



Circulation and zooplankton biomass distribution over the southern Patagonian shelf during late summer

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Abstract

In this article we use hydrographic data collected in the period 1994–2000 to analyze the summer distributions of temperature and salinity in the southern Patagonian shelf (Argentina). The objective is to infer the circulation patterns of the Patagonian shelf and to relate them to the zooplankton biomass distribution. The vertical structure of the hydrographic variables indicates the existence of two distinct regions. North of 51°S, the water column can be characterized as a two-layer system separated by a thermocline at approximately 50 m depth. South of 51°S, the density structure of the water column is nearly homogeneous. The two regions are separated by a front that extends in a northeast direction from the coastal region of the Grande Bay towards the continental slope. The circulation patterns inferred from the observed fields indicates that although the circulation in the southernmost portion of the Patagonian shelf, i.e., from Tierra del Fuego to the Grande Bay front, is towards the north, as predicted by previous studies, this northward flow turns offshore at the location of the Grande Bay front. This frontal region and the associated circulation pattern have not been previously described. The inferred circulation may enhance zooplankton production and accumulation over the coastal area of the Grande Bay—via increased primary production, by favoring both the enrichment and trapping of nutrients, and the retention of organisms.

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1. Introduction

The southern Patagonian Shelf, a region that extends from approximately 47°S to Cape Horn, encompasses a vital ecosystem that, although critical to the Argentinean fisheries, remains largely unexplored. In particular, there is a lack of understanding of the linkages between the

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ocean circulation and the plankton productivity of the ecosystem. Observations, for example, indicate that in the coastal waters near 51°S there is an increase of zooplankton during the austral summer, which might be related to the patterns of the oceanic circulation (Sabatini and Álvarez Colombo, 2001; Sabatini et al., 2000, 2001). The increase of zooplankton availability is likely to influence higher levels of the ecosystem and, hence, impact the local fisheries. For all its importance, however, we know relatively little on the coupling between physics and biology in these regions.

In this article, we analyze hydrographic and zooplankton data collected in the southern Patagonian Shelf during six austral summers. Our objectives are to describe the typically recurrent mesoscale features in order to develop hypothesis on the regional circulation patterns and to associate them with the local zooplankton activity. Unfortunately, the spatial and temporal resolution of our data set does not allow us to resolve intra-seasonal nor inter-annual variations, neither to define the small-scale circulation patterns that are more relevant to the physical–biological coupling. The combination of hydrographic and biological information, however, permits us to infer circulation patterns that are dynamically consistent with the results of existing numerical simulations and the zooplankton distribution.

This article has been organized as follows. After this introduction, in Section 2, we offer some background information over the circulation and ecosystem characteristics of the southern Patagonian shelf. In Section 3, we describe the data to be analyzed and the methods. In Section 4, we describe the circulation patterns inferred from the hydrographic data (Section 4.1), and the zooplankton distribution (Section 4.2). In Section 5, we summarize our results and combine them to make further inferences on the regional circulation and its effect on the ecosystem.

2. Background

The shelf circulation over the southern Patagonian region depends on the local wind forcing, the propagation of tidal waves, freshwater discharges

and the influence of the neighboring deep currents. The upper layers of the ocean are under the direct effect of the strong westerly and south-westerly winds which generate a dominant north–northeast flow (Forbes and Garraffo, 1988; Glorioso and Flather, 1995, 1997; Piola and Rivas, 1997; Glorioso, 2000). Although there are no observationally derived estimates of the circulation patterns in this region, numerical experiments indicate that south of 50°S the circulation is characterized by an anticyclonic cell, located between the coast and approximately 65°W, and a generally northward flow farther east (Fig. 7, Glorioso and Flather, 1995).

The Patagonian shelf has one of the strongest tidal regimes of the world, which generate large energy dissipation by bottom friction and strong vertical and lateral mixing. About 10% of the estimated total global dissipation takes place over the region (Simpson and Bowers, 1981; Glorioso and Flather, 1997). The propagation of the tidal wave over the Patagonian shelf dominates the high frequency portion of the variability spectrum (periods less than a day). The tidal amplitudes peak near the coast and decrease farther offshore. The largest values are observed in the latitudinal strip between 47°S and 51°S. Near the mouth of the Magellan Strait, for example, the amplitudes of the mean and spring tides are 7.1 and 9.0 m, respectively (Panella et al., 1991), while the amplitudes of the tidal velocities range between 0.8 and 1.0 m s⁻¹ (Michelato et al., 1991). The tidal amplitudes decrease farther south to 4.0 m at the tip of Tierra del Fuego.

There are two types of freshwater discharges over the Patagonian shelf. The first is related to the drainage of continental rivers along the coast of southern Patagonian, and the second to the inflow of diluted waters from the Magellan Strait (Panella et al., 1991). The main rivers of southern Patagonia are the Deseado, Santa Cruz, Coig, and Gallegos (Fig. 1). The Santa Cruz River has the largest discharge with an annual mean value of approximately 710 m³ s⁻¹, and a peak of 1250 m³ s⁻¹ at the end of the austral summer (March). Although there is only scant information about the magnitude of the relatively fresher waters from the Magellan Strait, the water mass

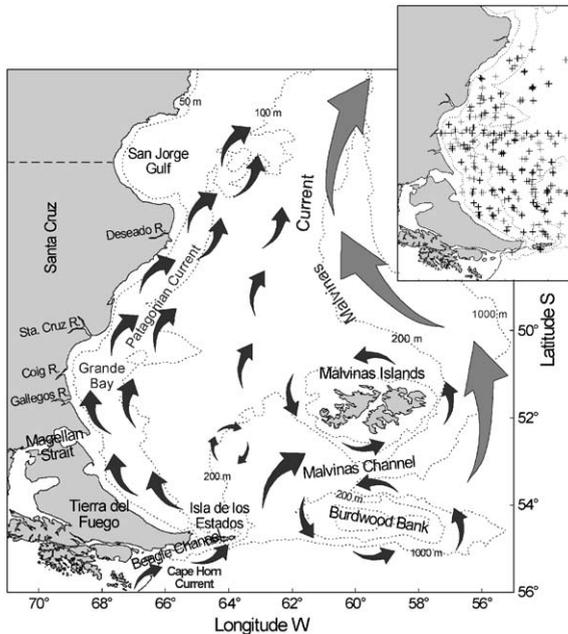


Fig. 1. General water circulation over the southern Patagonian shelf (modified after Piola and Rivas, 1997). Arrows are proportional to flux velocities. Local names used in the text are also indicated. Positions of the CTD stations occupied during the six cruises conducted in late summer (1994–2000) are shown in the inset. See also Table 1 for further sampling details.

structure of the Patagonian shelf is strongly influenced by a fresh water tongue that has its salinity minimum in that region and that is known as the Patagonian Current (Fig. 1). The main freshwater contributions to the Magellan discharge are continental runoff, local rainfall in the southeast Pacific (with annual averages larger than 5000 mm), and the entrainment of fluvial–glacial waters originated from the seasonal melting of glaciers. The resulting surface salinity of these waters range from 28.0 in the Pacific sector to 32.5 in the Atlantic. The magnitude of the volume discharge is largely unknown. Assuming a width of 40 km, a depth of 100 m and a mean velocity of 0.1 m s^{-1} the average transport should be of the order of 0.5 Sverdrup (Sv; $1 \text{ Sv} = 10^6 \text{ m}^3 \text{ s}^{-1}$). There are not long-term velocity measurements to validate this estimate. Lusquiños and Valdés (1971) reported values of $0.26\text{--}0.4 \text{ m s}^{-1}$ while Michelato et al. (1991) reported values of

1.0 m s^{-1} both from short time series. Those higher values, however, are likely to be biased by the strong tidal currents that characterize this region and do not necessarily represent a long-term average.

Two branches of the Antarctic Circumpolar Current influence the circulation over the southern Patagonian shelf. To the south, there is a direct inflow of cold Antarctic waters, mainly through the gap between Tierra del Fuego and Isla de los Estados, that has been dubbed the Cape Horn Current (Hart, 1946; Boltovskoy, 1970; Fig. 1). To the east, and over the continental slope, the narrow and deep northward jet known as the Malvinas Current occurs. The Malvinas Current is the western boundary current of the subpolar South Atlantic. After leaving the Drake Passage it meets the Burdwood Bank and bifurcates into a western and an eastern branch (Fig. 1). The waters of the westernmost branch are significantly diluted by continental runoff and ice melting (Lusquiños and Valdés, 1971; Piola and Gordon, 1989; Piola and Rivas, 1997; Guerrero et al., 1999).

The southern Patagonian Shelf is the habitat of various commercially important species, among them squid, southern blue whiting, Patagonian hoki, austral cod and Patagonian toothfish (Brunetti et al., 2000; Wöhler et al., 2000a, b; Hansen and Wöhler, 2000; Prenski, 2000). In the inner shelf the most abundant fish is the Patagonian sprat (Sánchez et al., 1995). The Patagonian hoki has become the largest resource to mitigate the recent collapse of the hake, one of the most commercially important resources of Argentina (e.g., Wöhler, 1999). Both Patagonian hoki and sprat are key ecological species acting as strong links between the pelagic and benthic trophic webs. High values of zooplankton biomass, mostly amphipods and copepods, are normally recorded during austral summer and early autumn in coastal waters between 51°S and 52°S . The zooplankton abundance is much lower elsewhere in the region (Sabatini and Álvarez Colombo, 2001; Sabatini et al., 2000, 2001). Squid and Patagonian hoki feed mainly on amphipods (Ivanovic and Brunetti, 1994; Sánchez, 1999) and Patagonian sprat is a zooplanktivorous species feeding mostly on copepods (Ramírez, 1976). The

latter is the main prey for other co-occurring fish species. Zooplankton distribution and variability may thus strongly influence higher trophic levels of the ecosystem, many of them under increasing commercial exploitation.

3. Methods

The data to be analyzed in this work were collected during six austral summers of the period 1994–2000 (Fig. 1, Table 1). At each station, temperature and salinity profiles were obtained by either a Sea-Bird 19 or a ME CTD. The calibration of the raw data was made by in situ bottle sampling and reversing thermometers (Table 1). The CTD data recorded on each cruise were interpolated onto a common 17×28 km grid from 48°S to 54.5°S and from the coast to 63°W (*kriging* method). Plots and basic statistics of the sea surface and bottom temperature, salinity and density fields were then estimated from those grids. All through the six cruises 13 stations spaced at about 35 km intervals were systematically occupied at fixed positions along a ca. 500 km cross-shelf transect at 51°S .

The stratification of the water column was estimated from the stability parameter Φ (Simpson, 1981) obtained from the vertical profiles of density at 1 m depth interval. The dependency of the Φ parameter on depth was removed by standardizing the values as

$$\Phi_{\text{STD}} = \Phi_{\text{OBS}}(Z_{\text{AVR}}/Z_{\text{OBS}}).$$

Values of the Simpson parameter $\Phi < 40 \text{ J m}^{-3}$ and $< 40 \text{ J m}^{-3}$ were used to denote vertically mixed and stratified waters, respectively. This Φ critical value was determined by comparison with unpublished ship data and infrared satellite images from waters of the northern Patagonian shelf and it is been currently used to separate the mixing and stratification fields in that region (e.g., Hansen et al., 2001; Sabatini and Martos, 2002). In this study, however, the isoline of 40 J m^{-3} was not used as an indicator of the location of fronts. There was, in fact, no single isoline that consistently marked all frontal positions, which were better denoted by the gradients. Herein we define as a front a region with large temperature or salinity horizontal gradients.

Zooplankton sampling was carried out with a high speed Nackthai sampler (Nellen and Hempel, 1969) provided with a $400 \mu\text{m}$ mesh size and flowmeter. The sampler was towed obliquely through the water column from near the sea bottom to surface. The methodology for the processing of the zooplankton samples and biomass estimates (wet weight) was described in detail elsewhere (Sabatini and Álvarez Colombo, 2001). The mean distribution of zooplankton biomass over the entire time series was plotted over the same grid as the physical parameters were. This may have introduced a certain amount of bias in the resulting pattern, since the number and location of the stations where zooplankton sampling was carried out varied substantially from cruise to cruise, and were much fewer than CTD stations. Even so it does represent the major

Table 1

Detail of the surveys carried out from 1994 to 2000 over the southern Patagonian shelf that provided the present data set on hydrography and zooplankton

Cruise code	Date	RV	CTD type	ΔSal	ΔTemp	CTD	NCK
OB-04/94	21 March–9 May 1994	Cap. Oca Balda	ME	0.080	0.011	93	33
OB-04/95	7–24 March 1995	Cap. Oca Balda	ME	0.068	n.d.	50	28
OB-04/97	15 March–4 April 1997	Cap. Oca Balda	ME	0.109	0.027	47	28
EH-03/98	4–28 March 1998	Dr. E. Holmberg	Sea-Bird 19	0.017	0.036	74	8
OB-03/99	10 March–2 April 1999	Cap. Oca Balda	Sea-Bird 19	0.026	n.d.	62	17
EH-03/00	24 March–17 April 2000	Dr. E. Holmberg	Sea-Bird 19	–0.005	n.d.	54	21

The CTD type and calibration errors in measuring salinity and temperature (ΔSal , ΔTemp), the number of CTD stations (CTD) and the number of zooplankton tows (NCK) accomplished during each cruise are indicated. Zooplankton sampling was carried out with a Nackthai sampler, $400 \mu\text{m}$ mesh size.

trends. Zooplankton statistics were instead calculated over the original estimates of biomass, without any kind of interpolation.

4. Results

4.1. Hydrography

Our description of the shelf circulation is based on vertical profiles of temperature and salinity collected during cruises carried out in the austral summer. The T–S structure of the Patagonian shelf region (Fig. 2) is characterized by three distinct water masses: Malvinas Water, i.e., water transported by the Malvinas Current, with salinities between 33.8 and 34.2, coastal water, with salinities less than 33.2, and shelf water formed by mixing of these two masses, with salinities ranging from 33.2 to 33.8 (Bianchi et al., 1982).

The temperature fields have a marked gradient from the northwest towards the southeast (Fig. 3). The maximum sea surface temperatures (SSTs)

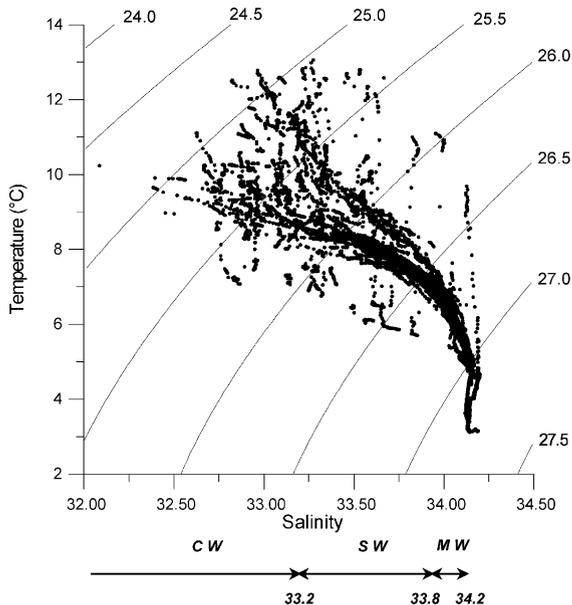


Fig. 2. T–S structure of the Patagonian shelf in late summer showing three distinctive water masses defined by their salinities, CW, coastal water; SW, shelf water; MW, malvinas water, i.e., water transported by the Malvinas Current (sensu Bianchi et al., 1982).

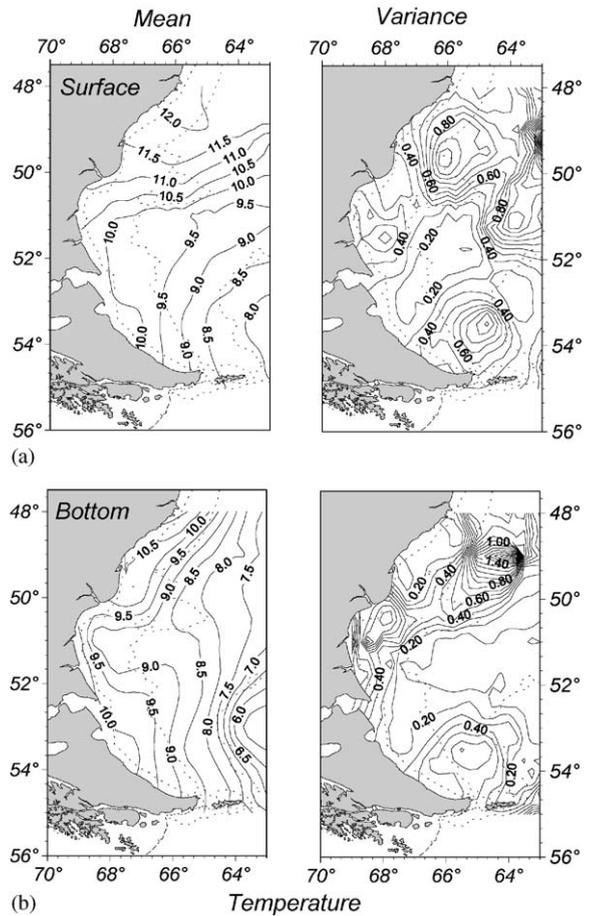


Fig. 3. Mean late summer temperatures and variances over the southern Patagonian shelf (1994–2000): (a) surface values and (b) bottom values.

recorded during our cruises, 11–13°C, are located in the north. The lowest SST values, 6–9°C, are located towards the southeast (Fig. 3a). The spatial patterns of bottom temperatures are similar to those of the SSTs (Fig. 3b), particularly south of 50°S. In the near shore region ($z < 100$ m), the vertical structure of the water column is highly homogeneous (see also Fig. 5), a feature that is likely to be associated with the strong vertical mixing caused by the large tidal currents that characterize this region (Glorioso and Flather, 1995). The quasi-isothermal structure of the near-shore region is not a ubiquitous characteristic of the entire surveyed area but only of its southernmost portion (Fig. 4). There is an abrupt change of

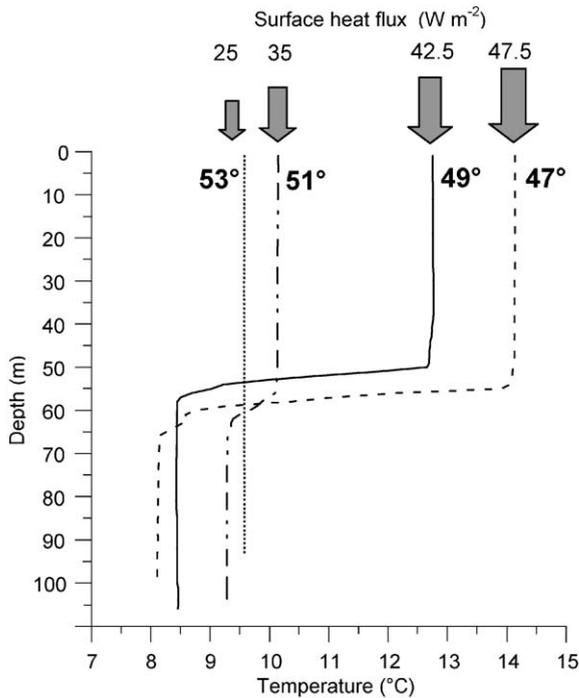


Fig. 4. Summer thermal stratification off southern Patagonia at varying latitudes from 47°S to 53°S (March 1999). Vertical temperature profiles from selected mid-shelf CTD stations, all of them precisely positioned on the 100 m isobath, are shown to exemplify the typical patterns. Arrows are proportional to the average heat flux at the sea surface (from Esbensen and Kushnir, 1981).

thermal structure near 51°S. To the north, the water column can be characterized as a two-layer system separated by a sharp thermocline at 50 m depth. To the south, it has a quasi-isothermal structure. Although a portion of the differences between stations can be attributed to latitudinal variations of the solar radiation, the magnitude of the SST gradients (Fig. 4) indicates that horizontal advection and vertical mixing are also important in this region. Note, for example, that while the SSTs decrease to the south (approximately 5°C from 47°S to 53°S) the bottom temperature actually increases (8°C at 47°S to 9.5°C at 53°S). The region where the thermal structure changes from a two-layer to a homogeneous system is characterized by sharp SST gradients of approximately 1°C per degree of latitude which indicates the existence of a frontal region. Interestingly, this

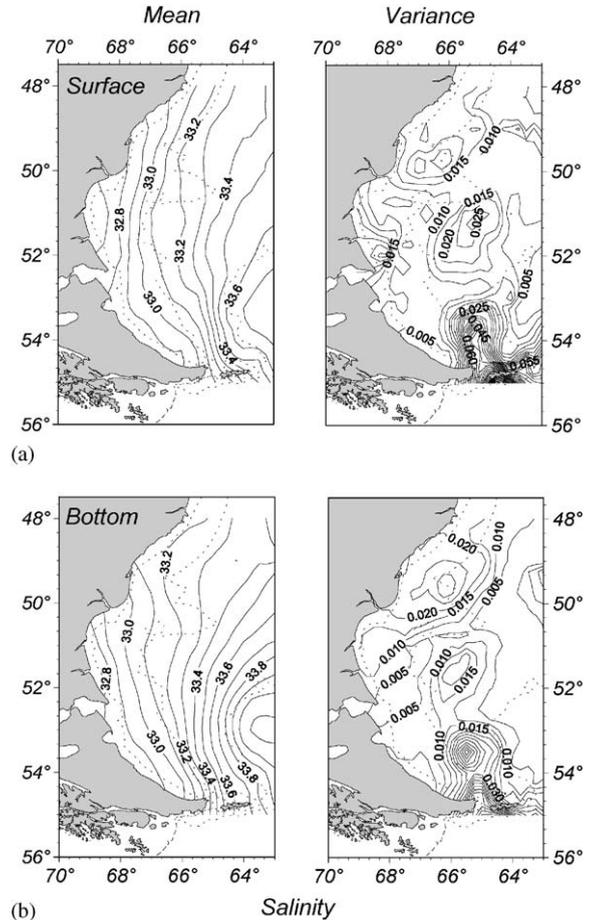


Fig. 5. Mean late summer salinities and variances over the southern Patagonian shelf (1994–2000): (a) surface values and (b) bottom values.

frontal region appears to be limited to the top portion of the water column since the signal at the bottom nearly disappears (Fig. 3a and b).

Salinity is a useful tracer to infer the influence of the neighboring deep circulation and the effects of freshwater discharges onto the continental shelf circulation. The overall pattern of the salinity distribution consists of a gradual increase offshore and a nearly homogeneous structure in the vertical (Fig. 5). The lowest surface salinity values of the region, 32.4–32.8, are located in the southwestern region where the salinity structure is highly influenced by the relatively fresh discharges from the Magellan Straits and the continental rivers in the Santa Cruz province. The highest salinities,

33.7–34.1, were recorded in the deepest part of the southeastern area. Unlike temperature, the spatial distribution of surface and bottom salinities are very similar (Fig. 5a and b).

The sharpest horizontal gradient of salinity observed during our surveying period was located between the southern tip of Tierra del Fuego and the eastern margin of the Isla de los Estados (at approximately 64°W and 54°S, Table 2). This salinity front is generated by the entrainment of cold and dense Subantarctic water in the Cape Horn Current (Fig. 1). Although of smaller magnitude, two other salinity gradients were also observed over the mid shelf between 50°S and 53°S, and in the coastal region of the Grande Bay. The former is related to the contrast between the coastal waters with the shelf waters (sensu Bianchi et al., 1982), while the later is likely to be related to freshwater discharges into the Grande Bay. The mouths of the three major rivers of southern Patagonia are close to each other, therefore their discharges are likely to overlap and reinforce, conforming thus a single large estuarine plume whose offshore penetration might be enhanced by the strong tidal currents that characterize this region. The interannual variations of amplitude and location of the different salinity fronts are summarized in Table 2.

Further insight into the dynamical characteristics of the hydrographic fields can be gained from the Simpson’s stability parameter, which repre-

sents the energy required to completely mix the water column (Simpson, 1981). The spatial distribution of the Simpson’s parameter indicates the existence of three dynamically distinct regions, which are separated, in a crude way, by the isoline of 40 J m^{-3} (Fig. 6). The first region is located north of approximately 51°S where the relatively high values of the Simpson parameter correspond to the strongly stratified two-layer system described above. The second region is confined to the middle and inner shelf south of 51°S (depths

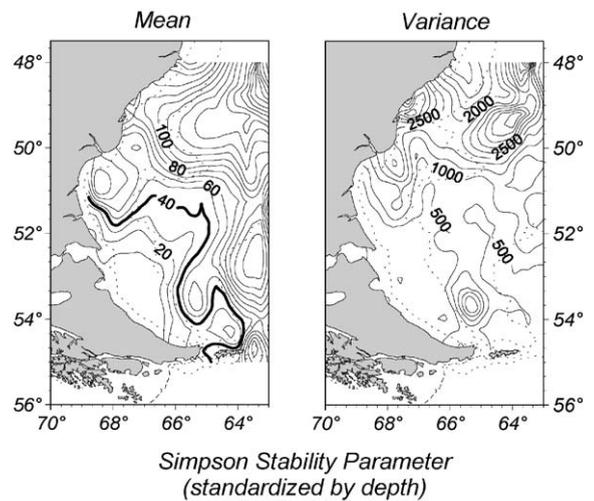


Fig. 6. Late summer stratification over the southern Patagonian shelf. Mean values and variances of the Simpson stability parameter standardized by depth (1994–2000).

Table 2

Year-to-year horizontal gradients (ΔS , $\text{psu } 10 \text{ km}^{-1}$) of the three main haline fronts occurring over the southern Patagonian shelf in summer

Year	(Shelf-break) water mass boundary front		(Coastal) tidal estuarine-plume front		(Mid-shelf) water mass boundary front	
	ΔS ($\text{psu } 10 \text{ km}^{-1}$)	Location	ΔS ($\text{psu } 10 \text{ km}^{-1}$)	Distance (km)	ΔS ($\text{psu } 10 \text{ km}^{-1}$)	Distance (km)
1994	0.11	64°W; 54°S	0.09	125	0.05	320
1995	0.07	64°W; 54°S	0.06	111	0.05	270
1997	0.12	64°W; 54°S	0.05	116	0.06	300
1998	0.09	64°W; 54°S	0.08	65	0.06	240
1999	0.08	64°W; 54°S	0.05	140	0.07	400
2000	0.08	64°W; 54°S	0.09	70	0.05	300
Series average	0.09		0.07	81	0.06	305

The approximate coordinates or the distance from shore at 51°S indicates their location.

less than 100 m), where the relatively small values of the Simpson parameter correspond with the quasi-homogeneous density structure observed during our cruises. The third region extends from the gap between Tierra del Fuego and the Isla de los Estados to the northeast and corresponds with the intrusion of the Subantarctic waters associated with the Cape Horn and the Malvinas Current.

As a consequence of the highly variable spatial (and inter-annual) stratification of the water column over the region, large variance values are associated with the Simpson parameter (Fig. 6). Standardized by depth values of this parameter (over the entire study period) ranged between a minimum of 0.004 J m^{-3} in the quasi-homogeneous coastal area south of 51°S in 1995 and a maximum of 267 J m^{-3} recorded in the strongly stratified northern area in 1999. The stabilization (and density structure) of the water column is mainly determined by temperature in the northern region, by salinity in the southern coastal region, and by a combination of temperature and salinity in the southern offshore region.

The previous analysis indicates that near 51°S there is rapid transition from a strongly stratified, two-layer system to the north, to a quasi-homogeneous system to the south in the inner shelf. It was noted that the boundary between these regions is well defined in temperature (Figs. 3 and 4) but not in salinity. The thermal front, however, is also apparent in the horizontal distribution of density (Fig. 7) which indicates that, by geostrophic balance, the meridional gradient of density (and temperature) is corresponded by zonal velocities. Since mass has to be conserved it is expected that this zonal velocity field will have regions of convergence and divergence of mass, i.e., regions of upwelling and downwelling. Our cruise data show that, as expected, the region of Grande Bay, near 51°S , is indeed characterized by rather complex circulation patterns. A cross-shelf section obtained during the 1994 cruise typifies the hydrography and circulation associated with this region (Fig. 8). The temperature profile shows a typically weak thermocline ($\Delta t = 0.07^\circ\text{C m}^{-1}$) and a small wedge of cooler water (8.5°C) on the bottom and very close to the shore (Fig. 8a). This

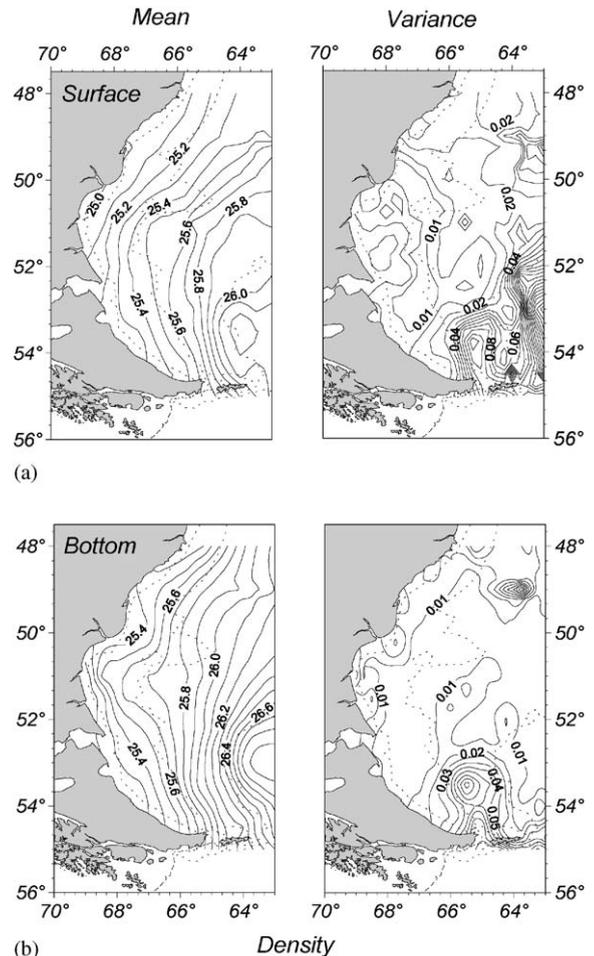


Fig. 7. Mean late summer densities and variances over the southern Patagonian shelf during summer (1994–2000): (a) surface values and (b) bottom values.

cold wedge was not always observed but it was absent in the summers of 1999 and 2000 (not shown). The salinity profiles show a strong gradient near the coast (Fig. 8b), associated with the estuarine-plume front mentioned earlier (the average salinity gradient was of $0.07 \text{ psu } 10 \text{ km}^{-1}$, Table 2). Farther offshore there is a second salinity gradient at approximately 300 km from the coast (Table 2). This haline front marks the boundary between the coastal and shelf water masses. The advection of subantarctic waters by the Malvinas Current is also evident over the outer continental shelf ($\sim 500 \text{ km}$) where there are sharp gradients of temperature and salinity in the deep layers. In

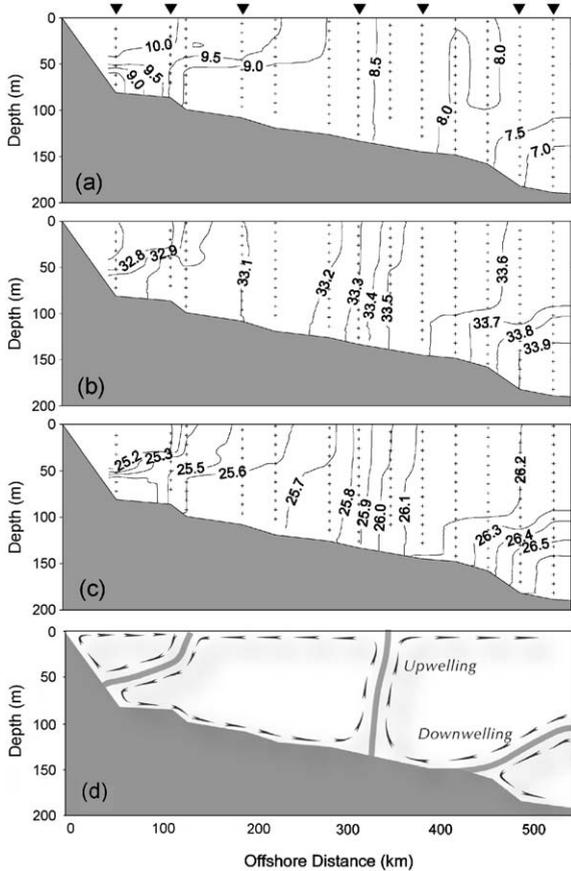


Fig. 8. Selected cross-shelf section off Grande Bay at 51°S from the March 1994 cruise. Vertical profiles of temperature (a), salinity (b) and density (c), and schematic baroclinic circulation across the shelf (d). Triangles at the top of the upper panel indicate the location of the fixed CTD stations along the sampling transect.

correspondence with the temperature and salinity fields the isopycnals show three retrograde fronts (Mooers et al., 1978) (Fig. 8c). The existence of these density fronts can be associated with baroclinic cells of circulation (Fig. 8d). The proposed scheme suggests the downwelling and inshore intrusion of cold and dense Malvinas water in the bottom boundary layer of the outer shelf, and a compensating offshore flow in the upper layers. The nearshore front is mostly controlled by the offshore penetration of a fresh-water plume feeding from the nearby river discharges and from relatively fresh waters advected from the Magellan Strait.

4.2. Zooplankton and trophic relationships

The spatial distribution of the zooplankton biomass reveals a “hot spot”, i.e., a region with values well above the background mean, over the coastal area of the Grande Bay up to ca. 200 km from shore (Fig. 9). There, the average summer values recorded during our cruises have an absolute maximum of 1000 mg m^{-3} . Peak values during individual years exceed 3500 mg m^{-3} (Table 3). The inherent variability in zooplankton distribution, most likely due to patchiness (see maximum and minimum figures realized over

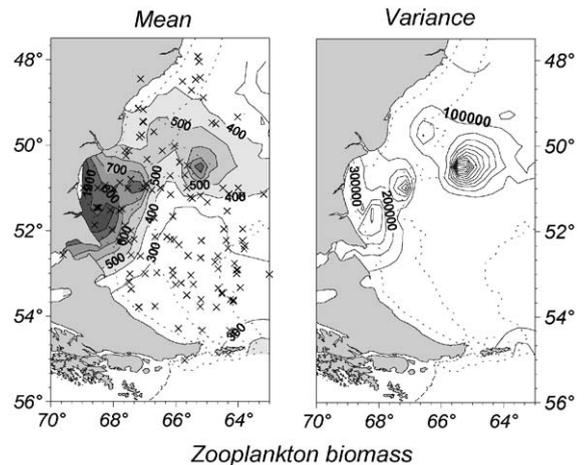


Fig. 9. Distribution of zooplankton biomass (wet weight, mg m^{-3}) over the southern Patagonian shelf during late summer. Mean values and variances estimated for summer seasons from 1994 to 2000. Nackthai sampler, $400 \mu\text{m}$ mesh size. Crosses correspond to the zooplankton stations occupied throughout the entire study period.

Table 3
Year-to-year range and mean values of zooplankton biomass (wet weight) off southern Patagonia over the surveyed period

Year	Maximum (mg m^{-3})	Minimum (mg m^{-3})	Mean (mg m^{-3})	N
1994	2776	18	629	33
1995	3559	92	851	28
1997	2728	60	432	28
1998	667	93	250	8
1999	1386	49	525	17
2000	657	41	293	21

the study period in Table 3), accounts for the large variance values of zooplankton biomass. In addition, some degree of uncertainty resulting from the interpolation of the field data in Fig. 9 should be considered. This latter is probably the reason for the large variances observed offshore in the northern region, where sampling was rather occasional throughout the cruises. On the contrary, maximum variances across the zooplankton “hot spot” seem more closely related to the large interannual variability of largests concentrations but also, although to a lesser extend, to the dissimilar sampling coverage between years (Table 3).

The overall composition of the zooplankton biomass is dominated by a relatively small number of taxa. Copepods compose the 30–40% of the total biomass while the contribution of amphipods and euphausiids varies between 5–45% and 20–30%, respectively. Species composition across the area of enhanced zooplankton biomass is illustrated from the data obtained at 51°S during the 1994 cruise (Fig. 10). The biomass at nearshore stations is dominated by the copepod *Calanus australis* and the amphipod *Themisto gaudichaudii*. Specific dominance changes offshore to the euphausiid *Euphausia lucens* and the copepod *Neocalanus tonsus*. Less abundant species are the copepods *Drepanopus forcipatus*, *Calanus simillimus* and *Clausocalanus brevipes*, the euphausiid *Thysanoessa gregaria*, and the chaetognats *Eukronia* spp. and *Saggita* spp. The latter group normally occurs only at offshore stations.

The spawning of fish is expected to follow the cycle of plankton production. The peak of late larvae and young juveniles should coincide with the peak of zooplankton biomass, matching the availability of suitable size prey in accordance with fish ontogeny (Cushing, 1975, 1996; Bollens et al., 1992). Hence, the spawning of local fish populations should be closely linked to the seasonal development of their prey populations. *Calanus australis* and *Drepanopus forcipatus* are the main prey species for the adults of Patagonian sprat (Ramírez, 1976). Through trophic transfer the contribution of these copepods may also be important to both Patagonian hoki (smaller than 59 cm) and Patagonian squid that feed almost exclusively on the amphipod

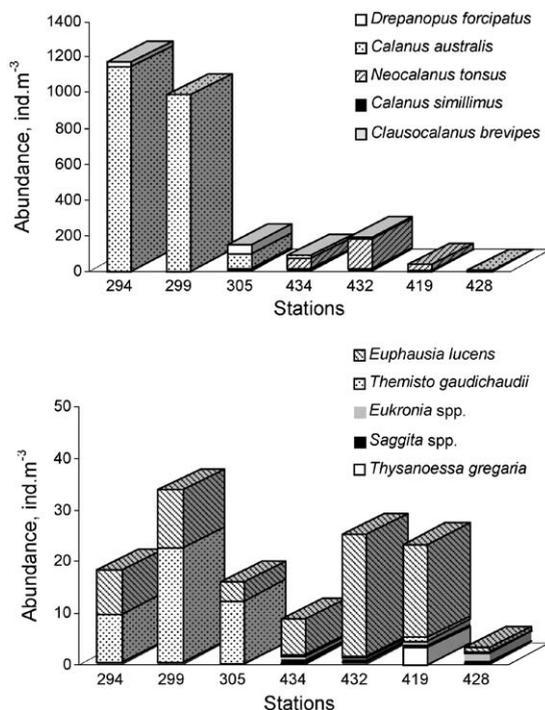


Fig. 10. Species composition across the area of enhanced zooplankton biomass at 51°S (Grande Bay). Data from the March 1994 cruise.

Themisto gaudichaudii (Sánchez, 1999; Ivanovic and Brunetti, 1994). Early stages of those copepods likely constitute the primary food source of larval and juvenile sprat, hoki and other fish species.

The large-sized zooplankton we observed during the summer seasons should therefore meet the energetic demands of late fish larvae and pelagic juveniles. Still preliminary evidences (authors' unpublished observations) indicate that earlier in spring (November) the small copepod *Drepanopus forcipatus* prevails over the larger *Calanus australis* in the area of Grande Bay, while large zooplankton such as amphipods and euphausiids are still absent or scarce. By then younger fish stages requiring lower rations are expected to co-occur.

5. Summary and discussion

According to our observations the mass structure of the Patagonian shelf can be separated in

two distinct regions. North of 51°S , the water column can be characterized as a two-layer system separated by a shallow thermocline at 50 m depth. South of 51°S the density structure of the water column becomes nearly homogeneous. The two regions are separated by a front that extends, in a northeastern direction, from the Grande Bay to the continental slope. Given the highly barotropic structure of the southern region it would be meaningless to calculate geostrophic currents from the T–S profiles. The spatial distribution of the tracers, however, indicates a generally northward circulation from Tierra del Fuego to the frontal region where the flow veers to the northeast (Fig. 11). The circulation patterns inferred from our observational data set do not agree with the results of numerical simulations that characterize the shelf circulation as a predominantly north–

northeast flow. Those simulations, however, may have missed the Grande Bay front because of the use of the outdated Hellerman and Rosenstein (1983) wind data. The recent numerical simulations by Palma et al. (2004) show that the Grande Bay front is reproduced by numerical models forced with the ECMWF winds (e.g., Trenberth et al., 1990) but not by those forced with the Hellerman and Rosenstein climatology. According to other experiments by Palma et al. (2004), density stratification and tidal mixing (associated with the protrusions of the bottom topography to the north of Grande Bay) contribute significantly to the sharpening of the front. If our hypotheses are correct, the Grande Bay front should be a ubiquitous feature of the coastal circulation since the wind stress curl structure over the Patagonian shelf does not show substantial qualitative changes with the seasons. It should be noted that seasonal stratification, although important for the frontal sharpening, is unlikely to be the main forcing for the frontal formation because the spatial scales associated with it are substantially larger than those indicated by the observations.

Although it is difficult to determine the regions of maximum dynamic variability, our observations show the largest variances in temperature and salinity in the passage between Tierra del Fuego and the Isla de los Estados and along the Grande Bay frontal region (Figs. 3 and 5–7). The variability of the southern region is likely to be driven by its connection to the highly energetic flow of the Antarctic Circumpolar Current, while that in the northern region by hydrodynamic instabilities of the front.

While it is not possible to separate the different contributions of the forcing to the shelf circulation it seems reasonable to surmise that the offshore portion of the shelf (say, east of 66°W) would be largely dominated by wind and inflows from the deep currents (i.e., the Cape Horn or Malvinas Currents) while the inshore portion by tides and river discharges. Wind forcing, in principle, should be important everywhere but the headlands of the Patagonian coast (particularly that at 50°S), might allow the development of meridional pressure gradients that arrest the wind forced circulation (Fig. 11). Numerical experiments (e.g., Glorioso

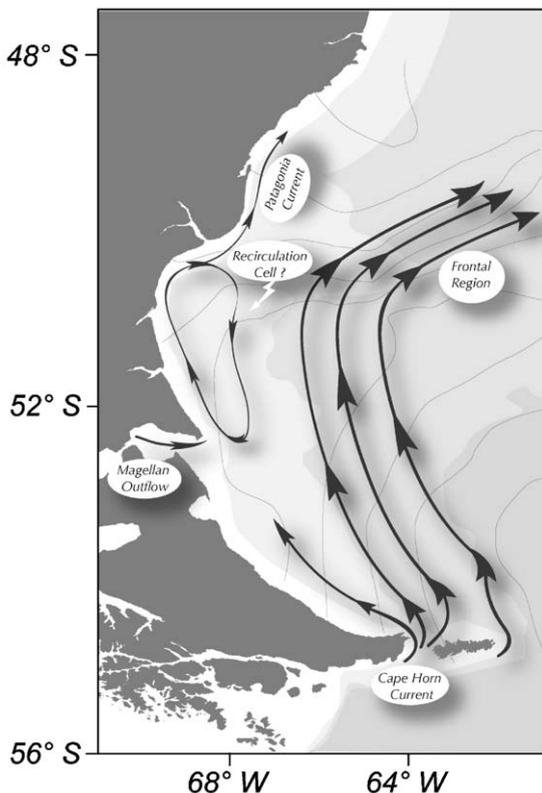


Fig. 11. Schematic illustration of the summer upper circulation over the southern Patagonian shelf inferred from the distribution of temperature and salinity.

and Flather, 1995) have shown that these pressure gradients generate a recirculation cell within the Grande Bay. The distribution of zooplankton biomass discussed in the previous section indicates that such a cell might indeed exist and contribute to the creation of a “zooplankton hot spot” in the Grande Bay. Unfortunately, our distribution of T-S does not allow us to properly resolve the oceanic circulation at these scales to either confirm or deny the existence of such a cell. For that reason the recirculation cell of Fig. 11 includes a question mark. Note that unlike the cells reported by Glorioso and Flather (1995) and Palma et al. (2004), the cell depicted in Fig. 11 is cyclonic. In these regards we should note that the schematic illustration of Fig. 11 represents the upper circulation while those of Glorioso and Flather or Palma et al. represent the vertically averaged circulation. It is still possible that the vertically integrated flow along the Grande Bay moves poleward but the northward plume of low salinity water from the Magellan Strait reported from observations can only be accounted by an equatorward surface current.

From a biological point of view the most interesting region of the southern Patagonian shelf is the Grande Bay, where our observations show the existence of a “zooplankton hot spot”. The production and accumulation of plankton in this region can be ascribed to nutrient enrichment and organisms retention. The nutrient enrichment is likely to be associated to land drainage, river discharges and runoff from the Magellan and Fuegian Channels, and frontal upwelling. Nitrates, for example, are in fact high ($5\text{--}12\ \mu\text{mol l}^{-1}$) all over the southern coastal area during late summer, and even higher offshore due to the supply from pure Subantarctic waters (Guglielmo and Ianora, 1995; Lusquiños, 1971). The accumulation of biomass should be linked to the oceanic circulation. Coastal discharges should, in principle, generate freshwater plumes that propagate to the north (in the southern hemisphere). The trapping of these nutrients in the Grande Bay, and the consequent increase and concentration of zooplankton biomass via enhanced primary production, might be related to the recirculation cell described in the previous paragraph and to the

close proximity of the frontal (northern) region. Note, for example, that the offshore maximum of the zooplankton biomass (Fig. 9) is located near the region where we identified the existence of an upwelling front (Fig. 8d).

The stratified areas to the north of Grande Bay might also benefit from the intense tidal mixing that takes place all over the southern Patagonian shelf. It is a well known phenomenon that, as soon as the thermocline has developed in spring, the phytoplankton bloom begins. Zooplankton does not generally benefit much from spring blooms because their numerical response time is far too long. However, regarding the currents and tides in the research area, there will follow a phenomenon typical for tidal fronts: the stratified area will shrink by erosion of the thermocline during periods of bad weather, and expand during silent periods, thus entraining nutrient rich water from the south all throughout the summer. This could enhance primary production and hence the zooplankton biomass. In the southern areas of the Grande Bay, however, where the water column is permanently mixed, the algal cells are continuously moved up and down and the amount of light that they receive it is limited to the time-span when they reach the surface during the day. This means that phytoplankton production will be very low (basically light limited), and a large amount of nutrients will be always available. The zooplankton production in those areas will be correspondingly low.

The zooplankton biomass distribution also shows conspicuous concentrations along the offshore extension of the Grande Bay front. The dynamics of this front cannot be explained from our present data set. Although, it seems possible that the currents associated to the frontal area generate eddies and an overall tendency of the front to meander. The formation of frontal eddies would entail an increased variability of the front position, and with this the possibility of transporting nutrient rich waters from the neighboring areas located to the south and offshore. Nutrient supply may be additionally increased by the mechanisms commonly associated with tidal fronts as described above. Enhanced zooplankton biomass along the front would result therefore from increased

primary production all through spring and summer.

On account of the above, the physical and biological conditions in the area of Grande Bay lead to a configuration that might be suitable for the spawning and nursery of fish populations. Current knowledge on the reproduction of austral fish species is yet too scant to explore this hypothesis. For all its ecological and assessment implications, however, it should be addressed in future research on recruitment of austral fishes. There is some evidence suggesting that the spawning of the Patagonian hoki, one of the most commercially important fishes of southern Patagonia, occurs in late spring to the south of Tierra del Fuego and Isla de los Estados, in near shore waters at 400–600 m depth (Machinandarena and Ehrlich, 1999). We surmise that the hoki larvae might drift northward to seek sheltered and food-rich coastal areas and reach the Grande Bay towards the summer for nursery purposes. According to our observations, the dominant zooplankton prey occurring there at that time should be suitable for juvenile hoki younger than age 3.

It was beyond the scope of this work to investigate the interannual differences in the physical and biological patterns off southern Patagonia, but rather to emphasize the outstanding characteristics that reoccur year-to-year. As progress for the present study, satellite images of chlorophyll in the area at different times of the year will be useful in testing the linkage between hydrography and zooplankton biomass through phytoplankton. Further examination of the hydro-meteorological forcing driving the biological patterns across and along the southern Patagonia shelf should be performed by way of biological-physical modeling. In this sense, three major hypothesis emerge from our results: (1) the circulation associated with the particular array of fronts occurring in the area of Grande Bay leads to enhanced phytoplankton production by ensuring constant nutrient supply throughout the spring-summer period; (2) the accumulation of zooplankton biomass during summer results from the concentration and retention of organisms within an area of high food availability; (3) this environment is a suitable region for the spawning and/or

nursery grounds of local fish such as Patagonian hoki.

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