathrm{m}^{-3}$. Lowest concentrations occurred in oceanic channels and around the Wollaston Islands (Fig. 11B).

South of the Penas Gulf it showed centers of abundance in oceanic waters although in the Magellanic sector its maxima occurred in the fjords. High abundance in the Magallanes Strait also were recorded by Guglielmo and Ianora (1997), who indicated that it was the dominant euphausiid. *E. vallentini* is endemic to the southern hemisphere, and characteristic of circumpolar SAAW, although it has been found to 38°S in the Humboldt Current System (Antezana, 1981).

3.4. Species richness

Siphonophores, chaetognaths and euphausiids all showed low species richness, with the broadest range in species number among the siphonophores (1–5 species per sample). The low number of siphonophores obtained in the Chilean fjords and channels, with 12 species, was similar to the value obtained in Scandinavian fjords where 15 species were found (Bamstedt, 1988). These values are low considering the 200 species of siphonophores known from the world oceans (Boltovskoy, 1999).

The maximum value reached for chaetognaths and euphausiids was four species in each taxon. Both groups are the small taxa, the chaetognaths

constituting around 100 species and the euphausiids 86 species (Boltovskoy, 1999). Similarly to the siphonophores, the species richness in both groups was very low in comparison to the species known in the oceans. Richard and Haedrich (1991) described four species of chaetognaths and six of euphausiids in Canadian fjords, while in the Scandinavian fjords, Sands (1980) found five species of chaetognaths and Bamstedt (1988) found four species of chaetognaths and three of euphausiids.

These results confirm that the zooplankton species richness of interior waters of southern Chile had low values when compared with similar communities occurring in the open ocean (Marín and Antezana, 1985; Guglielmo and Ianora, 1995, 1997). Similarly, low species richness was recently reported for the ichthyoplankton in these interior waters (Bernal and Balbontín, 1999).

3.5. Oceanographic characteristics and zooplankton fauna of interior waters

Present results have shown that under extreme oceanographic conditions ($T=0$–$14°C$, salinity $=0$–$34\,\mathrm{psu}$, $O_2=1.5$–$8\,\mathrm{ml\,l}^{-1}$) only a few zooplankton species have become successfully adapted to the interior waters. Some species such as *M. atlantica*, *L. conoidea*, *S. tasmanica*, and *E. vallentini* (Guglielmo and Ianora, 1997; Pagès and Orejas, 1999) have been able to quite successfully colonize the interior waters of the study area. It was notable that high concentrations of siphonophore eudoxids with mean values of $2249\times10^3\,\mathrm{m}^{-3}$ of *M. atlantica* and $3388\times10^3\,\mathrm{m}^{-3}$ of *L. conoidea*, were collected in the Magellanic fjords (Otway, Almirantazgo, and Agostini) outnumbering by six times the numbers of nectophores.

This is reflected by the occurrence of mono-and bi-specific populations represented by *M. atlantica*, *L. conoidea*, *S. tasmanica* and *E. vallentini*. This pattern is also observed in the Magallanes Strait where other taxa have been evaluated and strong monospecific dominance was observed such as that of *Oithona similis*, *Themisto gaudichaudi*, *Boreomysis rostrata* and *Discoconchoecia elegans* (Guglielmo and Ianora, 1995, 1997).
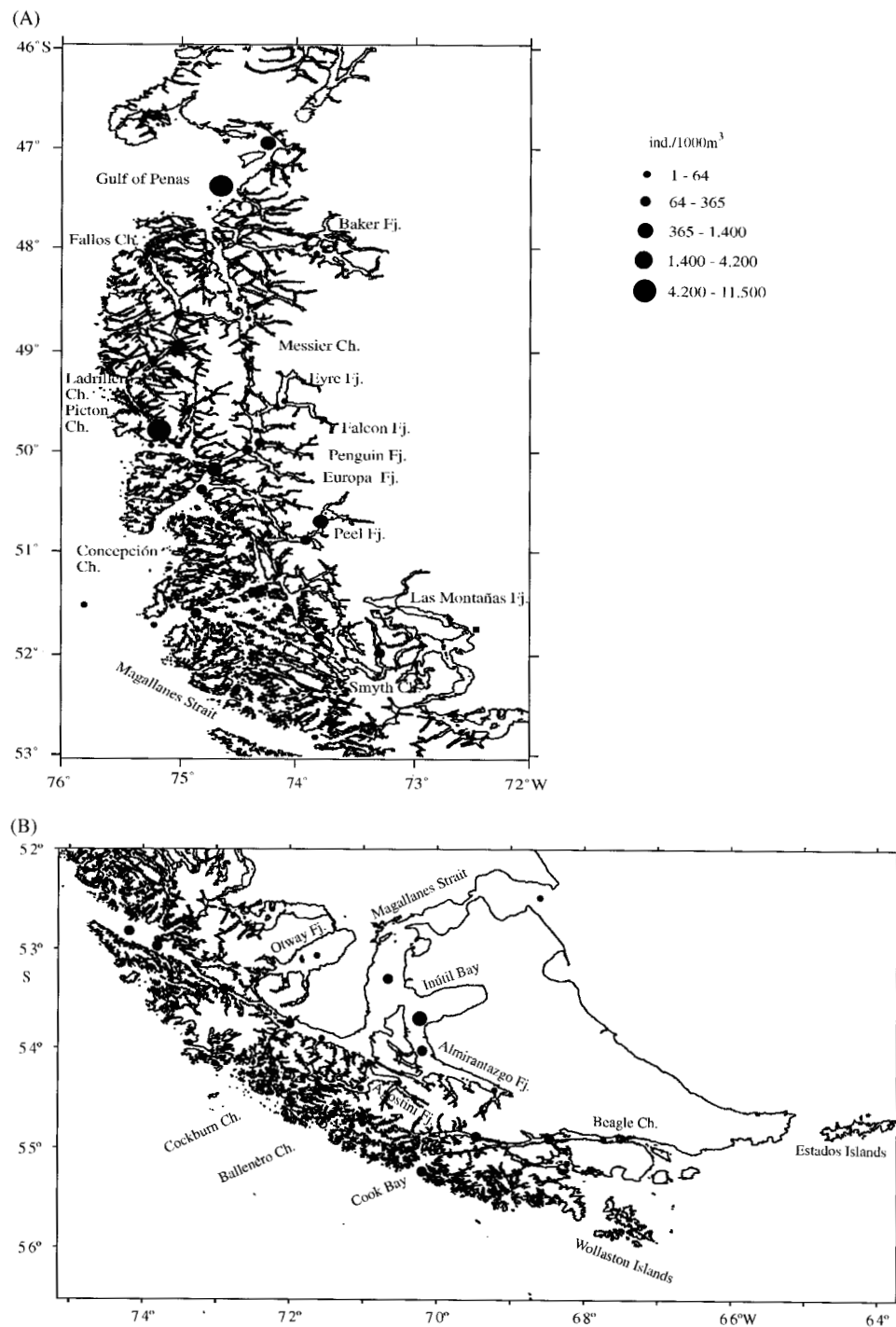
(A)

(B)

Fig. 11. Horizontal distribution of *E. vallentini* in the (A) Central Zone and (B) Southern Zone.

Similar patterns of dominance have been reported for fjords in the northern hemisphere where one or two species predominate, as occurs, for example, with *Dimophyes arctica, Aglantha digitale, Rathkea octopunctata, Eukrohnia hamata, Tomopteris helgolandica, Calanus helgolandicus, Thysanoessa raschii* (Bamstedt, 1988), *Oithona similis, Evadne nordmanni, Obelia spp.* and *Lensia conoidea* (Magnesen, 1988; Pagès et al., 1996).

In areas where SAAW penetrates into the interior waters such as the Guafo Entrance, Penas Gulf, Concepción Channel and the western mouth of the Magallanes Strait, as well as in the oceanic channels, additional epipelagic oceanic species such as *Abylopsis tetragona, Chelophyes appendiculata, Dimophyes arctica, Eudoxoides spiralis, Sphaeronectes fragilis, Sphaeronectes gracilis, Physophora hydrostatica, Sagitta enflata, Sagitta gazellae, Euphausia lucens* and *Thysanoessa gregaria* were founded. Some mesopelagic species such as *Vogtia pentacantha, Vogtia serrata, Eukrohnia bathyantarctica* and *Eukronia hamata* also were collected in these same areas, a few of which reached the interior waters in spite of the shallow sills at the entrances of these sectors. Most of these species are frequent inhabitants of temperate or warm waters (Alvariño, 1971; Pagès and Gili, 1992; Palma and Rosales, 1995), and their occurrence at these latitudes for some of them (*Abylopsis tetragona, Chelophyes appendiculata, Eudoxoides spiralis, Physophora hydrostatica, Sphaeronectes gracilis, Sphaeronectes fragilis, Sagitta enflata* and *Thysanoessa gregaria*) marks the southern limits of their distribution in the southern hemisphere.

The preceding, together with the presence of species common in EW such as *Lensia conoidea, Lensia meteori, Pyrostephos vanhoeffeni, Sagitta marri* and *Stylocheiron maximum*, suggests that the zooplankton fauna of austral Chilean fjords and channels are formed by a mixture of species from different biogeographic regions (Fig. 12).

Species such as *Lensia conoidea, Sagitta decipiens, Eukrohnia hamata*, and *E. bathyantarctica* collected in the interior Chilean waters also have been reported for waters with similar extreme temperature and salinity characteristics, such as Canadian and Scandinavian fjords (Bamstedt, 1988; Richard and Haedrich, 1991; Sands, 1980). This implies that these species are able to live under extreme oceanographic conditions.
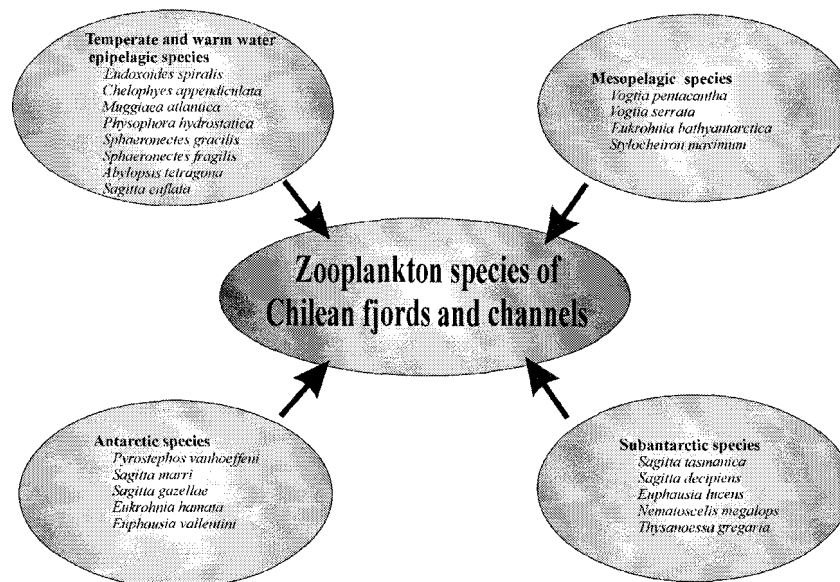

Fig. 12. Zooplankton species in the fjords and channels of southern Chile, and their different potential origins.

None of the species collected in the Chilean inner waters was found to be endemic. This lack of endemic character could be the result of the permanent water exchange between oceanic and interior waters due to surface and subsurface currents (Cáceres et al., 2002).

Finally, the results of this study suggest that the community structure of macrozooplankton in the interior waters is stable during the same season, since the dominant species found in spring are the same in the different years analyzed (1995, 1996 and 1998). Studies previously carried out in warm seasons (spring and summer) in the central and southern zones, also showed the same dominant species, including *Muggiaea atlantica* (Pagès and Orejas, 1999), *Sagitta tasmanica* (Ahumada, 1976; Guglielmo and Ianora, 1997) and *Euphausia vallentini* (Antezana, 1976; Guglielmo and Ianora, 1997).

4. Conclusions

1. The hydrography of the study area showed a marked spatial heterogeneity in temperature, salinity, and dissolved oxygen depending on the advection of Subantarctic Water (33–34 psu) and Equatorial Subsurface Water (33.8–34.2 psu) into the fjords and channels. The mixture of these waters with freshwater arising from precipitation, river runoff and local glacial meltwater forms Modified Subantarctic Water (32–33 psu) and Estuarine Water (1–32 psu), which contributes to the area's hydrographic heterogeneity.

2. The fjord and channel micro-basins are mostly filled with Subantarctic Water. Modified Subantarctic Water and Estuarine Water in its saltier fraction (25–32 psu) are also important components filling the upper part of the micro-basins, and sometimes they fill the whole water column.

3. Remnants of Equatorial Subsurface Water are present only up to Penas Gulf, flowing into the inner channels and filling their deeper parts up to where the topography allows their penetration.

4. The first report is now made for occurrence of the siphonophores *Physophora hydrostatica*, *Vogtia pentacantha* and *V. serrata* in fjords and channels of austral Chile, and the geographic distribution is broadened for most of the siphonophore and chaetognath species collected in the region.

5. The interior waters in the study area showed a decrease in zooplankton biomass and relative abundance from north to south.

6. The siphonophores, chaetognaths, and euphausiids of the interior waters were found to have a low degree of species richness, and presence of monospecific populations, as found for *Muggiaea atlantica*, *Sagitta tasmanica*, and *Euphausia vallentini*.

7. The macroplankton of interior waters was made up of a mixture of species from Antarctic, Subantarctic, and temperate epi- and mesopelagic waters.

Acknowledgements

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